

EXHIBIT 413

STATE OF CALIFORNIA
California Energy Commission

In the Matter of:

The Application for Certification
for the **CALICO SOLAR PROJECT**
(formerly SES Solar One)

Docket No. 08-AFC-13

REBUTTAL TESTIMONY OF VERNON BLEICH
ON BEHALF OF CALIFORNIA UNIONS FOR RELIABLE ENERGY
ON BIOLOGICAL RESOURCES
FOR THE CALICO SOLAR PROJECT

July 29, 2010

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I. Introduction

The Supplemental Staff Assessment for the Calico Solar Project (SSA) recognizes the potential for the project to eliminate habitat for bighorn sheep.¹ The footprint of the Project has been reduced by approximately 25%, and has been moved southward toward Interstate Highway 40, with the result that a smaller proportion of the south-facing slopes of the Cady Mountains will be impacted.² The SSA also indicates that the Applicant will provide access to concerned parties for the purposes of servicing an *existing* artificial water development that is currently heavily used by bighorn sheep in the southwestern portion of the Cady Mountains.³ Regardless, nearly 1,100 acres of habitat currently available to bighorn sheep for foraging will be permanently lost, and an additional 400 acres of spring foraging habitat will incur secondary impacts associated with noise impacts along the northern boundary of the Project.⁴ These losses, when coupled with other sources of disturbance (SunCatcher noise, avoidance of manmade structures and activity and surrounding habitat; increased disturbance from public traffic on a new northern boundary road; and the introduction or spread of non-native, invasive plants)⁵ to which sheep may be sensitive, are significant, and have the potential to negatively impact the population of bighorn sheep inhabiting the Cady Mountains.

Recognition of the potential for the Project to impact bighorn sheep habitat, and the resultant decrease in the size of the footprint of the Project are positive departures from the Staff Assessment, which largely failed to consider impacts to bighorn sheep. However, the conclusion that the Project "[i]s not expected to result in a significant loss of habitat" is wholly inappropriate.⁶ The SSA also recognizes that the Project has the potential to "[a]ct as a barrier to movement for sheep using the south side of the Cady Mountains or their foothills to traverse to [what are described in the SSA as] winter ranges in the Bristol Mountains"⁷ but Staff unfortunately has indicated that "[t]he proposed project is not expected to pose serious restrictions to movements for bighorn sheep."⁸ This is perplexing, because the Project site is located in an area identified as an essential biological connectivity area between the Bristol and Ord Mountains (Spencer et al. 2010).^{9 10}

¹ Calico Solar Plant Supplemental Staff Assessment (SSA) page C.2-5.

² SSA page C.2-100.

³ SSA page C.2-232.

⁴ SSA page C.2-5.

⁵ SSA page C.2-5.

⁶ SSA page C.2-93.

⁷ SSA page C.2-5.

⁸ SSA page C.2-93.

⁹ Spencer, W. D., P. Beier, K. Penrod, K. Winters, C. Paulman, H. Rustigian-Romsos, J. Strittholt, M. Parisi, and A. Pettler. 2010. California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California. Prepared for California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration.

¹⁰ SSA page C.2-16.

The Cady Mountains, which are inhabited by a population of at least 300 bighorn sheep,¹¹ represents the westernmost subpopulation of bighorn sheep in the Central Mojave Metapopulation and, because of its size, has a greater potential to produce emigrants than most other subpopulations that comprise the Central Mojave Metapopulation, and is the closest large population to the Newberry Mountains and Ord Mountains, which lie southwest of the Project site, albeit on the south side of Interstate Highway 40 (and which should not be considered a total barrier to movement, based on observations elsewhere).^{12 13} Moreover, the SSA fails to note the potential for the Project to impact the probability of animals immigrating into the Cady Mountains from the Newberry or Ord Mountains. Emigration, immigration, and gene flow are necessary components of metapopulation function, and likely occur at low rates within metapopulations of bighorn sheep;¹⁴ thus, Staff has erred (in the absence of information to the contrary) in concluding that the Project will not have a significant impact on bighorn sheep and that the Project does not pose serious restrictions to movement by bighorn sheep.¹⁵ This conclusion is especially onerous given that the Project is proposed within an area identified as an essential biological connectivity area between the Bristol and Ord Mountains.¹⁶

My testimony addresses three issues germane to this Project. First, I address the failure of the SSA to mitigation for the combined direct and indirect loss of nearly 3 square miles of bighorn sheep habitat. Secondly, I address the failure of the SSA to require mitigation for impacts of the Project to connectivity among bighorn sheep subpopulations comprising the Central Mojave Metapopulation. My third concern addresses the inappropriateness of what Staff has proposed as mitigation to offset impacts of project construction on bighorn sheep.

II. The SSA fails to mitigate for the loss of 1,500 acres of bighorn sheep habitat

Bighorn sheep are large, vagile mammals that occur largely in disjunct subpopulations that are distributed across the landscape and that comprise metapopulations.^{17 18 19 20} The majority of the area occupied by bighorn sheep is not

¹¹ SSA page C.2-93

¹² Torres, S., G. Mulcahy, B. Gonzales, A. Pauli, and N. Andrew. 2000. Human induced migration and homing behavior of a desert bighorn ram in the Whipple mountains, California: or, Herman, the trailer park ram. *Desert Bighorn Council Transactions* 44:13.

¹³ Telephone Conversation with Mr. Randy Botta, California Department of Fish and Game, regarding bighorn sheep use of habitat adjacent to Interstate Highway 8, 24 March 2010.

¹⁴ Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation* 37:179-190.

¹⁵ SSA, page C-2.94.

¹⁶ Spencer, W. D., P. Beier, K. Penrod, K. Winters, C. Paulman, H. Rustigian-Romsos, J. Strittholt, M. Parisi, and A. Pettler. 2010. California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California. Prepared for California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration.

¹⁷ Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation* 37:179-190.

¹⁸ Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conservation Biology* 4:383-390.

utilized on a permanent basis; instead, use of specific areas varies with environmental conditions, season, temperature, and other factors that affect resource availability and, ultimately, population performance.²¹ Although bighorn sheep occur over large areas, all areas utilized by bighorn sheep are necessary for their continued existence.²² The presence of bighorn sheep sign and remains adjacent to the Project site²³ provide compelling evidence that the site has been utilized by bighorn sheep in the past and that use would occur in the future in the absence of Project implementation. The SSA acknowledges that, "[i]t is likely that bighorn sheep use portions of the site for foraging and possibly inter-mountain movement to some degree."²⁴ Thus, the conclusion that the destruction of nearly 1,100 acres, and associated indirect impacts to another 400 acres, of bighorn sheep habitat (which total nearly 3 square miles in area) "[i]s not expected to result in a significant loss of habitat"²⁵ is not defensible.

It is inconceivable that the applicant is not being required to mitigate for the loss of nearly 3 square miles of habitat that clearly is of importance to bighorn sheep for foraging, at least on a seasonal basis. Such mitigation would best take one of two, or a combination of two, options, but first would require a detailed investigation of bighorn sheep in the Cady Mountains using radiotelemetry, which would provide data necessary to develop a habitat selection model that would be used to determine the most efficacious form of mitigation.

III. The SSA fails to mitigate for impacts to potential movements by bighorn sheep

As a result of the telemetry investigation, the Applicant would be able to make an informed decision regarding the type of mitigation to be implemented. Overall, the long-term objective should be one of enhancing the likelihood of persistence of bighorn sheep in the Cady Mountains, and maximizing the probability of maintaining connectivity between the Cady Mountains, and other ranges that comprise the Central Mojave Metapopulation. Epps et al. (2010) emphasized the importance of "[m]aintaining connectivity and the potential for recolonization by avoiding disruption of natural dispersal routes..." and further recommended bridging anthropogenic barriers to help ensure connectivity among subpopulations of bighorn sheep.²⁶ Consistent with this recommendation, the bridging of anthropogenic barriers was suggested by the Western

¹⁹ Bleich, V. C., J. D. Wehausen, R. R. Ramey II, and J. L. Rechel. 1996. Metapopulation theory and mountain sheep: implications for conservation. Pages 353-373 in D. R. McCullough (editor). *Metapopulations and wildlife conservation*. Island Press, Covelo, California.

²⁰ Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology* 44:714-724.

²¹ Wehausen, J. D. 2005. Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. Pages 37-50 in J. Goerriksen and J. M. Andre, editors. *Sweeney Granite Mountains Desert Research Center 1978-2003. A Quarter Century of Research and Teaching*. University of California Natural Reserve System, Riverside, California, USA.

²² Wilson, L. O. xx

²³ SSA, page C.2-93.

²⁴ SSA, page C.2-94.

²⁵ SSA, page C.2-94.

²⁶ Epps, C. W., J. D. Wehausen, P. J. Palsboll, and D. R. McCullough. 2010. Using genetic tools to track desert bighorn sheep colonizations. *Journal of Wildlife Management* 74:522-531.

Watersheds Project as one form of mitigation, but was summarily rejected. Unfortunately, and without evidence to the contrary, Staff clearly concluded "[t]hat land bridges are not necessary to mitigate the project's impacts to biological connectivity, including impacts to bighorn sheep connectivity."²⁷ Nevertheless, Staff has repeatedly acknowledged the potential for the Project to impact connectivity.²⁸

IV. Some proposed mitigation may be more harmful than helpful to bighorn sheep

Mitigation stipulated in BIO-23 is intended to offset the potential for disturbance of bighorn sheep during the construction phase of Project implementation.²⁹ As stipulated in BIO-23, construction activities are expected to cease whenever bighorn sheep are observed within 500 feet of any construction activity, and construction would be halted until bighorn sheep no longer are within 500 feet of that activity. Although this is a well-intentioned stipulation, it is my professional opinion that the uncertainty associated with the cessation and resumption of construction activities would, in reality, be of greater concern to bighorn sheep than would continuation of those activities. Bighorn sheep are highly adaptable creatures, and co-exist with *predictable* sources of disturbance in numerous situations that include ongoing mining activity,^{30 31 32 33} recreational pursuits,³⁴ interstate freeways,^{35 36} and urbanized areas.³⁷

A requirement that bighorn sheep repeatedly be exposed to the cessation and commencement of construction activities, as a function of the distance to those construction activities, is irresponsible considering the level of uncertainty associated with decisions to cease or begin construction. Bighorn sheep can habituate to disturbance if the disturbance is predictable in that it occurs in the same locations, is consistent, and is not perceived as threatening.^{38 39 40 41} Indeed, it is the lack of predictability of some

²⁷ SSA, page C.2-161.

²⁸ SSA, pages C.2-98, C.2-99, C.2-130.

²⁹ SSA, page C.2-331 – C.2-332

³⁰ Bleich, V. C., J. H. Davis, J. P. Marshal, S. G. Torres, and B. G. Gonzales. 2009. Mining activity and habitat use by mountain sheep (*Ovis canadensis*). *European Journal of Wildlife Research* 55:183-191.

³¹ Divine, D. D., and C. L. Douglas. 1996. Bighorn sheep monitoring program for the Eagle Mountain landfill project: phase one report. Cooperative National Park Studies Unit, National Biological Service, University of Nevada, Las Vegas, USA.

³² Jansen, B. D., P. R. Krausman, J. R. Heffelfinger, and J. C. deVos. 2006. Bighorn sheep selection of landscape features in an active copper mine. *Wildlife Society Bulletin* 34:1121-1126.

³³ Oehler M. W., Sr., V. C. Bleich, R. T. Bowyer, and M. C. Nicholson. 2005. Mountain sheep and mining: implications for conservation and management. *California Fish and Game* 91:149-178.

³⁴ Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. *Journal of Wildlife Management* 65:573-582.

³⁵ Telephone Conversation with Mr. Randy Botta, California Department of Fish and Game, regarding bighorn sheep use of habitat adjacent to Interstate Highway 8, 24 March 2010.

³⁶ Annual observations of Dr. Vernon Bleich with respect to bighorn sheep use of habitat adjacent to Interstate Highway 40 in the Marble Mountains, San Bernardino County, 1978 – 2006.

³⁷ Rubin, E. S., W. M. Boyce, C. J. Stermer, and S. G. Torres. 2002. Bighorn sheep habitat use and selection near an urban environment. *Biological Conservation* 104:251-263.

³⁸ Geist, V. 1975. On the management of mountain sheep: theoretical considerations. Pages 77-105 in J. B. Trefethen (editor). *The wild sheep in modern North America*. The Winchester Press, New York.

disturbance factor (which can be described as unexpected disturbance) that would be most detrimental to bighorn sheep.⁴² Repeated cessation and resumption of construction activities as a response to bighorn sheep approaching a construction site is a prime example of unexpected disturbance, and likely would be manifested in altered behavioral patterns, including the repeated disruption of foraging activities.⁴³

It is my professional opinion that bighorn sheep in the Cady Mountains will incur fewer intrusions upon their behavior if construction activities proceed in a predictable manner (i.e., they are ongoing constantly) that bighorn sheep can expect to occur, rather than in a manner that makes it impossible for a sheep to decide to approach or stay away from an ongoing activity. Thus, BIO-23 offers nothing in terms of mitigation for the loss of nearly 3 square miles of habitat and the potential disruption of connectivity but, instead, exacerbates that already unfortunate situation.

³⁹ Graham, H. 1980. The impact of modern man. Pages 288-309 in G. Monson and L. Sumner (editors). *The desert bighorn: its life history, ecology, and management*. University of Arizona Press, Tucson.

⁴⁰ Wehausen, J. D., L. L. Hicks, D. P. Garber, and J. Elder. 1977. Bighorn sheep management in the Sierra Nevada. *Transactions of the Desert Bighorn Council* 21:30-32.

⁴¹ Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. *Journal of Wildlife Management* 65:573–582.

⁴² Geist, V. 1975. On the management of mountain sheep: theoretical considerations. Pages 77-105 in J. B. Trefethen (editor). *The wild sheep in modern North America*. The Winchester Press, New York.

⁴³ Oehler M. W., Sr., V. C. Bleich, R. T. Bowyer, and M. C. Nicholson. 2005. Mountain sheep and mining: implications for conservation and management. *California Fish and Game* 91:149–178.

DECLARATION OF VERON C. BLEICH
CALICO SOLAR PROJECT
08-AFC-13

I, Vernon C. Bleich, declare as follows:

1. I recently retired from the California Department of Fish and Game, where I worked extensively and primarily with large mammals in the arid ecosystems that characterize eastern and southeastern California. As a private citizen, I currently offer expertise with respect to natural resource conservation issues.
2. I hold an M.A. degree in biology, and a Ph.D. in wildlife biology. My relevant professional qualifications and experience are set forth in the attached *curriculum vitae* and the attached testimony, and are incorporated herein by reference.
3. I prepared the testimony attached hereto and incorporated herein by reference as it relates to the Supplemental Staff Assessment prepared for the project known as the Calico Solar Project.
4. It is my professional opinion that the attached testimony is true and accurate.
5. I am personally familiar with the facts and conclusions described within the attached testimony and if called as a witness, I could testify competently thereto.

I declare under penalty of perjury that the foregoing is true and correct to the best of my knowledge and belief.

Dated: July 29, 2010.

Signed



At:

BISHOP, CA

Calico Solar – 08-AFC-13
DECLARATION OF SERVICE

I, Bonnie Heeley, declare that on July 29, 2010, I served and filed copies of the attached Rebuttal Testimony of Vernon Bleich on Behalf of California Unions for Reliable Energy on Biological Resources for the Calico Solar Project dated July 29, 2010. The original document, filed with the Docket Unit, is accompanied by a copy of the most recent Proof of Service list, located on the web page for this project at www.energy.ca.gov/sitingcases/calicosolar/CalicoSolar_POS.pdf. The document has been sent to both the other parties in this proceeding as shown on the Proof of Service list and to the Commission's Docket Unit electronically to all email addresses on the Proof of Service list; and by depositing in the U.S. mail at South San Francisco, CA, with first-class postage thereon fully prepaid and addressed as provided on the Proof of Service list to those addresses NOT marked "email preferred."

AND

By sending an original paper copy and one electronic copy, mailed and emailed respectively to:

CALIFORNIA ENERGY COMMISSION

Attn: Docket No. 08-AFC-13
1516 Ninth Street, MS 4
Sacramento, CA 95814-5512
docket@energy.state.us.ca.

I declare under penalty of perjury that the foregoing is true and correct. Executed at South San Francisco, CA, on July 29, 2010

_____/s/_____
Bonnie Heeley

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EXHIBIT 414

Curriculum Vitae

VERNON C. BLEICH

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Personal Interests:

Hockey (I am a former goaltender), family life, banjo, gardening, hunting, and fishing.

Professional Goals:

To help ensure the persistence of populations of large mammals and their habitats through the study of their ecology and behavior, to apply that knowledge in meaningful conservation efforts, and to impart that knowledge through professional activities including publications, teaching, and other public contacts.

Education:

Ph.D. University of Alaska Fairbanks (Wildlife Biology, 1993). Thesis: "Sexual Segregation in Desert-Dwelling Mountain Sheep."

M.A. California State University, Long Beach (Biology, 1973). Thesis: "Ecology of Rodents at the Seal Beach Naval Weapons Station, Fallbrook Annex, San Diego County, California."

B.S. California State University, Long Beach (Zoology, 1970).

Professional Background:

Senior Conservation Scientist, Eastern Sierra Center for Applied Population Ecology (2007 – present). I provide expertise on natural resource conservation issues, particularly as they relate to large mammals in desert, mountain, and plains environments.

Senior Environmental Scientist, California Department of Fish and Game (2001 – 2007; now retired). I served as the project leader for the Sierra Nevada Bighorn Sheep Recovery Program, a project to conserve mountain sheep in that range and restore them to formerly occupied habitats. I continued to function as the Regional Large Mammal and Desert

specialist, with an emphasis on mountain sheep and mule deer in southeastern California. I also served as chair of the Sierra Nevada Bighorn Sheep Scientific Advisory Group, and continued to serve as a member of the Peninsular Bighorn Sheep Recovery Team.

Senior Wildlife Biologist, California Department of Fish and Game (1999 - 2001). I served as the Regional Large Mammal and Desert Specialist, with an emphasis on mountain sheep and mule deer in southeastern California. At the request of the U.S. Fish and Wildlife Service I was appointed by the Department of Fish and Game to serve on the Peninsular Bighorn Sheep Recovery Team.

Senior Wildlife Biologist, California Department of Fish and Game (1993 - 1999). I served as the Regional Large Mammal Specialist and supervised the activities of 5 journeyman wildlife biologists in eastern California. Emphasis species included mountain sheep, mule deer, pronghorn, tule elk, and sage grouse in eastern California.

Associate Wildlife Biologist, California Department of Fish and Game (1986 - 1993). I served as the Regional mountain sheep specialist, and supervised the activities of 5 journeyman wildlife biologists in eastern California. Emphasis species included mountain sheep, mule deer, pronghorn, tule elk, and sage grouse in eastern California.

Project Leader, California Department of Fish and Game, Federal Aid in Wildlife Restoration Project W-26-D (1978 - 1986). I supervised 2 technicians, and planned and implemented habitat management projects designed to benefit waterfowl, sage grouse, mule deer, and mountain sheep in eastern California.

Assistant Wildlife Biologist, California Department of Fish and Game (1975 - 1978). I was an Area Biologist responsible for management of mule deer, mountain sheep, and the Endangered Stephens' kangaroo rat, as well as for environmental review activities in Riverside and San Bernardino counties, California.

Junior Aquatic Biologist, California Department of Fish and Game (1974 - 1975). I was responsible for fisheries management activities, with an emphasis on wild trout and the Endangered unarmored three-spined stickleback in Los Angeles and San Bernardino counties, California.

Park Ranger, Department of Recreation, City of Long Beach, California (1970 - 1973). I was responsible for public education activities, routine patrol, and coordination with other law enforcement agencies in El Dorado Regional Park, Long Beach, California.

Academic Appointments:

Research Professor, Department of Natural Resources and Environmental Science, University of Nevada, Reno (2007 - Present).

Affiliate Faculty, Department of Biological Sciences, Idaho State University, Pocatello, Idaho (2005 - Present)

Senior Research Associate, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska (1998 - Present).

Affiliate Assistant Professor of Wildlife Ecology, Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska (1993 - 1998).

Research Associate, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska (1993 - present).

Adjunct Assistant Professor of Natural Resource Science, Department of Natural Resource Science, University of Rhode Island, Kingston (1992 - 1994).

Instructor, Mt. San Jacinto College, San Jacinto, California. I instructed an introductory course entitled, "Wildlife Management" (1976 - 1986).

Assistant Professor, Department of Biology, Rio Hondo College, Whittier, California. I instructed lecture and laboratory sections of General Zoology (biology major emphasis), General Biology (general education emphasis), and Marine Biology (1973 - 1974).

Teaching Assistant, California State University, Long Beach. I instructed laboratory sections of General Biology (for non-majors) and General Zoology (for majors) (1972 - 1973).

Graduate Research Assistant, California State University, Long Beach. I prepared specimens and curated the collection of mammals (> 10,000 specimens) in the Bird and Mammal Museum, and instructed laboratory sections of General Ecology (for majors), General Mammalogy (for majors), and Advanced Mammalogy (1970-1972).

Graduate Student Supervision:

Chair of Graduate Committee:

Kevin L. Monteith (Ph.D.), Reproductive ecology of migratory and resident mule deer in the eastern Sierra Nevada, California. Idaho State University, Pocatello. Graduation expected June, 2010. Co-chair with Dr. R. T. Bowyer.

Michael W. Oehler (M.S.), Ecology of mountain sheep: effects of mining and precipitation. University of Alaska Fairbanks. *Graduated December 1999*. Current position: Wildlife Biologist, National Park Service, Theodore Roosevelt National Park, Medora, North Dakota. Co-chair with Dr. R. T. Bowyer.

Becky M. Pierce (Ph.D.), Predator-prey dynamics between mountain lions and mule deer: effects on distribution, population regulation, habitat selection and prey selection. University of Alaska Fairbanks. *Graduated May 1999*. Current position: Associate Wildlife Biologist, California Department of Fish and Game. Co-chair with Dr. R. T. Bowyer.

Graduate Committee Membership:

Cody J. McKee (M.S.), Ecology of mule deer in the eastern Mojave Desert, California. University of Nevada, Reno (Graduation expected June 2011).

Jeffrey T. Villepique (Ph.D.), Interactions between mountain lions and mountain sheep: an assessment of forage benefits and predation risk. Idaho State University, Pocatello (Graduation expected December 2010).

Sabrina Morano (Ph.D.), Reproductive biology of mule deer in the White Mountains, Inyo and Mono counties, California. University of Nevada, Reno (Graduation expected June 2011).

Jericho C. Whiting (Ph.D.), Behavior and ecology of reintroduced Rocky Mountain bighorn sheep. Idaho State University, Pocatello. *Graduated December 2008*. Current position: Wildlife Biologist, Idaho National Laboratory, Twin Falls.

Cody A. Schroeder (M.S.), Habitat selection by mountain sheep: forage benefits or risk of predation? Idaho State University, Pocatello. *Graduated September 2007*. Current position: Doctoral Student, University of Nevada, Reno.

Jason P. Marshal (Ph.D.), Foraging ecology and water relationships of mule deer in a Sonoran Desert environment. University of Arizona, Tucson. *Graduated May 2005*. Current position: Lecturer, University of the Witwatersrand, South Africa.

Heather E. Johnson (M.S.), Antler breakage in tule elk in Owens Valley, California: nutritional causes and behavioral consequences. University of Arizona, Tucson. *Graduated January 2004*. Current position: Doctoral Student and Research Associate, University of Montana, Missoula.

Jennifer L. Rechel (Ph.D. [Geography]), Influence of neighborhood effects and friction surfaces on the spatial distribution and movement strategies of desert-dwelling mountain sheep (*Ovis canadensis*). University of California, Riverside. *Graduated August 2003*. Current position: Wildlife Biologist, U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Riverside, California.

Holly B. Ernest (Ph.D.), Ecological genetics of mountain lions (*Puma concolor*) in California. University of California, Davis. *Graduated December 2001*. Current position: Research Geneticist, School of Veterinary Medicine, University of California, Davis.

Esther S. Rubin (Ph.D.), The ecology of bighorn sheep (*Ovis canadensis*) in the peninsular ranges of California. University of California, Davis. *Graduated December 2000*. Current position: Conservation Biologist, The Conservation Biology Institute, Borrego Springs, California.

Nancy G. Andrew (M.S.), Demography and habitat use of desert-dwelling mountain sheep in the East Chocolate Mountains, Imperial County, California. University of Rhode Island, Kingston. *Graduated May 1994*. Current position: Staff Environmental Scientist, California Department of Fish and Game.

Awards and Honors:

Honorary Lifetime Membership, 2010 (in recognition of long and continuing service to the Society for the Conservation of Bighorn Sheep)

Wild Sheep Biologist Wall of Fame Award, 2009 (in recognition of significant contributions to the conservation of wild sheep in North America) (Wild Sheep Foundation)

Lifetime Achievement Award, 2008 (In recognition of contributions toward the conservation of mountain sheep in California) (California Chapter of the Foundation for North American Wild Sheep)

Honor Plaque 2007 (Group Award, in recognition of outstanding contributions toward the recovery of mountain sheep in the Sierra Nevada) (Desert Bighorn Council)

State Statesman Award, 2006 (In recognition of outstanding contributions to the wild sheep of California) (Foundation for North American Wild Sheep)

Trail Blazer Award, 2004 (In recognition of efforts on behalf of mountain sheep conservation in California) (California Chapter of the Foundation for North American Wild Sheep)

Director's Achievement Award, 2004 (In recognition of editorial services for *California Fish and Game* (California Department of Fish and Game)

Annual Achievement Award, 2004 (In recognition of conservation of mule deer and their habitats) (Southern California Chapter, California Deer Association)

Alumni Achievement Award for Professional Excellence, 2002 (University of Alaska Alumni Association)

Outstanding Alumnus Award, 2002 (College of Science, Engineering, and Mathematics, University of Alaska Fairbanks)

Sustained Superior Accomplishment Award, 2002 (California Department of Fish and Game)

The Desert Ram Award, 2001 (Desert Bighorn Council)

Outstanding Publication Award for a Monograph, 1998 (The Wildlife Society)

Award of Appreciation, 1998 (San Fernando Valley Chapter of Safari Club International, CA)

Professional Membership, Boone and Crockett Club, 1998 (Boone and Crockett Club)

Certificate of Appreciation, 1997 (Society for the Conservation of Bighorn Sheep)

"Ol' Irongut" Award, 1996 (California Department of Fish and Game, Division of Air Services)

Resources Agency/University of California Fellowship, 1996 (Sponsored jointly by the California Resources Agency and the University of California, Davis)

Director's Achievement Award, 1992 (California Department of Fish and Game)

Outstanding Biology Department Alumnus, 1988 (California State University, Long Beach)

Professional of the Year, 1985 (Western Section of The Wildlife Society)

California Wildlife Officer of the Year, 1984 (Shikar-Safari Foundation)

Award of Honor, 1984 (Society for the Conservation of Bighorn Sheep)

Honorary Lifetime Membership, 1984 (Banning [California] Sportsman's Club)

Professional and Fraternal Memberships:

American Society of Mammalogists (Life Member)
The Boone and Crockett Club (Professional Member)
The Wildlife Society
Society for Conservation Biology
Southwestern Association of Naturalists
Wild Sheep Foundation
National Rifle Association
California Chapter, Foundation for North American Wild Sheep
Society for the Conservation of Bighorn Sheep
Minnesota-Wisconsin Chapter, Foundation for North American Wild Sheep

Licenses and Certifications:

California Community College Credential (# 45476, Lifetime)
State of California Blaster's License (# 2087)
Certified in Wildlife Capture Techniques (California Department of Fish and Game)
Certified Wildlife Biologist (1981 - The Wildlife Society)
California Hunter Safety Instructor (# 1984)

Other Professional Activities:

Editorial Activities:

Editor-in-Chief, *California Fish and Game* (2009 – present)

Associate Editor, *California Fish and Game* (1995 - 2009)

Editor, *Transactions of the Western Section of The Wildlife Society* (1988)

Associate Editor, *Transactions of the Western Section of The Wildlife Society* (1986-87)

Reviewer for Journals:

Conservation Biology, Journal of Wildlife Management, Wildlife Society Bulletin, Journal of Mammalogy, The Condor, California Fish and Game, Transactions of the Western Section of the Wildlife Society, Western North American Naturalist, Desert Bighorn Council Transactions, Southwestern Naturalist, Proceedings of the Northern Wild Sheep and Goat Council, Journal of Wildlife Diseases, Great Basin Naturalist, Bulletin of the Southern California Academy of Sciences, Journal of Zoology (London), Vida Silvestre Neotropical, Wildlife Biology, Wildlife Monographs, European Journal of Wildlife Research, Biological Conservation, Journal of Arid Environments (An average of about 12 reviews per year).

Other Activities:

2008 - Present: Member, Big Game Records Committee, Boone and Crockett Club

2007 - Present: Advisory Board Member, Texas Bighorn Society

2007 - Present: Science Advisor, Society for the Conservation of Bighorn Sheep

2006 - Present: Member, Ad Hoc Committee on Professional Membership, Boone and Crockett Club.

1998 - 2002: Coach and member of Board of Trustees, Sierra Roller Hockey League.

1995-96: Vice Chairman, The Desert Bighorn Council.

1994-98: Member, Board of Directors, The Wildlife Forensic DNA Foundation.

1993 - Present: Member, Wildlife Management Professional Advisory Committee, Foundation for North American Wild Sheep.

1991: Member, Committee on Support of Symposia and Conferences, The Wildlife Society.

1989-1993: Member, Board of Trustees, Friends of the Eastern California Museum; Vice-chairman, 1991-1992; Chairman, 1993.

1987-1988: Chairman, The Desert Bighorn Council.

1988: Co-chairman, Wildlife Water Development Symposium, Western Section of The Wildlife Society.

Refereed Publications:

Bleich, V. C. *In review.* Perceived threats to mountain sheep: levels of concordance among western states, provinces, and territories. Desert Bighorn Council Transactions.

Marshal, J. P., and **V. C. Bleich.** *In review.* Geographic variation in relationships between El Nino Southern Oscillation and mule deer harvest in California, USA. Canadian Journal of Zoology.

Holl, S. A., and **V. C. Bleich.** *In review.* Responses of large mammals to fire and rain in the San Gabriel Mountains, California. Southwestern Naturalist.

Marshal, J. P., **V. C. Bleich,** P. R. Krausman, A. Neibergs, M. L. Reed, and N. G. Andrew. *In review.* Habitat use and diets of mule deer and feral ass in the Sonoran Desert. Journal of Arid Environments.

Whiting, J. C., R. T. Bowyer, J. T. Flinders, **V. C. Bleich,** and J. G. Kie. *In press.* Sexual segregation and use of water by bighorn sheep: implications for conservation. Animal Conservation.

Villepique, J. T., B. M. Pierce, **V. C. Bleich,** and R. T. Bowyer. *In press.* Diets of mountain lions following a decline in mule deer numbers. Southwestern Naturalist.

Bleich, V. C. *In press.* Considerations for reprovisioning wildlife water developments: mountain sheep in desert ecosystems. California Fish and Game.

Gibson, R. M., **V. C. Bleich,** C. W. McCarthy, and T. L. Russi. *In press.* Recreational hunting can lower population size in Greater Sage-grouse. Studies in Avian Biology.

Schroeder, C. A., R. T. Bowyer, **V. C. Bleich,** and T. R. Stephenson. *In press.* Ramifications of sexual segregation for an endangered alpine ungulate: Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*. Arctic, Antarctic, and Alpine Research.

Bleich, V. C., J. P. Marshal, and N. G. Andrew. 2010. Habitat use by a desert ungulate: predicting effects of water availability on mountain sheep. Journal of Arid Environments 74:638-645.

Krausman, P. R., D. E. Naugle, M. R. Frisina, R. Northrup, **V. C. Bleich,** W. M. Block, M. C.

- Wallace, and J. D. Wright. 2009. Livestock grazing, wildlife habitat, and rangeland values. *Rangelands* 31(5):15-19.
- Holl, S. A., and V. C. Bleich. 2009. Reconstructing the San Gabriel Mountains bighorn sheep population. *California Fish and Game* 95:77-87.
- Clifford, D. L., B. A. Schumaker, T. R. Stephenson, V. C. Bleich, M. Leonard-Cahn, B. J. Gonzales, W. M. Boyce, and J. A. K. Mazet. 2009. Assessing disease risk at the wildlife-livestock interface: a study of Sierra Nevada bighorn sheep. *Biological Conservation* 142:2559-2568.
- Bleich, V. C., J. H. Davis, J. P. Marshal, S. G. Torres, and B. J. Gonzales. 2009. Mining activity and habitat use by mountain sheep. *European Journal of Wildlife Research* 55:183-191.
- Pease, K. M., A. H. Freedman, J. P. Pollinger, J. E. McCormack, W. Buermann, J. Rodzen, J. Banks, E. Meredith, V. C. Bleich, R. J. Schaefer, K. Jones, and R. K. Wayne. 2009. Landscape genetics of California mule deer (*Odocoileus hemionus*): the roles of ecological and historical factors in generating differentiation. *Molecular Ecology* 18:1848-1862.
- Duffy, L. K., M. W. Oehler, R. T. Bowyer, and V. C. Bleich. 2009. Mountain sheep: an environmental epidemiological survey of variation in metal exposure and physiological biomarkers following mine development. *American Journal of Environmental Sciences* 5:296-303.
- Marshal, J. P., J. W. Cain III, V. C. Bleich, and S. S. Rosenstock. 2009. Intrinsic and extrinsic sources of variation in the population dynamics of an arid-environment large herbivore. *Canadian Journal of Zoology* 87:103-111.
- Villepique, J. T., V. C. Bleich, R. A. Botta, B. M. Pierce, T. R. Stephenson, and R. T. Bowyer. 2008. Evaluating GPS collar error: a critical evaluation of Televilt POSREC-Science™ Collars and a method for screening location data. *California Fish and Game* 94:155-168.
- Bleich, V. C., H. E. Johnson, S. A. Holl, L. Konde, S. G. Torres, and P. R. Krausman. 2008. Fire history in a chaparral ecosystem: implications for conservation of a native ungulate. *Rangeland Ecology and Management* 61:571-579.
- Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2008. Body condition of desert mule deer is related to rainfall. *Southwestern Naturalist* 53:311-318.
- Marshal, J. P., V. C. Bleich, and N. G. Andrew. 2008. Evidence for interspecific competition between feral ass and mountain sheep in a desert environment. *Wildlife Biology* 14:228-236.
- Bleich, V. C., and R. A. Weaver. 2007. Status of mountain sheep in California: comparisons between 1957 and 2007. *Desert Bighorn Council Transactions* 49:55-67.

- Wehausen, J. D., and V. C. Bleich. 2007. Influence of aerial search time on survey results. *Desert Bighorn Council Transactions* 49:23-29.
- Bowyer, R. T., V. C. Bleich, X. Manteca, J. C. Whiting, and K. M. Stewart. 2007. Sociality, mate choice, and timing of mating in American bison (*Bison bison*): effects of large males. *Ethology* 113:1048-1060.
- Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology* 44:714-724.
- Bleich, V. C., T. R. Stephenson, B. M. Pierce, and M. J. Warner. 2007. Body condition of mule deer while injured and following recovery. *Southwestern Naturalist* 52:164-167.
- Johnson, H. E., V. C. Bleich, and P. R. Krausman. 2007. Mineral deficiencies in tule elk, Owens Valley, California. *Journal of Wildlife Diseases* 43:61-74.
- Johnson, H. E., V. C. Bleich, P. R. Krausman, and J. L. Koprowski. 2007. Effects of antler breakage on mating behavior in male tule elk (*Cervus elaphus nannodes*). *European Journal of Wildlife Research* 53:9-15.
- Bleich, V. C. 2006. Mountain sheep in California: perspectives on the past, and prospects for the future. *Biennial Symposium of the Northern Wild Sheep and Goat Council* 15:1-13.
- Marshal, J. P., V. C. Bleich, P. R. Krausman, M. L. Reed, and N. G. Andrew. 2006. [Invited paper] Factors affecting habitat use and distribution of mule deer in an arid environment. *Wildlife Society Bulletin* 34:609-619.
- Bleich, V. C., N. G. Andrew, M. J. Martin, G. P. Mulcahy, A. M. Pauli, and S. S. Rosenstock. 2006. [Invited paper] Quality of water available to wildlife: comparisons among artificial and natural sources. *Wildlife Society Bulletin* 34:627-632.
- Bleich, V. C., S. Nelson, P. J. Wood, H. R. Wood, and R. A. Noles. 2006. [Invited paper] Retrofitting gallinaceous guzzlers: enhancing water availability and safety for wildlife. *Wildlife Society Bulletin* 34:633-636.
- Marshal, J. P., P. R. Krausman, V. C. Bleich, S. S. Rosenstock, and W. B. Ballard. 2006. [Invited paper] Gradients of forage biomass and ungulate use near wildlife water developments. *Wildlife Society Bulletin* 34:620-626.
- Rominger, E. M., V. C. Bleich, and E. J. Goldstein. 2006. [Letter] Bighorn sheep, mountain lions, and the ethics of conservation. *Conservation Biology* 20:1041.
- Marshal, J. P., L. M. Lesicka, V. C. Bleich, P. R. Krausman, G. P. Mulcahy, and N. G. Andrew. 2006. Demography of desert mule deer in southeastern California. *California Fish and Game* 92:55-66.

- Bleich, V. C., B. M. Pierce, J. Jones, and R. T. Bowyer.** 2006. Variance in survival rates among young mule deer in the Sierra Nevada, California. *California Fish and Game* 92:24-38.
- Johnson, H. E., V. C. Bleich, and P. R. Krausman.** 2005. Antler breakage in tule elk, Owens Valley, California. *Journal of Wildlife Management* 69:1747-1752.
- Rosenstock, S. S., V. C. Bleich, M. J. Rabe, and C. Reggiardo.** 2005. Water quality at wildlife water sources in the Sonoran Desert, United States. *Rangeland Ecology and Management* 58:623-627.
- Marshal, J. P., P. R. Krausman, and V. C. Bleich.** 2005. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. *Rangeland Ecology and Management* 58:360-365.
- Bleich, V. C., J. T. Villepique, T. R. Stephenson, B. M. Pierce, and G. M. Kutliyev.** 2005. Efficacy of aerial telemetry as an aid to capture specific individuals: a comparison of two techniques. *Wildlife Society Bulletin* 33:332-336.
- Bleich, V. C.** 2005. [Invited paper] In my opinion: politics, promises, and illogical legislation confound wildlife conservation. *Wildlife Society Bulletin* 33:66-73.
- Wehausen, J. D., V. C. Bleich, and R. R. Ramey II.** 2005. Correct nomenclature for Sierra Nevada bighorn sheep. *California Fish and Game* 91:216-218.
- Oehler, M. W., V. C. Bleich, R. T. Bowyer, and M. C. Nicholson.** 2005. Mountain sheep and mining: implications for conservation and management. *California Fish and Game* 91:149-178.
- Marshal, J. P., P. R. Krausman, and V. C. Bleich.** 2005. Dynamics of mule deer forage in the Sonoran Desert. *Journal of Arid Environments* 60:593-609.
- Bleich, V. C., and S. G. Torres.** 2004. [Guest Editorial] International involvement in wildlife conservation. *Wildlife Society Bulletin* 32:1013-1014.
- Krausman, P. R., V. C. Bleich, J. W. Cain III, T. R. Stephenson, D. W. DeYoung, P. W. McGrath, P. K. Swift, B. M. Pierce, and B. D. Jansen.** 2004. Neck lesions in ungulates from collars incorporating satellite technology. *Wildlife Society Bulletin* 32:987-991.
- Marshal, J. P., V. C. Bleich, N. G. Andrew, and P. R. Krausman.** 2004. Seasonal forage use by desert mule deer in southeastern California. *Southwestern Naturalist* 49:501-505.
- Holl, S. A., V. C. Bleich, and S. G. Torres.** 2004. Population dynamics of bighorn sheep in the San Gabriel Mountains, California, 1967-2002. *Wildlife Society Bulletin* 32:412-426.
- Pierce, B. M., R. T. Bowyer, and V. C. Bleich.** 2004. Habitat selection by mule deer: forage benefits or risk of predation? *Journal of Wildlife Management* 68:533-541.

- Bleich, V. C., E. F. Cassirer, L. E. Oldenburg, V. L. Coggins, and D. L. Hunter.** 2004. Predation by a golden eagle, *Aquila chrysaetos*, on a juvenile mountain sheep, *Ovis canadensis*. *California Fish and Game* 90:91-93.
- Epps, C. W., D. R. McCullough, J. D. Wehausen, V. C. Bleich, and J. L. Rechel.** 2004. Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conservation Biology* 18:102-113.
- Long, E. S., D. M. Fecske, R. A. Sweitzer, J. A. Jenks, B. M. Pierce, and V. C. Bleich.** 2003. Efficacy of photographic scent stations to detect mountain lions. *Western North American Naturalist* 63:529-532.
- Bleich, V. C.** 2003. The potential for botulism in desert-dwelling mountain sheep. *Desert Bighorn Council Transactions* 47:2-8.
- Epps, C. W., V. C. Bleich, J. D. Wehausen, and S. G. Torres.** 2003. Status of bighorn sheep in California. *Desert Bighorn Council Transactions* 47:20-35.
- Oehler, M. W., Sr., R. T. Bowyer, and V. C. Bleich.** 2003. Home ranges of mountain sheep: effects of precipitation in a desert ecosystem. *Mammalia* 67:385-402.
- Weckerly, F. W., V. C. Bleich, C.-L. B. Chetkiewicz, and Mark A. Ricca.** 2003. Body weight and rumen-reticulum capacity in tule elk and mule deer. *Journal of Mammalogy* 84:659-664.
- Ernest, H. B., W. M. Boyce, V. C. Bleich, B. M. May, S. J. Stiver, and S. G. Torres.** 2003. Genetic structure of mountain lion (*Puma concolor*) populations in California. *Conservation Genetics* 4:353-366.
- Bleich, V. C., T. R. Stephenson, N. J. Holste, I. C. Snyder, J. P. Marshal, P. W. McGrath, and B. M. Pierce.** 2003. Effects of tooth extraction on selected biological parameters of female mule deer. *Wildlife Society Bulletin* 31:233-236.
- Marshal, J., P. R. Krausman, V. C. Bleich, W. B. Ballard, and J. S. McKeever.** 2002. Rainfall, el Nino, and dynamics of mule deer in the Sonoran Desert, California. *Journal of Wildlife Management* 66:1283-1289.
- Stephenson, T. R., V. C. Bleich, B. M. Pierce, and G. P. Mulcahy.** 2002. Validation of mule deer body composition using *in vivo* and post-mortem indices of nutritional condition. *Wildlife Society Bulletin* 30:557-564.
- Swift, P. K., V. C. Bleich, T. R. Stephenson, A. E. Adams, B. J. Gonzales, B. M. Pierce, and J. P. Marshal.** 2002. Tooth extraction from mule deer in the absence of chemical immobilization. *Wildlife Society Bulletin* 30:253-255.
- Bleich, V. C., C. S. Y. Chun, R. W. Anthes, T. E. Evans, and J. K. Fischer.** 2001. [Invited

Paper] Visibility bias and development of a sightability model for tule elk. *Alces* 37:315-327.

Drew, M. L., V. C. **Bleich**, S. G. Torres, and R. G. Sasser. 2001. Early pregnancy detection in mountain sheep using a pregnancy-specific protein B assay. *Wildlife Society Bulletin* 29:1182-1185.

Rosenstock, S. S., J. J. Herver, V. C. **Bleich**, and P. R. Krausman. 2001. Muddying the water with poor science: a reply to Broyles and Cutler. *Wildlife Society Bulletin* 29:734-738 [peer edited].

Bleich, V. C. 2001. On wildlife management in national monuments. *The Wildlifer* 306:59 [letter].

Andrew, N. G., V. C. **Bleich**, A. D. Morrison, L. M. Lesicka, and P. Cooley. 2001. Wildlife mortalities associated with artificial water sources in the Sonoran Desert. *Wildlife Society Bulletin* 29:275-280.

Thompson, J. R., V. C. **Bleich**, S. G. Torres, and G. P. Mulcahy. 2001. Translocation techniques for mountain sheep: does the method matter? *Southwestern Naturalist* 46:87-93.

Bleich, V. C., and B. M. Pierce. 2001. Accidental mass mortality of migrating mule deer. *Western North American Naturalist* 61:124-125.

Chao-chin, C., B. B. Chomel, R. W. Kasten, R. Heller, K. M. Kocan, H. Ueno, K. Yamamoto, V. C. **Bleich**, B. M. Pierce, B. J. Gonzales, P. K. Swift, W. M. Boyce, S. S. Jang, H.-J. Boulouis, and Y. Piemont. 2000. *Bartonella* spp. isolated from domestic and wild ruminants in North America. *Emerging Infectious Diseases* 6:306-311.

Singer, F. J., V. C. **Bleich**, and M. A. Gudorf. 2000. [Invited Paper] Restoration of bighorn sheep metapopulations in and near western national parks. *Restoration Ecology* 8(4S):14-24.

Bleich, V. C., and M. W. Oehler. 2000. [Invited paper] Wildlife education in the United States: thoughts from agency biologists. *Wildlife Society Bulletin* 28:542-545.

Rubin, E. S., W. M. Boyce, and V. C. **Bleich**. 2000. Reproductive strategies of desert bighorn sheep. *Journal of Mammalogy* 81:769-786.

Schaefer, R. J., S. G. Torres, and V. C. **Bleich**. 2000. Survivorship and cause-specific mortality in sympatric populations of mountain sheep and mule deer. *California Fish and Game* 86:127-135.

Pierce, B. M., V. C. **Bleich**, and R. T. Bowyer. 2000. Prey selection by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. *Journal of Mammalogy* 81:462-472.

- Swift, P. K., J. D. Wehausen, H. B. Ernest, R. S. Singer, A. M. Pauli, H. Kinde, T. E. Rocke, and V. C. Bleich. 2000. Desert bighorn sheep mortality due to presumptive type C botulism in California. *Journal of Wildlife Diseases* 36:184-189.
- Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? *Ecology* 81:1533-1543.
- Bleich, V. C. 1999. Wildlife conservation and wilderness management: uncommon objectives and conflicting philosophies. *North American Wild Sheep Conference Proceedings* 2:195-205.
- Bleich, V. C., and A. M. Pauli. 1999. Distribution and intensity of hunting and trapping activity in the East Mojave National Scenic Area, California. *California Fish and Game* 85:148-160.
- Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. *Journal of Mammalogy* 80:986-992.
- Bleich, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy* 80:283-289.
- Bleich, V. C., and B. M. Pierce. 1999. Expandable and economical radio collars for juvenile mule deer. *California Fish and Game* 85:56-62.
- Hill, S. D., and V. C. Bleich. 1999. Monitoring wildlife water sources using low Earth orbiting satellites (LEOS). *Wildlife Society Bulletin* 27:25-27.
- Andrew, N. G., V. C. Bleich, and P. V. August. 1999. Habitat selection by mountain sheep in the Sonoran Desert: implications for conservation in the United States and Mexico. *California Wildlife Conservation Bulletin* 12:1-30.
- Grigione, M. M., P. Burman, V. C. Bleich, and B. M. Pierce. 1999. Identifying individual mountain lions (*Felis concolor*) by their tracks: refinement of an innovative technique. *Biological Conservation* 88:25-32.
- Bleich, V. C. 1998. Importance of observer experience in determining age and sex of mountain sheep. *Wildlife Society Bulletin* 26:877-880.
- de Ropp, J. S., J. H. Theis, J. I. Mead, and V. C. Bleich. 1998. Limitations of nuclear magnetic resonance (NMR) analysis of fecal bile for taxonomic identification of contemporary and extinct mammals. *California Fish and Game* 84:112-118.
- Bleich, V. C., and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. *Great Basin Naturalist* 58:265-272.

- Pierce, B. M., V. C. Bleich, C. L.-B. Chetkiewicz, and J. D. Wehausen. 1998. Timing of feeding bouts of mountain lions. *Journal of Mammalogy* 79:222-226.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134:1-50.
- Andrew, N. G., V. C. Bleich, P. V. August, and S. G. Torres. 1997. Demography of mountain sheep in the East Chocolate Mountains, California. *California Fish and Game* 83:68-77.
- Andrew, N. G., L. M. Lesicka, and V. C. Bleich. 1997. An improved fence design to protect water sources for native ungulates. *Wildlife Society Bulletin* 25:823-825.
- Bleich, V. C., S. G. Torres, J. D. Wehausen, and T. A. Swank. 1996. [Invited paper] History of transplanting mountain sheep - California. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 10:164-166.
- Torres, S. G., V. C. Bleich, and J. D. Wehausen. 1996. Status of bighorn sheep in California, 1995. *Desert Bighorn Council Transactions* 40:27-34.
- Oehler, M. W., V. C. Bleich, and R. T. Bowyer. 1996. Error associated with LORAN-C: effects of aircraft altitude and geographic location. *Desert Bighorn Council Transactions* 40:19-21.
- Bleich, V. C. 1996. Interactions between coyotes (*Canis latrans*) and mountain sheep (*Ovis canadensis*). *Southwestern Naturalist* 41:81-82.
- Davis, J. L., C. L.-B. Chetkiewicz, V. C. Bleich, G. Raygorodetsky, B. M. Pierce, J. W. Ostergard, and J. D. Wehausen. 1996. A device to safely remove immobilized mountain lions from trees and cliffs. *Wildlife Society Bulletin* 24:537-539.
- Bleich, V. C., B. M. Pierce, J. L. Davis, and V. L. Davis. 1996. Thermal characteristics of mountain lion dens. *Great Basin Naturalist* 56:276-278.
- Main, M. B., F. W. Weckerly, and V. C. Bleich. 1996. [Invited Paper] Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* 77:449-461.
- Cronin, M. A., and V. C. Bleich. 1995. Mitochondrial DNA variation among populations and subspecies of mule deer in California. *California Fish and Game* 81:45-54.
- Bleich, V. C., and M. V. Price. 1995. Aggressive behavior of *Dipodomys stephensi*, an endangered species, and *Dipodomys agilis*, a sympatric congener. *Journal of Mammalogy* 76:646-651.
- Torres, S. G., V. C. Bleich, and J. D. Wehausen. 1994. Status of bighorn sheep in California, 1993. *Desert Bighorn Council Transactions* 38:17-28.
- Bleich, V. C., and S. G. Torres. 1994. [Invited Paper] California's mountain sheep management

program. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 9:186-195.

- Bleich, V. C., R. T. Bowyer, A. M. Pauli, M. C. Nicholson, and R. W. Anthes.** 1994. [Lead Article] Responses of mountain sheep *Ovis canadensis* to helicopter surveys: ramifications for the conservation of large mammals. *Biological Conservation* 45:1-7.
- Jaeger, J. R., J. D. Wehausen, **V. C. Bleich**, and C. L. Douglas. 1993. Limits in the resolution of LORAN-C for aerial telemetry studies. *Desert Bighorn Council Transactions* 37:20-23.
- Torres, S. G., **V. C. Bleich**, and A. M. Pauli. 1993. Status of bighorn sheep in California, 1992. *Desert Bighorn Council Transactions* 37:47-52.
- Torres, S. G., **V. C. Bleich**, and A. M. Pauli. 1993. An analysis of hunter harvest of mountain sheep in California, 1987-1992. *Desert Bighorn Council Transactions* 37:37-40.
- Jessup, D. A., W. L. Goff, D. Stiller, M. N. Oliver, **V. C. Bleich**, and W. M. Boyce. 1993. A retrospective serologic survey for *Anaplasma* spp. infection in three bighorn sheep (*Ovis canadensis*) populations in California. *Journal of Wildlife Diseases* 29:547-554.
- Thompson, J. R., and **V. C. Bleich**. 1993. A comparison of mule deer survey techniques in the Sonoran Desert of California. *California Fish and Game* 79:70-75.
- Bleich, V. C.** 1993. Comments on research, publications, and California's longest continuously published journal. *California Fish and Game* 79:42-43.
- Bleich, V. C., M. C. Nicholson, A. T. Lombard, and P. V. August.** 1992. Preliminary tests of mountain sheep habitat models using a geographic information system. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 8:256-263.
- Bleich, V. C., R. T. Bowyer, D. J. Clark, and T. O. Clark.** 1992. Quality of forages eaten by mountain sheep in the eastern Mojave Desert, California. *Desert Bighorn Council Transactions* 36:41-47.
- Bleich, V. C., S. G. Torres, D. A. Jessup, and G. P. Mulcahy.** 1992. Status of mountain sheep in California, 1991. *Desert Bighorn Council Transactions* 36:76-77.
- Krausman, P. R., **V. C. Bleich**, J. A. Bailey, D. Armentrout, and R. R. Ramey II. 1992. What is a minimum viable population? *Desert Bighorn Council Transactions* 36:68-75.
- Jaeger, J. R., J. D. Wehausen, and **V. C. Bleich**. 1991. Evaluation of time-lapse photography to estimate population parameters. *Desert Bighorn Council Transactions* 35:5-8.
- Bleich, V. C., and D. A. Jessup.** 1991. Status of bighorn sheep in California, 1990. *Desert Bighorn Council Transactions* 35:11-12.
- Bleich, V. C., and D. Racine.** 1991. Mountain beaver (*Aplodontia rufa*) from Inyo County,

- California. California Fish and Game 77:153-155.
- Bleich, V. C., J. G. Stahmann, R. T. Bowyer, and J. E. Blake.** 1990. Osteoporosis, osteomalacia, and cranial asymmetry in a mountain sheep (*Ovis canadensis*). *Journal of Wildlife Diseases* 26:372-376.
- Bleich, V. C.** 1990. On Calcium deficiency and brittle antlers. *Journal of Wildlife Diseases* 26:588.
- Bleich, V. C., J. D. Wehausen, and S. A. Holl.** 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conservation Biology* 4:383-390.
- Bleich, V. C., R. T. Bowyer, A. M. Pauli, R. L. Vernoy, and R. W. Anthes.** 1990. Responses of mountain sheep to aerial sampling using helicopters. *California Fish and Game* 76:197-204.
- Bleich, V. C., J. D. Wehausen, J. A. Keay, J. G. Stahmann, and M. W. Berbach.** 1990. Radiotelemetry collars and mountain sheep: a cautionary note. *Desert Bighorn Council Transactions* 34:6-8.
- Bleich, V. C., J. D. Wehausen, K. R. Jones, and R. A. Weaver.** 1990. Status of bighorn sheep in California, 1989 and translocations from 1971 through 1989. *Desert Bighorn Council Transactions* 34:24-26.
- Pauli, A. M., and V. C. Bleich.** 1988. Additional records of the spotted bat (*Euderma maculatum*) from California. *Great Basin Naturalist* 48:563.
- Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi.** 1987. Recruitment dynamics in a southern California mountain sheep population. *Journal of Wildlife Management* 51:86-98.
- Holl, S. A., and V. C. Bleich.** 1987. Mineral lick use by mountain sheep in the San Gabriel Mountains, California. *Journal of Wildlife Management* 51:381-383.
- Wehausen, J. D., V. C. Bleich, and R. A. Weaver.** 1987. Mountain sheep in California: a historical perspective on 108 years of full protection. *Western Section of The Wildlife Society Transactions* 23:65-74.
- Schwartz, O. A., V. C. Bleich, and S. A. Holl.** 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation* 37:179-190.
- Bleich, V. C.** 1986. Early breeding in free-ranging mountain sheep. *Southwestern Naturalist* 31:530-531.
- Schwartz, O. A., and V. C. Bleich.** 1985. Optimal foraging in Barn Owls? Rodent frequencies in diet and fauna. *Bulletin of the Southern California Academy of Science* 84:41-45.

- Bowyer, R. T., and V. C. Bleich. 1984. Distribution and taxonomic affinities of mule deer, *Odocoileus hemionus*, from Anza-Borrego Desert State Park, California. *California Fish and Game* 70:53-57.
- Bowyer, R. T., and V. C. Bleich. 1984. Effects of cattle grazing on selected habitats of southern mule deer. *California Fish and Game* 70:240-247.
- Bleich, V. C., and R. A. Weaver. 1983. "Improved" sand dams for wildlife habitat management. *Journal of Range Management* 36:130.
- Bleich, V. C. 1983. Comments on helicopter use by wildlife agencies. *Wildlife Society Bulletin* 11:304-306.
- Bleich, V. C. 1982. Additional notes on species richness of mammals at Bodie, California. *Southwestern Naturalist* 27:121-122.
- Bleich, V. C., L. J. Coombes, and J. H. Davis. 1982. Horizontal wells as a wildlife habitat improvement technique. *Wildlife Society Bulletin* 10:324-329.
- Bleich, V. C. 1982. An illustrated guide to aging the lambs of mountain sheep. *Desert Bighorn Council Transactions* 26:59-62.
- Bleich, V. C., L. J. Coombes, and G. W. Sudmeier. 1982. Volunteers and wildlife habitat management: twelve years together. *CAL-NEVA Wildlife Transactions* 1982:64-68.
- Bleich, V. C. 1982. Horizontal wells for mountain sheep: desert bighorn "Get the shaft". *Desert Bighorn Council Transactions* 26:63-64.
- Bleich, V. C., L. J. Coombes, and G. W. Sudmeier. 1982. Volunteer participation in California wildlife habitat management projects. *Desert Bighorn Council Transactions* 26:56-58.
- Paysen, T. E., J. A. Derby, H. Black, V. C. Bleich, and J. W. Mincks. 1980. A vegetation classification system applied to southern California. *USDA Forest Service General Technical Report PSW-45:1-33*.
- Bleich, V. C. 1979. *Microtus californicus scirpensis* not extinct. *Journal of Mammalogy* 60:851-852.
- Bleich, V. C., and B. Blong. 1978. A magnificent frigatebird in San Bernardino County, California. *Western Birds* 9:129.
- Bleich, V. C. 1978. Breeding bird census: annual grassland. *American Birds* 32:121.
- Bleich, V. C. 1977. *Dipodomys stephensi*. *Mammalian Species* 73:1-3.
- Schwartz, O. A., and V. C. Bleich. 1976. The development of thermoregulation in two species

of woodrats, *Neotoma lepida* and *Neotoma albigula*. *Comparative Biochemistry and Physiology* 54A:211-213.

Bleich, V. C. 1975. Roadrunner predation on ground squirrels in California. *Auk* 92:147-149.

Bleich, V. C., and O. A. Schwartz. 1975. Water balance and fluid consumption in the southern grasshopper mouse, *Onychomys torridus*. *Great Basin Naturalist* 35:62-64.

Bleich, V. C., and O. A. Schwartz. 1975. Observations on the home range of the desert woodrat, *Neotoma lepida intermedia*. *Journal of Mammalogy* 56:518-519.

Bleich, V. C. 1975. Diving times and distances in the Pied-billed Grebe. *Wilson Bulletin* 87:278-280.

Bleich, V. C., and O. A. Schwartz. 1975. Parturition in the white-throated woodrat. *Southwestern Naturalist* 20:271-272.

Schwartz, O. A., and V. C. Bleich. 1975. Comparative growth in two species of woodrats, *Neotoma lepida intermedia* and *Neotoma albigula venusta*. *Journal of Mammalogy* 56:653-656.

Bleich, V. C. 1974. Muskrats (*Ondatra zibethicus*) in Amargosa Canyon, Inyo and San Bernardino counties, California. *Murrelet* 55:7-8.

Bleich, V. C. 1974. Abnormal dentition in a grizzly bear. *Murrelet* 55:11.

Bleich, V. C., and O. A. Schwartz. 1974. Interspecific and intergeneric maternal care in woodrats (*Neotoma*). *Mammalia* 38:381-387.

Bleich, V. C., and O. A. Schwartz. 1974. Western range extension of Stephens' Kangaroo rat (*Dipodomys stephensi*), a threatened species. *California Fish and Game* 60:208-210.

Book Chapters and Proceedings of Symposia:

Bleich, V. C., and B. M. Pierce. 2005. [Invited contribution] Management of mountain lions in California. Pages 63-69 in E. L. Buckner and J. Reneau, editors. *Records of North American big game*. 12th edition. Boone and Crockett Club, Missoula, Montana, USA.

Rubin, E. S., and V. C. Bleich. 2005. [Invited contribution] Sexual segregation: a necessary consideration in wildlife conservation. Pages 379-391 in K. E. Ruckstuhl and P. Neuhaus, editors. *Sexual segregation in vertebrates: ecology of the two sexes*. Cambridge University Press, Cambridge, United Kingdom.

Bleich, V. C., J. G. Kie, E. R. Loft, T. R. Stephenson, M. W. Oehler, Sr., and A. L. Medina. 2005. [Invited contribution] Managing rangelands for wildlife. Pages 873-897 in C. E. Braun, editor. *Techniques for wildlife investigations and management*. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

- Pierce, B. M., and V. C. Bleich. 2003. [Invited Contribution] Mountain lion. Pages 744-757 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild Mammals of North America*. Second Edition. The Johns Hopkins University Press, Baltimore, Maryland.
- Torres, S. G., and V. C. Bleich. 1999. [Invited Contribution] Desert bighorn sheep: California. Pages 170-173 in D. E. Toweill and V. Geist, editors. *Return of royalty: a celebration of success*. Boone and Crockett Club, Missoula, Montana.
- Bleich, V. C., and S. G. Torres. 1999. [Invited Contribution] California bighorn sheep: California. Pages 130-133 in D. E. Toweill and V. Geist, editors. *Return of royalty: a celebration of success*. Boone and Crockett Club, Missoula, Montana.
- Bleich, V. C. 1998. [Invited Contribution] *Microtus californicus* (Peale 1848). Pages 90-92 in D. J. Haffner, E. Yensen, and G. L. Kirkland, Jr., editors. *North American rodents: status survey and conservation action plan*. International Union for the Conservation of Nature, Gland, Switzerland.
- Kie, J. G., V. C. Bleich, A. L. Medina, J. D. Yoakum, and J. W. Thomas. 1996. [Invited Contribution] Managing rangelands for wildlife. Pages 663-688 in T. A. Bookhout, editor. *Research and management techniques for wildlife and habitats*. Fifth edition. The Wildlife Society, Bethesda, Maryland.
- Bleich, V. C., J. D. Wehausen, R. R. Ramey II, and J. L. Rechel. 1996. [Invited Contribution] Metapopulation theory and mountain sheep: implications for conservation. Pages 353-373 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Covelo, California.
- Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1995. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Pages 102-109 in D. Ehrenfeld, editor. *Readings from Conservation Biology: wildlife and forests*. The Sheridan Press, Hanover, Pennsylvania. [Reprinted from *Conservation Biology* 4:383-390].
- Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1995. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Pages 71-78 in D. Ehrenfeld, editor. *Readings from Conservation Biology: the landscape perspective*. The Sheridan Press, Hanover, Pennsylvania. [Reprinted from *Conservation Biology* 4:383-390].
- Bleich, V. C. 1992. History of wildlife water developments, Inyo County, California. Pp. 100-106 in C. A. Hall, V. Doyle-Jones, and B. Widawski, editors. *The history of water: eastern Sierra Nevada, Owens Valley, White-Inyo Mountains*. University of California White Mountain Research Station, Bishop.
- Bleich, V. C., and D. B. Koch. 1992. [Abstract] Tule elk on private lands: species preservation, habitat protection, or wildlife commercialization? Page 78 in R. D. Brown, editor. *The*

biology of deer. Springer-Verlag, New York, New York.

- Bleich, V. C., C. D. Hargis, J. A. Keay, and J. D. Wehausen.** 1991. Interagency coordination and the restoration of wildlife populations. Pages 277-284 in J. Edelbrock and S. Carpenter, editors. Natural areas and Yosemite: prospects for the future. U.S. National Park Service, Denver Service Center, Denver, Colorado.
- Bleich, V. C.** 1990. [Invited Paper] Horizontal wells for wildlife water development. Pages 51-58 in G. K. Tsukamoto and S. J. Stiver, editors. Wildlife water development. Nevada Department of Wildlife, Reno.
- Bleich, V. C., and A. M. Pauli.** 1990. Mechanical evaluation of artificial watering devices built for mountain sheep in California. Pages 65-72 in G. K. Tsukamoto and S. J. Stiver, editors. Wildlife water development. Nevada Department of Wildlife, Reno.
- Bleich, V. C.** 1990. Affiliations of volunteers participating in California wildlife water development projects. Pages 187-192 in G. K. Tsukamoto and S. J. Stiver, editors. Wildlife water development. Nevada Department of Wildlife, Reno.
- Bleich, V. C.** 1990. Costs of translocating mountain sheep. Pages 67-75 in P. R. Krausman and N. S. Smith, editors. Managing wildlife in the southwest. Arizona Chapter of The Wildlife Society, Phoenix.
- Bleich, V. C., and S. A. Holl.** 1982. [Invited Paper] Management of chaparral habitat for mule deer and mountain sheep in southern California. Pages 247-254 in C. E. Conrad and W. C. Oechel, Technical Coordinators. Proceedings of the symposium on the dynamics and management of Mediterranean-type ecosystems. USDA Forest Service, General Technical Report PSW-58.
- Bleich, V. C.** 1982. [Invited Paper] Review comments. Pages 567-568 in C. E. Conrad and W. C. Oechel, Technical Coordinators. Proceedings of the symposium on the dynamics and management of Mediterranean-type ecosystems. USDA Forest Service, General Technical Report PSW-58.
- Bowyer, R. T., and V. C. Bleich.** 1980. Ecological relationships between southern mule deer and California black oak. Pages 292-296 in T. R. Plumb, Technical Coordinator. Proceedings of the Symposium on the ecology, management, and utilization of California oaks. USDA Forest Service, General Technical Report PSW-44.

Agency Reports:

- Hurley, K. et al. 2007. Recommendations for domestic sheep and goat management in wild sheep habitat. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming. Available at <http://www.mwvrc.org/bighorn/wafwawildsheepreport.pdf>

Sierra Nevada Bighorn Sheep Recovery Program [V. C. Bleich, H. E. Johnson, B. M. Pierce, C.

- R. Schroeder, T. R. Stephenson, and J. T. Villepique]. 2006. Sierra Nevada bighorn sheep in 2006. *Outdoor California* 67(2):10-17.
- Bleich, V. C.** 2005. Sierra Nevada bighorn sheep. Pages 226-227 in California Department of Fish and Game (compiler). The status of rare, threatened, and endangered plants and animals of California 2002-2004. California Department of Fish and Game, Sacramento, California, USA.
- Bleich, V. C.** 2005. Peninsular bighorn sheep. Pages 228-230 in California Department of Fish and Game (compiler). The status of rare, threatened, and endangered plants and animals of California 2002-2004. California Department of Fish and Game, Sacramento, California, USA.
- Sierra Nevada Bighorn Sheep Recovery Program [V. C. **Bleich**, B. M. Pierce, T. R. Stephenson, J. T. Villepique, and J. D. Wehausen]. 2004. Sierra Nevada Bighorn Sheep Progress Report 2003. *Outdoor California* 65(1):4-17.
- U.S. Fish and Wildlife Service [C. Benz, V. **Bleich**, W. Boyce, D. Craig, D. Graber, H. Quigley, P. Stine, S. Torres, and J. Wehausen]. 2003. Draft recovery plan for the Sierra Nevada bighorn sheep. U.S. Fish and Wildlife Service, Portland, Oregon.
- U.S. Fish and Wildlife Service [D. Armentrout, V. **Bleich**, W. Boyce, T. Davis, J. DeForge, D. Freeman, M. Jorgensen, S. Ostermann, E. Rubin, O. Ryder, P. Sorensen, S. Torres, and J. Wehausen]. 2000. Recovery plan for bighorn sheep in the peninsular ranges, California. U.S. Fish and Wildlife Service, Portland, Oregon.
- Singer, F., W. Adrian, F. Allendorf, J. Bailey, J. Berger, V. **Bleich**, M. Bogan, P. Brussard, S. Buskirk, N. T. Hobbs, T. Smith, D. Stevens, C. Van Riper III, E. Vyse, and G. White. 1996. Bighorn sheep in the Rocky Mountain region. National Biological Service, Ft. Collins, Colorado. 55 pp.
- Gudorf, M., P. Y. Sweanor, F. J. Singer, A. Blankenship, V. **Bleich**, T. Easterly, J. Emmerich, C. Eustace, L. Irby, D. Jaynes, B. Jellison, R. Kissell, J. Lindsay, J. Parks, T. Peters, K. Reid, S. Stewart, and T. Voss. 1996. Bighorn sheep habitat assessment of the greater Bighorn Canyon National Recreation Area. National Park Service and National Biological Service Cooperative Report, Bighorn Canyon National Recreation Area, Lovell, Wyoming. 43 pp.
- Gudorf, M., P. Sweanor, F. Singer, V. **Bleich**, J. Cordova, C. Hake, L. Lee, T. Lytle, P. Perrotti, S. Petersburg, and B. Sloan. 1995. Bighorn sheep habitat assessment of the greater Colorado National Monument area. National Park Service and National Biological Service Cooperative Report, Colorado National Monument, Fruita, Colorado. 52 pp.
- Holl, S. A., and V. C. **Bleich**. 1983. San Gabriel mountain sheep: biological and management considerations. USDA Forest Service, San Bernardino National Forest, San Bernardino, California. 136 pp.

Bleich, V. C. 1980. Amargosa vole study. California Department of Fish and Game, Nongame Wildlife Investigations Job Final Report W-54-R-10. 8 pp.

Gould, G. I., Jr., and **V. C. Bleich**. 1977. Amargosa vole study: progress report. Nongame Wildlife Investigations Job Progress Report W-54-R-10 California Department of Fish and Game, Sacramento. 4pp.

Bleich, V. C. 1975. Wildlife section including habitat and vegetation types in the Lake Mathews study area. Pages 84-130 in A study of the fish and wildlife resources of the Metropolitan Water District property at Lake Mathews with habitat improvement recommendations. California Department of Fish and Game, Long Beach.

Bleich, V. C. 1972. An annotated checklist of the mammals occurring in the Tecopa-Dumont Sand Dunes Study Area. Pages 75-77, appendix in M. A. Romero, editor. Amargosa Canyon-Dumont Dunes Proposed Natural Area. House of Impressions, Sun Valley, California.

Bleich, V. C. 1972. Checklist of the terrestrial vertebrates of the Seal Beach Naval Weapons Station, Fallbrook Annex, San Diego County, California. U.S. Navy, WPNSTAFBAINST 11015.2:7-13.

Book Reviews and Obituaries:

Weaver, R. A., and **V. C. Bleich**. *In press*. Bonnar Blong. Desert Bighorn Council Transactions.

Bleich, V. C. 1994. Marvin Wood, 1909-1994. Wild Sheep 17(4):8.

Bleich, V. C. 1992. [Review of] Midnight wilderness: journeys in Alaska's Arctic National Wildlife Refuge, by D. S. Miller. California Fish and Game 78:85-86.

Bleich, V. C. 1992. [Review of] Natural history of the White-Inyo Range, eastern California, edited by C. A. Hall, Jr. California Fish and Game 78:84-85.

Bleich, V. C. 1987. James C. Bicket, 1947-1986. Wildlife Society Bulletin 15:477-478.

Bleich, V. C. 1987. J. D. "Don" Landells, 1926-1986. Western Section of The Wildlife Society Transactions 22:iv.

Bleich, V. C. 1987. James C. Bicket, 1947-1986. Western Section of The Wildlife Society Transactions 22:v.

Bleich, V. C. 1979. [Review of] Wild geese, by M. A. Ogilvie. California Fish and Game 66:282-283.

Bleich, V. C. 1977. [Review of] Mammals of the world, by E. P. Walker. California Fish and Game 63:73.

Bleich, V. C. 1975. [Review of] *The carnivores*, by R. F. Ewer. *California Fish and Game* 61:255-256.

Popular Articles:

Bleich, V. C. 2009. A brief history of the CDFG bighorn sheep habitat enhancement program. *California Wild Sheep*, Winter 2009:8-10.

Bleich, V. C. 2009. Some thoughts on "Water dispensaries keep mountain bighorn sheep alive. *California Wild Sheep*, Fall 2009:28-30.

Bleich, V. C. 2009. Parting shots [letter]. *Bighorn (The Official Magazine of the Texas Bighorn Society)*, Spring 2009:30.

Bleich, V. C. 2009. Implications of fire history for conserving bighorn sheep. *Boone and Crockett Club Trophy Points 3* (July 2009). Available at:
http://www.boone-crockett.org/news/featured_story.asp?area=news&ID=52

Darby, N., J. Dungan, K. Stewart, V. **Bleich**, and D. Hughson. 2009. Responses of mule deer to experimental manipulation of water sources: preliminary results from the first year. *Mojave National Preserve Science Newsletter* 1:1-3.

Bleich, V. C., H. E. Johnson, S. A. Holl, L. Konde, S. G. Torres, and P. R. Krausman. 2009. Implications of fire history for conserving bighorn sheep. *California Wild Sheep*, Summer 2009:29.

Bleich, V. C. 2009. Some thoughts on water development in wilderness. *California Wild Sheep*, Spring 2009:8-9.

Bleich, V. C. 2008. Mountain sheep in California: some perspectives on the past, and prospects for the future (Part IV). *California Wild Sheep*, Fall 2008:14-15.

Bleich, V. C. 2008. Mountain sheep in California: some perspectives on the past, and prospects for the future (Part III). *California Wild Sheep*, Summer 2008:10-11.

Bleich, V. C. 2008. Mountain sheep in California: some perspectives on the past, and prospects for the future (Part II). *California Wild Sheep*, Spring 2008:12-13.

Bleich, V. C. 2007. Mountain sheep in California: some perspectives on the past and some prospects for the future (Part I). *California Wild Sheep*, Winter 2007:12-13.

Bleich, V. C. 2007. The Sierra Nevada bighorn sheep recovery program. *Conservation Connection* 16:11.

Bleich, V. C. 2007. The Sierra Nevada bighorn sheep recovery program. *California Wild Sheep*, Fall 2007:16-17.

- Bleich, V. C., and B. M. Pierce.** 2007. Management of mountain lions in California: history, basic biology, and citizen initiatives [part II]. *Conservation Connection* 15:12. Reprinted with permission from *Records of North American Big Game*, 12th Edition)
- Monteith, K. L., and **V. C. Bleich.** 2007. Mule deer fawn survival in central Sierra Nevada. *Outdoor California* 6(3):26-29.
- Bleich, V. C., and B. M. Pierce.** 2007. Management of mountain lions in California: history, basic biology, and citizen initiatives [part II]. *California Wild Sheep*, Summer 2007:8-9. Reprinted with permission from *Records of North American Big Game*, 12th Edition)
- Bleich, V. C., and B. M. Pierce.** 2007. Management of mountain lions in California: history, basic biology, and citizen initiatives [part I]. *Conservation Connection* 14:18-19. Reprinted with permission from *Records of North American Big Game*, 12th Edition)
- Bleich, V. C., and B. M. Pierce.** 2007. Management of mountain lions in California: history, basic biology, and citizen initiatives [part I]. *California Wild Sheep*, Spring 2007:18-19. Reprinted with permission from *Records of North American Big Game*, 12th Edition)
- Monteith, K. L., and **V. C. Bleich.** Mule deer fawn survival in the central Sierra Nevada. *California Deer*, Winter 2007:6-8.
- Bleich, V. C.** 2006. The potential for death at the waterhole. *Conservation Connection* 12:13. [Reprinted from *California Wild Sheep*, Fall 2006:8-9].
- Monteith, K. L., and **V. C. Bleich.** 2006. Fawn survival: central Sierra Nevada. *Mule Deer Foundation Magazine* 9:16-18.
- Bleich, V. C., and N. G. Andrew.** 2006. Bighorn sheep in California: how many are there, and how are they doing? *Foundation for North American Wild Sheep Conservation Connection* 11:5-6. [Reprinted from *California Wild Sheep*, Summer 2006:4-5].
- Bleich, V. C.** 2006. The potential for death at the waterhole. *California Wild Sheep*, Fall 2006:8-9.
- Bleich, V. C., and N. G. Andrew.** 2006. Bighorn sheep in California: how many are there, and how are they doing? *California Wild Sheep*, Summer 2006:4-5.
- Bleich, V. C.** 2002. Restoring bighorn sheep to the Sierra Nevada: a project of interest to the Boone and Crockett Club. *Fair Chase* 17(1):22-26.
- Bleich, V. C.** 2001. Restoring bighorn sheep to the Sierra Nevada: a new challenge for wildlife biologists. *Wild Sheep* 24(4):47-50,52.
- Bleich, V. C.** 2001. Summer ranges, winter ranges, and migratory mule deer: putting the parts of a puzzle in place. *Outdoor California* 62(4):20-23.

- Anderson, L. A., and V. C. Bleich. 2000. Desert bighorns in California: a success story for wildlife biologists and sheep hunters. *Fair Chase* 15(4):13-15.
- Bleich, V. C., B. M. Pierce, S. G. Torres, and T. Lupo. 2000. Using space age technology to study mountain lion ecology. *Outdoor California* 61(3):24-25.
- Torres, S. G., and V. C. Bleich. 2000. Mountain lions — California's elusive predator. *Outdoor California* 61(3):4-6.
- Bleich, V. C., and N. G. Andrew. 2000. Mountain sheep, mule deer, and burros in the brush: flourishing wild burros impact habitats and native big game. *Tracks* 17:10-12.
- Pauli, A. M., and V. C. Bleich. 1999. Gambel's quail hunting opportunities abundant within Mojave National Preserve. Pages 8-9,14 in A. J. Kenward, editor. *Upland Game California*. California Department of Fish and Game, Sacramento.
- Bleich, V. C. 1999. Desert deer investigation launched. *Outdoor California* 60(5):13-15.
- Bleich, V. C. 1999. [Letter] America's wilderness. *National Geographic Magazine* 195(3):xv.
- Bleich, V. C. 1997. Securing large carnivores. *Wildlife Control Technology* 4(2):39.
- Bleich, V. C. 1996. Assisting researchers can augment your income. *Wildlife Control Technology* 3(6):4.
- Pierce, B. M., and V. C. Bleich. 1996. Round Valley deer study. *Mule Deer* 2(4):10-13.
- Bleich, V. C. 1995. California's newest sheep hunting opportunity: the East Chocolate Mountains. *Wild Sheep* 18(4):19-22.
- Pierce, B. M., and V. C. Bleich. 1995. California deer management: the Round Valley investigation. *California Hunter Magazine* 4(4):32-33.
- Bleich, V. C., and S. G. Torres. 1995. The "book" rams are still out there. *Tracks* 12:9.
- Bleich, V. C., and S. G. Torres. 1993. History and current status of mountain sheep in California. *Wild Sheep* 16(4):15-19.
- Bleich, V. C. 1993. Sexual segregation in desert-dwelling mountain sheep. *Wild Sheep* 16(4):13-14.
- Bleich, V. C. 1993. Mountain sheep habitat: using a geographic information system. *Boone and Crockett Club News Journal* 8(4):39-40.
- Bleich, V. C. 1992. Round Valley deer facing long comeback trail. *Tracks* 9:9,15.

- Bleich, V. C.** 1990. Status of bighorn sheep in California: a brief synopsis. *Wild Sheep* 13(2):55.
- Bleich, V. C.** 1988. Distribution and early history of mountain sheep in California. Pages 1-3 *in* B. W. Wilson, editor. *California desert bighorn sheep: a guidebook for the hunter*. Society for the Conservation of Bighorn sheep, Los Angeles, California.
- Bleich, V. C.** 1988. Modern management of mountain sheep in California. Pages 4-6 *in* B. W. Wilson, editor. *California desert bighorn sheep: a guidebook for the hunter*. Society for the Conservation of Bighorn sheep, Los Angeles, California.
- Bleich, V. C.** 1983. Big game guzzlers and mountain sheep. *Outdoor California* 44(6):10.
- Davis, J. H., and V. C. Bleich.** 1980. Time-lapse photography: a new focus on wildlife. *Outdoor California* 41(4):7-9.
- Coombes, L. J., and V. C. Bleich.** 1979. Horizontal wells: the DFG's new slant on water for wildlife. *Outdoor California* 40(3):10-12.

Presentations at Professional Meetings

From 1972 to the present, I have been an author or coauthor of more than 100 presentations at professional meetings. I was selected to present a keynote address, "Ecology of mountain sheep: Ramifications for disease transmission and population persistence" at the April 2007 Workshop on Respiratory Disease in Mountain Sheep: Knowledge Gaps and Future Research which was held at the University of California, Davis. Details pertaining to these presentations are available upon request.

Grants and Fellowships

During 1973 through 2007, I competed successfully for and received project-specific funding in the amount of \$1,636,247 from internal and external sources. Details of grants and other funding received are available upon request.

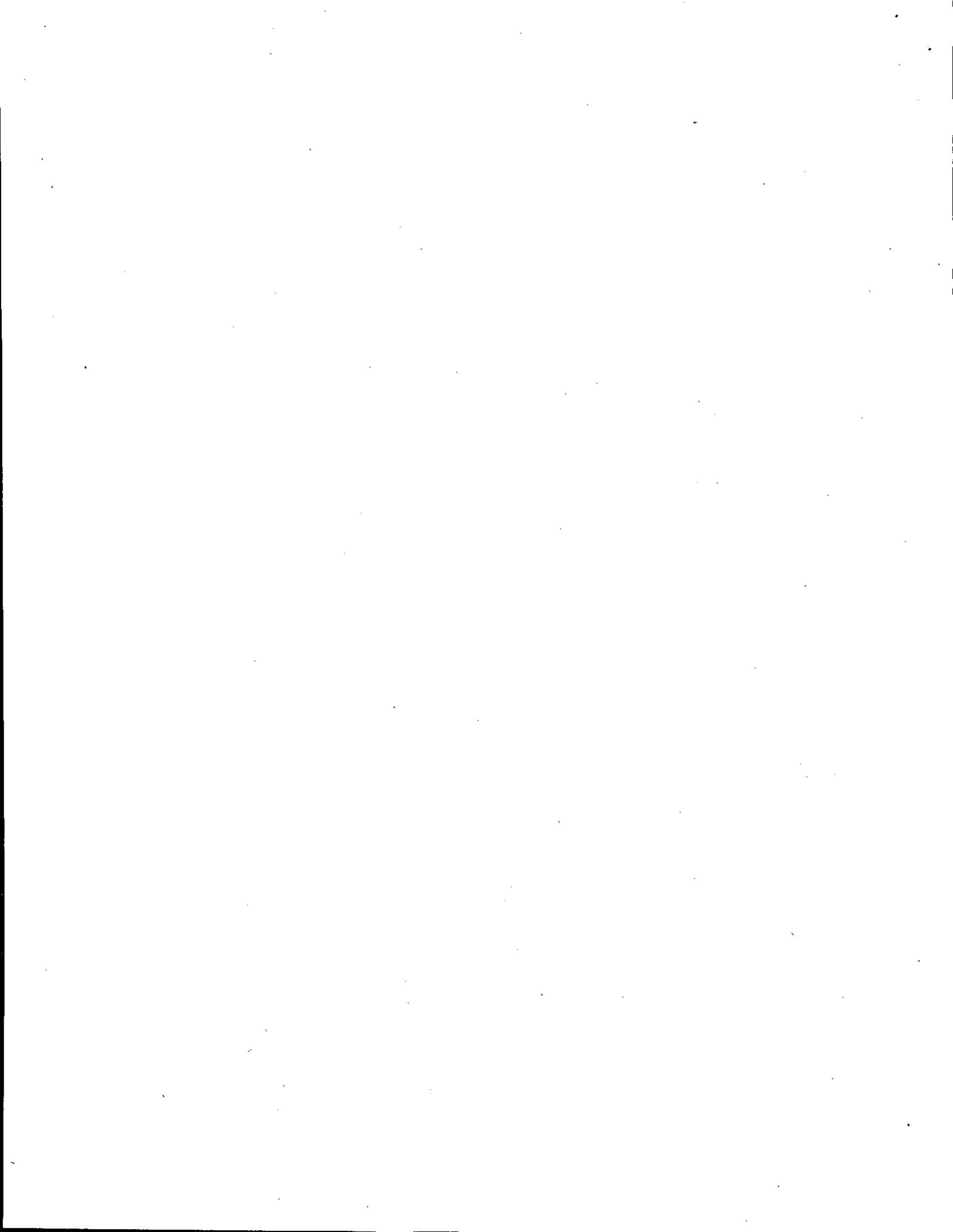
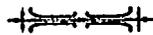


EXHIBIT 415

Bleich, V. C., J. D. Wehausen, R. R. Ramey II, and J. L. RecheI. 1996. Metapopulation theory and mountain sheep: implications for conservation. Pages 353-373 in D. R. McCullough, ed. *Metapopulations and wildlife conservation*. Island Press, Covelo, Calif.

15

Metapopulation Theory and Mountain Sheep: Implications for Conservation



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Researchers and managers traditionally have emphasized the need to protect steep, rocky terrain with which mountain sheep (*Ovis canadensis*) characteristically are associated (Bleich et al. 1990a). Management plans for this species in southwestern deserts commonly have defined mountain sheep populations on the basis of their geographic location, usually a single mountain range (Bureau of Land Management 1988). While mountain sheep occasionally cross the broad valleys that separate the majority of desert mountain ranges, little thought was previously given to the concept that sheep might regularly move between these desert mountain ranges (Schwartz et al. 1986). Wilson et al. (1980), however, emphasize that any areas used by mountain sheep might be essential for their survival, and recent telemetry investigations (Ough and deVos 1984; Jaeger 1994) suggest that intermountain movements occur frequently, necessitating an expanded concept of mountain sheep populations and habitat.

Andrewartha and Birch (1954) postulated that natural populations occurring over any substantial area will be composed of a number of local populations. Levins (1970) coined the term "metapopulation" to describe such systems of populations, but this concept has been applied only recently to wild populations (as in Shaffer 1985). Schwartz et al. (1986) first characterized the probable relationships of demes of mountain sheep inhabiting isolated mountain ranges of the American Southwest as metapopulations, and they used an area of the eastern Mojave Desert of California as an example. Bleich et al. (1990a) discussed another, more southern Mojave Desert "metapopulation" relative to the juxtaposition of traditional mountain sheep habitat and movements by sheep between these islands of rocky terrain; these authors

emphasized the need to maintain opportunities for movement between disjunct habitat patches (corridors) to ensure genetic diversity within metapopulations. Ramey (1993) further advocated a management approach that recognizes the metapopulation structure of wild sheep. Subsequently, the U.S. Bureau of Land Management embarked on a landscape-level plan that emphasizes the spatial and geographic relationships of mountain sheep habitat.

Metapopulation concepts recently have become fashionable among conservation biologists (Hanski 1991). Habitat fragmentation has created numerous situations where once-continuous distributions of species have come to resemble metapopulations but may not function as such. Hanski and Gilpin (1991) have cautioned that the dynamics of such fragmented populations generally are poorly understood and must be adequately explored before correct management prescriptions can be developed. Mountain sheep, however, have a naturally fragmented distribution (Bleich et al. 1990a) and may meet many of the predictions consistent with the structure of metapopulations. Indeed, Hanski and Gilpin note that "delimitation of local populations is often subjective, unless the environment consists of discrete habitat patches—which is the situation that has prompted metapopulation thinking and to which metapopulation thinking most naturally applies." Mountain sheep occur in such discrete habitat patches.

To date, metapopulation concepts have been applied to mountain sheep only from a genetic standpoint (Schwartz et al. 1986; Ramey 1993). Metapopulation theory is based as much on the spatial relationships of habitat patches (Gilpin 1987), however, as on the demographic consequences of extinctions and colonizations within the metapopulation (Hanski 1991). Applications of the metapopulation concept generally have been limited to species that are known to meet the demographic assumptions of the models (Hanski and Gilpin 1991). Because the dynamics of most mountain sheep populations are not well known, the application of metapopulation theory to the management of these ungulates has not been widely implemented.

The metapopulation model requires a colonization rate adequate to balance local extinctions, but colonization has been considered a rare event in mountain sheep (Geist 1971). In contrast, extinctions of populations are well documented (Wehausen et al. 1987; Torres et al. 1994), which appears consistent with the metapopulation model. Most of these extinctions have been human in cause, however, many from diseases contracted from domestic sheep (Foreyt and Jessup 1982; Goodson 1982; Jessup 1985; Onderka et al. 1988; Foreyt 1989) and may not result in an equilibrium that could have existed prior to such changes. Thus, a fundamental question about the dynamics of mountain sheep metapopulations concerns rates of natural extir-

pation and colonization. From a conservation standpoint, however, these questions are academic. Mountain sheep metapopulations have been altered considerably and the primary management question is: What strategy will best assure their continued viability?

Mountain Sheep and the Metapopulation Model

In this chapter we explore how well mountain sheep in California fit the assumptions of a metapopulation model, how anthropogenic changes have altered metapopulation structure, and what the most appropriate management approaches for conservation of this species are. We use topography and historical distributions of mountain sheep in eastern and southern California to delineate probable metapopulations that existed prior to their alteration by human activity. We test the hypothesis that mitochondrial DNA (mtDNA) haplotype frequencies differ among our geographically defined metapopulations, as a validation of their biological reality. Because colonization by females should occur more readily within metapopulations than between them, and because mtDNA is maternally inherited, mtDNA patterns should reflect colonization patterns of females (with the possible rare exceptions of males that might have been sampled outside their natal mountain ranges). We also present direct evidence of colonizations and natural extinctions and discuss substructuring of populations that result in a multitiered structure of mountain sheep metapopulations. Finally, we explore anthropogenic changes to these metapopulations and discuss management strategies that might best enhance the long-term persistence of wild sheep in the deserts of North America.

Geographic Metapopulations

Mountain sheep once were widespread in California, with populations concentrated in the northeast, the Sierra Nevada, and the Mojave and Sonoran deserts in the southeastern part of the state (Figure 15.1*a*). There were more than 92 historic populations of this species when mountain ranges in desert regions (Figure 15.2) or winter ranges of sheep in the Sierra Nevada are considered to represent geographically distinct populations.

We restricted our analyses to the central and southeastern parts of California (the Sierra Nevada and the deserts) where at least 60 populations occur (Torres et al. 1994). Most of these populations occupy public lands managed by a host of federal agencies (Bureau of Land Management, Forest Service, Department of Defense, National Park Service). Three "subspecies" of mountain sheep (Cowan 1940) have legal status in California (California

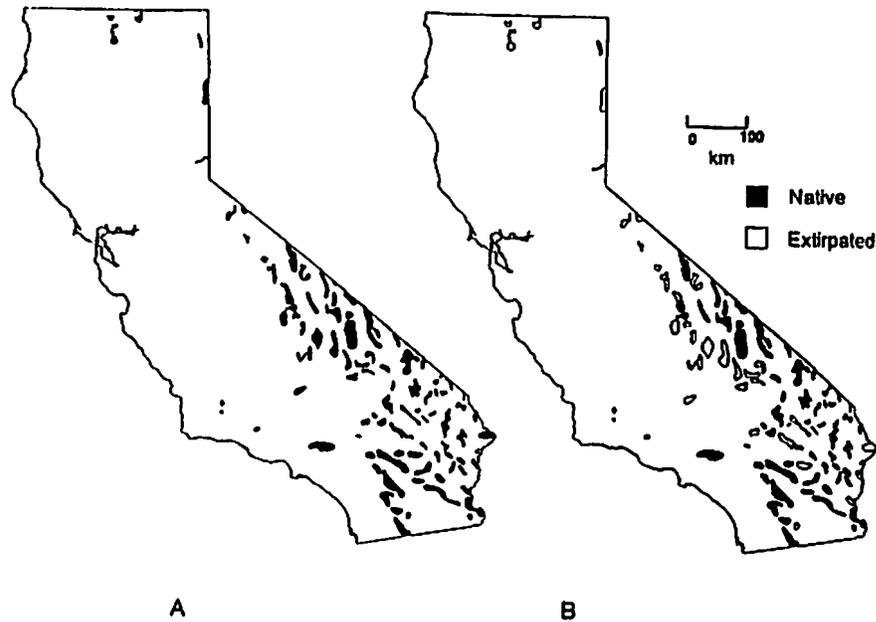


Figure 15.1. A. Historical distribution of mountain sheep in California, circa 1850. B. Extant and extirpated populations of mountain sheep in California, circa 1970.

Fish and Game Commission 1995) despite lack of biological support for one of these (Ramey 1993; Wehausen and Ramey 1993). In this chapter we treat mountain sheep in California collectively as *O. canadensis*.

To define the historical distribution of mountain sheep, we relied on data summarized by Wehausen et al. (1987) and Torres et al. (1994), which included only those geographic areas for which there is reliable evidence for the prior existence of permanent populations. We also mapped extant populations, including both native or translocated animals. Each area was delineated on a 1:100,000 USGS topographic map using the contour line that best defined the individual mountain range or the range known to be used by individual populations within large mountain masses (such as the Sierra Nevada).

We used a geographic information system (ARC/INFO, Environmental Systems Research Institute, Redlands, California) for spatial analyses. We created contour lines at various distances around each mapped population (buffer distance) and defined potential metapopulations by the connectivity of those lines. We then considered the relationship between buffer distance and resultant number of metapopulations in the context of known vagility of females to define metapopulations for further analysis. Additionally, we used



Figure 15.2. Typical habitat of mountain sheep in the southeastern California deserts is on mountain ranges separated by intervening low-desert expanses. Photo by V. C. Bleich.

the geographic information system (GIS) to determine changes in metapopulations within historical times prior to and following the construction of fenced, interstate highways in the desert regions of California. We used an extensive data set ($N > 10,000$ aerial telemetry locations) obtained during 1983–1994 to document movements within and between “geographic” metapopulations. We also used telemetry data and direct observations (Wehausen 1979, 1992; Holl and Bleich 1983; Andrew 1994; Jaeger 1994) that documented the existence of multiple demes of ewes within geographic areas that previously had been thought to contain only single populations.

By 1970, the number of native populations in California had been reduced to 52, with the largest proportion of these occurring in the Mojave and Sonoran deserts (Figure 15.1*b*). Mountain sheep are extinct in northeastern California and in 22 desert mountain ranges, as are 11 populations in the Sierra Nevada. Moreover, this species purportedly disappeared from three areas in the Transverse Ranges, far removed from what is considered typical habitat of mountain sheep. Because no extant populations of this species occur north of Lake Tahoe and management options in northeastern California are limited by the presence of domestic livestock (Northeastern California Bighorn Sheep Interagency Advisory Group 1991), we limit

further discussion to the area south of Lake Tahoe.

When we examined the relationship between buffer distance and the resultant number of metapopulations, the number of metapopulations declined rapidly with increasing buffer distance up to 7.5 km; beyond 7.5 km the slope of this relationship decreased markedly (Figure 15.3). Consequently, we chose a 7.5-km buffer distance to define metapopulations, whereby mountain sheep occupying ranges lying less than 15 km from one another are part of the same metapopulation. Using the probable distribution of mountain sheep in 1850, the 7.5-km buffer distance resulted in the definition of 13 metapopulations in southeastern California, of which 8 were insular populations (Figure 15.4*a*). Of the remaining 5 metapopulations, 2 consisted of paired populations and 3 contained from 10 to 50 subpopulations. Despite many extirpations, in 1970 the number of metapopulations remained similar to that in 1850 because additional metapopulations created via fragmentation were balanced by the loss of isolated, small metapopulations (insular populations and population pairs; Figure 15.4*b*). As a result, the mean number of populations composing these remaining metapopulations (including insular populations) declined from 7.7 to 4.0. Since 1970, as a result of the proliferation of the interstate highway system, these metapop-

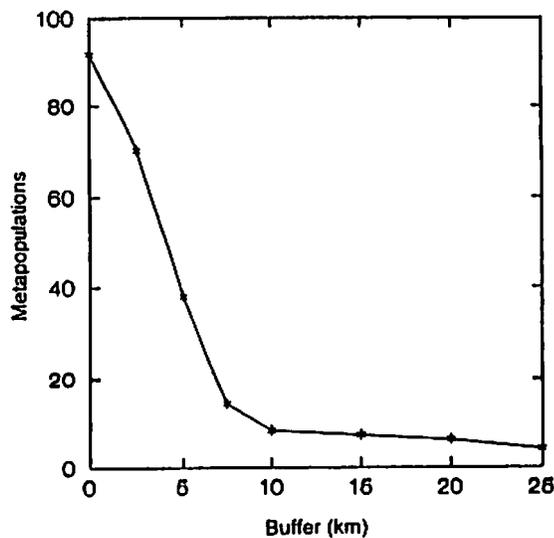


Figure 15.3. The relationship between the number of spatially defined metapopulations declines rapidly with increasing distance from the base of the mountain up to 7.5 km. Beyond that point, the number of metapopulations remains almost constant as distance increases.

ulations have experienced additional fragmentation (Figure 15.4c) and the mean number of populations composing each metapopulation has declined to 2.6. This situation has been ameliorated slightly through reestablishment of populations via translocation (Bleich 1990; Bleich et al. 1990b), but some of these were not considered in a larger landscape perspective and resulted in the establishment of six additional insular populations (Figure 15.4c).

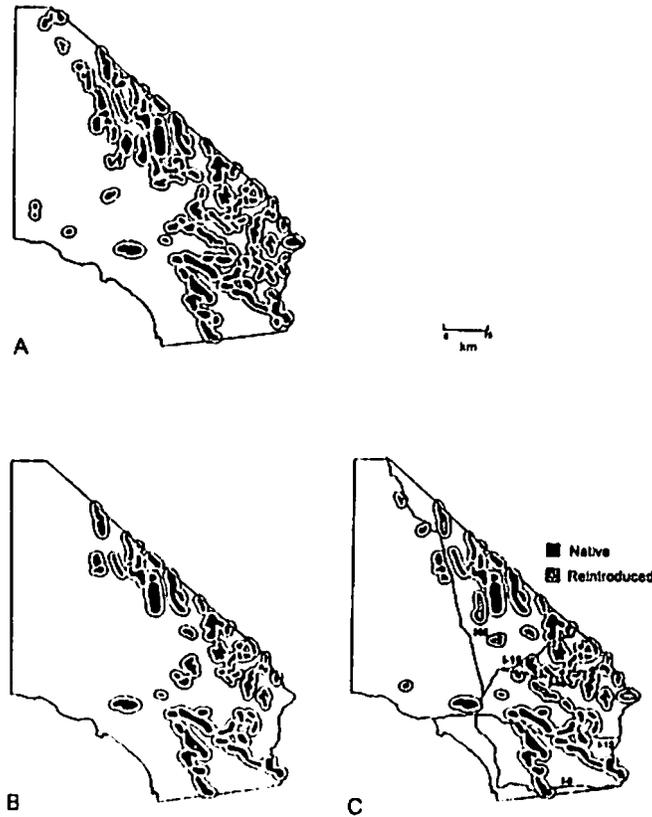


Figure 15.4. A. We delineated 13 spatially defined metapopulations in southeastern California, using populations of mountain sheep extant circa 1850. Of these, 8 were insular populations, and 2 were composed of 2 populations each; the remaining 3 consisted of from 10 to 50 populations. B. In 1970, the number of spatially defined metapopulations in southeastern California remained similar to that circa 1850 because additional metapopulations created by fragmentation were offset by the loss of isolated, small metapopulations (insular populations and population pairs). C. Since 1970, proliferation of the interstate highway system in southeastern California (I-8, I-10, and other routes) has further fragmented mountain sheep metapopulations.

Haplotype Frequencies

Mitochondrial DNA data were available from 164 mountain sheep inhabiting 18 mountain ranges within our study area (Ramey 1993). We tabulated mtDNA data by metapopulation and haplotype and tested for differences in the relative frequencies of mtDNA haplotypes among metapopulations with a G -test (Zar 1984). We eliminated three rare haplotypes that Ramey (1993) detected in only six individuals, due to their small contribution to the data set and because their inclusion would have resulted in less powerful tests. Hence our analyses were based on mtDNA from 158 individuals that occurred in 18 mountain ranges.

Haplotype frequencies (Figure 15.5) differed significantly ($G = 212.3$, $df = 20$, $P < 0.001$) among six metapopulations defined by the distribution of mountain sheep in 1850 (Figure 15.4a). All sheep sampled from the Sierra Nevada had a unique haplotype, and 64.3 percent of those from the White Mountains/Death Valley metapopulation had yet another unique haplotype, both of which strongly influenced this result. Consequently, we eliminated those metapopulations and repeated our analysis. Again, significant differences existed in the haplotype frequencies among the four southern metapopulations ($G = 65.4$, $df = 6$, $P < 0.001$). Because the San Gabriel Mountains are so isolated from the other southern metapopulations, we further compared the haplotype frequencies among the three desert metapopulations and significant differences persisted ($G = 53.1$, $df = 4$, $P = 0.001$). Finally, we compared the two largest metapopulations within the desert and significant differences again persisted ($G = 10.6$, $df = 2$, $P = 0.005$).

Defining Metapopulations

The probability of a sheep crossing between mountain ranges is a function of the distance between habitat patches (Gilpin 1987) and differs between sexes (Ramey 1993) because males and females follow different strategies to maximize reproductive fitness (Bleich 1993). Schwartz et al. (1986) summarized evidence that mountain sheep can traverse intermountain distances greater than 20 km. Our spatial definition of metapopulations (that is, occupying mountain ranges located less than 15 km from one another) was selected, in part, because of the philopatric tendencies of females, even though some intermountain movements by females have exceeded this distance (Ough and deVos 1984; Jaeger 1994).

Genetics and Population Substructuring

Schwartz et al. (1986) and Bleich et al. (1990a) have documented considerable opportunity for intermountain movements by males and females within metapopulations. The results of our mtDNA analyses are consistent with in-

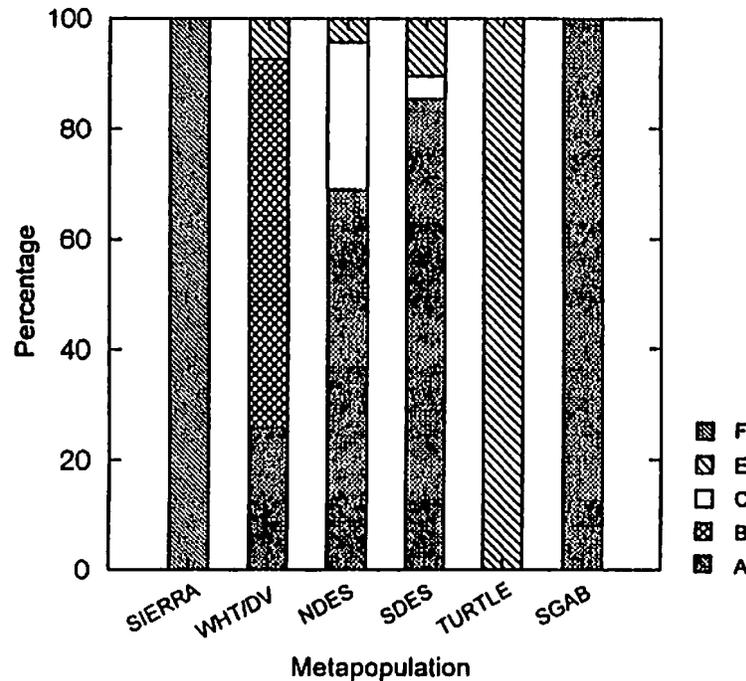


Figure 15.5. The frequency of five mtDNA haplotypes differed among six spatially defined metapopulations that were extant circa 1850 in southeastern California. SIERRA = Sierra Nevada metapopulation ($n = 9$); WHT/DV = White Mountains–Death Valley metapopulation ($n = 27$); NDES = Northern Desert metapopulation ($n = 45$); SDES = Southern Desert metapopulation ($n = 48$); TURTLE = Turtle Mountains metapopulation ($n = 10$); SGAB = San Gabriel Mountains metapopulation ($n = 19$).

frequent movements by females between our defined metapopulations and suggest that our geographic definition reflects biological reality.

The typical view of a mountain sheep population as a group of individuals occupying a particular mountain range is an oversimplification of their demography and genetics (Wehausen 1992; Ramey 1993). Despite documented seasonal movements and dispersal events, most females occupy relatively predictable home ranges that often are restricted to a limited part of a particular mountain range and may have little or no overlap with ranges of other groups of females (Andrew 1994; Jaeger 1994).

Geist (1971) has noted strong fidelity of females to specific winter ranges in the Rocky Mountains. Subsequently, Festa-Bianchet (1986) suggested that females with similar home ranges consist largely of related individuals; such groups, therefore, may represent matriline. Elsewhere in the Rocky

Mountains, Stevens and Goodson (1993) have described a similar population structure. In the Mojave Desert, evidence for population substructuring has been reported by Wehausen (1992), Cunningham et al. (1993), Jaeger (1994), and V. Bleich (unpublished data). Similar evidence has been found in the Sierra Nevada (Wehausen 1979) and San Gabriel Mountains (Holl and Bleich 1983).

Because of the conservative dispersal behavior of female mountain sheep, nuclear gene flow probably occurs primarily through the movements of males between mountain ranges, which occur much more often than for females (Ramey 1993). If female substructuring reflects matriline (Avisé 1995), however, it should be reflected in geographic patterns of mtDNA haplotypes. The finding that the three isolated "metapopulations" in our data set each exhibited a single haplotype (Figure 15.5) is consistent with this interpretation on a large geographic scale. These three populations were geographically more isolated from adjacent mountain ranges and thus would be expected to receive fewer immigrants. It is possible that each was founded by a lone female, resulting in a single matriline.

That female demes may represent matriline has important implications for both conservation and metapopulation concepts regarding mountain sheep. If the conservative behavior of female sheep results in infrequent emigrations leading to the founding of subpopulations that are matriline, then matriline may be the real operational metapopulation units. Similarly, metapopulation dynamics will be driven by the extirpation and founding of matriline, rather than by the larger and more complex demographic units previously postulated. If such populations are extirpated, they are unlikely to recover or be reestablished via recruitment of nonindigenous females (Avisé 1995) because of the characteristically low dispersal rates of female mountain sheep. Founder events (possibly involving a single female), lineage sorting within populations (that is, matrilineal groups), and low rates of mtDNA gene flow between populations are the most likely factors contributing to the observed patterns of mtDNA variation in southeastern California (Ramey 1993). Low frequency of female dispersal may lead to local fixation of mtDNA haplotypes, even if the population was founded by more than one female having different haplotypes. The much higher rate of intermountain movement by males (Ramey 1993) presumably is important in maintaining heterozygosity of nuclear genes and helps assure potential success of colonizing females.

Substructuring of female populations and differences in male-female dispersal distances (Ough and deVos 1984; Ramey 1993) have important implications for mountain sheep genetics, demography, and management.

Combining data from subpopulations may obscure independent dynamics, as Wehausen (1992) has documented for the Old Woman Mountains; one subpopulation was increasing while the other was decreasing in size. The concept of population substructuring has been incorporated into a recovery and conservation plan for the Sierra Nevada (Sierra Bighorn Interagency Advisory Group 1984). More recently, Stevens and Goodson (1993) have cautioned about similar situations in the Rocky Mountains. Without careful attention to substructuring within populations, managers could operate under the false premise that the overall population was increasing when in fact a segment of it was heading toward extinction.

Evidence for Natural Extirpations

The phenomenon of natural, independent extirpations of subpopulations within a metapopulation is an important component of metapopulation theory. Losses of mountain sheep populations are well documented (Wehausen et al. 1987; Torres et al. 1994), but the causes of these extirpations are rarely known. Some losses presumably resulted from unregulated market hunting during the latter part of the nineteenth century (Buechner 1960; Wehausen 1985). Other extirpations resulted from diseases contracted from domestic sheep (*Ovis aries*) that seasonally were herded through desert regions and pastured in summer at higher elevations in the Sierra Nevada, White, and Sweetwater mountains (Jones 1950; Wehausen 1988). Experimental mixing of domestic sheep and native mountain sheep has repeatedly resulted in fatal pneumonia among native sheep (Onderka and Wishart 1988; Foreyt 1989; Callan et al. 1991).

The number of extirpations of mountain sheep that have resulted from nonanthropogenic causes is speculative. Predation can significantly reduce local populations (Wehausen 1992) and may have been responsible for some local extinctions. Similarly, extended drought and resultant poor forage conditions and limited surface water (drying up of springs) may have caused the disappearance of several populations in southeastern California (Weaver and Mensch 1971).

Colonization Events

Colonization is considered a rare event among mountain sheep (Geist 1971), and reliable documentation of such behavior is lacking. Exploratory behavior probably is a necessary precursor to changes in the distribution of females and may occur in varying degrees from intramountain to intermountain movements. Colonizations likely begin with the exploration of unoccupied areas, followed by establishment of seasonal migrations, some of which may become

emigrations. A lamb born after its mother's emigration to a new range may be more likely to remain there (and contribute to colonization). A lamb born within its mother's natal range is less likely to subsequently emigrate.

Although mountain sheep inhabiting arctic and alpine ecosystems frequently exhibit migratory behavior (Geist 1971; Geist and Petocz 1977; Wehausen 1980; Holl and Bleich 1983; Festa-Bianchet 1986), few instances of migration have been described in desert ecosystems. Since 1984, we have documented seasonal movements by female sheep between six pairs of mountain ranges in the eastern Mojave Desert. Most of these have been migrations representing seasonal visits to neighboring mountain ranges, and females have given birth in at least five of these seasonally occupied ranges (Table 15.1). In one instance, a yearling female emigrated from her natal range, established a permanent home range, and produced at least one offspring in the neighboring mountain range. Observations of female sheep in mountain ranges far removed from permanent populations ($\bar{x} = 51.5$ km, $n = 4$; McQuivey 1978) may represent additional evidence of exploratory and migratory behavior by females. Further use of radiotelemetry is likely to yield additional information on exploratory and seasonal movements and occasional colonization events.

Implications of Metapopulation Theory for Conservation

There are four probable causes of metapopulation extinction (Hanski 1991). First, if extirpation rates of local populations exceed colonization rates, then extinction of the metapopulation is inevitable. Metapopulation persistence is contingent on the factors affecting extinction and colonization rates of populations within the metapopulation. Gilpin and Soulé (1986) have described four population extinction vortices: demographic, distribution, genetic, and adaptation, each with a potential role in the persistence of local populations. Mountain sheep are large, iteroparous mammals, and populations can persist for considerable periods with little recruitment because of their longevity (Wehausen 1992). They are also physiologically buffered from short-term environmental changes; for instance, they can live year-round in some hot deserts with no surface water (Krausman et al. 1985). Because of these characteristics, mountain sheep will not be as affected by the demographic and distribution extinction vortices as smaller, more r -selected species. They may, however, be more susceptible to genetic and adaptation extinction vortices due to lower population densities and longer generation times.

The rate of loss of genetic heterozygosity within a metapopulation is inversely related to the number of occupied habitat patches (Gilpin 1991). It is likely, however, that demographic processes are more important than genetics in the long-term persistence of populations within metapopulations (Lande

TABLE 15.1.
Evidence for migration and colonization of vacant habitats (emigration) by female mountain sheep in the Mojave and Sonoran deserts of California

Type of event and location (source/destination)	Birth occurring	Number of events
<i>Migration</i>		
Old Woman/Ship Mts.	No	1
Old Woman/Iron Mts.	Yes	1
Old Dad Peak/Cowhole Mt.	Yes	3
Kingston/Mesquite Mts.	Yes	14
Clark/Spring Mts.	Yes	20
Marble/Bristol Mts.	Yes	4
<i>Emigration</i>		
Marble/Bristol Mts.	Yes	1

1988; Caro and Laurenson 1994). Although Berger's (1990) conclusion that populations of less than 50 sheep will not survive for more than 50 years seems to bode poorly for the persistence of mountain sheep metapopulations, a reanalysis of data from California indicates much lower extinction probabilities (J. Wehausen, unpublished data). Traditional thinking suggests that small habitat patches are less important as sources of colonizers than large patches because the latter support larger populations and thus send out more colonists (Gilpin 1991). This does not mean, however, that smaller patches play no role in the metapopulation process. While smaller populations may receive more genetic variation than they export and thus contribute little to the effective size of metapopulations (Gilpin 1991), they may in some cases be critical stepping-stone populations in a larger colonization process (Gilpin 1987), making them important in the long-term conservation of mountain sheep in the American Southwest (Bleich et al. 1990a). Small populations and small patches of suitable habitat should not be undervalued (Krausman and Leopold 1986).

The second cause of metapopulation extinction (Hanski 1991) occurs where only two stable equilibria exist, such that metapopulations below a certain size are destined to extinction while larger ones may persist. Metapopulations above a certain size can become extinct if stochastic processes cause them to drop below that threshold. Such an outcome, which depends on immigration contributing to the dynamics of individual populations, is unlikely to be important to mountain sheep, given their low vagility and concomitant low colonization rates.

Immigration-extinction stochasticity is a third potential cause of metapopulation extinction when the number of local populations is small (Hanski 1991). Fragmentation of desert regions of eastern California has led to a decline in the average size of the extant mountain sheep metapopulations, making them more vulnerable to such extinction.

The fourth potential cause of metapopulation extinction involves regional stochasticity (Hanski 1991) because correlated dynamics tend to reduce metapopulation persistence (Hanski 1989). Weaver and Mensch (1971) have implied that a long drought period may have caused the extinction of several populations, and such an outcome would be consistent with the concept of correlated dynamics. However, Wehausen (1992) found differing dynamics of populations within metapopulations as well as between subpopulations within a mountain range, both of which would favor longer metapopulation persistence. Where regionally correlated stochasticity occurs, the low dispersal rates of mountain sheep may bode poorly for the long-term persistence of metapopulations of this species.

Lessons

Although numerous extirpations have occurred and anthropogenic barriers have fragmented historical metapopulations, our analysis suggests that 19 extant metapopulations currently exist in the Great Basin, Mojave, and Sonoran deserts and in the Sierra Nevada of California. Habitat fragmentation is the most significant threat faced by this species. Unoccupied habitat patches represent an important aspect of mountain sheep metapopulation dynamics because these areas may be the sites of future populations (Nunney and Campbell 1993). Moreover, given their potential importance to evolutionary processes, suboptimal habitats and peripheral populations should not be overlooked (Hoffmann and Parsons 1991; Lesica and Allendorf 1995).

Managers might best consider reestablishing extirpated populations in proximity to occupied habitat, thereby enhancing the probability of dispersing males encountering females. Because female dispersal appears to be rare, nuclear gene flow via male immigration from adjacent occupied patches is more apt to occur than the establishment of additional populations by females dispersing from translocation sites. In essence, the maintenance of existing metapopulations should precede the establishment of new metapopulations.

The California Department of Fish and Game has reestablished six populations that were spatially isolated from the nearest extant population, and

one of these is isolated from all other populations by an interstate highway. In retrospect, these translocations probably had limited value to the long-term persistence of mountain sheep as a species unless establishment of a large, continuous population or a metapopulation is possible at each site. But the establishment of isolated populations may be appropriate in certain situations—for example, to avoid catastrophic loss of a rare ecotype. Because population subdivision often prevents the spread of pathogens (Dobson and May 1986), management policy for the ecotype of mountain sheep occurring in the Sierra Nevada has recommended that newly established populations be disjunct from each other (Sierra Bighorn Interagency Advisory Group 1984). In this way, managers have reduced the probability of an epizootic depleting this ecological race. The ultimate success of this approach, however, may depend on establishing adequate metapopulations in each of these isolated locations.

Most metapopulations of mountain sheep are distributed across lands managed by a diversity of agencies, and there are not many examples (such as, Keay et al. 1987; Bleich et al. 1991) of the interagency coordination needed in comprehensive management programs (Bailey 1992). Indeed, interagency competition and bureaucratic inertia frequently have thwarted the preservation of biodiversity on public lands (Grumbine 1990). A landscape-level approach to management of lands (Agee and Johnson 1988) is necessary to ensure that reserves of adequate size are established and protected. Moreover, interagency cooperation is necessary to implement the strategies whereby such reserves are managed for the long-term persistence of large carnivores and ungulates (Salwasser et al. 1987).

Maintaining viable populations of mountain sheep in North America is contingent on protecting habitats for this species, but habitat protection alone will not be sufficient in many cases (Soulé et al. 1979; Belovsky et al. 1994). Public lands, including those harboring occupied and unoccupied habitats of mountain sheep, offer opportunities for the long-term conservation of these specialized ungulates. The apparent conformance of this species to the predictions of metapopulation models dictates that government agencies cooperate to ensure that opportunities for colonization are not precluded by further fragmentation of habitats through thoughtless blocking of movement corridors.

The ramifications of a metapopulation structure for mountain sheep conservation are clear: managers must ensure that anthropogenic extirpations are minimized and that opportunities for natural recolonization by females and the migration of nuclear genes via males are not impeded. For mountain sheep, the future is now. Adequate planning and interagency cooperation will

best serve the future of this species. Opportunities to develop proactive, rather than reactive, conservation strategies should not be wasted (Wilcove 1987).

Acknowledgments

We thank J. Barrette and M. C. Nicholson for suggesting the method used to define geographic metapopulations; A. M. Pauli for assistance with analyses; M. E. Gilpin for conversations that helped shape the direction of this chapter; and R. T. Bowyer, P. R. Krausman, and S. G. Torres for helpful comments on the manuscript. This is a contribution from the California Department of Fish and Game's Mountain Sheep Management Program.

REFERENCES

- Agee, J. K., and D. K. Johnson, eds. 1988. *Ecosystem Management for Parks and Wilderness*. Seattle: University of Washington Press.
- Andrew, N. G. 1994. Demography and habitat use of desert-dwelling mountain sheep in the East Chocolate Mountains, Imperial County, California. M.S. thesis, University of Rhode Island, Kingston.
- Andrewartha, H. G., and L. C. Birch. 1954. *The Distribution and Abundance of Animals*. Chicago: University of Chicago Press.
- Avisé, J. C. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to conservation. *Conservation Biology* 9:686-690.
- Bailey, J. A. 1992. Managing bighorn habitat from a landscape perspective. *Biennial Symposium of the Northern Wild Sheep and Goat Council* 8:49-57.
- Belovsky, G. E., J. A. Bissonette, R. D. Dueser, T. C. Edwards, Jr., C. M. Luecke, M. E. Ritchie, J. B. Slade, and F. H. Wagner. 1994. Management of small populations: Concepts affecting the recovery of endangered species. *Wildlife Society Bulletin* 22:307-316.
- Berger, J. 1990. Persistence of different-sized populations: An empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91-98.
- Bleich, V. C. 1990. Costs of translocating mountain sheep. Pages 67-75 in P. R. Krausman and N. S. Smith, eds., *Managing Wildlife in the Southwest*. Phoenix: Arizona Chapter of The Wildlife Society.

- . 1993. Sexual segregation in desert-dwelling mountain sheep. Ph.D. thesis, University of Alaska, Fairbanks.
- Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1990a. Desert-dwelling mountain sheep: Conservation implications of a naturally fragmented distribution. *Conservation Biology* 4:383–390.
- Bleich, V. C., J. D. Wehausen, K. R. Jones, and R. A. Weaver. 1990b. Status of bighorn sheep in California, 1989, and translocations from 1971 through 1989. *Desert Bighorn Council Transactions* 34:24–26.
- Bleich, V. C., C. D. Hargis, J. A. Keay, and J. D. Wehausen. 1991. Interagency coordination and the restoration of wildlife populations. Pages 277–284 in J. Edelbrock and S. Carpenter, eds., *Natural Areas and Yosemite: Prospects for the Future*. Denver: USDI National Park Service.
- Buechner, H. K. 1960. The bighorn sheep in the United States: Its past, present, and future. *Wildlife Monographs* 4:1–174.
- Bureau of Land Management. 1988. Rangewide plan for managing habitat of desert bighorn sheep on public lands. Washington, D.C.: USDI Bureau of Land Management.
- Callan, R. J., T. D. Bunch, G. W. Workman, and R. E. Mock. 1991. Development of pneumonia in desert bighorn sheep after exposure to a flock of exotic wild and domestic sheep. *Journal of the American Veterinary Medical Association* 198:1052–1056.
- California Fish and Game Commission. 1995. *Fish and Game Code of California*. Longwood, Fla.: Gould Publications.
- Caro, T. M., and M. K. Laurenson. 1994. Ecological and genetic factors in conservation: A cautionary tale. *Science* 263:485–486.
- Cowan, I. M. 1940. Distribution and variation in the native sheep of North America. *American Midland Naturalist* 24:505–580.
- Cunningham, S. C., L. Hanna, and J. Sacco. 1993. Possible effects of the realignment of U.S. Highway 93 on movements of desert bighorns in the Black Canyon area. Pages 83–100 in P. G. Rowlands, C. van Riper III and M. K. Sogge, eds., *Proceedings of the First Biennial Conference on Research in Colorado Plateau National Parks*. Washington, D.C.: USDI National Park Service.
- Dobson, A. P., and R. M. May. 1986. Disease and conservation. Pages 345–365 in M. E. Soulé, ed., *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, Mass.: Sinauer Associates.
- Festa-Bianchet, M. 1986. Seasonal dispersion of overlapping mountain sheep ewe groups. *Journal of Wildlife Management* 50:325–330.
- Foreyt, W. J. 1989. Fatal *Pasteurella haemolytica* pneumonia in bighorn sheep

- after direct contact with clinically normal domestic sheep. *American Journal of Veterinary Research* 50:341-344.
- Foreyt, W. J., and D. A. Jessup. 1982. Fatal pneumonia of bighorn sheep following association with domestic sheep. *Journal of Wildlife Diseases* 18:163-168.
- Geist, V. 1971. *Mountain Sheep: A Study in Behavior and Evolution*. Chicago: University of Chicago Press.
- Geist, V., and R. G. Petocz. 1977. Bighorn sheep in winter: Do rams maximize reproductive fitness by spatial and habitat segregation from ewes? *Canadian Journal of Zoology* 55:1802-1810.
- Gilpin, M. E. 1987. Spatial structure and population vulnerability. Pages 125-139 in M. E. Soulé, ed., *Viable Populations for Conservation*. Cambridge: Cambridge University Press.
- . 1991. The genetic effective size of a metapopulation. *Biological Journal of the Linnean Society* 42:165-175.
- Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pages 19-34 in M. E. Soulé, ed., *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, Mass.: Sinauer Associates.
- Goodson, N. J. 1982. Effects of domestic sheep grazing on bighorn sheep populations: A review. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 3:287-313.
- Grumbine, R. E. 1990. Viable populations, reserve size, and federal lands management: A critique. *Conservation Biology* 4:127-134.
- Hanski, I. 1989. Metapopulation dynamics: Does it help to have more of the same? *Trends in Ecology and Evolution* 4:113-114.
- . 1991. Single-species metapopulation dynamics: Concepts, models and observations. *Biological Journal of the Linnean Society* 42:17-38.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3-16.
- Hoffmann, A. A., and P. A. Parsons. 1991. *Evolutionary Genetics and Environmental Stress*. Oxford: Oxford University Press.
- Holl, S. A., and V. C. Bleich. 1983. San Gabriel mountain sheep: Biological and management considerations. San Bernardino, Calif.: USDA Forest Service, San Bernardino National Forest.
- Jaeger, J. R. 1994. Demography and movements of mountain sheep (*Ovis canadensis nelsoni*) in the Kingston and Clark mountain ranges, California. M.S. thesis, University of Nevada, Las Vegas.
- Jessup, D. A. 1985. Diseases of domestic livestock which threaten bighorn sheep populations. *Desert Bighorn Council Transactions* 29:29-33.

- Jones, F. L. 1950. A survey of the Sierra Nevada bighorn. M.A. thesis, University of California, Berkeley.
- Keay, J. A., J. D. Wehausen, C. D. Hargis, R. A. Weaver, and T. E. Blankinship. 1987. Mountain sheep reintroduction in the central Sierra: A cooperative effort. *Transactions of the Western Section of the Wildlife Society* 23:60-64.
- Krausman, P. R., and B. D. Leopold. 1986. The importance of small populations of desert bighorn sheep. *Transactions of the North American Wildlife and Natural Resources Conference* 51:52-61.
- Krausman, P. R., S. Torres, L. L. Ordway, J. J. Hervert, and M. Brown. 1985. Diel activity of ewes in the Little Harquahala Mountains, Arizona. *Desert Bighorn Council Transactions* 29:24-26.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.
- Lesica, P., and F. W. Allendorf. 1995. When are peripheral populations valuable for conservation? *Conservation Biology* 9:753-760.
- Levins, R. 1970. Extinction. Pages 77-107 in M. Gesternhaber, ed., *Some Mathematical Questions in Biology*. Providence, R.I.: American Mathematical Society.
- McQuivey, R. P. 1978. The desert bighorn sheep of Nevada. Biological Bulletin 6. Reno: Nevada Department of Wildlife.
- Northeastern California Bighorn Sheep Interagency Advisory Group. 1991. California bighorn sheep recovery and conservation guidelines for northeastern California. Alturas, Calif.: Modoc National Forest.
- Nunney, L., and K. A. Campbell. 1993. Assessing minimum viable population size: Demography meets population genetics. *Trends in Ecology and Evolution* 8:234-239.
- Onderka, D. K., and W. D. Wishart. 1988. Experimental contact transmission of *Pasteurella haemolytica* from clinically normal domestic sheep causing pneumonia in Rocky Mountain bighorn sheep. *Journal of Wildlife Diseases* 24:663-667.
- Onderka, D. K., S. A. Rawluk, and W. D. Wishart. 1988. Susceptibility of Rocky Mountain bighorn sheep and domestic sheep to pneumonia induced by bighorn and domestic livestock strains of *Pasteurella haemolytica*. *Canadian Journal of Veterinary Research* 52:439-444.
- Ough, W. D., and J. D. deVos, Jr. 1984. Intermountain travel corridors and their management implications for bighorn sheep. *Desert Bighorn Council Transactions* 28:32-36.
- Ramey, R. R., II. 1993. Evolutionary genetics and systematics of North American mountain sheep: Implications for conservation. Ph.D. thesis, Cornell University, Ithaca.

- Salwasser, H., C. Schonewald-Cox, and R. Baker. 1987. The role of interagency cooperation in managing for viable populations. Pages 159–173 in M. E. Soulé, ed., *Viable Populations for Conservation*. Cambridge: Cambridge University Press.
- Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation* 37:179–190.
- Shaffer, M. L. 1985. The metapopulation and species conservation: The special case of the northern spotted owl. Pages 86–99 in R. Gutiérrez and A. Carey, eds., *Ecology and Management of the Northern Spotted Owl in the Pacific Northwest*. General Technical Report PNW-185. Portland: USDA Forest Service.
- Sierra Bighorn Interagency Advisory Group. 1984. Sierra Nevada bighorn sheep recovery and conservation plan. Bishop, Calif.: Inyo National Forest.
- Soulé, M. E., B. A. Wilcox, and C. Holtby. 1979. Benign neglect: A model of faunal collapse in the game reserves of East Africa. *Biological Conservation* 15:259–272.
- Stevens, D. J., and N. J. Goodson. 1993. Assessing effects of removals for transplanting on a high-elevation bighorn sheep population. *Conservation Biology* 7:908–915.
- Torres, S. G., V. C. Bleich, and J. D. Wehausen. 1994. Status of bighorn sheep in California, 1993. *Desert Bighorn Council Transactions* 38:17–28.
- Weaver, R. A., and J. L. Mensch. 1971. Bighorn sheep in northeastern Riverside County. California Department of Fish and Game, Wildlife Management Administrative Report 71-1:1–8.
- Wehausen, J. D. 1979. Sierra Nevada bighorn sheep: An analysis of management alternatives. Cooperative Administrative Report. Bishop, Calif.: Inyo National Forest and Sequoia, Kings Canyon, and Yosemite National Parks.
- . 1980. Sierra Nevada bighorn sheep: History and population ecology. Ph.D. thesis, University of Michigan, Ann Arbor.
- . 1985. A history of bighorn management in the Sierra Nevada. Pages 99–105 in D. Bradley, ed., *State of the Sierra Symposium, 1985–86*. San Francisco: Pacific Publishing.
- . 1988. The historical distribution of mountain sheep in the Owens Valley region. Pages 97–105 in *Mountains to Deserts: Selected Inyo Readings*. Independence, Calif.: Friends of the Eastern California Museum.
- . 1992. Demographic studies of mountain sheep in the Mojave Desert: Report IV. Unpublished report. Bishop, Calif.: California Department of Fish and Game.

- Wehausen, J. D., and R. R. Ramey II. 1993. A morphometric evaluation of the peninsular bighorn subspecies. *Desert Bighorn Council Transactions* 37:1-10.
- Wehausen, J. D., V. C. Bleich, and R. A. Weaver. 1987. Mountain sheep in California: A historical perspective on 108 years of full protection. *Western Section of the Wildlife Society Transactions* 23:65-74.
- Wilcove, D. S. 1987. From fragmentation to extinction. *Natural Areas Journal* 7:23-29.
- Wilson, L. O., J. Blaisdell, G. Welsh, R. Weaver, R. Brigham, W. Kelly, J. Yoakum, M. Hinks, J. Turner, and J. DeForge. 1980. Desert bighorn habitat requirements and management recommendations. *Desert Bighorn Council Transactions* 24:1-7.
- Zar, J. H. 1984. *Biostatistical Analysis*. Englewood Cliffs, N.J.: Prentice-Hall.

EXHIBIT 416

Optimizing dispersal and corridor models using landscape genetics

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Summary

1. Better tools are needed to predict population connectivity in complex landscapes. ‘Least-cost modelling’ is one commonly employed approach in which dispersal costs are assigned to distinct habitat types and the least-costly dispersal paths among habitat patches are calculated using a geographical information system (GIS). Because adequate data on dispersal are usually lacking, dispersal costs are often assigned solely from expert opinion. Spatially explicit, high-resolution genetic data may be used to infer variation in animal movements. We employ such an approach to estimate habitat-specific migration rates and to develop least-cost connectivity models for desert bighorn sheep *Ovis canadensis nelsoni*.

2. Bighorn sheep dispersal is thought to be affected by distance and topography. We incorporated both factors into least-cost GIS models with different parameter values and estimated effective geographical distances among 26 populations. We assessed which model was correlated most strongly with gene flow estimates among those populations, while controlling for the effect of anthropogenic barriers. We used the best-fitting model to (i) determine whether migration rates are higher over sloped terrain than flat terrain; (ii) predict probable movement corridors; (iii) predict which populations are connected by migration; and (iv) investigate how anthropogenic barriers and translocated populations have affected landscape connectivity.

3. Migration models were correlated most strongly with migration when areas of at least 10% slope had 1/10th the cost of areas of lower slope; thus, gene flow occurred over longer distances when ‘escape terrain’ was available. Optimal parameter values were consistent across two measures of gene flow and three methods for defining population polygons.

4. Anthropogenic barriers disrupted numerous corridors predicted to be high-use dispersal routes, indicating priority areas for mitigation. However, population translocations have restored high-use dispersal routes in several other areas. Known intermountain movements of bighorn sheep were largely consistent with predicted corridors.

5. Synthesis and applications. Population genetic data provided sufficient resolution to infer how landscape features influenced the behaviour of dispersing desert bighorn sheep. Anthropogenic barriers that block high-use dispersal corridors should be mitigated, but population translocations may help maintain connectivity. We conclude that developing least-cost models from similar empirical data could significantly improve the utility of these tools.

Key-words: bighorn sheep, connectivity, fragmentation, GIS, isolation, least-cost model, metapopulation, *Ovis canadensis*, roads, translocation.

Journal of Applied Ecology (2007) **44**, 714–724
doi: 10.1111/j.1365-2664.2007.01325.x

Introduction

Defining and maintaining connectivity of natural populations has become a conservation priority (Moilanen *et al.* 2005). As natural populations become increasingly fragmented by habitat destruction and the creation of dispersal barriers such as roads, extinction probabilities for some populations will increase due to demographic and genetic factors associated with reduced dispersal (Hanski 1999; Hedrick 2005). Greater recognition that isolation of protected areas will lead to faunal relaxation (the gradual loss of species, e.g. Soule, Wilcox & Holtby 1979) has resulted in world-wide efforts to link protected areas using corridors, buffer zones and mixed-use areas. Models that incorporate land use, habitat quality, human activities and other factors are often employed to aid the mapping of landscape connectivity and prioritize land acquisitions (e.g. Hunter, Fisher & Crooks 2003; Nikolakaki 2004). However, identifying the optimal locations of wildlife corridors has proved to be difficult and controversial, in part because the details of how different species disperse across landscapes are often inadequately understood.

The advent of geographical information systems (GIS) analysis as a tool for identifying corridors and defining population connectivity has led to the widespread application of techniques such as 'least-cost' modelling (Adriaensen *et al.* 2003) and 'friction' analyses (Ray, Lehmann & Joly 2002; Joly, Morand & Cohas 2003; Sutcliffe *et al.* 2003; Nikolakaki 2004). Models created through these approaches are based typically on raster maps that divide landscapes into many cells with unique values that depict different habitat or vegetation types, elevation, slope or other landscape features. Cells are given weights or 'resistance values' reflecting the presumed influence of each variable on movement of the species in question. Least-cost routines (see Adriaensen *et al.* 2003), then, are employed to: (i) calculate the relative cost of all possible routes among populations or islands of core habitat; (ii) determine the least costly route for animal movement between pairs of populations or core areas of habitat; and (iii) plot these most probable routes on maps for use in conservation planning. 'Cost' is related to probability of transit and may not be defined explicitly; energetic costs, increased risk of predation or costs associated with reduced forage availability are among the reasons why an animal might avoid or be less able to traverse a landscape feature.

Although the least-cost approach has been employed widely (e.g. Adriaensen *et al.* 2003; Beazley *et al.* 2005; Rouget *et al.* 2006), this approach has two major drawbacks. First, the underlying models of dispersal (i.e. what resistance values are assigned to different landscape categories) are based rarely on anything more than informed opinions from experts. Where empirical data are available, dispersal costs are typically inferred from presence/absence or abundance data in

different habitats, but such data may reflect habitat use rather than dispersal cost. Second, although these techniques define the most probable route according to the cost weighting system, the actual cost of a route over which dispersal can occur is unknown. Therefore, despite the increasing need and frequent application of such tools, these largely untested models are of uncertain value for conservation planning and management.

Population genetics approaches offer additional tools that can be applied to questions of dispersal and connectivity. Selectively neutral genetic markers can provide indices of gene flow derived from differences in allele frequencies between individuals or populations (Waser & Strobeck 1998). The emerging field of 'landscape genetics' uses high-resolution genetic data to determine the influence of landscape features such as fields (Vos *et al.* 2001) or highways (Keller & Largiader 2003; Epps *et al.* 2005) on gene flow and dispersal (Manel *et al.* 2003). However, developing dispersal models from genetic data entails large data sets and certain assumptions.

In particular, migration (in the sense of gene flow) operates at a different time scale than dispersal. Genetic data may reflect long-term dispersal patterns, but the time-period represented is variable and depends partly on the effective size (N_e) of the populations. Time to equilibrium between migration and drift is proportional to N_e (Slatkin 1993). Therefore, among populations with small N_e , estimates of genetic distance or gene flow should reflect more recent dispersal patterns than estimates among populations with large N_e . Simulated data can be used to describe more clearly the time scale for a given data set (e.g. Epps *et al.* 2005), but in general the time scale represented is unknown. Furthermore, migration reflects effective dispersal, i.e. dispersal followed by reproduction. Individuals that disperse and do not reproduce will not be represented unless they are sampled directly. This could be advantageous if effective dispersal is the process of interest, but might not be as useful when considering, for instance, the role of dispersing individuals in spreading disease. Finally, sex-biased dispersal must be considered; gene flow estimates derived from nuclear DNA may largely represent movements of the least philopatric sex. Despite these possible limitations, genetic analyses may provide comprehensive pictures of dispersal that are otherwise unavailable (Koenig, VanVuren & Hooge 1996).

Efforts to develop more sophisticated models of migration from genetic data that consider species' dispersal behaviour are increasingly common. One such approach is to examine the correlation of gene flow with measures of 'effective geographical distance' (EGD) among populations, in addition to measures of geographical distance or the presence or absence of specific elements such as roads (Michels *et al.* 2001). EGD is a composite measure of dispersal distance between populations that incorporates both geographical distance and landscape features hypothesized to affect

dispersal. Recent examples of EGD include distances along riparian areas (Vignieri 2005), elevation change (Spear *et al.* 2005) and least-cost models that use a cost weighting surface based on assumed habitat value (Coulon *et al.* 2004; Spear *et al.* 2005; Vignieri 2005). EGD often explains more variation in gene flow between individuals or populations than geographical distance alone. This suggests that gene flow and dispersal patterns may not always fit a simple nearest-neighbour model, and it is important to test alternate hypotheses. However, genetic-based studies of dispersal rarely have examined more than a few alternate models of dispersal, and efforts to combine least-cost models with genetic data have been limited by a priori assumptions used to build the models. For instance, Vignieri (2005) used knowledge of preferred habitat for the Pacific jumping mouse *Zapus trinotatus* Rhoads to assign a lower dispersal cost to riparian and low-elevation habitat; however, that dispersal cost appeared arbitrary with respect to magnitude.

We propose that the effectiveness of combining least-cost and genetics-based approaches can be tested by comparing the ability of multiple least-cost models based on different landscape characteristics and a range of parameter values to explain observed variation in gene flow. Past analyses appear only to have tested hypotheses about which landscape factors affect dispersal. To translate least-cost models into effective conservation tools that identify active movement corridors and rank them according to predicted levels of gene flow, we also propose to estimate empirically how gene flow varies with EGD and determine the maximum EGD over which gene flow will occur.

In this paper we present methods to (1) test assumptions underlying least-cost connectivity models using genetic data; (2) predict landscape connectivity; and (3) test alternative management scenarios. We use estimates of gene flow among populations of desert bighorn sheep *Ovis canadensis nelsoni* Merriam to test the effectiveness of different least-cost GIS models and to optimize parameter values. We employ the following: (1) two methods for estimating gene flow among populations; (2) estimates of EGD derived from least-cost GIS models based on slope and distance with a wide range of parameter values; (3) three methods of defining population polygons used as the basis of our spatial analyses; (4) partial Mantel tests to assess correlation between gene flow estimates and EGD from alternate least-cost models; (5) regression of gene flow estimates on EGD to determine the maximum EGD over which gene flow is detectable; (6) identification and ranking of dispersal corridors using the best-fitting model of EGD; and (7) use of that model to identify probable movement corridors among populations of desert bighorn sheep while considering alternate management scenarios. Finally, we discuss the application of these techniques to conservation and management of species occupying fragmented habitats.

DESERT BIGHORN SHEEP AND PREVIOUS DISPERSAL MODELS

Desert bighorn sheep are desert-adapted ungulates native to the south-western United States. Preferred habitat is generally steep, rocky, arid terrain. In California, desert bighorn sheep populations are typically small, often < 50 individuals (Epps *et al.* 2003) and located in small mountain ranges isolated by varying expanses of low-lying desert habitat. The metapopulation-like distribution of desert bighorn sheep results in frequent extinction and recolonization of populations (Schwartz, Bleich & Holl 1986; Bleich, Wehausen & Holl 1990), and it is recognized that appropriate management requires consideration of population connectivity (e.g. determining when translocation of bighorn sheep may be needed to re-establish recently extirpated populations; Bleich *et al.* 1996). Bleich *et al.* (1996) proposed a model of population connectivity that considered populations < 15 km apart as likely to be connected by dispersal and hypothesized that interstate highways were barriers to dispersal. That model was used to determine management units above the level of individual populations. Low-resolution genetic markers [mitochondrial DNA (mtDNA) control region restriction fragment length polymorphism (RFLP) data] were used to verify that detectable genetic differences existed between management units.

Population genetics data from 26 populations of desert bighorn sheep in the Mojave and Sonoran Desert regions of California were used to investigate the spatial scale of gene flow and the role of anthropogenic (human-made) barriers such as interstate highways, urban areas and canals (Epps *et al.* 2005). Epps *et al.* (2005) tested whether estimates of gene flow and genetic distance (Nm and F_{ST}) were correlated with simple linear distance between populations and the presence of anthropogenic barriers. Those analyses confirmed that little or no gene flow had occurred across those barriers and that gene flow occurred primarily among populations < 15 km apart. However, habitat features expected to favour bighorn dispersal (e.g. areas with topographic relief sufficient to provide escape terrain for predator evasion) were not considered. Owing to considerable variation in the amount of escape terrain in low-lying areas among populations, we hypothesized that a least-cost model of migration based on topography could significantly improve our ability to predict the degree to which populations are linked by dispersal.

Materials and methods

OVERALL APPROACH: USING GENETIC DATA TO OPTIMIZE PARAMETER VALUES FOR A LEAST-COST MODEL

We used a matrix-based regression approach to test whether gene flow among populations of desert bighorn

sheep varied as a function of distance and topography or distance alone, and to identify which model of distance and topography best approximated the effect of these variables on gene flow. First, we calculated a series of matrices (X_1 – X_i) of effective geographical distances (EGD) among populations. Each matrix represented estimates of EGD between all population pairs among 26 populations of desert bighorn sheep in California, USA (Fig. 1), resulting from a unique set of parameter values (i unique combinations). Next, a matrix (Y) depicting the presence or absence of anthropogenic barriers (fenced highways, canals and urban areas) among those 26 populations was generated to control for the effect of those barriers on gene flow. Finally, a matrix (Z) of gene flow estimates between all population pairs was developed. We used partial Mantel tests to assess the correlation of Z (gene flow) with each matrix X_i (EGD), while controlling for the effect of Y (anthropogenic barriers). In that manner parameter values for the EGD model resulting in the strongest correlation between X and Z were identified. That exercise was repeated using three different methods to define the geographical extent of each population, as well as a second method of estimating gene flow, to examine how sensitive model fitting was to those variables. The optimized model of EGD was then used in later analyses of corridor length and location. Our methods are detailed in the following sections.

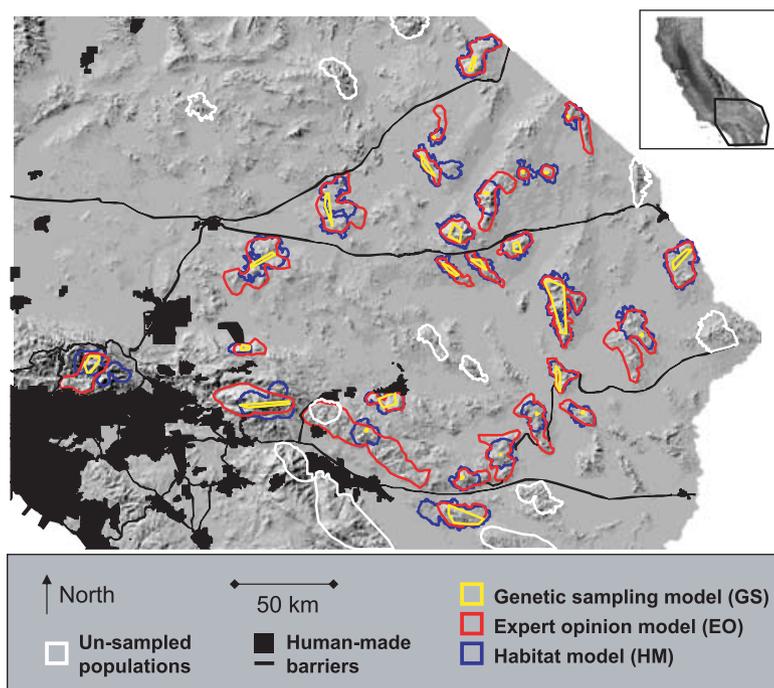


Fig. 1. Topography (hill-shade) and distribution of desert bighorn sheep in south-eastern California, United States. Coloured polygons represent genetically sampled populations used to develop the dispersal model. GS polygons are minimum convex polygons around genetic sample locations. EO polygons were hand-drawn based on topography and expert opinion on bighorn sheep distribution. HM polygons were developed either from a GIS habitat model (described in Appendix S2) or from 95% density kernels based on radio-telemetry locations. Population polygons not used for model development (outlined in white) are based on the HM or EO models. Anthropogenic barriers indicated include fenced interstate highways, canals and urban areas.

DEVELOPING LEAST-COST GIS MODELS TO CALCULATE EGD

We used slope as the variable for identifying the relative resistance or migration value of habitat between population polygons. We compiled 30 m Digital Elevation Model (DEM) data [US Geological Survey (USGS) 2003 series] for our study area and estimated slope for each 30 m cell using ArcGIS 9.0 (ESRI, Redlands, CA, USA). To simplify the models of bighorn migration as a function of topography and distance, we defined a ‘slope cut-off’ value for each model. Grid cells with slope greater than the cut-off value (‘slope’ cells) were considered more suitable (lower resistance) for bighorn dispersal than grid cells with slope lower than the cut-off (‘flat’ cells). We tested three slope cut-off values (5%, 10% and 15%), based on our assessment of radio telemetry data that suggested bighorn sheep are found mainly in habitat of at least 10% slope (3386 locations across the study area; unpublished data; California Department of Fish and Game). For each cut-off value tested, we generated six grids representing a wide range of different resistance values (weights) for slope cells. Thus, relative to the fixed cost of ‘1.0’ for a flat cell, slope cells were given weights of 0.7, 0.5, 0.3, 0.1, 0.05 or 0.01 for each respective cost grid, yielding 18 different least-cost models and thus 18 matrices of different estimates of EGD (X_i). For example, the model of EGD with 15% slope cut-off and slope cell weight of 0.1 considered cells with slope < 15% as 10 times more costly to cross than cells with slope > 15%. Slope grids were resampled at 90 m resolution to reduce calculation time.

ESTIMATING GENETIC DISTANCE AND GENE FLOW AMONG POPULATIONS

We used genetic data from 26 populations of desert bighorn sheep in California to develop the matrix of population pairwise gene flow estimates (Z). We identified 392 different individuals from data for 14 microsatellite loci using DNA extracted from faeces, tissue or blood, using two to six replicate polymerase chain reactions (PCRs) (see Epps *et al.* 2005). We used ARLEQUIN (Schneider, Roessli & Excofier 2000) to estimate population pairwise F_{ST} values and transformed these to Nm values via the standard Wright–Fisher model $F_{ST} = 1/(1 + 4Nm)$ as our primary index of relative gene flow. Due to the restrictive assumptions of this model, Nm is unlikely to represent the actual number of migrants per generation (Whitlock & McCauley 1999) but can indicate relative levels of gene flow, particularly when migration rates exceed mutation rates (Slatkin 1993).

As a second measure of gene flow, we estimated migration rates (M) using MIGRATE (Beerli & Felsenstein 2001). Because computation time for the full data set of 26 populations was estimated at about 2 years, we restricted analyses to a subset of nine populations. MIGRATE estimates migration rates among populations

using maximum-likelihood Markov chain Monte Carlo (MCMC) methods, and is an effort to improve migration rate estimates beyond the usual F_{ST} -based statistics (see Appendix S1 in Supplementary material for details).

USING GENE FLOW ESTIMATES TO TEST ALTERNATIVE PARAMETER VALUES

We used PATHMATRIX (Ray 2005) to calculate the least-cost paths among the 26 genetically sampled populations. This extension for ArcView version 3.2 (ESRI) uses a cost grid (here, derived from a given model of EGD) to (1) calculate least-cost paths among all pairs of population polygons; (2) generate the matrix \mathbf{X}_i of EGD; and (3) map each least-cost path. Each estimate of EGD between a population pair is calculated as:

$$\text{EGD} = \sum x_j w_j \quad \text{eqn 1}$$

where x_j is the linear distance across each grid cell j and w_j is the weight for that cell (determined here by whether the slope value is above or below the slope cut-off), summed over all the cells in a given path. All possible paths are evaluated, but only the EGD of the least-costly path is reported in matrix \mathbf{X}_i . Finally, we \log_{10} -transformed values in each matrix \mathbf{X}_i to linearize the relationship of distance with Nm (Epps *et al.* 2005).

The presence of anthropogenic barriers (fenced highways, canals and urban areas) was found previously to affect gene flow strongly among these populations (Epps *et al.* 2005). We chose to correct for this effect by including barrier presence/absence as a second predictor matrix \mathbf{Y} when assessing correlation between EGD and gene flow. Otherwise, if barriers were incorporated into each least-cost grid during the model-fitting process (by assigning large cost values to any grid cell where a barrier was present), appropriate cost values would vary for each least-cost grid. Inappropriate cost values would disrupt the otherwise linear relationship between gene flow (Nm) and $(\log_{10})\text{EGD}$. Moreover, those barriers have been present for only 40–60 years and have presumably affected gene flow at a different time scale than topography. Finally, barriers could be mitigated and therefore should be considered separately. We incorporated barriers formally into the underlying cost grid only when using the final best-fitting model to define active corridors (as described below). Barriers were recorded as present for any population pair with a barrier interposed; the map of barriers was compiled as described by Epps *et al.* (2005).

We used partial Mantel tests (Smouse, Long & Sokal 1986; Manly 1991) to estimate the partial correlation of matrix \mathbf{Z} (Nm or MIGRATE M) with each matrix \mathbf{X}_i , while controlling for the presence of anthropogenic barriers by including matrix \mathbf{Y} as a second predictor matrix. Tests were conducted using XLSTAT (Addinsoft, New York, USA). Partial Mantel tests determine the correlation of a response matrix \mathbf{Z} to a predictor matrix

\mathbf{X} , while removing a spurious correlation resulting from a second predictor matrix \mathbf{Y} that may be correlated with both \mathbf{Z} and \mathbf{X} . We used the value of the partial correlation coefficient r resulting for each \mathbf{X}_i to compare graphically the relative fit of each model of EGD. We also estimated r for the null model (\mathbf{X}_0) matrix of straight-line distances (\log_{10} -transformed) between population polygons.

While partial Mantel tests are controversial due to potential underestimation of type I error (Raufaste & Rousset 2001; Rousset 2002), Castellano & Balletto (2002) argued that this concern has been overstated. Moreover, because we compared the partial correlation coefficient of distance matrices while using the same second predictor matrix \mathbf{Y} in all tests, and did not compare P -values, such underestimation is unlikely to affect our conclusions.

DEFINING POPULATION POLYGONS

Most metrics of gene flow use populations as the basic unit of comparison, defined theoretically as groups of freely interbreeding individuals. In practice, defining the spatial extent of populations may be difficult. To calculate accurate distances among populations, population map polygons must depict habitat used regularly by interacting individuals. To test how sensitive parameter optimization for the least-cost models was to population polygon definition, we repeated EGD calculations using three different methods to define population polygons.

Our first polygon model ['Genetic sampling' (GS); Fig. 1] used minimum convex polygons drawn around the locations in each mountain range where DNA samples were actually collected. If samples were collected at only one location such as a waterhole, we used a circle with diameter of 1 km centred on the sampling point. This approach would be useful for species where the extent of each population sampled is not defined clearly by the habitat patch and is likely to provide a conservatively small habitat area. The second polygon model ['expert opinion' (EO); Fig. 1] used the population polygons defined by Epps *et al.* (2005). These polygons were drawn on the basis of both the topographic extent of each mountain range and expert opinion regarding the distribution of bighorn sheep in each location, derived from field observations and helicopter surveys. Bleich *et al.* (1996) used a similar approach to define population polygons for management purposes. Expert opinion may often be the only available means to define populations for many species.

The final polygon model tested ['habitat model' (HO); Fig. 1] was a GIS model based on slope and distance to perennial water sources. It was designed to provide repeatable polygons depicting desert bighorn sheep distribution and to predict the probable distribution of new populations in vacant habitat. The model was developed using radio telemetry locations of desert bighorn sheep in five populations (California Department.

of Fish and Game, unpublished data) and expert opinion to inform model fit (see Appendix S2).

IDENTIFYING AND RANKING DISPERSAL CORRIDORS USING THE BEST-FITTING DISPERSAL MODEL

After examining graphically correlation coefficients from Mantel tests for all X_i matrices, repeated for three sets of population polygons and Z matrices based on two different estimates of gene flow, we chose the best-fitting model of EGD by selecting the values of slope cut-off and slope weight that resulted in the strongest correlation coefficients. We then used that best-fitting model to identify probable movement corridors between bighorn sheep populations, after selecting a population polygon model based both on performance and practical considerations.

To identify probable movement corridors, we used two regression-based procedures. We first estimated the maximum effective dispersal distance (the greatest effective geographical distance separating population polygons over which gene flow can be detected; hereafter, EGD_{MAX}) for desert bighorn sheep. This was performed via regression of population pairwise estimates of Nm on estimates of EGD from the best-fitting model for population pairs without intervening barriers. Gene flow, as measured by Nm between populations, is expected to decline with increasing distance until an asymptote at a 'background' non-zero level of Nm is reached. At distances greater than this point, current gene flow is unlikely but some degree of genetic similarity exists because of descent from common ancestors or recurrent mutations (Slatkin 1993). Because we could not identify a regression model that adequately described the rapid decline of Nm to a non-zero asymptote, we used XLSTAT version 2006.2 (Addinsoft) to perform nonparametric regression (Härdle 1992) of Nm on EGD from the best-fitting dispersal model. Nonparametric regression is essentially a smoothing method for predictive purposes. We used the LOWESS method with the tri-weight kernel and bandwidth equal to the standard deviation, based on the underlying model of a second-degree polynomial. We defined our estimate of EGD_{MAX} as the point at which the predicted values from the nonparametric regression first stopped decreasing (excluding initial fluctuations at high Nm).

We defined active dispersal corridors as those least-cost paths with total cost $< EGD_{MAX}$. However, because nonparametric regression does not generate a general predictive equation for gene flow as a function of EGD, we modelled this relationship with a negative exponential regression function for $EGD < EGD_{MAX}$ (where an adequate fit could be achieved) and used the resulting equation to predict relative gene flow over active dispersal corridors.

To identify probable dispersal corridors on the current landscape, we added barriers to the cost grid of

the best-fitting migration model. Because Epps *et al.* (2005) determined that those barriers had eliminated recent gene flow, we assigned barrier cells a cost equivalent to EGD_{MAX} to make them impermeable. After adding polygons for un-sampled populations to the population map, we used PATHMATRIX to calculate and map all least-cost paths between populations with a total cost less than EGD_{MAX} . This was repeated without human-made barriers in the cost-grid to examine how mitigation of those barriers might affect landscape connectivity. To investigate the role that translocations have played in maintaining population connectivity in south-eastern California, we repeated the first analysis but removed five populations re-established by the California Department of Fish and Game through translocations. The relative strength of each corridor was assessed using the exponential decay model to estimate Nm as a function of EGD.

MODEL VALIDATION

Current radio-telemetry data were insufficient to validate the presence of dispersing bighorn sheep in the predicted least-cost corridor routes. Radio-telemetry locations were typically collected monthly; intermountain movements are relatively rare and time spent moving between mountain ranges may be of short duration. However, radio-collared or marked individuals have been detected after moving between mountain ranges. We compiled a list of all such movements as well as those inferred from anecdotal reports. We then evaluated whether least-cost paths from the best-fitting model linked each pair of ranges for which intermountain movements were detected.

Results

Effective geographical distance (EGD) based on topography was more strongly negatively correlated with gene flow (both Nm , as calculated from population pairwise F_{ST} values, and M , as estimated by MIGRATE) than straight-line distance in almost all cases, with an absolute increase of the correlation coefficient r of up to 23% (Fig. 2). EGD models based on 5% slope cut-off performed more poorly than models based on 10% or 15% slope in all cases. The 15% slope cut-off performed slightly better than the 10% cut-off over most (but not all) tests (Fig. 2). For all slope cut-off values, all population polygon models and both measures of gene flow, best-fitting models resulted when sloped terrain had 1/20th to 1/10th the cost of movement across flat terrain (Fig. 2), with the slope weight of 0.10 most often favoured. Therefore, the EGD model employing the 15% slope cut-off and slope weight of 0.10 (hereafter referred to as the 15/0.10 model) was used for further corridor modelling. Stronger correlation coefficients (r) were observed when using EO model population polygons (Fig. 2). However, the differences in r were not large, and

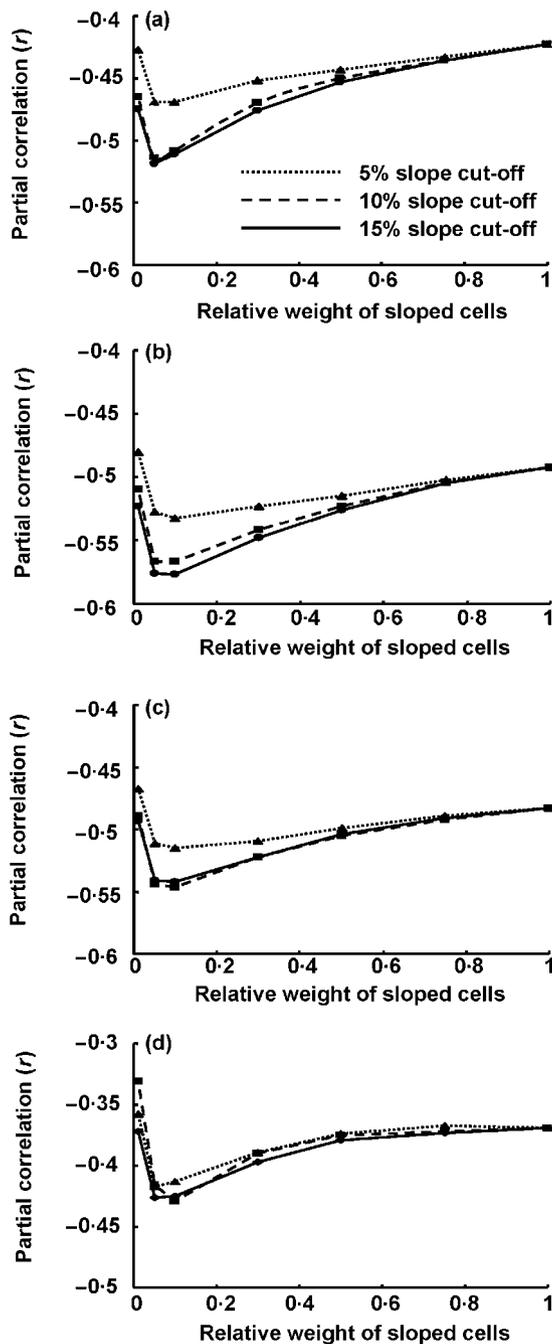


Fig. 2. Coefficients (r) for partial correlation of gene flow (Nm) with effective geographical distance from least-cost models, while correcting for anthropogenic barriers. Models use slope cut-off values of 5%, 10% and 15% and relative weights for slope cells of 0.01–1.0, for (a) GS polygons; (b) EO polygons; (c) HM polygons; and (d) a subset of nine populations using estimates of gene flow (M) from MIGRATE with HM polygons. The slope weight of 1.0 represents the shortest straight-line distance between population pairs.

optimal slope cut-off values and weights were similar, indicating low sensitivity to the choice of population polygon model. We chose HM polygons to calculate EGD_{MAX} and model different corridor scenarios because this model can be used easily where bighorn sheep are currently absent or their distribution is poorly understood.

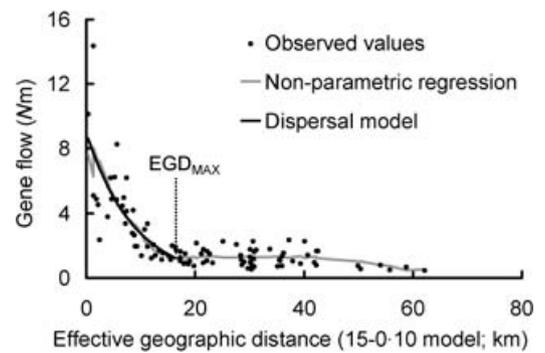


Fig. 3. Population pairwise estimates of gene flow (Nm) (for population pairs without intervening anthropogenic barriers) plotted against effective geographical distance (EGD) from the best-fitting model. Maximum effective dispersal distance (EGD_{MAX} , indicated with dashed arrow) was defined as the smallest EGD (after initial fluctuations) at which the slope of the line of predicted values generated by the nonparametric regression (grey line) stopped decreasing. Non-linear regression (black line) was conducted on all points below EGD_{MAX} to generate a predictive model for gene flow as a function of EGD. Above EGD_{MAX} , dispersal was assumed to be negligible.

From nonparametric regression of population pairwise Nm values on estimates of EGD from the 15/0.10 model, we estimated the maximum effective dispersal distance (EGD_{MAX}) as 16.4 km-cost-units (corresponding to 16.4 km of flat terrain or 164 km of sloped terrain; Fig. 3). From regression of Nm values on EGD (km scale) for all values $< EGD_{MAX}$ (Fig. 3), we derived the following negative exponential model:

$$Nm = 9.141 * e^{-0.112 * EGD} - 0.219 \quad \text{eqn 2}$$

We used equation 2 to estimate the relative strength of gene flow across active dispersal corridors with $EGD < EGD_{MAX}$ (Fig. 4).

The connectivity of the current landscape suggested that nearly all populations are currently linked to another population by at least one possible dispersal corridor (black lines, Fig. 4a). However, in some cases these corridors had costs nearing EGD_{MAX} , making significant gene flow unlikely (narrow-width corridor lines, Fig. 4a). Comparison with corridors mapped in the absence of human-made barriers (yellow lines, Fig. 4a) indicated that those barriers have disrupted several regions of formerly high connectivity and resulted in complete isolation for at least one population. Mapping of corridors with and without populations re-established successfully by translocation (Fig. 4b) demonstrated that those translocations have helped maintain corridors for gene flow across a large region in the centre of the study area and several other areas, thereby greatly reducing the isolation of several native populations.

We identified 31 pairs of mountain ranges in the study area between which intermountain movements of bighorn sheep have been detected or inferred (Appendix S3). Of 22 pairs between which movements were detected via radio-telemetry or observation of

marked animals, 21 pairs were linked by a predicted dispersal corridor. Of nine pairs between which movements were suggested on the basis of anecdotal reports, all were linked by predicted dispersal corridors.

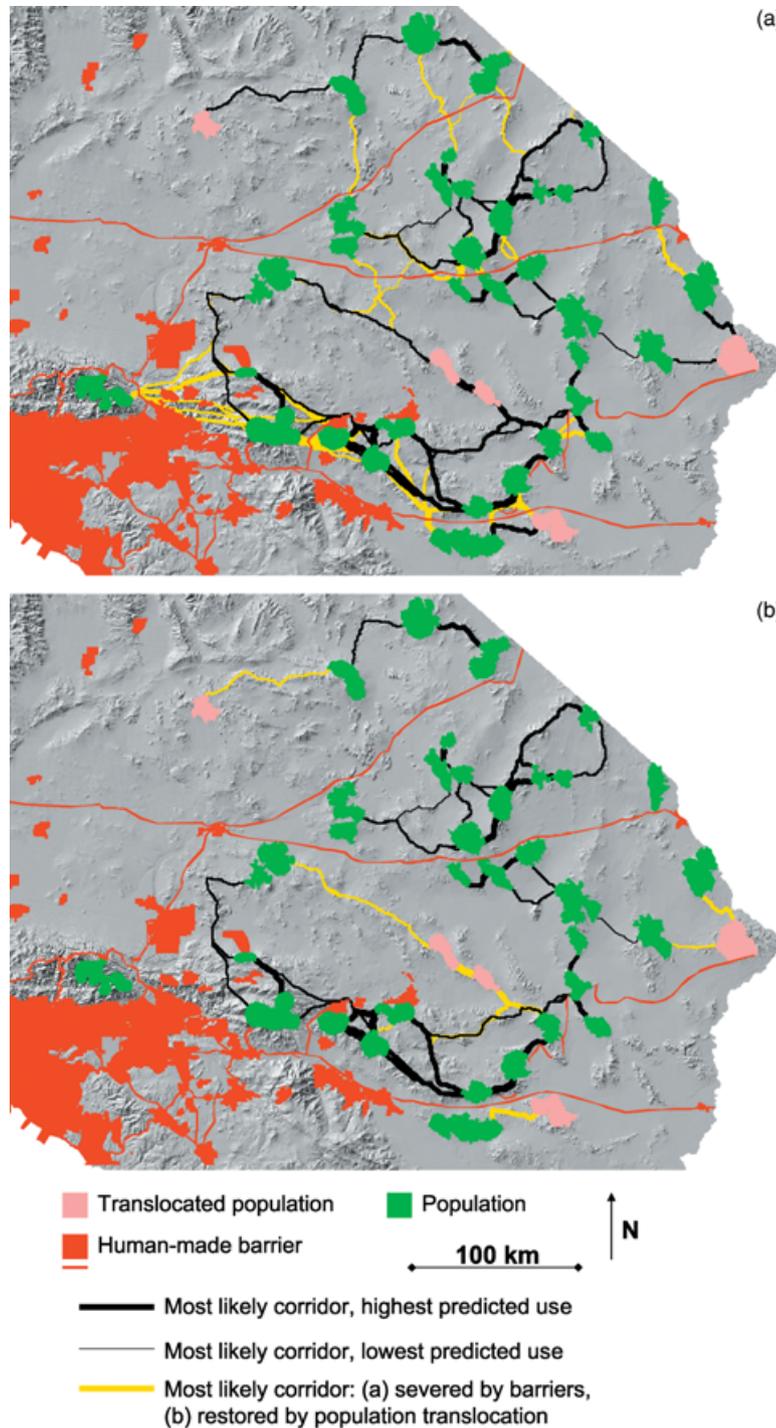


Fig. 4. Dispersal corridors predicted by the best-fitting dispersal model (15/0-10) and the HM population model, depicted with hill-shade topography. Black lines indicate least-costly corridor routes for corridors with cost $< EGD_{MAX}$, yellow lines indicate least-costly corridor routes that (a) were severed by anthropogenic barriers; or (b) were re-established by translocated populations. Corridors are presented based on (a) all extant populations within the study area, with and without current anthropogenic barriers considered; and (b) extant populations with and without those successfully re-established by translocation, with current anthropogenic barriers considered.

Discussion

Migration models that incorporated topography explained substantially more variation in gene flow than models that considered only geographical distance. While the models presented here reflect a small portion of possible models, we found that the best-fitting cost weights and slope cut-off values were consistent across different population polygon models and different measures of gene flow (Fig. 2). While time-consuming, we suggest that testing more than one type of gene flow estimate or population polygon model is important as a sensitivity analysis. Greater confidence in our results was derived from the concordance among models tested.

Inferring active dispersal corridors via the best-fitting migration model for desert bighorn sheep in California resulted in several conclusions. Most importantly, anthropogenic barriers currently fragment several regions that previously exhibited high connectivity (Fig. 4a), suggesting priority locations for the mitigation of these barriers. Additionally, mapping dispersal corridors including populations re-established by translocation (Fig. 4b) demonstrated that our models can be used to improve connectivity: if population establishment in an empty habitat patch could link existing populations by active dispersal corridors, a population translocation to that patch might receive higher priority. Potential future barriers can also be evaluated explicitly in this manner and avoided or mitigated at the time of construction. Finally, the successful restoration of several major dispersal corridors connecting otherwise isolated populations suggests that translocation could be used to restore critical nodes of population connectivity for other species.

These applications of the best-fitting migration model demonstrate the value of this tool for conservation and management. Because we parameterized this model from real data, we can have higher confidence that it models correctly the behaviour of bighorn sheep. We suggest reporting the effective geographical distance (EGD) values or predicted relative gene flow to rank corridors. Here, we scaled corridor widths by Nm to portray relative predicted corridor effectiveness (Fig. 4).

Comparison of the population polygon models suggested that, in this case at least, the definition of population extent did not affect greatly the parameterization of the migration model. Even the most restrictive polygon model (GS polygons, based on the location of the genetic samples collected) exhibited model-fitted curves of the same shape as those generated by the EO and HM polygons. This suggests that fitting least-cost dispersal models may be possible even in situations where the geographical extent of populations is difficult to define. If there is no clear basis at all for defining populations, it should also be possible to develop models in this fashion based on individual pairwise genetic comparisons (e.g. Vignieri 2005). Because this model-testing exercise was designed to examine migration, we caution against over-interpreting differences in

absolute model fit between the population polygon models.

The number of populations in the genetic data set (26) was large, and such a sample might be considered prohibitive to applying this technique for other species. However, results obtained from testing dispersal models using MIGRATE M estimates for the nine-population subset were entirely consistent with those from the full data set (Fig. 3d). Thus, even relatively few populations may suffice to fit such dispersal models.

The connectivity network derived from the genetic analyses confirmed that knowledge of bighorn sheep behaviour (i.e. preference for steep terrain) could be incorporated into a connectivity design, even to the extent of identifying where additional population nodes could be reintroduced to improve the overall connectivity of the bighorn sheep metapopulations. This, in turn, suggests that core and corridor analyses for other species, based on behaviour and proper weighting of landscape variables, could provide important tools for management and conservation. Many aspects of this approach bear further investigation. For instance, rather than use the cumbersome 'trial and error' testing of model parameters, it may be possible to determine the best-fitting model mathematically. However, no mathematical solution will be possible once the number of parameter estimates exceeds the number of population pairs with genetic data. Setting up a few biologically plausible alternative models for testing and exploring restricted subsets of parameter space may be the most practical strategy.

Another aspect worthy of investigation is how best to determine when one model represents a 'significant' improvement over another. Model-selection techniques such as Akaike's information criterion (AIC) may be of little value when the identity of the predictor variables does not change among models. For this reason, we selected the best models using a graphical assessment of model fit. In the end, once the appropriate range of model parameters is identified, slight variations in model fit resulting from small differences in cost weights are likely to be unimportant. In our case, fitting corridors based on slope supported the behavioural inference that bighorn sheep prefer to travel over sloped terrain offering security from predators, regardless of minor differences between 10% and 15% slope cut-offs. Small changes in model parameters may become more important when considering whether an individual corridor is likely to be used or not. For this reason, we reiterate that the relative likelihood of corridor use should be considered, rather than merely a 'corridor or not-corridor' assessment.

MODEL VALIDATION

Known intermountain movements by bighorn sheep correlated well with our corridor model, with the exception of one marked individual that apparently crossed an interstate highway. This observation

highlights the difference between individual dispersal events and the broad patterns of movement over time inferred by our analyses of gene flow. Occasional movements may far exceed those predicted by our migration model. Whether bighorn sheep follow routes consistent with the least costly paths among ranges is also unclear. Acquiring enough data points to verify the complete movement paths of dispersing bighorn sheep will probably require the use of GPS collars set to collect multiple locations per day. Until then, path locations predicted by our model should be considered as hypotheses for further testing.

LIMITATIONS OF THE APPROACH

While the field of landscape genetics is making rapid strides in developing analyses of gene flow that consider complicated landscape features, our approach still has a number of limitations. For instance, such a modelling exercise is better suited to dealing with common landscape characteristics that affect large numbers of populations, given the low statistical power of matrix correlation tests. In this analysis, the south-westernmost populations inhabit mountain ranges with thick forests and chaparral. Those habitat elements probably strongly limit movement by bighorn sheep because of increased predation risk. We did not consider those elements in model development because of the small number of populations affected; thus, connectivity in that region may have been overstated.

A second limitation to our model is that it reflects more effectively the potential for gene flow rather than colonization of empty habitat patches. Desert bighorn sheep have sex-biased dispersal: males are much more likely to travel long distances between populations, while females are probably the limiting factor in colonization events. Because the model described here is fitted using nuclear genetic markers, it represents both male- and female-mediated gene flow. A correction for the reduced movement of females possibly could be generated from radio-telemetry data or mtDNA, although the variability in estimates of gene flow from mtDNA (resulting from its behaviour as one linked locus) makes its use inherently imprecise. This limitation may be important to consider when using these models for management decisions; for example, determining when translocation may be necessary for population re-establishment.

Determining how to model landscape features such as anthropogenic barriers proved to be a complex issue. We dealt with those barriers in a separate analytical framework during model fitting and brought them back into the final model. This approach seemed appropriate because roads have been present on the landscape for only a short period of time. Moreover, road impacts can be mitigated and therefore corridor design should be assessed as a function of the mitigated landscape. A further technical limitation is that the width of interstate highway corridors and other barriers

varies; ideally, the estimated cost of the barrier should be applied to any path crossing the barrier but not on a per-pixel basis (where that cost is accumulated for each pixel encountered). Other, more integrative approaches may be of value in other systems.

Finally, an important caveat is that we used migration, a long-term process, to make inferences about current patterns of bighorn sheep dispersal. Variation in allele frequencies used to estimate migration may be affected by other factors such as population bottlenecks (Whitlock & McCauley 1999). Moreover, if past conditions are reflected more strongly than current dispersal patterns, management decisions using these models might be flawed. However, the small size of these populations and the detectable effect of barriers present for only six to seven generations (Epps *et al.* 2005) suggest that in this case we can still make useful inferences about movement of bighorn sheep on the recent landscape as well as identify factors likely to affect connectivity on the current landscape. Because dispersal is a complex process and the reasons that an individual animal does or does not disperse are unclear, and may not be reduced to simple models, fitting least-cost models using genetic data is probably most effective at identifying broad-scale patterns of gene flow resulting from landscape features that have been present for at least a few generations.

IMPROVING CORRIDOR MODELS AND PLANS TO MAINTAIN OR RE-ESTABLISH CONNECTIVITY

Our study suggests that developing least-cost models from genetic data can improve significantly the quality of and confidence in models of dispersal, migration and connectivity. Other types of data on movement could be used in a similar approach (e.g. Sutcliffe *et al.* 2003). Least-cost models have been employed worldwide to plan landscape-scale conservation strategies, to design reserves and to assess the effects of habitat fragmentation on many species. In some cases those models may have been applied uncritically with respect to their underlying assumptions. While developing genetic data or other data on movement may be a difficult task for many species, it may at least be possible to inform such models using data from species with similar biological characteristics.

Acknowledgements

We thank T. W. Epps, A. Hendricks, E. Kaufman, L. Konde and J. Thorne for assistance in developing the concepts of fitting least-cost models, G. Sudmeier and the late B. Campbell of the Society for the Conservation of Bighorn Sheep for information on water distribution, as well as F. He, P. Beier and two anonymous reviewers for helpful comments on the manuscript. GIS analyses were conducted in the Geospatial Informatics and Imaging Facility (GIIF) of the University of California,

Berkeley (UCB) and funded by the Resource Assessment Program of the California Department of Fish and Game. This is professional paper 056 of the Eastern Sierra Center for Applied Population Ecology. We also thank D. McCullough, P. Palsbøll, G. Roderick and the many individuals who assisted during the collection of the genetic data; funding for that portion of the project was provided by the National Science Foundation, the Agricultural Experiment Station of UCB, the Golden Gate Chapter of Safari Club International and the UCB chapter of Sigma Xi.

References

- Adriaenssens, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H. & Matthysen, E. (2003) The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, **64**, 233–247.
- Beazley, K., Smandych, L., Snaith, T., MacKinnon, F., Austen-Smith, P. & Duinker, P. (2005) Biodiversity considerations in conservation system planning: map-based approach for Nova Scotia, Canada. *Ecological Applications*, **15**, 2192–2208.
- Beerli, P. & Felsenstein, J. (2001) Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences USA*, **98**, 4563–4568.
- Bleich, V.C., Wehausen, J.D. & Holl, S.A. (1990) Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conservation Biology*, **4**, 383–390.
- Bleich, V.C., Wehausen, J.D., Ramey, R.R. & Rechel, J.L. (1996) Metapopulation theory and mountain sheep: implications for conservation. *Metapopulations and Wildlife Conservation* (ed. D.R. McCullough), pp. 353–373. Island Press, Covelo.
- Castellano, S. & Balletto, E. (2002) Is the partial Mantel test inadequate? *Evolution*, **56**, 1871–1873.
- Coulon, A., Cosson, J.F., Angibault, J.M., Cargnelutti, B., Galan, M., Morellet, N., Petit, E., Aulagnier, S. & Hewison, A.J.M. (2004) Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. *Molecular Ecology*, **13**, 2841–2850.
- Epps, C.W., Bleich, V.C., Wehausen, J.D. & Torres, S.G. (2003) Status of bighorn sheep in California, 2004. *Desert Bighorn Council Transactions*, **47**, 20–35.
- Epps, C.W., Palsboll, P.J., Wehausen, J.D., Roderick, G.K., Ramey, R.R.I.I. & McCullough, D.R. (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters*, **8**, 1029–1038.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, New York.
- Hardle, W. (1992) *Applied Nonparametric Regression*. Cambridge University Press, Cambridge, UK.
- Hedrick, P.W. (2005) *Genetics of Populations*. Jones and Bartlett Publishers, Boston.
- Hunter, R.D., Fisher, R.N. & Crooks, K.R. (2003) Landscape-level connectivity in coastal Southern California, USA, as assessed through carnivore habitat suitability. *Natural Areas Journal*, **23**, 302–314.
- Joly, P., Morand, C. & Cohas, A. (2003) Habitat fragmentation and amphibian conservation: building a tool for assessing landscape matrix connectivity. *Comptes Rendus Biologies*, **326**, S132–S139.
- Keller, I. & Largiader, C.R. (2003) Recent habitat fragmentation caused by major roads leads to reduction of gene flow and

- loss of genetic variability in ground beetles. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, **270**, 417–423.
- Koenig, W.D., VanVuren, D. & Hooge, P.N. (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution*, **11**, 514–517.
- Manel, S., Schwartz, M.K., Luikart, G. & Taberlet, P. (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution*, **18**, 189–197.
- Manly, B.F.J. (1991) *Randomization and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Michels, E., Cottenie, K., Neys, L., De Gelas, K., Coppin, P. & De Meester, L. (2001) Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. *Molecular Ecology*, **10**, 1929–1938.
- Moilanen, A., Franco, A.M.A., Eary, R.I., Fox, R., Wintle, B. & Thomas, C.D. (2005) Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proceedings of the Royal Society, Series B, Biological Sciences*, **272**, 1885–1891.
- Nikolakaki, P. (2004) A GIS site-selection process for habitat creation: estimating connectivity of habitat patches. *Landscape and Urban Planning*, **68**, 77–94.
- Raufaste, N. & Rousset, F. (2001) Are partial Mantel tests adequate? *Evolution*, **55**, 1703–1705.
- Ray, N. (2005) PATHMATRIX: A geographical information system tool to compute effective distances among samples. *Molecular Ecology Notes*, **5**, 177–180.
- Ray, N., Lehmann, A. & Joly, P. (2002) Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. *Biodiversity and Conservation*, **11**, 2143–2165.
- Rouget, M., Cowling, R.M., Lombard, A.T., Knight, A.T. & Graham, I.H.K. (2006) Designing large-scale conservation corridors for pattern and process. *Conservation Biology*, **20**, 549–561.
- Rousset, F. (2002) Partial Mantel tests: reply to Castellano and Balletto. *Evolution*, **56**, 1874–1875.
- Schneider, S., Roessli, D. & Excofier, L. (2000) *ARLEQUIN: A Software for Population Genetics Data Analysis*, version 2.000. Genetics and Biometry Laboratory, Department of Anthropology, University of Geneva, Geneva.
- Schwartz, O.A., Bleich, V.C. & Holl, S.A. (1986) Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation*, **37**, 179–190.
- Slatkin, M. (1993) Isolation by distance in equilibrium and non-equilibrium populations. *Evolution*, **47**, 264–279.
- Smouse, P.E., Long, J. & Sokal, R. (1986) Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology*, **35**, 627–632.
- Soule, M.E., Wilcox, B.A. & Holtby, C. (1979) Benign neglect: a model of faunal collapse in the game reserves of East Africa. *Biological Conservation*, **15**, 259–272.
- Spear, S.F., Peterson, C.R., Matocq, M.D. & Storfer, A. (2005) Landscape genetics of the blotched tiger salamander (*Ambystoma tigrinum melanostictum*). *Molecular Ecology*, **14**, 2553–2564.
- Sutcliffe, O.L., Bakkestuen, V., Fry, G. & Stabbetorp, O.E. (2003) Modelling the benefits of farmland restoration: methodology and application to butterfly movement. *Landscape and Urban Planning*, **63**, 15–31.
- U.S. Geological Survey (2003) 30m digital elevation model for the coterminous United States. USGS, Washington, D.C.
- Vignieri, S.N. (2005) Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*). *Molecular Ecology*, **14**, 1925–1937.
- Vos, C.C., Antonisse-De Jong, A.G., Goedhart, P.W. & Smulders, M.J.M. (2001) Genetic similarity as a measure for connectivity between fragmented populations of the moor frog (*Rana arvalis*). *Heredity*, **86**, 598–608.
- Waser, P.M. & Strobeck, C. (1998) Genetic signatures of interpopulation dispersal. *Trends in Ecology and Evolution*, **13**, 43–44.
- Whitlock, M.C. & McCauley, D.E. (1999) Indirect measures of gene flow and migration: F-ST not equal 1/(4Nm+1). *Heredity*, **82**, 117–125.

Received 24 August 2006; final copy received 13 March 2007
Editor: Fangliang He

Supplementary material

The following supplementary material is available for this article.

Appendix S1. Estimating migration rates *M* using MIGRATE software.

Appendix S2. Defining the Habitat Model population polygons.

Appendix S3. Reported intermountain movements by desert bighorn sheep in the study area.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01325.x>

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EXHIBIT 417

CHAPTER X NUTRIENT PREDICTABILITY, BIRTHING SEASONS, AND LAMB RECRUITMENT FOR DESERT BIGHORN SHEEP

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Key words: desert bighorn sheep, *Ovis canadensis nelsoni*, diet quality, fecal nitrogen, nutrient predictability, lambing seasons, lamb recruitment, lamb survival



Introduction

Desert bighorn sheep (*Ovis canadensis*) were once widespread throughout the desert mountain ranges of the southwestern United States and northern Mexico, and persist in many of those ranges (Buechner 1960). As herbivores living in arid environments, their ability to procure nutrients is substantially limited by the phenological patterns of the vegetation they feed on. Nutrient content of diets varies with the amount of green, growing plant tissue available to be eaten. The youngest, most rapidly growing, plant tissue

typically provides the highest digestibility (Van Soest 1982). Sheep maximize their nutrient intake through very selective feeding, eating the most nutritious species and plant parts available. Patterns of nutrient intake determine when the nutrient-expensive process of gestation and lactation will be most successful and how successful it will be relative to lamb survival.

Deserts are characterized by scant precipitation, such that potential evapotranspiration greatly exceeds precipitation overall and soil moisture conditions are not conducive to plant growth for much of the year (Major 1977). Climatic patterns vary across North American deserts in overall temperature (low elevation hot to high elevation cold alpine deserts) and seasons of rainfall (MacMahon 1979). In addition, precipitation is typically quite variable between years (Wagner 1981). Because plant phenology is closely tied to rainfall, nutrient availability for bighorn sheep inhabiting deserts also is quite limited annually. An important question relative to life history and demographic patterns of desert bighorn sheep is the predictability of nutrient availability.

The birthing season for wild sheep in North America varies with latitude. Syntheses of available data have suggested two basic patterns: (1) a short (about 1-2 month) birthing season in late spring and early summer in northern climates that shifts slightly earlier with declining latitude; and (2) a long season (numerous months) in desert ecosystems of southwestern United States and adjacent Mexico (Bunnell 1982, Thompson and Turner 1982). In some desert areas births have been documented throughout the year (Krausman et al. 1999). Bunnell (1982) presented the shift between the two birthing patterns as an abrupt change at a latitude of about 38 degrees.

A related question is what underlies this purported sudden change in birthing patterns. Based on limited data from one bighorn sheep population in New Mexico, Lenarz (1979) hypothesized that the protracted lambing seasons of desert bighorn sheep represented an evolved gambling strategy to an environment that is unpredictable in nutrient availability. That explanation has been widely accepted (Bailey 1980, Bunnell 1982, Thompson and Turner 1982, Krausman et al. 1999), but simulations by Lenarz and Conley (1982) cast some doubt on this characterization of the reproductive strategy of desert bighorn sheep.

Drawing on the work of Beatley (1974) on phenological triggers in Mojave Desert ecosystems, Lenarz (1979) calculated the probability of obtaining 2.5 cm (1 inch) of rain in each month for his study area in New Mexico. From those results Lenarz (1979:671) concluded the following: "in 3 of 10 years plant productivity will not begin until August or will fail altogether. The relationship between precipitation and plant productivity makes forage availability in deserts relatively unpredictable."

Here I examine the question of nutrient predictability using long-term data on diet quality patterns of bighorn sheep from three populations in the Eastern Mojave Desert of California. I analyze patterns of nutrient availability relative to timing of birthing and the survivorship of lambs.

Study Populations

The populations investigated were (SE to NW) the Turtle Mountains, Old Woman Mountains, Marble Mountains, and Old Dad Mountain. They form a transect about 150 km in length that passes through the Granite Mountains. Only 3 years of data are available from the Turtle Mountains, which are used in just one analysis. Of the four mountain ranges studied, the Turtle Mountains is the only one that is decidedly Sonoran Desert, supporting species like Ocotillo (*Fouquieria splendens*) and Ironwood (*Olneya tesota*). The three Mojave Desert ranges form a transect about 100 km long. The Old Woman Mountains are the highest, topping out at about 1600 m and contain sparse pinyon-juniper woodland at the highest elevations. Volcanic and limestone substrates are essentially lacking. The Marble Mountains is the lowest range, peaking out at about 1,150 m. It is primarily a volcanic range with some limestone at the

southern end of the habitat used by sheep. Old Dad Mountain peaks out at about 1300 m and is a combination of a large limestone massive and outlying volcanic ridges, some of which have considerable deposits of blow sand (Bleich et al 1997).

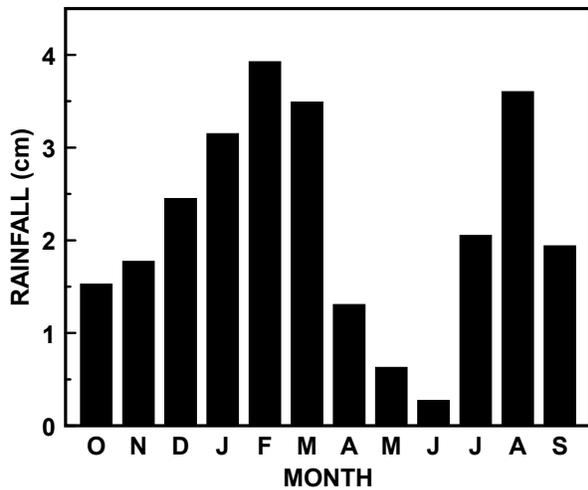


Figure 1. Mean monthly rainfall for Mitchell Caverns in the south Providence Mountains, 1959-2002.

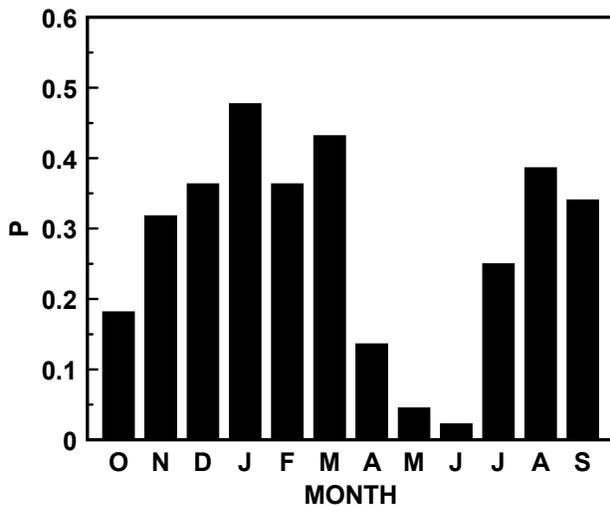


Figure 2. Probability of receiving 2.5 cm of precipitation by month at Mitchell Caverns in the south Providence

The Mojave Desert is something of a hybrid between cold Great Basin and hot Sonoran Desert ecosystems that bound it. Temperatures are intermediate. Precipitation patterns also are intermediate (Figure 1), showing the bimodal pattern of the Sonoran Desert, but with a predominance of winter rainfall that characterizes the Great Basin Desert. For 44 years of data from Mitchell Caverns in the south Providence Mountains, 64 percent of the annual rainfall occurred during the winter-spring season (November-May) and 36% during the hot season (June-October). There is considerable inter-annual variation in rainfall. By the criteria of Lenarz (1979), the eastern Mojave Desert is less predictable than the Chihuahuan Desert ecosystem that he investigated. His peak probabilities of receiving 2.5 cm of rainfall were 0.70 and 0.74 for the months of July and August, respectively, whereas for the eastern Mojave Desert no month even reaches 0.5 (Figure 2). Consequently, unpredictable patterns of diet quality for bighorn sheep in the eastern Mojave Desert would be expected if Lenarz's (1979) criteria are meaningful, while a regular periodicity in diet quality would not be consistent with this expectation.

Methods

Diet quality of sheep was tracked via % nitrogen in feces (FN). FN tracks apparent digestibility of the diet in a curvilinear relationship (Wehausen 1995). The natural log of FN was used to linearize that relationship, and this measure was expressed on an organic matter (ash-free) basis (lnFOMN) because this increases its resolution as an index of diet quality (Wehausen 1995). For the bighorn sheep populations in this study, this index varied from 0.3 to 1.2. For domestic sheep, those values would correspond to a range of about 50-75% apparent digestibility (Wehausen 1995), which also may apply to bighorn sheep; both sheep species have similar

digestive systems, including a very large rumen and reticulum relative to body size (Hanley 1982, Krausman et al. 1993).

Fecal samples mostly were collected fresh from female groups of sheep seen. Where sheep could not be found, very recent tracks were found and followed to find fecal droppings. Those samples were backdated by the estimated age of the tracks. Sampling of feces was approximately monthly. During seasons of rapid phenological change in the vegetation, this interval was somewhat shortened in some years, while during periods of phenological stasis the sampling interval was increased to 2 months in some years. For most samplings, equal amounts of each sample were composited for analysis by commercial labs to produce a single data point. Where separate analyses were made for each sample, the mean was used.

Diet quality over multiple months, rather than single months, is most meaningful relative to many questions, such as lamb recruitment. Consequently, I have measured the area under diet quality curves for the periods of interest (e.g. February through June) using a linear relationship between adjacent points. Because sampling was not on the same day of the month each year, I standardized integrated values by dividing by the number of days between the first and last sampling points.

The three long-term data sets analyzed consisted of continuous diet quality curves for 15-18 years depending on the population. To investigate the question of temporal predictability of diet quality, I calculated for each month the proportion of the years in which the diet quality index reached 0.6 and 0.7. Those values represent modest increases in diet quality relative to the minimum of 0.3. For domestic sheep, these respective values correspond to increases in apparent digestibility of about 8 and 10.5%.

As a test of Lenarz's (1979) approach to using precipitation data, I investigated actual influences of precipitation in individual months on diet quality for the longest data set (Marble Mountains) via simple and multiple linear

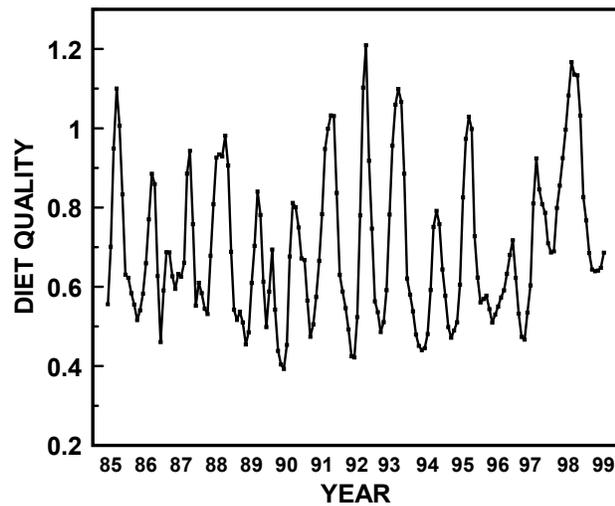


Figure 3. Diet quality (% fecal organic matter nitrogen) for bighorn sheep in the Old Woman Mountains, 1984-1999.

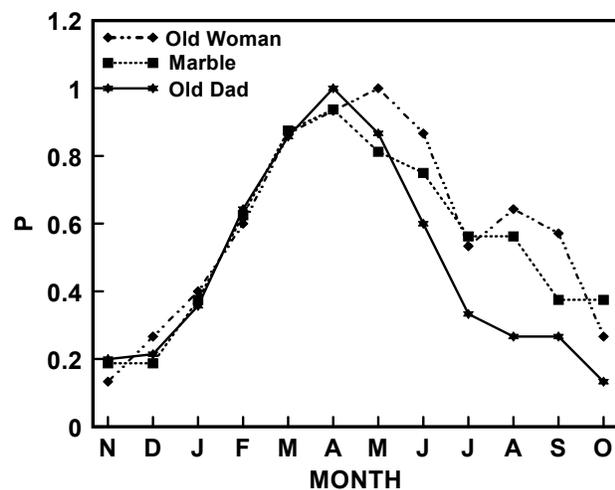


Figure 4. Probability by month that the natural log of fecal organic matter nitrogen equals or exceeds 0.6 for bighorn sheep at Old Dad Mountain and the Marble and Old Woman Mountains, California.

regression, and the use of logged variables to investigate curvilinear relationships.

I investigated the influence of February-June diet quality on recruitment of lambs to the beginning of summer via regression analysis. Lamb recruitment was measured as the ratio of lambs per 100 ewes from direct samplings in late spring and analysis of automated cameras placed at water sources at the beginning of the hot season.

Results and Discussion

Diet Quality Patterns and Predictability

Contrary to predictions from Lenarz's (1979) hypothesis and analytic methods, diet quality curves from the study area show a clear periodicity (Figure 3) and temporal predictability (Figure 4). What is unpredictable is not when peak diet quality will occur, but the amplitude of that peak. Figure 4 depicts the probabilities of only a modest increase in diet quality ($\ln\text{FOMN} = 0.6$). Increasing that threshold level of diet quality narrows the time period in which it is likely to be reached and lowers the peak probability of actually reaching that level. The lowest threshold tested was reached in every year sampled for each population (Figure 4). Increasing that threshold to 0.7 already lowered the probability of reaching it to less than 1 (Figure 5). Further increases in that threshold will further lower that peak probability, while also narrowing the time period.

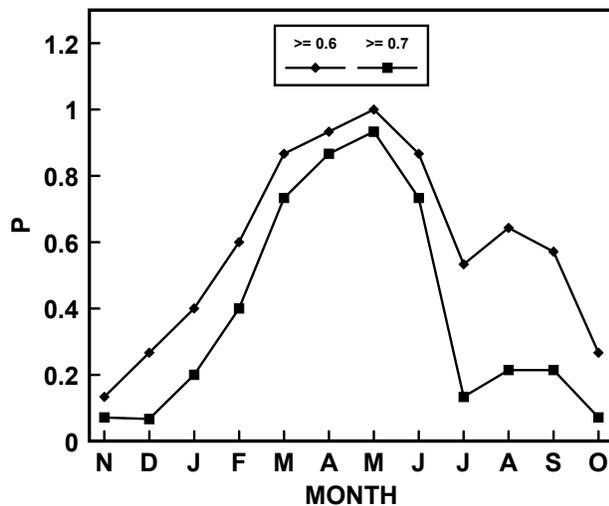


Figure 5. Probability by month that the natural log of fecal organic matter nitrogen equal or exceeds 0.6 and 0.7 for bighorn sheep in the Old Woman Mountains, California

The pattern that emerges in Figure 4 is the important result, rather than the threshold chosen. That pattern demonstrates that there is a predictable timing of the winter-spring growing season that determines diet quality for the sheep. In contrast, forage growth from summer rainfall yields minimal nutritional gains for these sheep (Figs. 4 & 5). The winter-spring rising pattern in Figure 4 is remarkably coincident among the 3 study populations, suggesting that this growing season is regional in nature. This also is indicated by the pattern of diet quality for the February-June period for 1985 - 2002; the patterns for the 4 populations sampled correlate closely (Figure 6A). The variance among years represents the

unpredictable aspect of nutrient availability to these sheep in the primary growing season. This variance can be termed amplitude predictability, to be distinguished from the high temporal predictability for the populations sampled. Lenarz (1979) failed to distinguish these two separate aspects of resource predictability.

Variables Driving Diet Quality Patterns

The interannual variance in winter-spring diet quality (Figure 6A) is driven by rainfall patterns. The single month with the greatest rainfall effect on spring diet quality in the Marble Mountains is February, followed by October. When those two months are combined in a multiple linear regression, together they explain 64% of the variation. In that multiple regression, the slope associated with October rainfall is 67% greater than February (Table 1); thus a unit of rainfall in October generates considerably more nutrition for sheep than an equivalent amount in February. Rainfall in October and February has different effects on vegetation growth. Fall rainfall is important for initiating the growth of cold-tolerant species: annuals, herbaceous perennials, and perennial grasses (Beatley 1974, Turner and Randall 1989). February rainfall is important for continuance of growth of those cold-tolerant species that might have been initiated earlier, but also is important for growth of cold-intolerant perennial species during spring (Beatley 1974). When October rainfall is expressed as logged values along with February rainfall, the model improves slightly, suggesting some curvilinearity in the effect of October rainfall (Table 1).

The forage species initiated by fall rains provide the first new green growth eaten by sheep. Those species determine diet quality for sheep in winter and account for the initial rise in the growing season curve in Figure 4. As the growing season progresses with warming temperatures, numerous cold-intolerant perennial species initiate growth and flowering. The peak in digestibility of sheep diets (Figure 4) coincides with the peak in growth and flowering of perennial species. However, the greater influence of early precipitation on February-June diet quality speaks to the critical importance of the earliest rise in diet quality in winter. Because the dependent variable analyzed begins with the February sampling, early precipitation determines the diet quality level at that first sampling, from which the curve rises to the spring peak. Also, in the years of high peak diet qualities, species whose growth was initiated by the early rains are still available and eaten at the time of that peak.

When rainfall is combined for adjacent pairs of months, the best 2 independent variables are October + November, and January + February, which together explain 75% of the variation in February - June diet quality. For those longer time periods, the distinction between the role of precipitation in initiating early plant growth and contributing to later growth begins to blur; the slope of the earlier rainfall variable is only 17% larger than the later one (Table 1). A single independent variable of total rainfall for October through April explains yet 6% more of the variation in winter-spring diet quality in a curvilinear relationship (Figure 7, Table 1). Eliminating December and March rainfall from that cumulative rainfall explains yet another 4% of the variation. However, there is no clear biological explanation why December and March

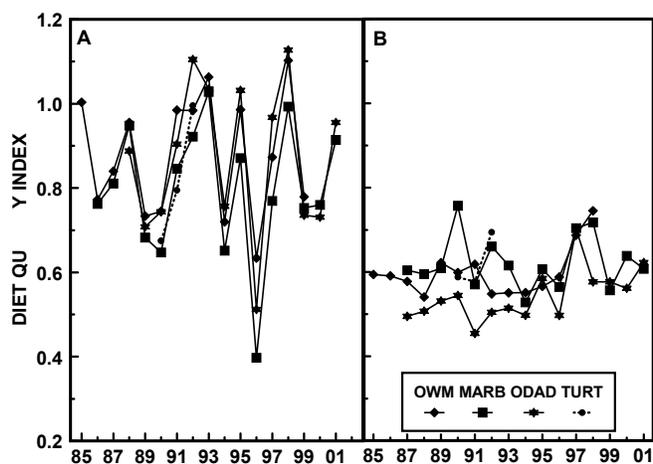


Figure 6. February-June (A) and July-October (B) diet quality by year for bighorn sheep at Old Dad Mountain, and the Marble, Old Woman, and Turtle Mountains, California.

Table 1. Results (independent variables, slopes, coefficients of determination, and total model probabilities) of regression analyses of February-June diet quality of bighorn sheep in the Marble Mountains on precipitation in different time periods.

X ₁	X ₂	B ₁	B ₂	R ²	P
Feb		0.020		0.401	0.006
Feb	Oct	0.021	0.035	0.636	0.001
Feb	lnOct	0.020	0.043	0.674	<0.001
Jan-Feb		0.017		0.554	0.001
Jan-Feb	Oct-Nov	0.018	0.021	0.752	<0.001
lnOct-Apr		0.198		0.808	<0.001

rainfall would not contribute to sheep diet quality. Consequently, that finding is treated here as a statistical artifact.

While the left side of the rising curve in Figure 4 is essentially identical for the 3 populations sampled, the declining pattern in late spring and summer is notably different among them. That variation reflects important habitat differences between the mountain ranges sampled. Temperature exhibits a classic inverse relationship with elevation (Major 1977), and strongly affects plant growth (Hoefs and Cowan 1979, Wehausen 1980). In high mountain ranges, sheep and other large herbivores typically use altitudinal migration to increase their nutrient intake by following the growing season as it progresses up mountain slopes (Hebert 1973; Hoefs 1979; Wehausen 1980, 1983). Sheep in desert mountain ranges also can do this to a limited extent. The extended peak in the Old Woman Mountains (Figure 4) is an example that reflects the higher elevation there.

The diet quality curve for Old Dad Mountain declines more rapidly than the other two populations and remains lower through the hot season (Figure 4). This reflects differences in the availability of 1 forage species, catclaw acacia (*Acacia greggii*), which is readily available to the sheep in the Old Woman and Marble Mountains, but is lacking for the Old Dad sheep. Catclaw acacia is a very deep-rooted deciduous member of the pea family that leafs out about mid April and carries green leaves throughout the hot season until November or later. It elevates the diet quality of sheep throughout the hot season where available (Figure 6B).

The curves for all 3 mountain ranges in Figure 4 show a changing pattern beginning in August that represents the diet quality response to summer rains. Summer rains clearly produce much less nutrient availability for sheep than cold season rains. Indeed, summer diet quality in the best years barely overlaps diet quality in the worst years for the winter-spring period (Figure 6A, B). There are a number of reasons for this, of which temperature is fundamental. Cold season precipitation mostly occurs as soaking rains that persist for long periods as soil moisture because of subsequent cool temperatures. In contrast, much of summer rainfall runs out of the mountain ranges as flash floods to habitats not used by sheep. What moisture makes it into the soil in sheep habitat evaporates rapidly due to hot temperatures. Just as rainfall in different periods of the cool season cannot be equated in terms of effects on nutrient availability, cool

season rain is very different from that in the hot season relative to effects on diet quality of sheep.

Lenarz's (1979) simplistic analysis of rainfall data relative to nutrient predictability for bighorn sheep failed to predict diet quality patterns in part because it failed to account for the important influence of temperature and season on vegetation response to rainfall. Among those influences are important cumulative effects of rainfall in the cool season (Figure 7) that cannot be accounted for by analyses that treat months independently.

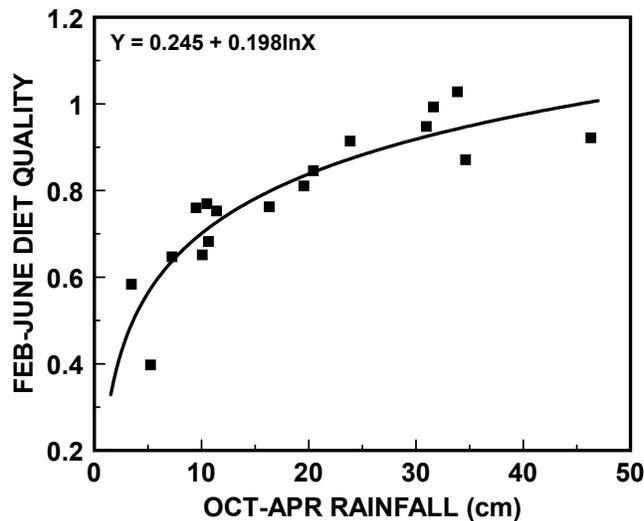


Figure 7. The relationship between February-June diet quality for bighorn sheep in the Marble Mountains and October-April rainfall at Mitchell Caverns in the south Providence Mountains, California.

patchy in distribution compared with winter rains. The other is that mountain ranges closer to the Colorado River and Sonoran Desert are more likely to receive summer rainfall. This influence can be seen in Figure 4 in the differences among populations in the amount of rise in the predictability of August and September diet quality.

Birthing Seasons of Desert Bighorn

The high temporal predictability of diet quality found here leads to the expectation that the birthing season should occur in the late winter and spring. Contrary to suggestions by Lenarz (1979) and others, the birthing seasons of desert bighorn sheep typically show a clear winter-spring peak that is aligned well with diet quality patterns. Two studies have produced excellent data on birthing dates for telemetered female bighorn sheep. In the Sonoran Desert of southwestern Arizona, Witham (1983) found a January - February birthing peak, with about 76% of 215 lambs born during January-March over a 4-year period. In the Sonoran Desert Peninsular Ranges of California, Rubin et al. (2000) recorded a consistent birthing peak in March for 133 lambs born over a 4-year period. This latter pattern is representative of the eastern Mojave Desert of California (Wehausen 1991), where the birthing peak occurs in March and April.

Peak diet quality mostly occurs in April in the region of this study. Consequently, there is a tendency for the peak of birthing to occur somewhat earlier than the peak in nutrient

There are also differences in plant species responses to cool and hot season rains that influence diet quality differences between those two periods. Relatively few species respond to hot season rains compared with cool season rains. Also, tropical grasses have different biochemical pathways (C4) and structural chemistry that typically make their peak digestibilities for ungulates lower than temperate (C3) grasses (Van Soest 1982). The same probably holds for hot season versus cold season grasses in the Mojave Desert.

In contrast to winter-spring diet quality patterns, there is little correlation in summer diet quality patterns among the populations sampled (Figure 6B). One reason for this is that summer rains are very

availability. There is a good reason for this. The survival of lambs to summer is strongly influenced by the amount of body growth they put on in spring (see below). The earlier they are



born, the more body mass they can accumulate during the spring growing season before diet quality plummets in late spring. However, the earlier the births, the higher the probability that diet quality will be insufficient for females at the end of gestation and early lactation. What mediates these opposing forces is the body condition of females. Females in better condition can ovulate earlier and potentially use their body reserves to get through a period of insufficient nutrient intake (Wehausen 1984). Cook et al. (2004) documented this relationship

between body condition and ovulation date for elk. Witham (1983) found birthing peaks to shift between January and February in different years. I have observed similar shifts of a month in the eastern Mojave Desert of California. Those year-to-year shifts probably reflect differences in body condition of females the previous year.

Witham (1983) and Rubin et al. (2000) both documented tails of the birthing curve that extend into summer. This also occurs in the eastern Mojave Desert. However, this distribution tail amounts to a small proportion of lambs produced. July-September births accounted for less than 2% of the births in Arizona (Witham 1983) and less than 5% in the Peninsular Ranges (Rubin et al. 2000). Using total length of the birthing season as the basis of hypotheses on reproductive strategies of desert bighorn sheep is therefore inappropriate given this lack of uniformity in the distribution of births within those periods.

The characterization of protracted birthing seasons of desert bighorn sheep as an abrupt latitudinal change from the northern pattern (Bunnell 1982) does not accurately represent the geography of this phenomenon. The timing of the beginning of the birthing season is a parameter of considerable importance in that it largely sets the length of the birthing season. The beginning of the birthing season shows clinal change from hot to cold desert ecosystems. For monthly categories, this initiation varies from November in the hot Sonoran Desert to (late) April in the southern Great Basin Desert (Table 2). Data are mostly lacking from further north in the heart of the cold desert, where native sheep appear not to begin birthing until May (Wehausen 1991). Thus, the more northern desert regions exhibit relatively short birthing seasons that are northern in character. However, the change in the initiation of lambing seasons is not strictly latitudinal (Table 2); instead, it simply reflects habitat differences such as elevation. The San Gabriel Mountains on the north side of the Los Angeles Basin is a prime example of this (Table 2).

Results of translocations of bighorn sheep suggest that different birthing seasons across the desert region may have a strong genetic basis. The Nevada Department of Wildlife has moved sheep from the southern warm-desert end of that state to northern cold desert ecosystems, where the early (February) initiation of birthing has persisted, but is about 3 month earlier than would be appropriate for the ecosystem to which they were moved (Wehausen 1991). Similarly, sheep moved from the Corn Creek pens at the Desert Game Range in Nevada to the Los Angeles Zoo maintained an intermediate timing of birthing initiation (Hass 1993).

Table 2. Month in which the birthing season begins for some native bighorn sheep populations in the southwestern United States.

Population	Latitude	Beginning Month	Source
SW Arizona	33	November	Witham 1983
Old Woman Mts., CA	34.5	December	pers. obs.
Marble Mts., CA	34.5	January	Wehausen 1991
Peninsular Ranges, CA	33	February	Rubin et al. 2000
Old Dad Mt., CA	35	February	pers. obs.
River Mts., NV	36	February	Hass 1993
Inyo Mts., CA	37	March	pers. obs.
Corn Cr., NV	37	March	Hass 1993
Canyonlands, UT	38.5	March	Douglas 1991
San Gabriel Mts., CA	34.5	April	Holl and Bleich 1983
White Mts., CA	37.5	April	Wehausen 1991
Sierra Nevada, CA	37	April	Wehausen 1991

Rather than a gambling strategy, the protracted birthing season of bighorn sheep in warm and hot desert regions is probably due to relaxed selection. I suggest that the operative variable is temperature. While annual temperature regimes underlie patterns of plant phenology and nutrition (Figure 4), temperature also affects the risk of losing a newborn to hypothermia (Bunnell 1980). This latter selective constraint on the birthing season declines from cold northern and high mountain ecosystems to hot deserts, effectively disappearing in the hot Sonoran Desert. A related phenomenon is that in warmer environments adult females in poorer body condition can more readily survive the winter cold season because less fat will be needed to maintain body temperature. This also means that the acceptable ratio of allocation of resources between body maintenance and current reproductive effort can shift in favor of reproduction. This would allow females to successfully give birth earlier and still meet overall nutrient needs even when conditions are not optimal.

The probability of a lamb surviving to adulthood is greatly influenced by the timing of its birth; thus, natural selection can be expected to closely tailor lambing seasons. Relaxed selection relative to birthing seasons means that lambs born over long time periods in warm desert environments all have a high enough probability of surviving and reproducing that natural selection has not censored any part of those time periods, as it has in colder climates. The lack

of uniformity in the distribution of births across those time periods, however, points to variation in the probability of lambs born at different times surviving to adulthood.

The advantage of longer birthing seasons lies with flexibility. There appears to be a threshold body condition that females must reach for ovulation to occur. In northern environments with short birthing seasons, there is a short time window in which that can occur. If conception fails after the first ovulation, there is unlikely to be more than a second opportunity for a female to conceive where birthing seasons are short (Bunnell 1980). If conception does not occur during the breeding season, a female must wait nearly a year until the next one. In contrast, the long breeding season of sheep in warmer desert environments provides considerably more opportunity for females to gain the necessary body condition to ovulate and to ovulate numerous times until conception occurs if necessary. Long breeding seasons mean that the period between consecutive births can vary considerably in both directions from 1 year, as mediated by prior nutrient intake and expenditures. For bighorn sheep in the Sonoran Desert of Arizona, Witham (1983) reported the period between consecutive births to vary from 279 to 446 days. In short, the flexibility afforded by longer birthing periods gives females the opportunity to produce more offspring in a lifetime.

Nutrient Availability and Lamb Survival

The variance among years in diet quality for bighorn sheep in the Mojave Desert has important implications for lamb survival. The primary loss of lambs occurs prior to summer. Unless a water source dries up during the hot season, there is almost no loss of lambs between late spring and fall (unpubl. data). However, depending on diet quality, there can be a large loss of lambs prior to the hot season. That loss exhibits an interesting relationship with diet quality that indicates 2 opposing factors are operating on lamb mortality. Up to a February-June diet quality value of almost 1, spring lamb recruitment increases linearly with increasing diet quality, as expected. However, this relationship reverses sharply with higher diet qualities (Figure 8). The point of change corresponds to 23.4 cm of October-April rainfall at Mitchell Caverns. The year 1990 is a notable outlier in this relationship (Figure 8) and is treated as such. That year was the second of 2 consecutive years of low rainfall in the growing season, which likely accounts for its outlier status.

The pattern in Figure 8 is consistent with similar patterns previously elucidated (unpubl. data). In the initial years of this research, bighorn sheep in the Old Woman and Marble Mountains suffered from a disease syndrome that killed most lambs during spring. During those disease episodes, the relationship between lamb recruitment and February-June diet quality for both populations was the same pattern as Figure 8, except that the meeting of the two curves was shifted greatly to the left to where the peak lamb recruitment was only 30 lambs:100 ewes, compared with 61:100 in Figure 8.

The disease syndrome that previously affected the sheep in the Marble and Old Woman Mountains is poorly understood, but is conjectured to have a virus as the ultimate cause, similar to what affected the bighorn sheep in the Peninsular Ranges of California for numerous years (Wehausen et al 1986, DeForge et al. 1995). The lamb recruitment patterns in the Marble and Old Woman Mountains during those disease episodes were consistent with an insect vectored virus, such as bluetongue. While diet quality of sheep benefits from increasing growing season precipitation (Table 1, Figure 7), so do insect populations. It is possible that the declining lamb recruitment phase in Figure 8 is also due to a disease that is adequately spread among sheep by arthropods only during very wet years.

There appears to be a linear increase in spring lamb recruitment relative February-June diet quality up to the inflection point (Figure 8). However, February-June diet quality follows a curvilinear relationship with rainfall (Figure 7). A noteworthy aspect of that curvilinearity is the initial steep increase in diet quality with small gains in rainfall. Thus, small initial increases in rainfall translate to large gains in lamb recruitment.

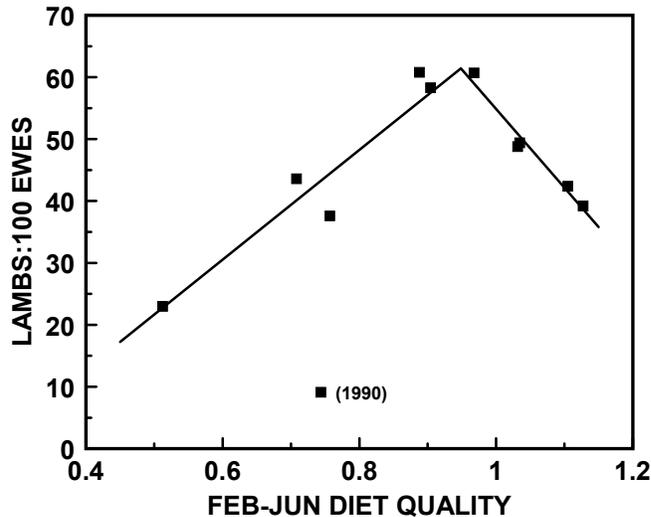


Figure 8. The relationship between lamb recruitment rate in early summer and winter-spring diet quality for bighorn sheep at Old Dad Mountain, California.

birthing seasons of desert bighorn sheep are a gambling strategy response to an unpredictable environment. There is also a lack of support for the idea that there is an abrupt change from northern short birthing periods to long birthing seasons in desert bighorn sheep. Instead, the evidence suggests that the birthing season of desert bighorn sheep varies according to habitat, from long seasons in the southern hot desert to short seasons typical of northern environments in the cold desert of the Great Basin. A key variable in this variation is the timing of the beginning of the birthing season, which varies from November in the hot Sonoran Desert to May in the Great Basin Desert.

The unpredictable aspect of nutrient availability for bighorn sheep in the eastern Mojave Desert is the amplitude of the winter-spring growing season. While geographically consistent, the amplitude of the spring peak varied considerably from year to year. That variation is driven by the amount of rainfall during October-April. Rainfall at different times of year has decidedly different effects on diet quality of sheep. This is even the case within the October-April period, with rainfall in the earlier part of that period having a greater effect on diet quality than later rainfall. Temperature plays a strong role in how rainfall affects subsequent diet quality of sheep.

October-April rainfall probably has a small effect on the timing of the birthing season the following year through its effect on subsequent body condition of females and the effect of body condition on timing of ovulation. In contrast, the amount of rainfall during October-April has a major effect on the survivorship of lambs to summer. That relationship is more complex than expected, with strong gains in survivorship up to about 23 cm of rainfall, but decreasing

Conclusions

Like most scientific questions, it is important to break the concept of resource predictability into its constituent components (Colwell 1974). For nutrient availability to desert bighorn sheep, temporal predictability should be distinguished from amplitude predictability. For the Mojave Desert ecosystems studied here, the temporal predictability of nutrient availability for bighorn sheep is high. The primary growing season occurs consistently in winter and spring, a timing that reflects both temperature and precipitation patterns.

The timing of births matches that pattern of nutrient availability, contrary to the common explanation that the long

survivorship associated with rainfall beyond that amount. This phenomenon deserves further research attention.

The data sets used here allowed analyses of patterns of nutrient availability because of their length (15-18 years). However, because each year represents but a single data point for most analyses, in some ways these data sets allow only the beginning of an understanding of the complexities of this ecosystem. Additional decades of data would allow considerable refinement of that understanding.

Acknowledgments

I thank the California Department of Fish and Game for funding this research, and the following individuals for their help in the collection of data: L. Brown, M. Hansen, J. Hart, J. Jaeger, T. Manning, and R. Ramey

Literature Cited

- Bailey, J. A. 1980. Desert bighorn, forage competition, and zoogeography. *Wildlife Society Bulletin* 8:208-216.
- Beatley, J. C. 1974. Phenological events and their environmental triggers in Mojave desert ecosystems. *Ecology* 55:856-863.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildl. Monogr.* No. 134. 50pp.
- Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. *Wildl. Monogr.* No. 4. 174pp.
- Bunnell, F. L. 1980. Factors controlling lambing period of Dall's sheep. *Canadian Journal of Zoology* 58:1027-1031.
- Bunnell, F. L. 1982. The lambing period of mountain sheep: synthesis, hypotheses, and tests. *Canadian Journal of Zoology* 60:1-14.
- Colwell, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55:1148-1153.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurito, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monograph* 155:1-61.
- DeForge, J. R., E. M. Barrett, S. D. Ostermann, M. C. Jorgensen, and S. G. Torres. 1995. Population dynamics of peninsular bighorn sheep in the Santa Rosa Mountains, California, 1983-1994. *Desert Bighorn Council Trans.* 39:50-67.
- Douglas, C. L. 1991. Predicting bighorn lamb survival from weather patterns in Canyonlands National Park., Utah. National Park Service, University of Nevada, Las Vegas, Contribution No. CPSU/UNLV 031/08.
- Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. *Journal of Range Management* 35:146-151.
- Hass, C. C. 1993. Reproductive ecology of bighorn sheep in alpine and desert environments. Ph.D. diss. Univ. of North Dakota, Grand Forks. 166pp.
- Hebert, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. thesis, Univ. of British Columbia. 357pp.
- Hoefs, M. 1979. Flowering plant phenology at Sheep Mountain, Southwest Yukon Territory. *Canadian Field-Naturalist* 93:183-187.
- Hoefs, M., and I. M. Cowan. 1979. Ecological investigation of a population of Dall sheep (*Ovis dalli dalli* Nelson). *Syesis* 12, supplement 1: 1-81.
- Krausman, P. R., J. D. Wehausen, M. C. Wallace, and R. C. Etchberger. 1993. Rumen characteristics of desert races of mountain sheep and desert mule deer. *Southwestern Naturalist* 38:172-174.
- Krausman, P. R., A. V. Sandoval, and R. C. Etchberger. 1999. Natural history of desert bighorn sheep. Pages 139-191 in R. Valdez and P. R. Krausman, eds. *Mountain sheep of North America*. Univ. of Ariz. Press., Tucson.
- Lenarz, M. S. 1979. Social structure and reproductive strategy in desert bighorn sheep (*Ovis canadensis mexicana*). *Journal of Mammalogy* 60:671-678.
- Lenarz, M. S. and W. Conley. 1982. Reproductive gambling in bighorn sheep (*Ovis*): a simulation. *Journal of Theoretical Biology* 98:1-7.

- MacMahon, J. A. 1979. North American deserts: their floral and faunal components. Pages 21-82 in D. W. Goodall, R. A. Perry, and K. M. W. Howes, eds. *Arid-land ecosystems: structure, functioning and management*, Vol 1. Cambridge Univ. Press.
- Major, J. 1977. California climate in relationship to vegetation. Pages 11-73 in M. G. Barbour and J. Major, eds. *Terrestrial vegetation of California*. John Wiley and Sons.
- Rubin, E. S., W. M. Boyce, and V. C. Bleich. 2000. Reproductive strategies of desert bighorn sheep. *Journal of Mammalogy* 81:769-786.
- Thompson, R. W., and J. C. Turner. 1982. Temporal geographic variation in the lambing season of bighorn sheep. *Canadian Journal of Zoology* 60:1781-1793.
- Turner, F. B., and D. C. Randall. 1989. Net productivity by shrubs and winter annuals in southern Nevada. *Journal of Arid Environments* 17:23-36.
- Van Soest. 1982. *Nutritional ecology of the ruminant*. O & B Books, Inc., Corvallis OR. 373pp.
- Wagner, F. H. 1981. Population dynamics. Pages 125-168 in D. W. Goodall, R. A. Perry, and K. M. W. Howes, eds. *Arid-land ecosystems: structure, functioning and management*, vol. 2. Cambridge University Press., Cambridge.
- Wehausen, J. D. 1980. *Sierra Nevada bighorn sheep: history and population ecology*. Ph.D. Thesis, Univ. of Mich., Ann Arbor, MI. 240pp.
- Wehausen, J. D. 1983. *White Mountain bighorn sheep: an analysis of current knowledge and management alternatives*. Inyo National Forest Administrative Report, Bishop, CA 93 pp.
- Wehausen, J. D. 1984. Comment on desert bighorn as relicts: further considerations. *Wildlife Society Bulletin* 12:82-85.
- Wehausen, J. D. 1991. Some potentially adaptive characters of mountain sheep populations in the Owens Valley region. Pages 256-267 in C. A. Hall, Jr., V. Doyle-Jones, and B. Widawski, eds. *Natural history of eastern California and high-altitude research*. White Mountain Research Sta. Symp. Vol. 3., Bishop, CA.
- Wehausen, J. D. 1995. Fecal measures of diet quality in wild and domestic ruminants. *Journal of Wildlife Management* 59:816-823.
- Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987b. Recruitment dynamics in a southern California mountain sheep population. *J. Wildl. Manage.* 51:86-98.
- Witham, J. H. 1983. *Desert bighorn sheep in Southwest Arizona*. Ph.D. diss., Colorado State University, Fort Collins. 81pp.

EXHIBIT 418

MOUNTAIN SHEEP AND MINING: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

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Opportunities to quantitatively assess responses of ungulates to mineral extraction have been limited. Reasons for this dearth of research include a lack of adequate funding, available personnel, and logistical constraints. In 1992, a request was submitted to the Bureau of Land Management by a mining company for permission to extract and process gold ore in the Panamint Range, Inyo County, California, near a spring presumed to be critically important to mountain sheep, *Ovis canadensis*. Ensuing compliance with the National Environmental Policy Act resulted in funds to monitor effects of mining activities on mountain sheep inhabiting that area. Because funding was not released until ~8 months prior to construction and operation of the mine, we were unable to adequately address the pre-mining ecology of sheep in the “affected” area. We therefore employed a simultaneous treatment-control study designed to test several hypotheses regarding effects of mining activities on habitat selection, demographics, home-range dynamics, foraging activities, and composition and quality of diet for mountain sheep during 1995-1997. During our 3-yr study, we radiocollared and monitored 86% ($n = 19$) of all adult female sheep known to exist within the mined (treatment) and nonmined (control) areas. Size of annual home ranges, composition of diet, and ratios of young to adult females did not differ between female sheep

inhabiting mined and nonmined areas. The nonmined area contained more annual plants, succulents, and perennial forbs than did the mined area, whereas abundance of shrubs, quality of forage, and relative abundance of carnivores did not differ between sites. During spring, female sheep adjacent to the mine spent more time foraging and had a lower-quality diet than those in the nonmined area. Conversely, during summer and autumn, female sheep from the mined area spent less time foraging than those in the nonmined area, but continued to have a lower-quality diet. All females were nearest water in summer compared with other seasons. During all seasons, females selected sites with more mixed-woody scrub, lower elevations, steeper slopes, and less visibility than available at random locations. We observed the greatest disparities between study areas in time spent foraging and diet quality during summer. In summer, females from the mined area were nearest to the mine; amount of explosives used, frequency of blasting, and amount of ore hauled from the mine were greatest during that period. Because of their reliance on a source of permanent water adjacent to the mine during summer and autumn, we hypothesize that female sheep from the mined area spent more time vigilant during those seasons and, consequently, less time foraging than conspecifics in the nonmined area. If outcomes we observed persist for mountain sheep in the mined area, reduced nutrient intake could have demographic consequences for that subpopulation. Thus, providing a reliable source of water away from the mine, or reducing mining activity during summer, may benefit mountain sheep that currently use areas adjacent to the mine.

INTRODUCTION

Among ungulates, exposure to human activities has been linked to temporary abandonment of areas of traditional use (Kuck et al. 1985, Bleich et al. 1994), shifts in centers of activity (Van Dyke and Klein 1996), and localized extirpations (DeForge et al. 1981). Quantitative data regarding effects of mineral extraction on mountain sheep, *Ovis canadensis*, however, are few. Some researchers have investigated responses of mountain sheep to activities typically associated with mining (e.g., helicopter disturbance—Stockwell et al. 1991, Bleich et al. 1994; human disturbance—Hicks and Elder 1979, Leslie and Douglas 1980, Krausman and Etchberger 1995, Papouchis et al. 2001; and water development—Krausman and Etchberger 1995), but those authors did not address the issue of mining activities and their effects on mountain sheep.

We studied the ecology of female mountain sheep adjacent to a heap-leach gold mine in the Mojave Desert. We measured variables from two subpopulations of female sheep inhabiting distinct geographic areas within a single mountain range (i.e., mined and nonmined) to test hypotheses regarding potential influences of mining on habitat selection, home-range dynamics, and foraging ecology of those large herbivores. We predicted that if mining had no effect on sheep, there would be no differences in selection of habitat and size of home ranges between females occupying those two areas. We also predicted that after considering potential influences of resources and

predators, female sheep would select habitat in a manner similar to that of sheep from the nonmined area, if there were no effects of mining activities. Among mountain sheep, vigilant behavior increases in areas with low levels of visibility (Risenhoover and Bailey 1985, Frid 1997, Rachlow and Bowyer 1998), and is affected by the presence of perceived threats (Berger 1978, Festa-Bianchet 1988, Berger 1991, Stockwell et al. 1991)—such behavior reduces time spent foraging, and might result in differences between mined and nonmined areas. Therefore, if mountain sheep near the mine were unaffected by mining activities, we hypothesized that after considering availability of forage, there would be no difference in time spent foraging between areas. Further, if quality of forage differed between sites, we predicted that individuals consuming lower-quality forage would spend more time foraging to meet their nutrient requirements (Leslie and Douglas 1979). Finally, if abundance of predators differed between areas, we predicted that after considering availability and quality of forage, mountain sheep in areas with more predators would spend more time vigilant (Berger 1978, Rachlow and Bowyer, 1998) and, consequently, less time foraging (Molvar and Bowyer 1994, Bowyer et al. 2001). Effects of mining cannot be addressed or mitigated without considering influences of these factors on the ecology of free-ranging mountain sheep.

METHODS

Study Area

Our study was conducted in the Mojave Desert on the west-facing slope of the Panamint Range, Inyo County, California, USA (Fig. 1). The subpopulation of female sheep living near the mine was centered on Redlands Spring (36°56'37"N, 117°10'43"W) in the southern end of our study area, whereas the center of our control population (i.e., nonmined) was located ~22 km to the north (37°09'34"N, 117°09'50"W) (Fig. 2).

Elevations range from 305 m on the valley floor to 3,368 m at Telescope Peak. Mean (\pm SE) annual rainfall from 1911 to 1994 at the weather station ~30 km from our study site (Greenland Ranch-Furnace Creek, California) was 4.7 ± 0.33 cm, and temperature was highly variable; daytime high temperatures ranged from $>40^\circ\text{C}$ during summer (May-August), to -7°C during spring (January-April, Fig. 3; Death Valley National Park Service files). We used climatological data collected from Greenland Ranch-Furnace Creek, and data on timing of parturition (Welles and Welles 1961) to define three seasons. Spring was 1 January-30 April, which incorporated most of parturition, and was typified by cool temperatures ($\bar{x} = 25^\circ \pm 5.7^\circ\text{C}$) and relatively greater precipitation ($\bar{x} = 0.59 \pm 0.99$ cm) than other seasons. Summer was 1 May-31 August; that period was extremely hot ($\bar{x} = 43^\circ \pm 3.8^\circ\text{C}$) with low rainfall ($\bar{x} = 0.21 \pm 0.51$ cm). Autumn (and the concomitant mating season) extended from 1 September to 31 December, and was characterized by cooler temperatures ($\bar{x} = 29^\circ \pm 9.9^\circ\text{C}$), and lower precipitation than spring ($\bar{x} = 0.37 \pm 0.77$ cm).

Six vegetation communities were delineated within the study area from a LANDSAT-TM scene with cells of 25-m resolution: 1) alkali playa (305 m elevation), which occurred on relatively flat areas of the valley floor; 2) desert saltbush, *Atriplex canescens*, scrub,

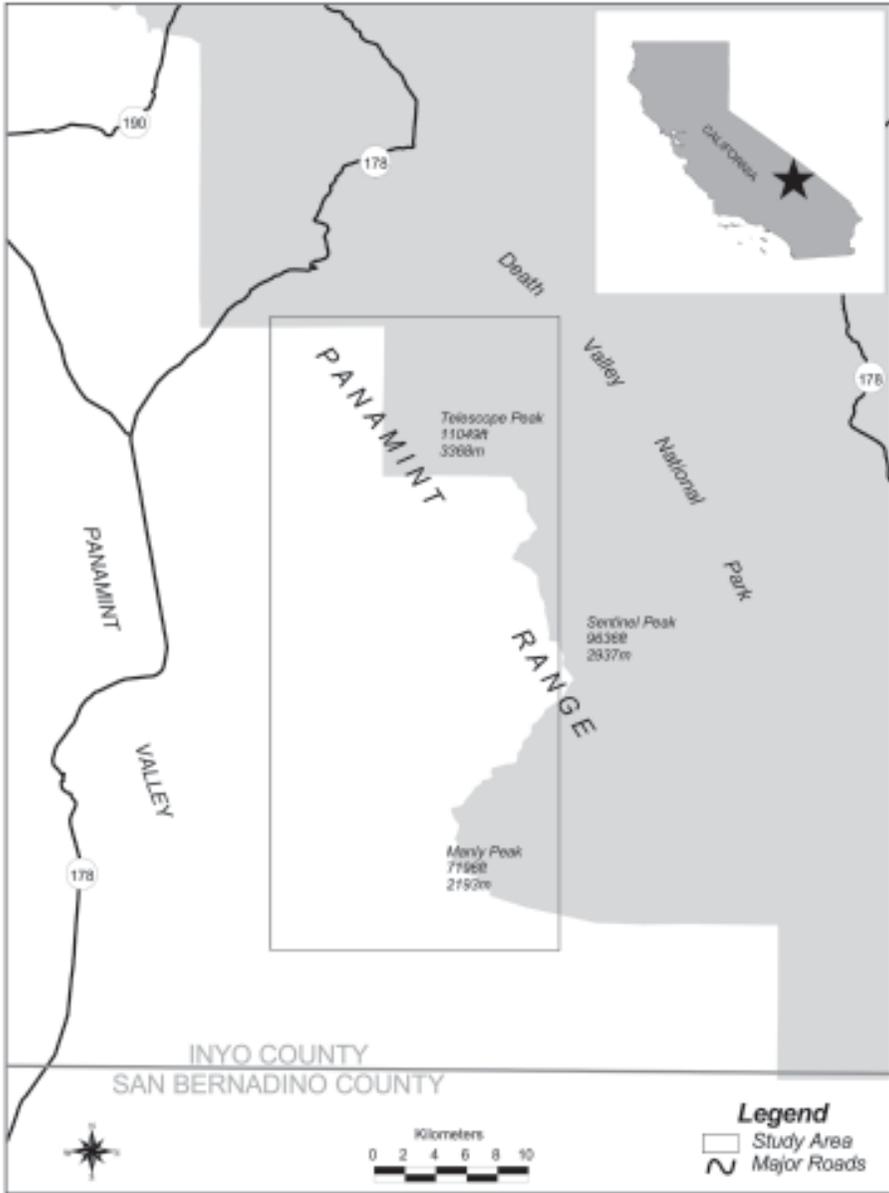


Fig. 1. Location of our study areas in the Panamint Range, Inyo County, California, USA, 1995-1997.

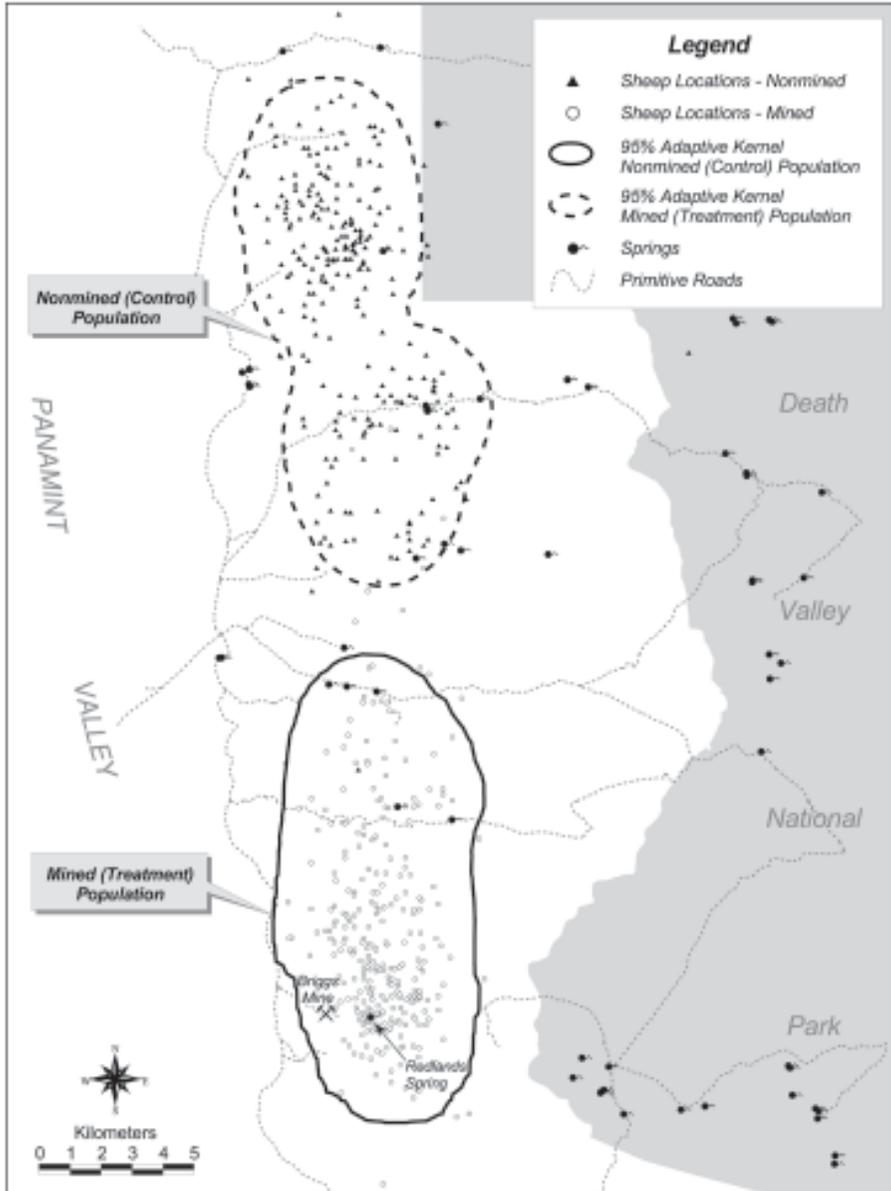


Fig. 2. Telemetry locations of female mountain sheep, and 95% adaptive kernel polygons for populations of sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, 1995-1997.

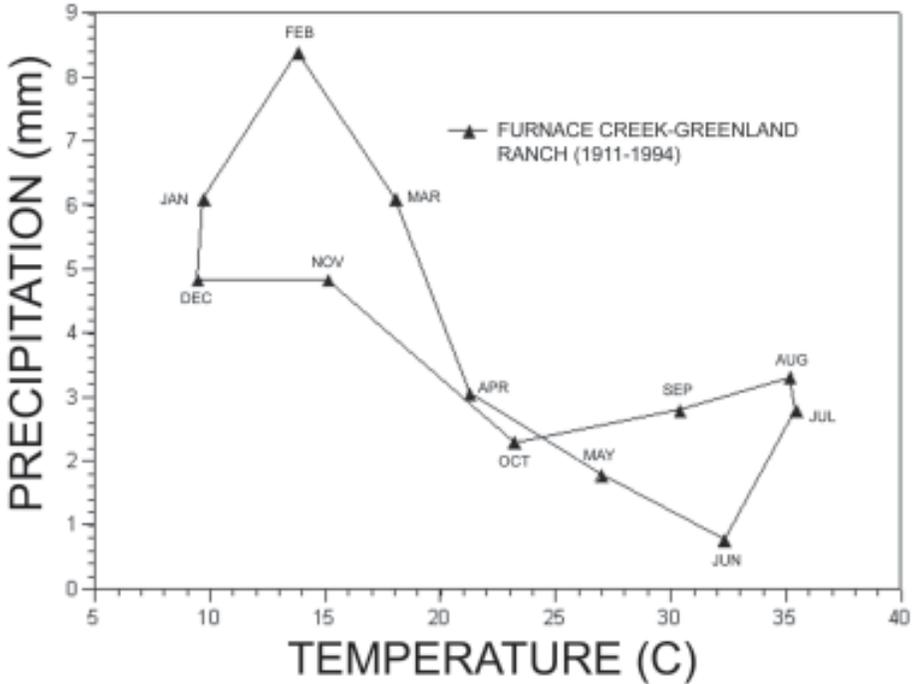


Fig. 3. Climograph of mean monthly temperature and precipitation at Furnace Creek, Inyo County, California, USA, 1911-1994.

which was adjacent to playas and characterized by microphyllous shrubs; 3) creosote bush, *Larrea tridentata*, scrub, which occurred from 300 to 1,640 m elevation; 4) Mojave mixed woody-scrub (1,400-2,300 m elevation), with shadscale, *A. confertifolia*, and blackbush, *Coleogyne ramosissima*, as predominant species; 5) Mojave-woodland scrub (2,300-3,300 m elevation), which was dominated by pinyon pine, *Pinus monophylla*, and juniper, *Juniperus osteosperma*; and 6) bristlecone pine, *Pinus longaeva*, forest, which occurred at elevations >3,300 m. There were 9 and 13 permanent springs, respectively, within mined and nonmined areas.

Mountain sheep occurred in the Panamint Range at relatively low densities (72 adult females/1,000 km; Oehler et al. 2003); other ungulates that inhabit the area include feral asses, *Equus asinus*, and mule deer, *Odocoileus hemionus*. Large mammalian carnivores present include coyotes, *Canis latrans*, bobcats, *Lynx rufus*, and mountain lions, *Puma concolor* (Welles and Welles 1961). Nevertheless, predation on desert sheep by those carnivores was thought to be negligible (Welles and Welles 1961, Weaver¹ 1972).

¹Weaver, R. A. 1972. Desert bighorn sheep in Death Valley National Monument and adjacent areas. California Department of Fish and Game Wildlife Management Administrative Report 72-4.

Most lands within the study area were administered by the U.S. National Park Service or the U.S. Bureau of Land Management and, as a result of the California Desert Protection Act of 1994, most roads in this area were closed to motorized vehicles. The few roads not included in wilderness areas were accessible only by four-wheel drive vehicles; access was extremely limited. During the cooler portions of the year (November-March), roads open to the public were used by 10-15 vehicles/weekend, and 5-10 hikers/week, whereas in summer vehicular traffic and hiking in those areas was rare (D. Brenner, National Park Service, personal communication).

In December 1995, Canyon Resources Corporation began construction of an open-pit gold mine (hereafter the Briggs Mine) near Redlands Spring (Fig. 2); excavation, crushing, and on-site processing of ore began in March, July, and October 1996, respectively. The Briggs Mine was projected to process ~19.3 million metric tons of ore on site during the 7-year life of the mine, and to disturb 1,333 ha of land within the 2,350-ha project area.

Capture and Aerial Telemetry of Mountain Sheep

We captured adult (>1 yr old) female sheep during June and October 1995, June 1996, and January 1997 with a helicopter and net-gun (Krausman et al. 1985a); all aspects of animal handling complied with protocols set forth by the California Department of Fish and Game (Jessup et al.² 1986), and were consistent with methods adopted by the American Society of Mammalogists (Ad Hoc Committee on Acceptable Field Methods. 1987). We categorized all females and young observed or captured during fieldwork as adults or young (individuals of either sex <1 yr old). We fitted sheep captured in June 1995 with standard VHF telemetry collars (Telonics®, Mesa, Arizona), and animals captured during subsequent efforts with activity-sensing collars (Advanced Telemetry Systems®, Isanti, Minnesota).

We attempted to locate all radiocollared sheep weekly during June, July, and August, and in alternate weeks during the remainder of the year using a fixed-wing aircraft (Krausman et al.³ 1984). We located collared sheep between 0900 and 1400 h, Pacific Standard Time, and locations were estimated with either LORAN-C or Global Positioning System (GPS) instruments aboard the aircraft. Because of error associated with LORAN-C (Jaeger et al. 1993, Oehler et al. 1996), we derived a correction factor (Patric et al. 1988) to adjust geographic coordinates obtained using that technology. On average, coordinates obtained from LORAN-C technology indicated the aircraft was 41 m west and 127 m north of the target. Global Positioning Systems are less subject to geographic variability in accuracy than LORAN-C (Leptich et al. 1994), and we did

²Jessup, D. A., W. E. Clark, and M. A. Fowler. 1986. Wildlife restraint handbook. Third edition. California Department of Fish and Game, Rancho Cordova, California, USA.

³Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1984. Radio tracking desert mule deer and bighorn sheep with light aircraft. Pages 115-118 in *Deer in the southwest: a workshop* (P. R. Krausman and N. Smith, editors.). School of Renewable Natural Resources, University of Arizona, Tucson, USA.

not correct sheep locations obtained via GPS. Accuracy of telemetry locations was 177 m (i.e., a circle with radius of 177 m) for an investigation of mule deer in the San Bernardino Mountains, California (Nicholson et al. 1997). Because we used the same pilot as Nicholson et al. (1997) for our flights, we reasoned that the error within our study area would be similar. To be conservative, and because we occasionally used another pilot, we increased the radius of the circle to 200 m.

Habitat Analyses

Unless specifically indicated, hereafter our references to “habitat” are general in nature and apply to the suite of variables we analyzed relative to locations of sheep (e.g., slope, aspect, viewshed, vegetation communities, etc.). We tested locations for each animal for lack of independence with the multiresponse-sequence procedure (MRSP) of BLOSSOM statistical software (Solow 1989, Slauson et al.⁴ 1991) and eliminated locations until no significant ($P \geq 0.05$) autocorrelation was detected (Nicholson et al. 1997). We pooled telemetry locations of female sheep by area (mined vs. nonmined) to define areas of available habitat and used the program CALHOME (Kie et al. 1996) to construct a 100% minimum convex polygon around those locations. Resulting polygons were buffered by 1,000 m to account for undetected movements (Bleich et al. 1997), and to avoid biases in assessing habitat selection from only within the home ranges of sheep (Kie et al. 2002). We then generated random locations within each buffered polygon with the same frequency as sheep locations used to construct that polygon. Next, we used a Geographic Information System (GIS; ARC/INFO®, Environmental Systems Research Institute, Redlands, California) to generate a circle with a radius of 200 m around each sheep (i.e., potential telemetry error) and random location; area within those circles was used to calculate relative use and availability of habitat attributes (Andrew et al. 1999, Nicholson et al. 1997).

We generated a three-dimensional model of terrain for the study area from USGS 7.5' digital elevation models (DEM) with 30-m resolution using the GRID module of ARC/INFO. The DEM provided information on elevation, slope, and aspect associated with each telemetry location. Because resolution of the DEM was 30 m, the radius of the circle used to assess associated features was 210 m (i.e., 30 m x 7 pixels). We used the product of the *SD* of slope and the mean angular deviation of aspect inside each circle as an index to terrain diversity (Nicholson et al. 1997). We used the GIS to estimate visibility (i.e., the viewshed) from each female sheep and random location to examine the role of visibility in habitat selection among female sheep. The GIS calculated the two-dimensional area that would be visible from a height of 1 m (approximate eye-level of a sheep) within a circle having a radius of 1,000 m.

A GIS layer of vegetation communities was developed for the study area from the LANDSAT-TM scene. Because alkali playa, desert-saltbush scrub, and the bristlecone-

⁴Slauson, W. L., B. S. Cade, and J. D. Richards. 1991. User's manual for BLOSSOM statistical software. United States Fish and Wildlife Service, National Ecology Research Center, Fort Collins, Colorado, USA.

pine forest represented <0.5% of the available plant communities, and because female sheep were not located in those vegetation types, we eliminated them from further consideration. We also digitized the locations of roads and springs from USGS 7.5' quadrangle maps to evaluate those factors relative to use of habitat by sheep.

We used stepwise logistic regression (PROC LOGISTIC; SAS Institute Inc. 1997) with an α -to-enter and stay of 0.15 (Agresti 1990) to identify variables that might be important in differentiating random locations from those used by sheep (Nicholson et al. 1997). For our habitat analyses, we treated the individual animals as our sampling unit to eliminate inflated sample sizes associated with using individual telemetry locations as sampling units. Using variables selected by logistic regression, we calculated a vector of means for each female sheep during each season (i.e., three vectors for each female). Because availability of the habitat variables we measured does not change by season, we calculated a single vector of means for those variables at the random locations in each of the mined and nonmined areas. Finally, we generated a vector of differences for each female sheep during each season (i.e., sheep minus the random vector from its corresponding area); resulting vectors became dependent variables in a two-way multivariate analysis of variance (MANOVA; Johnson and Wichern 1988) to test hypotheses regarding selection of habitat. Main effects in the habitat model were area (mined and nonmined) and season (spring, summer, and autumn); significance of the model was determined with Wilks' lambda (Johnson and Wichern 1988). We determined selection or avoidance of habitat variables following the methods of Nicholson et al. (1997) and Bowyer et al. (1999). Additionally, we used a two-way ANOVA (random vs. sheep location, and season, as main effects) to compare distances from the Briggs Mine to sheep locations in mined and nonmined areas.

Home-range Analyses

Prior to calculating adaptive-kernel home ranges for each female sheep, we used CALHOME to estimate the parameter for the optimum smoothing of the 95% adaptive kernel for that sheep (Worton 1989, Kie et al. 1996). Next, we calculated 95% adaptive-kernel home ranges based on 60-120% (in increments of 10%) of that smoothing parameter; the value that minimized the least squares cross-validation score for each individual data set was then used as the smoothing parameter for calculating 95, 50, and 10% adaptive-kernel home ranges for that animal (Kie et al. 1996). We considered the 10% adaptive-kernel home range to be the center of activity for a particular sheep; we then used the GIS to measure distances from that centroid of the home range to permanent springs and roads.

To determine if we had an adequate number of locations to estimate home ranges for each mountain sheep, we first plotted the area within 95% adaptive-kernel home range against cumulative sample size, and then estimated the sample size necessary to compute the home range using the nonlinear procedure in SPSS (SPSS Inc. 1993): home-range size = $A(1 - e^{-bn})$, where A is the asymptote of the equation, e is the base of the natural log, n is the sample size, and b is a constant. Data sets that did not attain 90% of that asymptotic value were eliminated from further analyses (Nicholson et al. 1997).

We tested hypotheses regarding home-range size with data from seasons combined, because of inadequate numbers of locations within seasons. We analyzed size of home ranges using a two-sample *t*-test, and a one-way analysis of covariance (ANCOVA) with area as the main effect, and distances from the center of activity to nearest spring and road as covariates. We used the multi-response permutation procedure (MRPP) of BLOSSOM statistical software (Slauson et al.⁴ 1991) to test our assumption that sheep assigned to mined and nonmined populations inhabited unique geographic areas.

Foraging Behavior

We collected data on head position (i.e., up vs. down) of female mountain sheep fitted with activity collars (mined, $n = 8$; nonmined, $n = 10$) via two remote recording stations (Receiver Model 2100, Data Logger Model DCC-5400, Advanced Telemetry Systems, Isanti, Minnesota) deployed from March 1996 to September 1997. The telemetry frequency of each sheep was scanned at 15-min intervals until either that frequency was received and a pulse rate could be ascertained, or for a maximum of 1 min. If that frequency was not received within 1 min., the datalogger proceeded to the next frequency in its memory and repeated the previously described process. Each time a frequency was received and a corresponding pulse rate was determined for that frequency, that observation (i.e., an instantaneous scan; Altmann 1974) was coded as either head-up or head-down; the resulting data were then pooled by individual animal at 1-hour intervals. We used a two-sample *Z*-test for proportions (Remington and Schork 1970) to evaluate the ability of the recording system to correctly quantify the proportion of time an animal spent with its head in a particular position, and to compare the proportion of time spent feeding with the position of the head. We further evaluated bias of the recording system following the methods of Hansen et al. (1992).

We conducted validation tests for concordance between direct visual observation and the recording system at the Bighorn Institute, Palm Desert, California, USA. One desert sheep was fitted with an activity collar (Advanced Telemetry Systems, Isanti, Minnesota), and the position of its head was recorded every 30 seconds using our electronic system. We conducted instantaneous-scan sampling (Altmann 1974) simultaneously with the collection of electronic data to serve as a measure of the "true" activity of the collared animal at that instant; we recorded head position (up or down) and the activity in which the animal was engaged (e.g., feeding, bedded, walking, etc.) at the same time the datalogger recorded its observation. We used data on head position to test the system for accuracy, whereas information on feeding was used to establish a relationship between head position and time spent feeding (Bradshaw et al. 1997). During validation of data collection by our remote system, the proportion of head-up and head-down observations recorded by the datalogger and the observer ($n = 1,277$) did not differ ($Z = 0.775, P = 0.441$); the recording system underestimated head-down positions by 1.2%. Additionally, no significant difference existed in the proportion of time in the head-down position (as indexed by the recorder) and the proportion of time spent foraging in direct observations ($Z = 0.163, P = 0.873$). Bias

associated with foraging was minimal with the electronic system, which overestimated observed foraging by 0.2%; consequently, we assumed that a head-down signal indicated a foraging animal, whereas a head-up signal was consistent with activities other than foraging.

Response to Blasting

Because we knew the days on which blasting occurred at the Briggs mine, we used days since blasting as our measure of response to that potential disturbance. We used a weighted mixed-model ANOVA (PROC MIXED; SAS Institute Inc. 1997) to test for the effect of blasting on head position (i.e., foraging vs. nonforaging); this model is appropriate when data contain both fixed and random components, and exhibit heterogeneous variances (SAS Institute Inc. 1997). Number of observations for each female during a particular day and hour were used to weight proportional data. Fixed effects were area, season, number of days since blasting (day of the blast, 1-3 days post-blasting, and >3 days post-blasting), and time of day (0100-0459, 0500-0859, 0900-1259, 1300-1659, 1700-2059, and 2100-0059 h). Individual animals (nested within area) were considered a random component, and were included to account for individual variation among animals; interactions incorporating that term also were considered random effects (SAS Institute Inc. 1997). The interaction season \times time period \times animals nested within area was used to test for differences between areas resulting from ecological processes (i.e., seasonal and diurnal patterns), whereas days since blasting \times time period \times animals nested within area was used to test for effects of blasting.

Forage Abundance and Quality

We quantified vegetation using step-point sampling along 100-m transects that were located randomly (Bowyer and Bleich 1984, Bleich et al. 1997) within mined and nonmined areas. We compared relative abundance between those areas using MANOVA and univariate *F*-tests. Samples of 12 forage species (five samples/species/area/month), consumed by mountain sheep (Bleich et al. 1992), were collected from July 1995 to June 1996 for analyses of percent crude protein (nitrogen \times 6.25), in vitro dry matter digestibility (IVDMD), and moisture content following the methods of Bleich et al. (1992). Species of perennial forbs sampled were desert mallow, *Sphaeralcea ambigua*, desert trumpet, *Eriogonum inflatum*, and Rixford eriogonum, *E. rixfordii*. Perennial grasses were needlegrass, *Stipa speciosa*, and three-awn, *Aristida glauca*; representative species of shrubs included bedstraw, *Galium stellatum*, burro-weed, *Ambrosia dumosa*, desert holly, *Atriplex hymenelytra*, brittle bush, *Encelia farinosa*, Mormon-tea, *Ephedra nevadensis*, California buckwheat, *Eriogonum fasciculatum*, and mesquite, *Prosopis glandulosa*.

We analyzed IVDMD and moisture of perennial forbs and shrubs separately using three-way ANOVA (main effects were area, season, and forage class). Crude protein of perennial forbs and shrubs was analyzed with a three-way ranked ANOVA (Conover and Iman 1981) with the same factors. Because of nonconstant variances when grass

was incorporated into the overall model, that forage class was analyzed separately with a two-way ANOVA (area and season as main effects).

Diet Quality and Composition

We used a combination of telemetry (aerial and ground-based) and field observations to locate female groups for collection of fresh fecal pellets (i.e., <1-week-old) each month (June 1995-September 1997) within our study areas. We collected samples on approximately the same date each month, and stored them appropriately (Jenks et al. 1990) prior to conducting analyses. Because the California Department of Fish and Game had collared adult males ($n = 10$) in our study area as part of another project, we were able to use telemetry and direct observation to avoid areas inhabited predominantly by males (Bleich et al. 1997), thereby avoiding biases that might be introduced if we included their samples in our analyses. We attempted to collect ≥ 5 pellet groups (25 pellets per group) from each area each month. We determined percent fecal nitrogen for each sample as described previously for forage samples; this measure provided an index to diet quality (Bleich et al. 1997).

We used composited fecal samples (Bleich et al. 1997) collected between June 1995 and August 1996 to index composition of diets. Species of plants in fecal samples were determined at the Forage Analysis Laboratory, University of Arizona, with the microhistological technique described by Sparks and Malechek (1968). Plant fragments were categorized as perennial forbs, perennial grasses, shrubs, or succulents for statistical analyses (Bleich et al. 1997). Diet composition was analyzed with a two-way MANOVA with forage classes as dependent variables and area and season as main effects, whereas fecal nitrogen was evaluated with a two-way ANOVA with area and season as main effects.

Additional Analyses

We indexed relative abundance of carnivores on each area by noting when they were encountered during helicopter flights, and by collecting carnivore feces in the field. Feces were enumerated and pooled within each area, and feces per kilometer of line transect for each area was compared with a t -test (Bleich et al. 1997).

We compared the ratios of young to adult females observed during fieldwork and helicopter surveys using a binomial approach (Bowyer 1991). We calculated 95% CI for estimates, and compared ratios between areas for a particular period with the 95% CI ; where CI overlapped, we assumed the ratio of young to adult females did not differ during that period (Bowyer 1991).

When multi-factor ANOVA was employed, all individual factor levels and their interactions were evaluated; significant models ($P \leq 0.05$) were explored further with Tukey's honestly significant difference (HSD) to determine where differences occurred. We analyzed data using the software PC SAS (SAS Institute Inc. 1997) and SPSS (Statistical Package for the Social Sciences 1993). We used a Bonferroni correction (Kleinbaum et al. 1988) when conducting multiple comparisons. We examined

assumptions of each statistical test and transformed data as necessary to meet those assumptions. Bivariate correlations were evaluated with a Pearson product-moment correlation (Zar 1984). An $\alpha = 0.05$ was adopted for all tests. Unless otherwise noted, we present means and standard errors for descriptive statistics.

RESULTS

Capture and Aerial Telemetry

We captured 8 female sheep (5 in 1995 and 3 in 1996) in the mined area, and 11 (8 in 1995 and 3 in 1996) in the nonmined area; no deaths of animals occurred during our capture efforts. During 45 h of extensive capture and survey efforts with a helicopter, we observed only 22 individual adult females within the specific area encompassing both study sites (Fig. 2), of which 19 (86%) were radiocollared during some portion of this study. We conducted 70 telemetry flights during June 1995–October 1997; female sheep were located 653 times (340 on the mined and 313 on the nonmined areas); the number of locations/female was 48.6 ± 5.8 on the mined and 39.1 ± 3.9 on the nonmined area. Additionally, our initial assignment of females to discrete populations (Fig. 2; i.e., mined or nonmined) was supported by their differing spatial distributions (MRPP; $\delta = -124.340, P < 0.001$).

Habitat Selection

Number of independent locations per female sheep in our analyses was 43.3 ± 4.4 in the mined and 34.1 ± 3.8 in the nonmined areas. The logistic-regression model, which exhibited good fit ($X^2 = 4.54, P = 0.85$), identified four variables as useful in distinguishing between random sites and those used by female sheep: percentage of the mixed-woody-scrub plant community ($X^2 = 108.80, P < 0.001$), elevation ($X^2 = 17.88, P < 0.001$), percent slope ($X^2 = 22.89, P < 0.001$), and percent visibility ($X^2 = 3.03, P < 0.001$; Table 1). Females from mined and nonmined areas, however, did not differ in how they used habitat (MANOVA, $F_{8,70} = 0.988, P = 0.452$). When compared to random locations, both groups selected sites in the mixed-woody scrub plant community at lower elevations, on steeper slopes, and with less visibility (Fig. 4).

Distance to permanent springs did not enter the logistic-regression model; however, because of an *a priori* hypothesis concerning its importance to desert sheep, we used a two-way ANOVA (area and season as main effects) to address that variable. When data from both areas were pooled, distance from water to random sites and to those used by female sheep differed significantly ($F_{5,1151} = 4.34, P = 0.013$). After controlling for availability of water, female sheep from the mined area were significantly nearer water than those from the nonmined area during autumn ($F_{1,364} = 9.27, P = 0.002$). During spring and summer, however, distance to water was not significantly different between areas ($F_{1,232} = 2.69, P = 0.102$ and $F_{1,544} = 0.06, P = 0.799$, respectively). In general, females from both areas were nearer water than were random locations during summer (Table 1).

Within the mined area, significant differences occurred in the spatial distribution

Table 1. Habitat characteristics of random locations and of female mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, during 1995-1997. Sample sizes are in parentheses.

Habitat variables	Area												
	Random (576)			Mined			Nonmined			Nonmined			
	\bar{x}	SE		Spring (65)	Summer (150)	Autumn (88)	Spring(53)	Summer (124)	Autumn(96)	\bar{x}	SE		
Dist. to springs (m)	1,925	40		2,060	1,608	83	1,922	97	2,113	133	84	2,238	89
Dist. toroads (m)	1,846	50		1,501	1,579	56	1,814	83	1,508	133	89	1,363	93
Dist. to Briggs Mine (m)	12,059	367		2,975	2,091	167	3,267	340	19,698	651	21,092	320	20,960
Sin aspect ^a	-0.43	0.02		-0.52	0.03	0.02	-0.43	0.04	-0.48	0.04	-0.40	0.03	-0.45
Cos aspect ^b	-0.07	0.02		-0.04	0.04	0.04	-0.07	0.05	-0.13	0.06	-0.21	0.04	-0.10
Slope (%) ^c	26.1	0.3		27.5	0.8	0.5	28.6	0.6	27.1	0.7	29.9	0.6	26.7
Terrain index ^d	526	12		664	31	545	573	30	575	39	498	20	534
Elevation (m) ^e	1,324	25		1,128	39	1,164	1,256	27	1,112	40	1,250	27	1,157
Visibility (ha) ^{e,e}	0.61	0.02		47.0	3.4	51.4	45.9	2.8	49.7	3.8	59.6	2.6	55.1
Creosote-bush	7.3	1.0		3.7	2.2	0.9	0.7	0.0	3.9	2.4	0.9	0.6	2.9
Juniper-woodland	11.6	1.3		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.8	1.0
Mixed-woodyscrub ^c	79.56	1.6		95.5	2.6	99.1	100	0.0	96.1	2.4	98.4	1.0	96.0

^aN-S aspects.

^bE-W aspects.

^cV variables selected by logistic regression model for differentiating random locations from those used by female sheep.

^dSD slope times angular deviation of aspect (Nicholson et al. 1997).

^eViewshed analysis from ARC/INFO; area (ha) visible to a sheep (1 m in height) to a maximum distance of 1000 m based on topographic relief.

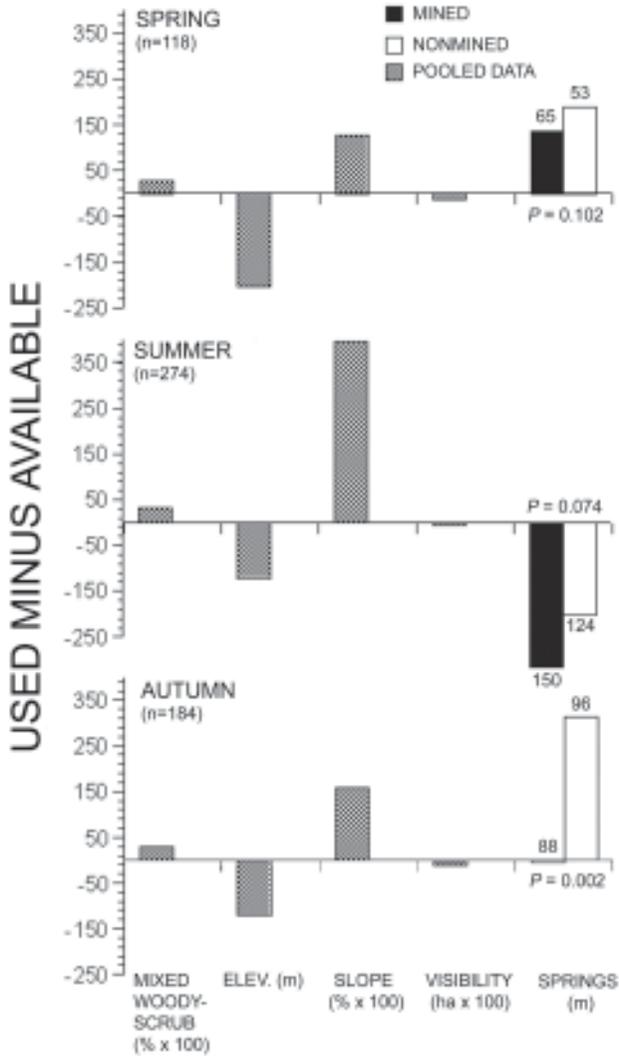


Fig. 4. Selection (used minus available) of habitat variables by female mountain sheep in the Panamint Range, Inyo County, California, USA, during 1995-1997. Mixed woody-scrub, elevation, slope, and visibility were significant variables in a logistic regression model ($X^2 = 4.54$, $P = 0.85$) for differentiating sheep locations from random locations. P -values for distance to springs are from ANOVA, and numbers above or below bars represent number of sheep locations used in that analysis.

of sheep and random locations relative to the Briggs Mine (two-way ANOVA, $F_{5,605} = 19.00, P < 0.001$); females were consistently nearer the mine than were random locations (ANOVA, $F_{1,605} = 67.09, P < 0.001$). Moreover, there were significant differences between seasons in the distances that sheep occurred from the mine ($F_{2,302} = 6.68, P < 0.001$); female sheep were closer to the mine during summer ($2,091 \pm 166$ m) than in autumn ($3,267 \pm 340$ m), whereas during spring they were at an intermediate distance from the mine ($2,975 \pm 326$ m); distance from the mine in spring did not differ from that in summer.

Home Range

We determined that a mean minimum sample of 26.7 ± 2.4 telemetry locations in the mined ($n = 7$) and 26.5 ± 2.6 in the nonmined ($n = 8$) areas were required for home range estimation; four individuals lacked an adequate sample and were eliminated from our analyses. Mean sizes of annual home ranges did not differ significantly between areas (Table 2). Moreover, sizes of home ranges did not differ after controlling for effects of distance to the nearest permanent spring (ANCOVA, $F_{1,12} = 0.482, P = 0.501$), or road (ANCOVA, $F_{1,12} = 0.325, P = 0.579$).

Table 2. Size of annual home ranges (ha) of female mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, during 1995-1997. *P*-values from two-sample *t*-tests are for within-row comparisons of mined versus nonmined areas.

Home Range Model	Area						<i>P</i>
	Nonmined ($n = 8$)			Mined ($n = 7$)			
	\bar{x}	SE	CV	\bar{x}	SE	CV	
Adaptive Kernel							
95%	6,926	834	34	6,222	806	34	0.557
50%	1,230	193	44	954	118	33	0.260
Min. Convex Polygon							
95%	4,006	445	31	3,467	396	30	0.395

Foraging Behavior

We collected 10,241 and 7,023 h of data on head position (hereafter foraging, or foraging activity) for sheep inhabiting the mined ($n = 8$) and nonmined ($n = 10$) areas, respectively (Fig. 5). Number of days since blasting occurred had a significant effect on the proportion of time that females spent foraging ($F_{4,334} = 17.68, P < 0.001$). When a reduced model (all main effects and the interaction days since blasting \times time period \times animals nested within area) was conducted by season, the three-way interaction was highly significant during all 3 seasons. That effect was greatest in summer ($Z = 8.07, P < 0.001$), intermediate during spring ($Z = 7.49, P = 0.001$), and smallest during autumn ($Z = 6.81, P = 0.001$).

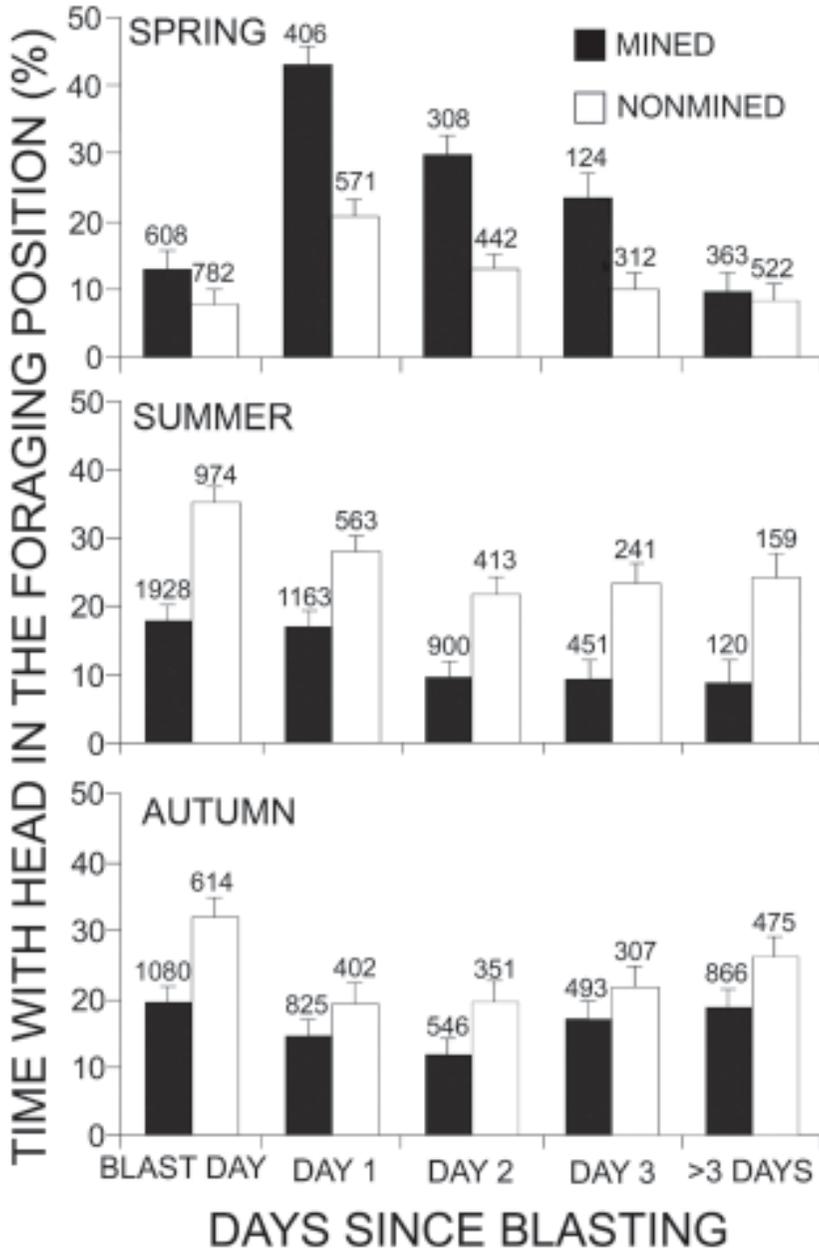


Fig 5. Percent time with the head in a foraging position (indexed by tip-switch collars) for female mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, during 1996-1997. Value of bars (+ 1 SE) are least-squares means from mixed-model ANOVA (PROC MIXED; SAS 1997); numbers above bars are total hours of data collected for that bar.

We further examined number of days between blasts for the mined area with a two-way MANOVA, with days between blasting and amount of explosives per blast as dependent variables, and season as the class variable. We noted significant differences among seasons ($F_{4,400} = 3.58, P = 0.007$), which were not the result of differences in the amount of explosives used per blast during spring ($20,462 \pm 1,362$ tons), summer ($23,204 \pm 905$ tons), or autumn ($22,020 \pm 1,280$ tons) ($F_{2,201} = 1.61, P = 0.202$), but rather number of days between blasts ($F_{2,201} = 5.76, P = 0.004$). There were significantly fewer days between blasts during summer (1.5 ± 0.2) and spring (2.2 ± 0.3) than during autumn (3.0 ± 0.4) ($F_{2,203} = 5.76, P = 0.004$). There were 3,397,878 metric tons of ore removed from the pit during spring, 4,785,498 in summer, and 2,552,166 during autumn. Amount of ore hauled each month was positively correlated with tons of explosives used during that month ($r^2 = 0.83, P < 0.001$).

Forage Abundance

We quantified vegetation on 24 and 36 transects in the mined, and nonmined areas, respectively (Fig. 6), and documented significant differences between areas in types of ground cover ($F_{1,58} = 12.21, P < 0.001$). Transects on the nonmined area were characterized by more annuals ($F_{1,58} = 48.55, P < 0.001$), forbs ($F_{1,58} = 7.16, P = 0.009$), and bare ground ($F_{1,58} = 8.41, P = 0.005$) than those in the mined area, whereas abundance of succulents ($F_{1,58} = 3.79, P = 0.056$) and shrubs ($F_{1,58} = 0.00, P = 0.99$) did not differ between areas.

Forage Quality

We collected 1,152 forage samples within mined ($n = 578$) and nonmined ($n = 574$) areas. No significant differences occurred in moisture content of perennial forbs and shrubs between areas, but differences existed among seasons ($F_{11,191} = 1.88, P = 0.044$), with shrubs possessing a higher moisture content than perennial forbs during spring ($F_{3,77} = 3.35, P = 0.023$; Fig. 7). Similarly, there were no significant differences between areas in IVDMD of perennial forbs or shrubs ($F_{1,191} = 2.90, P = 0.090$); nevertheless, IVDMD of perennial forbs and shrubs differed significantly among seasons ($F_{1,191} = 24.62, P < 0.001$). Shrubs had consistently higher IVDMD than did perennial forbs during spring ($F_{1,77} = 22.15, P < 0.001$) and summer ($F_{1,63} = 6.30, P = 0.015$), but that relationship was not as apparent during autumn ($F_{1,49} = 3.30, P = 0.075$). Conversely, when an overall model considered crude protein of perennial forbs and shrubs, there were no area or seasonal effects ($F_{11,191} = 0.90, P = 0.546$).

When perennial grasses were analyzed separately, there were significant differences in protein between seasons ($F_{5,23} = 7.52, P < 0.001$); further examination revealed differences were attributable to perennial grasses having higher protein content during spring in both mined ($F_{2,11} = 6.55, P = 0.017$) and nonmined ($F_{2,11} = 9.87, P = 0.005$) areas. Likewise, significant differences occurred in IVDMD ($F_{5,23} = 6.42, P < 0.001$) and moisture content ($F_{5,23} = 4.52, P = 0.008$) of perennial grasses from mined and nonmined areas. Again, differences were driven largely by the effects of spring; IVDMD was

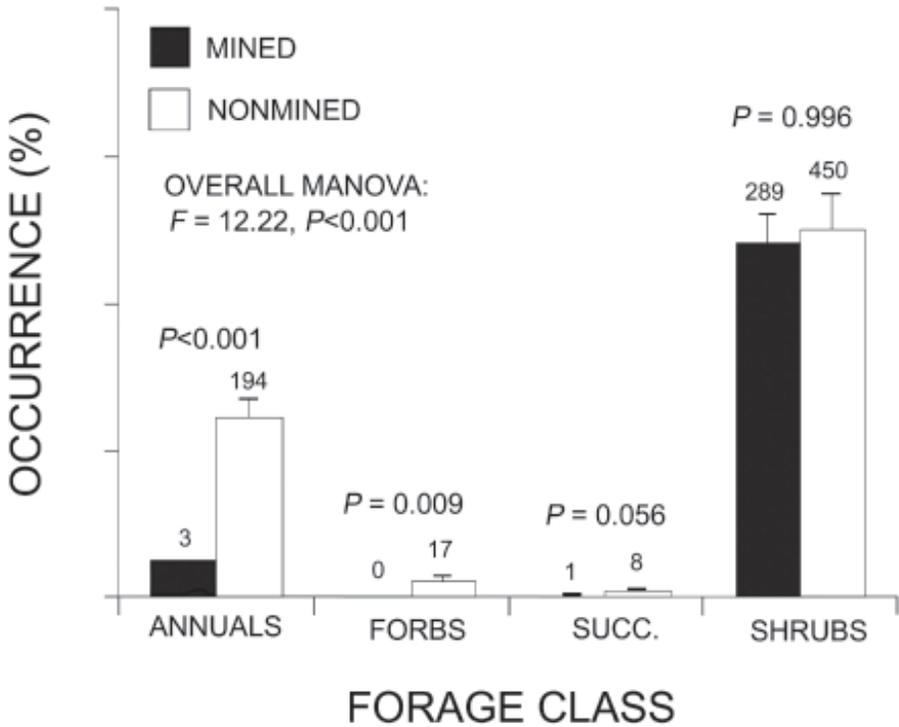


Fig. 6. Mean ($\pm 1 SE$) vegetative cover (%) in habitats used by radiocollared female mountain sheep from mined ($n = 24$ transects) and nonmined ($n = 36$ transects) areas in the Panamint Range, Inyo County, California, during 1995-1997. Numbers above bars indicate occurrence (i.e., "hits") of that type of vegetation on all transects, and P -values are from univariate F tests. Grasses were not detected on transects in either area, and percentage of bare ground was significantly greater ($P = 0.005$) in mined (87%) than the nonmined area (81%).

significantly higher ($F_{1,5} = 29.58, P = 0.005$) on the mined than the nonmined area ($\bar{x} = 66.4 \pm 4.7$ and $\bar{x} = 42.5 \pm 5.9\%$, respectively) during spring. Moisture content of perennial grasses did not differ between areas ($F_{2,23} = 2.18, P = 0.157$), but was significantly higher in both areas during spring than in autumn ($F_{2,11} = 7.39, P = 0.013$). Overall, there was a clear trend in both areas for increased quality of forage among all classes during spring (Fig. 7).

Diet Quality and Composition

We collected 175 individual fecal groups from the mined area and 184 from the nonmined area for assessing quality of diet. There were significant area and seasonal effects on quality of diets (two-way ANOVA; $F_{13,358} = 32.18, P < 0.001$; Fig. 8). Female

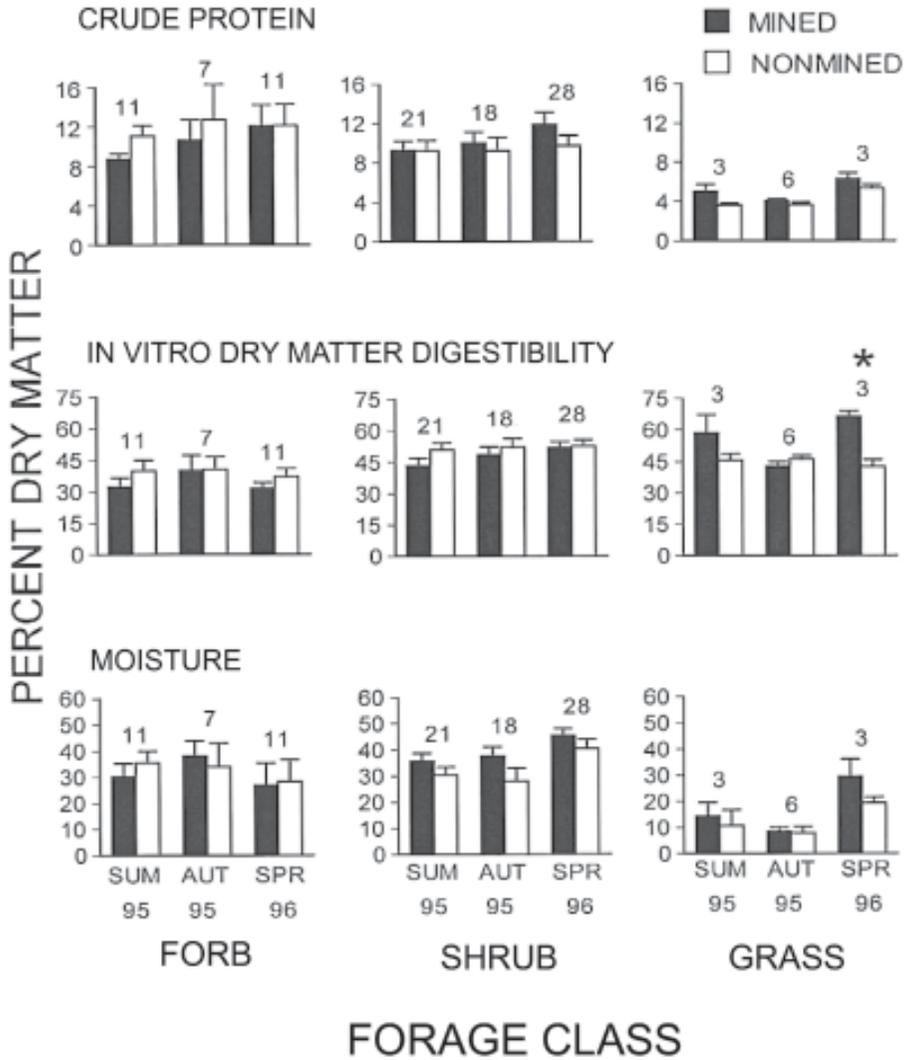


Fig. 7. Percent dry matter crude protein (top), *in vitro* dry matter digestibility (middle), and moisture (bottom) content of forage classes ($\bar{x} \pm SE$) eaten by mountain sheep in the Panamint Range, Inyo County, California, during 1995-1996. Asterisk indicates significant difference ($P < 0.01$) between areas and numbers above bars represent sample size from each area in the comparison.

sheep on the nonmined area had consistently higher levels of fecal nitrogen than conspecifics in the mined area (Fig. 8). Moreover, diet quality was highest during spring (Fig. 8), which was consistent with forage classes having higher levels of crude protein, moisture, and increased digestibility during that season (Fig. 7). Although level of tannins in shrubs may have increased fecal nitrogen, this is unlikely to have occurred because there was not a consistent or significant correlation between fecal nitrogen and the amount of shrubs in the diets of sheep from mined ($r^2 = 0.882$, $P = 0.118$), or nonmined ($r^2 = -0.268$, $P = 0.732$) areas.

No significant differences occurred between areas in the proportions of forage classes in the diet of female sheep (two-way MANOVA, $F_{8,32} = 1.27$, $P = 0.292$). During all seasons, shrubs were the most prevalent vegetation type in diets of females from both areas (Table 3). Overall, diets of female sheep contained an average of 55% shrubs, 30% forbs, 11% succulents, and 4% grasses.

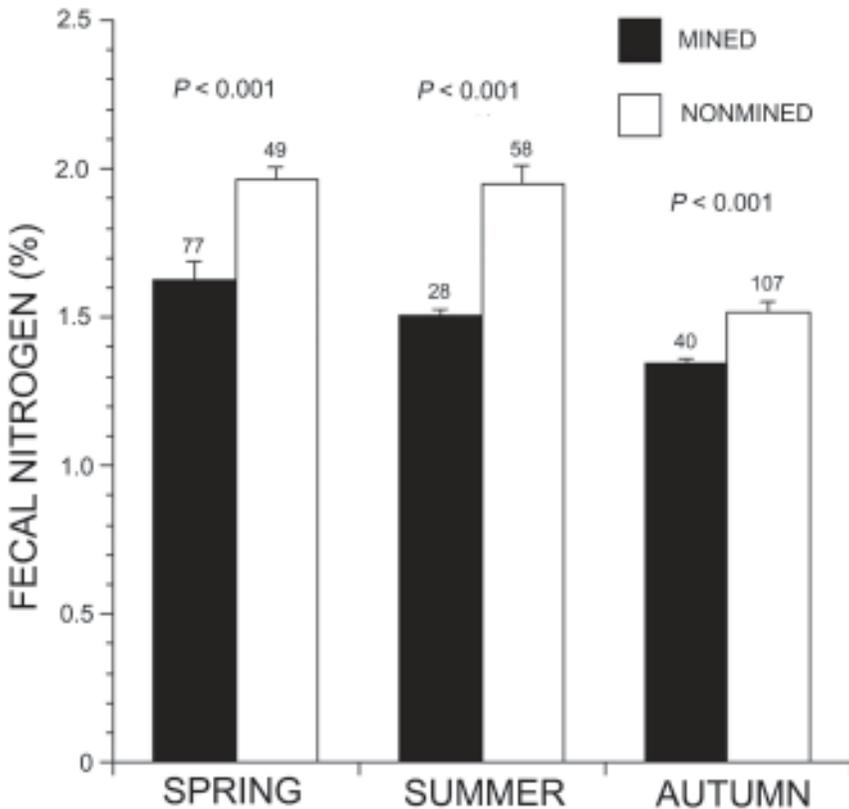


Fig. 8. Mean percent fecal nitrogen of female mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, during 1995-1997. Numbers above bars indicate sample size, bars represent 1 SE, and P -values are from two-sample t -tests.

Table 3. Percent of forage classes in the diets of female mountain sheep indexed from microhistological analyses of their feces, from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, during 1995-1996.

Area	Percentage of forage class ^a							
	Forb		Grass		Shrub		Succulent	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Spring								
Mined (3) ^b	34.4	2.3	1.1	0.6	53.5	2.4	11.1	0.7
Nonmined (3)	26.4	8.3	4.1	0.6	53.9	8.9	15.6	1.0
Summer								
Mined (7)	27.1	3.8	4.5	1.4	59.3	5.1	9.2	1.7
Nonmined (6)	31.0	5.7	5.9	1.0	52.9	4.9	10.3	2.4
Autumn								
Mined (2)	35.4	5.5	1.5	1.5	48.9	3.4	14.3	0.6
Nonmined (4)	31.3	5.2	1.8	1.4	57.5	8.1	9.4	3.8

^aOverall MANOVA (area and season) was not significant ($F_{8,32} = 1.27, P = 0.292$).

^bNumber of composite fecal samples for that season.

Mortality and Indices to Predator Abundance

There were seven mortalities of female sheep in the nonmined area, and two in the mined area. In the nonmined area, two mortalities were attributed to predation by mountain lions, one fell to its death, and causes of death for the other four could not be ascertained. Similarly, causes of mortality for two female sheep in the mined area could not be determined. No differences existed in the ratio of young to adult females between mined and nonmined areas (Table 4).

From July 1995 to September 1997, we sampled transects totaling 24 and 34 km in length for carnivore feces from the mined and nonmined areas, respectively. When feces encountered on transects were pooled by area, there was no significant difference ($t_{22} = -1.91, P = 0.077$) in the number of feces/km between mined (1.6 ± 0.3) and nonmined (1.0 ± 0.1) sites. No carnivores were sighted during the course of fieldwork on either study area; however, most work was performed during the day. Additionally, no carnivores were observed on the study area while conducting captures of sheep (~45 h of helicopter flight-time).

DISCUSSION

Collared mountain sheep constituted 86% of the adult female sheep observed in our two study areas. Overall, we observed few effects that we could attribute to mining on the demography or other characteristics of populations of female sheep inhabiting mined and nonmined areas. For instance, proportion of young to adult females was not

Table 4. Young and adult female mountain sheep observed during aerial surveys near mined and nonmined areas in the Panamint Range, Inyo County, California, USA, during 1995-1997.

Date	Area	Young (<i>n</i>)	Females (<i>n</i>)	P_t^b	95% CI (P)
Jun 1995 ^a					
	Mined	5	7	0.416	0.132-0.700
	Nonmined	6	8	0.428	0.290-0.909
Oct 1995 ^a					
	Mined	1	4	0.200	0.000-0.551
	Nonmined	6	10	0.375	0.138-0.612
Jun 1996 ^a					
	Mined	4	8	0.333	0.117-0.549
	Nonmined	5	14	0.260	0.007-0.513
Jan 1997 ^a					
	Mined	3	4	0.428	0.054-0.802
	Nonmined	2	4	0.666	0.281-1.000
Oct 1997 ^a					
	Mined	3	4	0.428	0.054-0.802
	Nonmined	3	6	0.333	0.019-0.647

^aProportion of young to adult females did not differ between areas during that survey as indicated by overlap of 95% confidence intervals.

^bRatio and confidence intervals (CI) determined following methods of Bowyer (1991).

different between areas during any of the 3 years we monitored those subpopulations (Table 4). Moisture content, crude protein, and IVDMD of forage classes were highest for both areas in spring, intermediate in summer, and lowest during autumn (Fig. 7). Those outcomes are consistent with patterns in the quality of forage observed for other ranges inhabited by sheep in desert environments (Bleich et al. 1997, Krausman et al. 1989). Digestibility of grass was highest in the mined area during spring, but that was the only difference we detected in forage quality between areas (Fig. 7). We observed no differences in composition of diets of female sheep from mined and nonmined areas, although differences existed between forage classes consumed across seasons (Table 3). The former outcome is probably the result of the similarity in quality (Fig. 7) and availability of forage species (i.e., shrubs) between sites (Fig. 6), whereas the latter is likely a consequence of how desert plants with differing life-history strategies respond to variation in precipitation (Beatley 1974). Thus, female sheep from both areas used forage classes differentially, depending on seasonal quality and availability. Differences in availability of forage (as indexed by vegetative cover) between areas were minimal and limited to percentage of annual plants and perennial forbs (Fig. 6).

Size of annual home ranges for females did not differ significantly between areas (Table 2). Indeed, there was substantial individual variation and no clear pattern in

those data (Table 2). Berger (1991) suggested that use of steep rocky habitats was more pronounced for post-parturient female mountain sheep when compared with those without young. In contrast, females without offspring were more likely to forage in areas away from escape terrain, where quality of forage was better, but perceived risk of predation higher (Berger 1991)—those factors could result in large home ranges for females without young. Thus, variability in sizes of home range in our study may have occurred because not all collared females had young at heel, a hypothesis we could not test because we were unable to ascertain the reproductive status of every female during aerial telemetry flights. Nonetheless, the large proportion of the population that was collared and the lack of a difference in ratios of young to adult females between study areas make this interpretation unlikely.

Females from both areas selected sites with more mixed woody-scrub, lower elevations, steeper slopes, and less visibility than at random locations during all seasons (Fig. 4, Table 1). Several researchers (Berger 1991, Bleich et al. 1997, and others) have reported that female sheep consistently used steep and rugged terrain that was close to water. That strategy likely represents a tradeoff between decreased forage quality in steep rocky habitats and decreased rates of predation on neonates (Berger 1991, Bleich et al. 1997, Rachlow and Bowyer 1994, 1998). Following precipitation in early spring, the proportion of grasses increased in the diets of sheep from the nonmined area, but not for those in the mined area (Table 3). That females in the nonmined area apparently increased their use of that resource is consistent with other studies that noted an increase in the consumption of graminoids by mountain sheep following periods of precipitation (Wehausen and Hansen 1988, Berger 1991). Berger (1991) proposed that pre-parturient females that foraged at low elevations on open slopes traded an increased risk of predation for the opportunity to maximize nutrient intake, a hypothesis supported by research on other ungulates (Bowyer et al. 1999, Kie 1999, Barten et al. 2001). Females from the nonmined area had higher levels of fecal nitrogen during spring than did those from the mined area (Fig. 8); such an outcome would be consistent with the aforementioned strategy suggested by Berger (1991). Although females from both areas used areas lower in elevation than random locations, females from the mined area may have been reluctant to forage on the lowest elevation slopes adjacent to the mine during spring because of the proximity of those sites to activities associated with the mine.

Patterns of foraging were not similar between subpopulations of female sheep (Fig. 5), and interpretation of those results during spring was not straightforward. If females in the mined area were precluded from foraging on graminoids during spring by mining activities, they may have had to forage more intensively (i.e., spent more time foraging) in steep areas where forage quality was lower (Bleich et al. 1997). Indeed, quality of diet was lower for female sheep in the mined area during spring (Fig. 8). Although mountain sheep may habituate to human-caused disturbances (Morgantini and Worbets 1988), those ungulates have been reported to avoid areas where disturbance was extreme (Leslie and Douglas 1980, Berger 1991, Stockwell et al. 1991), and did not appear to habituate to extreme disturbances such as helicopter overflights (Bleich et al. 1994).

Availability and juxtaposition of water within each area may be the most parsimonious

explanation for differences we observed in foraging ecology between groups of female mountain sheep inhabiting mined and nonmined areas during summer. Indeed, females from both areas were nearer water during summer than other seasons (Table 1). Sources of permanent water were fewer and more dispersed in the mined area. Moreover, female sheep in that area relied almost exclusively on Redlands Spring, which was adjacent to the mine, to meet their metabolic needs for water during summer. In contrast, females in the nonmined area used several springs. Turner⁵ (1973) reported that daily needs for water for desert mountain sheep was about 4% of their body mass, and that this amount could not be obtained from forage during the hot summer. Desert sheep have been reported to inhabit ranges without sources of perennial water (Krausman et al. 1985b); nevertheless, that result would not preclude water affecting the distribution of sheep in other areas. For instance, free water strongly affected the distributions of other ungulates, even in situations where water was abundant and therefore could not be limiting those populations (Bowyer 1981, Stewart et al. 2002).

Alderman et al. (1989) reported that in the Little Harquahala Mountains, Arizona, where permanent water was not available, desert sheep likely met their metabolic needs by using pools of free-standing water that accumulated in depressions in the substrate after occasional thunderstorms. During our investigation, however, summer thundershowers were rare (Oehler et al. 2003); the lack of summer rain likely would have limited areas that could be used by desert sheep during that season. As a consequence of their reliance on Redlands Spring during summer, female mountain sheep in the mined area also were closest to the Briggs Mine during that season (Table 1).

Several studies have reported that the magnitude of a response to a disturbance is a function of the proximity to the stimulus (MacArthur et al. 1982, Stockwell et al. 1991, Bleich et al. 1994). Stockwell et al. (1991) concluded that mountain sheep in the Grand Canyon, Arizona, foraged more efficiently as distance from helicopter disturbance increased. Similarly, MacArthur et al. (1982) reported mountain sheep in Alberta, Canada, exposed to low-flying aircraft (90-250 m), exhibited a 3.5-fold increase in heart rate over those exposed to high-flying aircraft (>400 m). Results from our analyses of foraging behavior and diet quality suggest that female sheep in the mined area were disturbed by activities associated with the Briggs Mine during summer. That outcome is consistent with the interval between blasting being shortest during summer (1.5 ± 0.2 days). Moreover, amount of ore hauled (an index to vehicle activity) from the mine pit also was highest during summer, and was strongly correlated with the amount of explosives used at the mine.

Patterns of decreased foraging by mountain sheep in the mined area during summer and autumn (Fig. 5) may have been the result of those females spending more time vigilant and, concomitantly, less time foraging (Berger 1991, Stockwell et al. 1991). That conclusion is in keeping with sheep in the mined area obtaining lower-quality diets during summer than sheep from the nonmined area (Fig. 8) as a consequence of decreased foraging efficiency (Berger 1991, Stockwell et al. 1991, Molvar and Bowyer

⁵Turner, J. C. 1973. Water, energy and electrolyte balance in the desert bighorn sheep *Ovis canadensis*. Dissertation, University of California, Riverside, USA.

1994, Bowyer et al. 2001). Likewise, summer was when the greatest disparity in quality of diets of sheep occurred (Fig. 8). Differences in levels of foraging during autumn were similar to those of summer for sheep in the mined area (i.e., consistently lower than the nonmined area; Fig. 5); however, interpretation is less clear than for summer.

During autumn, as daytime temperatures (Oehler et al. 2003) and metabolic needs for water decreased, levels of foraging were most similar between areas, and may have been an outcome of sheep from the mined area moving away from Redlands Spring (Table 1) and, consequently, away from the mine. Moreover, an increased interval between blasts at the mine, and subsequently less ore being removed during autumn than summer, may have ameliorated disturbances to sheep. Quality of forage was lowest during autumn (Fig. 7); however, decreased water requirements (Turner⁵ 1973) associated with lower temperatures probably allowed sheep in the mined area to venture further from Redlands Spring in search of higher-quality forage. We hypothesize that the resultant increase in foraging by sheep in the mined area during autumn (Fig. 5), and the small difference in quality of diets between areas (Fig. 8), are the result of those animals moving away from the area of disturbance as physiological demands for water became less severe.

A combination of four factors offers the best explanation for our results: 1) proximity of Briggs Mine to the primary source of water used by females in the mined area; 2) a limited number of permanent sources of water in the mined area; 3) lack of rainfall during summer and autumn (Oehler et al. 2003); and 4) philopatric behavior of female mountain sheep (Geist 1968), which lessened the tendency to disperse from the disturbance caused by mining. In concert, those factors likely resulted in females remaining near the mine where disturbance was greatest, particularly during summer when metabolic needs for water also were highest. Leslie and Douglas (1980) reported that female mountain sheep in Nevada altered their watering patterns in response to construction activities near a primary source of water. In contrast, we did not observe such a result, presumably because of the high degree of fidelity of females to Redlands Spring and the scarcity of other nearby sources of free water.

Demographic consequences in response to disturbance are difficult to document because of high variability in observed population parameters (e.g., young to female ratios); therefore, less-direct measurements are of value for these types of investigations. For example, small changes in diet quality can result in important nutritional changes in females over time, and thereby affect subsequent reproductive efforts (White 1983). Also, nutrition, as affected by forage quality and efficiency of foraging (Berger 1979), can be linked to nutrition of females, and thereby survivorship of young ungulates (Keech et al. 2000). Such consequences can be especially important to desert mountain sheep, particularly in marginal environments, where recruitment is comparatively low (Rubin et al. 2000). If the outcomes we observed persist in the mined area, we hypothesize that reduced nutrient intake could have demographic consequences for that subpopulation.

Because observed differences were most pronounced during summer, a reduction of mining activities during that season may benefit sheep occupying areas near the mine. Most females have young at heel during spring, and shifting mining activity from

summer to spring might be detrimental. Increasing the interval between blasting, which would result in a decrease in overall mining activity during summer, may ameliorate the apparent effects of mining on sheep during that season. Intensity of mining, as indexed by days between blasting, amount of explosives used, and amount of ore hauled from the pit, was lowest during autumn. Although we have no direct data on levels of potential auditory disturbance from the sound caused by blasting, amount of explosives used undoubtedly provides an index to such stimuli. If a shift in mining activity is necessary to offset lost mine production in summer, we suggest that autumn is the best time for the concomitant increase in activities. Creation of additional sources of permanent water away from the mine also may help reduce reliance of females on Redlands Spring and, hence, reduce potential negative effects of mining on foraging behavior. We observed few effects of mining on demography or other characteristics of mountain sheep populations; however, we caution that because of the unique distribution of water in our study area, that our conclusions should not be generalized to other circumstances where the juxtaposition of critical resources might differ, thereby detrimentally affecting the demographics of mountain sheep.

ACKNOWLEDGMENTS

This study was supported by the Institute of Arctic Biology and Department of Biology and Wildlife at the University of Alaska Fairbanks, Department of Biological Sciences at Idaho State University, U.S. National Park Service, California Department of Fish and Game, North Dakota Game and Fish Department, Canyon Resources Corporation, the U.S. Bureau of Land Management, the and the San Fernando Valley Chapter of Safari Club International. We thank W. Allsup, R. Anthes, C. Baker, R. Barry, J. Bauer, J. DeForge, S. DeJesus, T. Evans, E. Forner, B. Gonzales, S. Hager, M. Miller, B. Nuckolls, D. Oehler, L. Oehler, M. Oehler, Jr., A. Pauli, K. Pindel, D. Racine, E. Rextad, J. Schlachter, K. Schwaegerle, J. Sedinger, C. Sexton, T. Swank, R. Teagle, D. Threloff, S. Torres, and K. Whitten for their assistance. We also thank Canyon Resources Corporation for facilitating our research at the mine. This is a contribution from the California Department of Fish and Game Mountain Sheep Conservation Program, and is Professional Paper 016 from the Eastern Sierra Center for Applied Population Ecology.

LITERATURE CITED

- Ad Hoc Committee on Acceptable Field Methods. 1987. Acceptable field methods in mammalogy. *Journal of Mammalogy* 68(suppl.):1-18.
- Agresti, A. 1990. *Categorical data analysis*. John Wiley & Sons, New York, New York, USA.
- Alderman, J. A., P. R. Krausman, and B. D. Leopold. 1989. Diel activity of female desert bighorn sheep in western Arizona. *Journal of Wildlife Management* 53:264-271.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- Andrew, N. G., V. C. Bleich, and P. V. August. 1999. Habitat selection by mountain sheep in the Sonoran Desert: implications for conservation in the United States and Mexico. *California Wildlife Conservation Bulletin* 12:1-30.

- Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. *Journal of Wildlife Management* 65:77-92.
- Beatley, J. C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856-863.
- Berger, J. 1978. Group size, foraging and anti-predator ploys: an analysis of bighorn sheep decisions. *Behavioral Ecology and Sociobiology* 4:91-100.
- Berger, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Animal Behaviour* 41:61-77.
- Bleich, V. C., R. T. Bowyer, D. J. Clark, and T. O. Clark. 1992. Analysis of forage used by mountain sheep in the eastern Mojave Desert, California. *Desert Bighorn Council Transactions* 36:41-47.
- Bleich, V. C., R. T. Bowyer, A. M. Pauli, M. C. Nicholson, and R. W. Anthes. 1994. Mountain sheep *Ovis canadensis* and helicopter surveys: ramifications for the conservation of large mammals. *Biological Conservation* 45:1-7.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134:1-50.
- Bowyer, R. T. 1981. Activity, movement, and distribution of Roosevelt elk during rut. *Journal of Mammalogy* 62:574-582.
- Bowyer, R. T. 1991. Timing of parturition and lactation in southern mule deer. *Journal of Mammalogy* 72:138-145.
- Bowyer, R. T., and V. C. Bleich. 1984. Effects of cattle grazing on selected habitats of southern mule deer. *California Fish and Game* 70:240-247.
- Bowyer, R. T., D. R. McCullough, and G. E. Belovsky. 2001. Causes and consequences of sociality in mule deer. *Alces* 37:371-402.
- Bowyer, R. T., V. Van Ballenberghe, J. G. Kie, and J. A. K. Maier. 1999. Birth-site selection in Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy* 80:1070-1083.
- Bradshaw, C. J. A., S. Boutin, and D. M. Hebert. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. *Journal of Wildlife Management* 61:1127-1133.
- Conover, W. J., and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* 35:124-130.
- DeForge, J. R., J. E. Scott, G. W. Sudmeier, R. L. Graham, and S. V. Segreto. 1981. The loss of two populations of desert bighorn sheep in California. *Desert Bighorn Council Transactions* 25:36-38.
- Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts of forage quality, forage quantity, and predator avoidance. *Oecologia* 75:580-586.
- Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53:799-808.
- Geist, V. 1968. On the interrelation of external appearance, social behavior and social structure of mountain sheep. *Zeitschrift für Tierpsychologie* 25:199-215.
- Hansen, M. C., G. W. Garner, and S. G. Fancy. 1992. Comparison of 3 methods for evaluating activity of Dall's sheep. *Journal of Wildlife Management* 56:661-668.
- Hicks, L. L., and J. M. Elder. 1979. Human disturbance of Sierra Nevada bighorn sheep. *Journal of Wildlife Management* 43:909-915.
- Jaeger, J. R., J. D. Wehausen, V. C. Bleich, and C. L. Douglas. 1993. Limits in the resolution of LORAN-C for aerial telemetry studies. *Desert Bighorn Council Transactions* 37:20-23.
- Jenks, J. A., R. B. Soper, R. L. Lochmiller, and D. M. Leslie, Jr. 1990. Effects of exposure on nitrogen and fiber characteristics of white-tailed deer feces. *Journal of Wildlife Management* 54:389-391.

- Johnson, R. A., and D. W. Wichern. 1988. Applied multivariate statistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management* 64:450-462.
- Kie, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* 80:1114-1129.
- Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. CALHOME: a program for estimating animal home ranges. *Wildlife Society Bulletin* 24:342-344.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* 83:530-544.
- Kleinbaum, D. G., L. L. Kupper, and K. E. Muller. 1988. Applied regression analysis and other multivariate methods. Second edition. Duxbury Press, Belmont, California, USA.
- Krausman, P. R., J. J. Herver, and L. L. Ordway. 1985a. Capturing deer and mountain sheep with a net-gun. *Wildlife Society Bulletin* 13:71-73.
- Krausman, P. R., S. Torres, L. L. Ordway, J. J. Herver, and M. Brown. 1985b. Diel activity of ewes in the Little Harquahala Mountains, Arizona. *Desert Bighorn Council Transactions* 29:24-26.
- Krausman, P. R., B. D. Leopold, R. F. Seegmiller, and S. G. Torres. 1989. Relationships between desert bighorn sheep and habitat in western Arizona. *Wildlife Monographs* 102:1-66.
- Krausman, P. R., and R. C. Etchberger. 1995. Response of desert ungulates to a water project in Arizona. *Journal of Wildlife Management* 59:292-300.
- Kuck, L., G. L. Hompland, and E. H. Merrill. 1985. Elk calf response to simulated mine disturbance in southeast Idaho. *Journal of Wildlife Management* 49:751-757.
- Leptich, D. J., D. G. Beck, and D. E. Beaver. 1994. Aircraft-based LORAN-C and GPS accuracy for wildlife research on inland study sites. *Wildlife Society Bulletin* 22:561-565.
- Leslie, D. M., Jr., and C. L. Douglas. 1979. Desert bighorn sheep of the River Mountains, Nevada. *Wildlife Monographs* 66:1-56.
- Leslie, D. M., Jr., and C. L. Douglas. 1980. Human disturbance at water sources of desert bighorn sheep. *Wildlife Society Bulletin* 8:284-290.
- MacArthur, R. A., V. Geist, and R. H. Johnston. 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. *Journal of Wildlife Management* 46:351-358.
- Molvar, E. M., and R. T. Bowyer. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy* 75:621-630.
- Morgantini, L. E., and B. W. Worbets. 1988. Bighorn sheep use of a gas well site during servicing and testing: a case study of impact and mitigation. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 6:159-164.
- Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. *Journal of Mammalogy* 78:483-504.
- Oehler, M. W. Sr., V. C. Bleich, and R. T. Bowyer. 1996. Error associated with LORAN-C: effects of aircraft altitude and geographic location. *Desert Bighorn Council Transactions* 40:19-21.
- Oehler, M. W. Sr., R. T. Bowyer, and V. C. Bleich. 2003. Home ranges of mountain sheep: effects of precipitation in a desert ecosystem. *Mammalia* 69:337-354.
- Patric, E. F., T. P. Husband, C. G. McKiel, and W. M. Sullivan. 1988. Potential of LORAN-C for wildlife research along coastal landscapes. *Journal of Wildlife Management* 32:553-557.

- Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. *Journal of Wildlife Management* 65:573-582.
- Rachlow, J. L., and R. T. Bowyer. 1994. Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? *Journal of Mammalogy* 75:328-337.
- Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *Journal of Zoology (London)* 245:457-465.
- Risenhoover, K. L., and J. A. Bailey. 1985. Foraging ecology of mountain sheep: implications for habitat management. *Journal of Wildlife Management* 49:797-804.
- Rubin, E. S., W. M. Boyce, and V. C. Bleich. 2000. Reproductive strategies of desert bighorn sheep. *Journal of Mammalogy* 81:769-786.
- SAS Institute, Inc. 1997. SAS/STAT software changes and enhancements through release 6.12 ed. SAS Institute, Cary, North Carolina, USA.
- Solow, A. R. 1989. A randomization test for independence of animal locations. *Ecology* 70:1546-1549.
- Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscope technique. *Journal of Range Management* 21:264-265.
- Statistical Package for the Social Sciences. 1993. SPSS for windows: base system user's guide. Release 6.0. SPSS, Chicago, Illinois, USA.
- Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy* 83:229-244.
- Stockwell, C. A., G. C. Bateman, and J. Berger. 1991. Conflicts in national parks: a case study of helicopters and bighorn sheep time budgets at the Grand Canyon. *Biological Conservation* 56:317-328.
- Tilley, J. M., and R. A. Terry. 1963. A two-stage technique for the *in vitro* digestion of forage crops. *Journal of the British Grassland Society* 18:104-111.
- Van Dyke, F., and W. C. Klein. 1996. Response of elk to installation of oil wells. *Journal of Mammalogy* 77:1028-1041.
- Wehausen, J. D., and M. C. Hansen. 1988. Plant communities as the nutrient base of mountain sheep populations. Pages 256-268 in *Plant biology of eastern California* (C. A. Hall, Jr., and V. Doyle-Jones, editors). University of California, White Mountain Research Station, Bishop, California, USA.
- Welles, R. E., and F. B. Welles. 1961. *The bighorn of Death Valley*. National Park Service, Washington, D.C., USA.
- White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40:377-384.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.
- Zar, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Received: 9 May 2004

Accepted: 15 September 2004

EXHIBIT 419

Genetics and the Conservation of Mountain Sheep *Ovis canadensis nelsoni*

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ABSTRACT

Recent hypotheses have proposed that mountain sheep were suffering from inbreeding depression. Here we present an alternative hypothesis. We have examined sheep migration abilities, the distances required for migration, and sheep mating patterns to challenge the inbreeding hypothesis and conclude that the sound application of more traditional wildlife management techniques will likely preclude short- and long-term genetic problems.

INTRODUCTION

Recent symposia, texts, and journal articles have begun to focus the techniques of population genetics on the problems of conservation (e.g. Soulé & Wilcox, 1980; Schonewald-Cox *et al.*, 1983; Lehmkuhl, 1984).

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Biol. Conserv. 0006-3207/86/\$03-50 © Elsevier Applied Science Publishers Ltd, England, 1986. Printed in Great Britain

ranges (Hansen, 1980); (3) a polygynous mating system (Wishart, 1978); and (4) the assumption that because of cultural features (construction by humans) developed in the last century, sheep do not leave the mountains and disperse across the relatively flat ground that occurs between desert ranges (Bailey, 1980). Through these mechanisms a small N_e would be maintained.

In this paper, using existing data, we challenge the hypothesis of inbreeding depression in *Ovis canadensis nelsoni*. Our hypothesis is based on the following: relatively large population sizes of mountain sheep in desert ranges; documented mountain sheep vagility; male breeding strategies that were largely unrecognised; the ability of mountain sheep to cross cultural obstacles; and the low levels of migration (number of sheep migrating into a range and breeding) necessary in a species to preclude inbreeding depression.

METHODS

We chose to evaluate the hypothesis of inbreeding depression in those desert-dwelling mountain sheep occupying an approximately 50 000 km² triangle in California and Nevada bordered on the north by Interstate Highway 15, on the south by Interstate Highway 40, on the west where these highways merge in Barstow, California, and on the east by the Colorado River. This triangle is bounded by cultural and natural features which may partially restrict the movement of sheep to within that triangle, but it is also an area in which there are no cultural features that should provide serious limitations to migration; as such, it is typical of much of the area occupied by mountain sheep in California. Estimated populations of sheep in each range in California are the latest (1984), based on aerial and ground observations by the California Department of Fish and Game. The estimates from the Nevada ranges are those of McQuivey (1978).

RESULTS AND DISCUSSION

Figure 1 shows the estimated number of adult sheep in the triangle and in several ranges adjacent to the study area. Also shown are the estimated effective population sizes based on the frequent observation of a ram:ewe

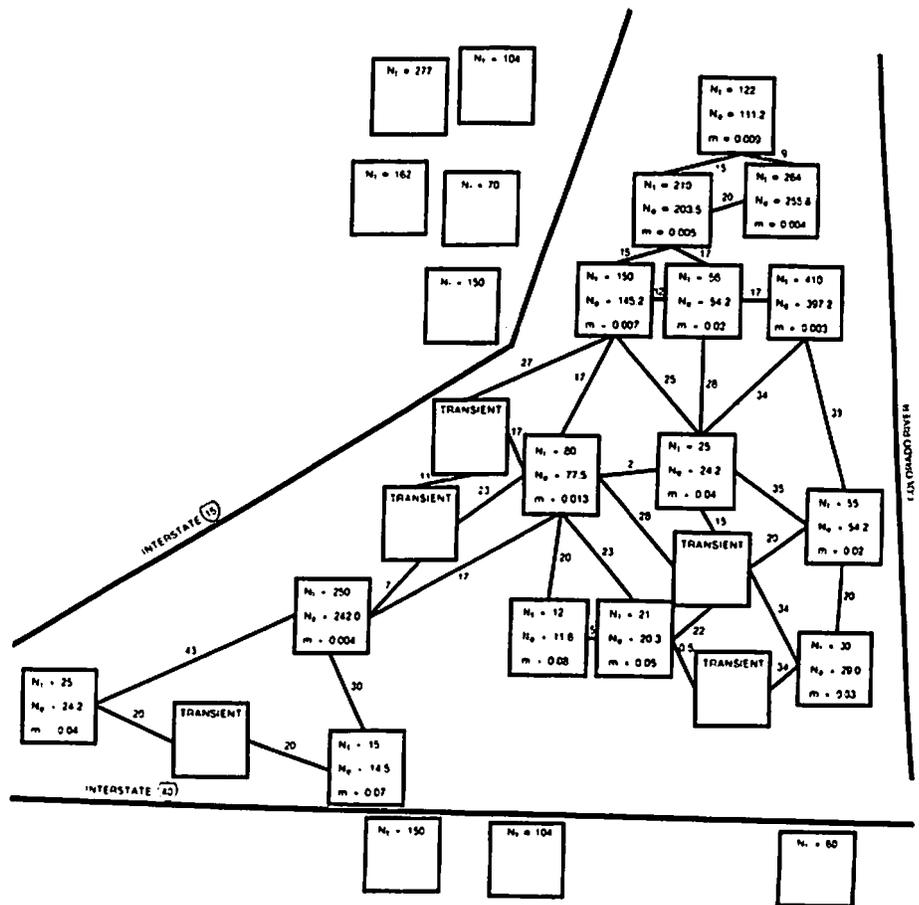


Fig. 1. In our triangular study area in the Mohave Desert of California and Nevada we report the estimated total population of desert-dwelling mountain sheep (N_t), effective population size (N_e), and the required migration rate (m) to maintain an equilibrium coefficient of inbreeding of 0.2. Distances between ranges are in kilometres, and the map is only roughly to scale.

ratio of 70:100 (Aldous, 1957; Leslie & Douglas, 1979; Wehausen *et al.*, in press), and the distance in kilometres between proximal ranges. The rate of migration into a range with a given effective population size was estimated with the formula: $F = 1/(4N_e m + 1)$ (Crow & Kimura, 1970 p. 269; Hartl, 1980 p. 195) where F is the equilibrium coefficient of inbreeding in a substructured population, here set to 0.2 (see below); N_e is as described above; and m the migration rate per generation, obtained

by solving the equation with the N_e given for each range. An F of 0.2 is achieved when $N_e m = 1$, a widely regarded rule of thumb that, when applicable, effectively makes subpopulations nearly panmictic (Camin & Ehrlich, 1958; Futuyma, 1979, p. 281). F can be further described as the probability for homozygosity under the conditions of drift and migration in subdivided populations (Spiess, 1977, p. 653). Figure 2 shows the relationship between F and $N_e m$.

Migration capabilities of mountain sheep may be underestimated; available intermountain range movement data are presented in Table 1. These documented movements suggest no complete philopatry to a sheep's natal area and less hesitancy to negotiate cultural features than previously thought. Also, there is the potential for much previously undetected intermountain movement.

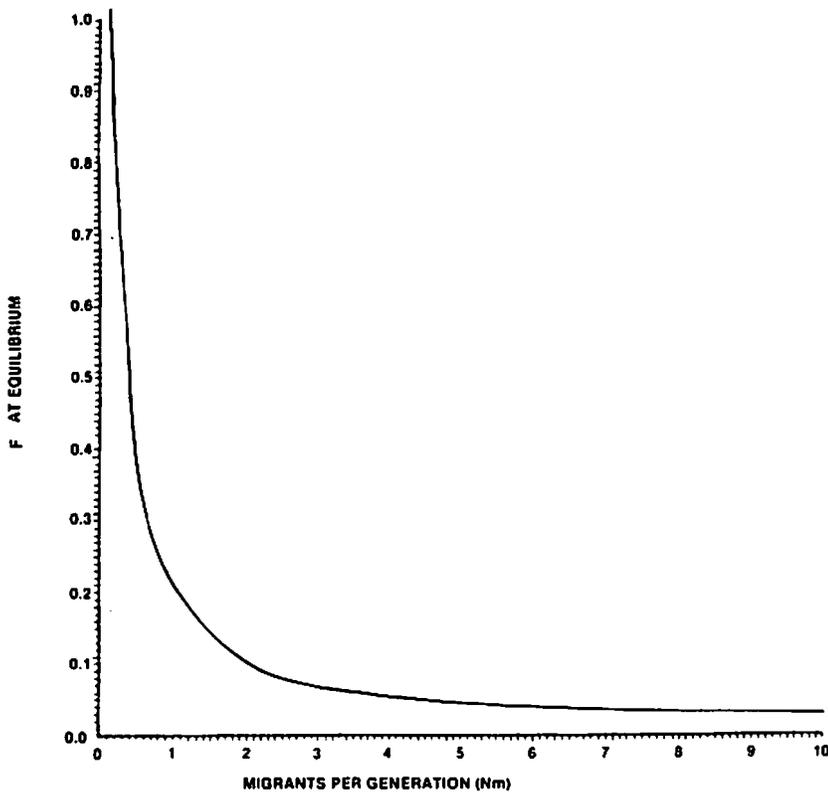


Fig. 2. The relationship between equilibrium inbreeding rate (F) and the number of migrants ($N_e m$) per generation is shown (after Hartl, 1980).

TABLE 1
A Summary of Intermountain Movements by Mountain Sheep

<i>Movement</i>	<i>Source</i>
17 interrange movements by radio-tagged rams (\bar{X} = 19.8 km, SE = 2.11, n = 17).	Ough & deVos (1984)
4 interrange movements by radio-tagged ewes (\bar{X} = 17.4 km, SE = 4.95, n = 4).	
Rams and ewes in ranges with no resident populations. Data are distances to nearest resident population. (\bar{X} = 19.7 km, SE = 1.9, n = 25).	McQuivey (1978)
17.5 km movement across open desert and other movements of 30.6, 32.2, 40.2 and 51.5 km.	Cochran & Smith (1983)
Rapid movement of rams and ewes following a transplant. Crossed fences, highways, and flat terrain.	Elenowitz (1982)
Ewes and lambs crossed Interstate 10 (4 lane with fences) in SW Arizona	Witham & Smith (1979)
Sheep crossing US Highway 95 used by thousands of vehicles annually.	King & Workman (1983)
Observed young ram leave Old Dad Peak and disappear across flatland. Routinely cross railroad tracks in the Cady Mountains.	V. C. Bleich (unpublished)
Sheep drowned while crossing Colorado River.	C. Douglas (pers. comm.)
Other interrange movements.	Simmons (1980) Russo (1956)

Relative to the movements referenced above, the distances involved, and our hypothesised rates of migration ranging from 0.003 to 0.08 (Fig. 1), it is highly plausible that movements do occur at such rates. Some of the desert ranges have such large herds that they may be approaching overpopulation (V. C. Bleich, unpublished data); however, the role of such dense populations in motivating additional dispersal is unknown. We suggest that the triangular study area should be more appropriately thought of as a single metapopulation (Levins, 1970) rather than a completely or even mostly subdivided population. If so,

there are over 1600 sheep estimated to be in the study area and several large adjacent populations (Fig. 1). A population of this magnitude would satisfy the previously stated requirement of at least 500 animals necessary for long-term, evolutionary fitness of a population. Additional considerations concerning the genetic health of these sheep include the fact that populations on most ranges have remained static or have increased since a 1969 survey, and several populations have dramatically increased, one from 25 to 250 animals and another from 20 to 150 animals (Bleich, 1983). Rapidly increasing populations have more copies of genes; hence variation is less subject to stochastic loss (Templeton & Read, 1983).

Although several parameters in our model may be imprecise or not universally agreed upon, the application of the model is still robust and our basic conclusions are not modified. For example, a lower inbreeding coefficient, $F = 0.1$, changes the range of migration rates to 0.005 for the largest populations and to 0.19 for the smallest. These rates still seem plausible given the vagility of mountain sheep.

There are other general biological and genetic mechanisms that are frequently overlooked by those predicting inbreeding depression in mountain sheep. Yellow-bellied marmots (Schwartz & Armitage, 1980), black-tailed prairie dogs (Hoogland, 1982), and olive baboons (Packer, 1979) have been reported to systematically avoid extreme inbreeding. Mechanisms for avoiding inbreeding included the following: young males left or were forced from the social group; dominant males were dead or deposed before their daughters were sexually mature; daughters suppressed oestrus in the presence of their fathers; and there was behavioural avoidance of close relatives during mating. The extent to which these or similar mechanisms may operate in mountain sheep is unknown.

There has been a misconception that the dominant ram does all the mating within a mountain sheep group (e.g. DeForge *et al.*, 1979). Hogg (1984) reported other breeding strategies in *O. canadensis* which he termed tending, coursing, and blocking. These strategies, which were not uncommon, allowed less dominant sheep to mate successfully. Geist (1971) noted that young rams also bred, and Turner (1976) provided evidence that young rams, and even male lambs, provided genetic contributions before reaching 'behavioural puberty'. Both of the above breeding behaviours would serve to increase effective population size.

During droughts or other unfavourable stochastic environmental

conditions (Samson *et al.*, 1985), N_e in desert subpopulations could be reduced (or populations eliminated), and the magnitude of the effects of this genetic bottleneck would be a function of its duration. This has several ramifications. It would be during such times that inbreeding would be most likely to occur. However, it also means that, like domestic animals, mountain sheep have been exposed to episodes of inbreeding and those that survived are likely to be those that carry relatively few deleterious genes. Following a bottleneck, the genetic variance of the metapopulation would be increased assuming resumption of migration. Other unknown factors that might change our estimates of N_e include the possibility of different average generation lengths for males and females and the variance in survival of offspring.

Some claims that inbreeding depression is impacting wild mountain sheep ignore some of the basic mechanisms of natural selection. An allele with a strong or dominant deleterious effect, such as that proposed by DeForge *et al.* (1979), would quickly be removed from the population by natural selection. Selection would likely act in a heterotic manner, promoting retention of remaining variation in the herd (Beardmore, 1983).

In conclusion, we think that conservation concerns regarding desert-dwelling mountain sheep as they relate to their genetic structure may be overemphasised relative to other more immediate habitat-related problems. Concerns about inbreeding depression are most appropriate in closely inbred captive herds (Sausman, 1982, 1984). The only published evidence of inbreeding depression in a natural population is that reported for great tits by Greenwood *et al.* (1978), and the effect in that population was slight. Also, the effect of genetic uniformity caused by inbreeding and population bottlenecks is unknown. The northern elephant seal experienced a bottleneck and has low genetic variability, but populations have increased to several thousand since effective management was begun (Bonnell & Selander, 1974), although this does not guarantee long-term genetic health. In contrast, the cheetah has critically low genetic variability and is experiencing its debilitating effects (O'Brien *et al.*, 1985).

Induced migration as a management strategy (Frankel, 1983) for the genetic improvement of mountain sheep herds does not seem to be presently warranted, especially given the cost of \$2000 to \$3000 per sheep relocated (V. C. Bleich, unpublished data) and the unknown success of introducing a new animal into an established social system (Elenowitz, 1982). Traditional wildlife management techniques, such as

proper utilisation, habitat protection and improvement, maintenance of dispersal corridors, re-introductions to ranges where sheep have become extinct, control of interspecific competition from domestic and feral animals, and control of diseases transmitted from livestock, would be most cost-effective (Bailey, 1980; Hansen, 1982). If such management techniques are implemented properly and in a timely manner, short- and long-term genetic health problems of these mountain sheep can be reduced or eliminated.

The genetic variation and population numbers of such a substructured population are going to be a dynamic topography with some inbreeding, extinction, recolonisation, and strong population growth in areas possessing good habitat for the species. Schonewald-Cox (1983) categorised the protection to species provided by different kinds of reserves. The mountain sheep discussed in this paper occupy a level 7 or 8 reserve, a type which has the promise of species preservation and evolution for long time periods because of the maintenance of genetic variation. In general, desert-dwelling mountain sheep populations are sufficiently abundant and juxtaposed, and areas of habitat are still sufficiently large to allow the continued existence of this species throughout much of its historic range. While we realise that there may be instances where isolated, small populations may inbreed, we believe that the future outlook is encouraging.

ACKNOWLEDGEMENTS

We wish to thank Russell B. Campbell, Thomas E. Kucera, Christine Schonewald-Cox, Robert D. Seager, Michael E. Soulé and John D. Wehausen for thoughtful discussions and comments and for reading earlier drafts of this paper. A portion of this research was funded by the Foundation for North American Wild Sheep and the Society for the Conservation of Bighorn Sheep. This is a contribution from California Federal Aid in Wildlife Restoration Project W-26-D, Wildlife Habitat Development.

REFERENCES

- Aldous, M. C. (1957). Status of bighorn sheep on the Desert Game Range. *Desert Bighorn Council Trans.*, 35-7.

- Bailey, J. A. (1980). Desert bighorn, forage competition and zoogeography. *Wildl. Soc. Bull.*, 8, 208-16.
- Beardmore, J. A. (1983). Extinction, survival and genetic variation. In *Genetics and conservation. A reference for managing wild animal and plant populations*, ed. by C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and W. L. Thomas, 125-51. Menlo Park, CA, Benjamin/Cummings.
- Berwick, S. H. (1968). *Observations on the decline of the Rock Creek, Montana, population of bighorn sheep*. MS thesis, University of Montana, Missoula.
- Bleich, V. C. (1983). Big game guzzlers and mountain sheep. *Outdoor California*, 44, 10.
- Bonnell, M. L. & Selander, R. K. (1974). Elephant seals: Genetic variation and near extinction. *Science, Washington DC*, 184, 908-9.
- Buechner, H. E. (1960). The bighorn sheep in the United States, its past, present, and future. *Wildl. Monogr.*, 4, 1-174.
- Camin, J. H. & Ehrlich, P. R. (1958). Natural selection in water snakes (*Natrix sipedon*) on islands in Lake Erie. *Evolution*, 12, 504-11.
- Cochran, M. H. & Smith, E. L. (1983). Intermountain movements by a desert bighorn ram in western Arizona. *Desert Bighorn Council Trans.*, 1-2.
- Crow, J. F. & Kimura, M. (1970). *An introduction to population genetics theory*. New York, Harper and Row.
- DeForge, J. R., Jenner, C. W., Plechner, A. J. & Sudmeier, G. W. (1979). Decline of bighorn sheep (*Ovis canadensis*), the genetic implications. *Desert Bighorn Council Trans.*, 63-5.
- DeForge, J. R., Scott, J., Sudmeier, G. W., Graham, R. L. & Segreto, S. V. (1981). The loss of two populations of desert bighorn sheep in California. *Desert Bighorn Council Trans.*, 36-8.
- Elenowitz, A. (1982). Preliminary results of a desert bighorn transplant in the Peloncillo Mountains, New Mexico. *Desert Bighorn Council Trans.*, 8-11.
- Frankel, O. H. (1983). The place of management in conservation. In *Genetics and conservation. A reference for managing wild animal and plant populations*, ed. by C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and W. L. Thomas, 1-14. Menlo Park, CA, Benjamin/Cummings.
- Franklin, I. R. (1980). Evolutionary changes in small populations. In *Conservation biology. An evolutionary-ecological perspective*, ed. by M. E. Soulé and B. A. Wilcox, 135-50. Sunderland, MA, Sinauer Associates.
- Futuyma, D. J. (1979). *Evolutionary biology*. Sunderland, MA, Sinauer Associates.
- Geist, V. (1971). *Mountain sheep*. Chicago, IL, University of Chicago Press.
- Greenwood, P. J., Harvey, P. H. & Perrins, C. M. (1978). Inbreeding and dispersal in the great tit. *Nature, Lond.*, 271, 52-4.
- Hansen, C. G. (1980). Habitat. In *The desert bighorn*, ed. by G. Monson and L. Sumner, 64-79. Tucson, AZ, University of Arizona Press.
- Hansen, M. C. (1982). Desert bighorn sheep: another view. *Wildl. Soc. Bull.*, 10, 133-40.
- Hartl, D. L. (1980). *Principles of population genetics*. Sunderland, MA, Sinauer Associates.

- Hogg, J. T. (1984). Mating in bighorn sheep: Multiple male strategies. *Science, Washington DC*, 225, 526-9.
- Hoogland, J. L. (1982). Prairie dogs avoid extreme inbreeding. *Science, Washington DC*, 215, 1639-41.
- King, M. M. & Workman, G. W. (1983). Preliminary report on desert bighorn movements on public lands in southeastern Utah. *Desert Bighorn Council Trans.*, 4-6.
- Lehmkuhl, J. F. (1984). Determining size and dispersion of minimum viable populations for land management planning and species conservation. *Environ. Mgmt*, 8, 167-76.
- Leslie, D. M. & Douglas, C. L. (1979). Desert bighorn sheep of the River Mountains, Nevada. *Wildl. Monogr.*, 66.
- Levins, R. (1970). Extinctions. In *Some mathematical questions in biology*, ed. by M. Gerstenhaber, 77-107. *Lectures on mathematics in the life sciences*, 2. Providence RI, American Mathematics Society.
- McQuivey, R. P. (1978). The desert bighorn sheep of Nevada. *Nevada Dep. Wildl., Biol. Bull.*, 6, 1-81.
- Ough, W. D. & deVos, J. C. Jr (1984). Intermountain travel corridors and their management implications for bighorn sheep. *Desert Bighorn Council Trans.*, 32-6.
- O'Brien, S. J., Roelke, M. E., Marker, L., Newman, A., Winkler, C. A., Meltzer, D., Colly, L., Evermann, J. F., Bush, M. & Wildt, D. E. (1985). Genetic basis for species vulnerability in the cheetah. *Science, Washington DC*, 227, 1428-34.
- Packer, C. (1979). Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.*, 27, 1-36.
- Russo, J. P. (1956). The desert bighorn sheep in Arizona. *Arizona Game and Fish Dep. Wildl. Bull.*, 1, 1-153.
- Samson, F. B., Perez-Trejo, Salswasser, H., Ruggiero, L. F. & Russ, T. L. (1985). On determining and managing minimum population size. *Wildl. Soc. Bull.*, 13, 425-33.
- Sausman, K. A. (1982). *Desert Bighorn Council Trans.*, 26-31.
- Sausman, K. A. (1984). Survival of captive-born *Ovis canadensis* in North American zoos. *Zoo Biol.*, 3, 111-21.
- Schonewald-Cox, C. M. (1983). Conclusions: Guidelines to management: A beginning attempt. In *Genetics and conservation. A reference for managing wild animal and plant populations*, ed. by C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and W. L. Thomas, 414-46. Menlo Park, CA, Benjamin/Cummings.
- Schonewald-Cox, C. M., Chambers, S. M., MacBryde, B. & Thomas, W. L. (1983). *Genetics and conservation. A reference for managing wild animal and plant populations*. Menlo Park, CA, Benjamin/Cummings.
- Schwartz, O. A. & Armitage, K. B. (1980). Genetic variation in social mammals: The marmot model. *Science, Washington DC*, 207, 665-7.
- Seton, E. T. (1929). *Lives of game animals*, 3, New York, Doubleday Page.

- Simmons, N. M. (1980). Behavior. In *The desert bighorn*, ed. by G. Monson and L. Sumner, 122-44. Tucson, University of Arizona Press.
- Soulé, M. E. (1980). Thresholds for survival: maintaining fitness and evolutionary potential. In *Conservation biology. An evolutionary-ecological perspective*, ed. by M. E. Soulé and B. A. Wilcox, 151-70. Sunderland, MA, Sinauer Associates.
- Soulé, M. E. & Wilcox, B. A. (1980). *Conservation biology. An evolutionary-ecological perspective*. Sunderland, MA, Sinauer Associates.
- Spiess, E. B. (1977). *Genes in populations*. New York, John Wiley.
- Templeton, A. R. & Read, B. (1983). The elimination of inbreeding depression in a captive herd of Speke's gazelle. In *Genetics and conservation. A reference for managing wild animal and plant populations*, ed. by C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and W. L. Thomas, 241-62. Menlo Park, CA, Benjamin/Cummings.
- Turner, J. C. (1976). Initial investigation into the reproductive biology of the desert bighorn ram, *Ovis canadensis nelsoni*, *O. c. cremnobates*. *North American Wild Sheep Conf., Trans.*, 2, 22-5.
- Wehausen, J. D., Bleich, V. C., Blong, B. & Russ, T. L. (in press). Recruitment dynamics in a southern California mountain sheep population. *J. Wildl. Mgmt.*
- Welles, R. E. (1962). What makes a valid observation? *Desert Bighorn Council Trans.*, 29-40.
- Wilcox, B. A. (1980). Insular ecology and conservation. In *Conservation biology. An evolutionary-ecological perspective*, ed. by M. E. Soulé and B. A. Wilcox, 95-118. Sunderland, MA, Sinauer Associates.
- Wilson, L. O. (1974). The need for genetic research in desert bighorn sheep. *Desert Bighorn Council Trans.*, 50-2.
- Wishart, W. (1978). Bighorn sheep. In *Big game of North America*, ed. by J. L. Schmidt and D. L. Gilbert, 161-71. Harrisburg, PA, Stackpole Books.
- Witham, J. H. & Smith, E. L. (1979). Desert bighorn movements in a southwestern Arizona mountain complex. *Desert Bighorn Council Trans.*, 20-5.

EXHIBIT 420

Desert-dwelling Mountain Sheep: Conservation Implications of a Naturally Fragmented Distribution

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Abstract: *Mountain sheep (Ovis canadensis) are closely associated with steep, mountainous, open terrain. Their habitat consequently occurs in a naturally fragmented pattern, often with substantial expanses of unsuitable habitat between suitable patches; the sheep have been noted to be slow colonizers of vacant suitable habitat. As a result, resource managers have focused on (1) conserving "traditional" mountainous habitats, and (2) forced colonization through reintroduction. Telemetry studies in desert habitats have recorded more intermountain movement by desert sheep than was previously thought to occur. Given the heretofore unrecognized vagility of mountain sheep, we argue that existing corridors of "nontraditional" habitat connecting mountain*

Resumen: *Los borregos cimarrones (Ovis canadensis) exhiben una asociación cercana con terrenos montañosos escarpados y abiertos. En consecuencia, su hábitat ocurre en un patrón naturalmente fragmentado, frecuentemente con grandes extensiones de hábitat impropio separando las áreas apropiadas; y se ha notado que los borregos cimarrones son lentos en colonizar hábitat apropiado vacante. Como resultado de estas observaciones, gerentes de recursos naturales han enfocado su atención en (1) conservación de hábitat montañoso "tradicional" y (2) colonización forzada por reintroducción. Estudios telemétricos en hábitates desiertos han demostrado más movimiento entre sierras que antes se creía que ocurría. Dado la tendencia de vagar hasta ahora no reconocido de los borregos cimarrones, proponemos que corredores actuales de hábitat no tradicional que conectan sierras merecen consideración adecuada para conservación. Además, se debe reconocer la importancia para poblaciones relativamente aisladas de los borregos cimarrones de áreas pequeñas de hábitat montañoso que, aunque*

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Paper submitted January 25, 1989; revised manuscript accepted November 7, 1989.

ranges be given adequate conservation consideration. Additionally, small areas of mountainous habitat that are not permanently occupied but that may serve as "stepping stones" within such corridors must be recognized for their potential importance to relatively isolated populations of mountain sheep. We discuss the potential importance of such corridors to other large, vagile species.

Introduction

Wilcox and Murphy (1985:884) echoed an increasingly common concern when they stated, "That current ecological theory is inadequate for resolving many of the details should not detract from what is obvious and accepted by most ecologists: habitat fragmentation . . . is the primary cause of the present extinction crisis." Indeed, fragmentation has been a central theme of much recent literature dealing with conservation biology (e.g., Soulé & Wilcox 1980; Schonewald-Cox et al. 1983; Harris 1984; Lehmkuhl 1984; Schwartz et al. 1986; Soulé 1986; and Chepko-Sade & Halpin 1987). Both community-level (e.g., Wilcove et al. 1986) and population-level (e.g., Ralls et al. 1986; Allendorf & Leary 1986) theory have been applied to current conservation problems. The former has been concerned with species diversity and the latter with the long-term integrity of gene pools. Two primary approaches are used to maintain adequate gene pools in fragmented situations (1) periodic induced migration (Frankel 1983); and (2) maintaining or creating corridors to connect fragments (Schonewald-Cox 1983; Simberloff & Cox 1987; Noss 1987). This paper addresses the long-term maintenance of genetically viable populations of desert-dwelling mountain sheep (*Ovis canadensis* ssp.) via the latter approach. In addition, we discuss the related topic of protecting islands of habitat that do not support permanent populations but may be used occasionally, serving as important "stepping stones" in migration corridors.

Philopatry in Desert-dwelling Mountain Sheep

Mountain sheep, in general, are closely associated with steep, mountainous, open terrain (Geist 1971), which results in naturally disjunct demes. This habitat preference reflects two basic adaptations of mountain sheep relative to predation (1) great agility on rocks; and (2) keen vision to detect predators at sufficient distances to make escape probable.

Following the early decimation of mountain sheep in North America, it became evident that this species was inherently slow to recolonize vacant habitat. Consequently, reintroductions became an important management technique, dating back as far as the 1930s. Geist (1967, 1971) was the first to propose a general theory

no ocupadas de manera permanente, pueden facilitar el movimiento de los borregos cimarrones dentro de dichos corredores. Se señala la importancia de estos corredores para otras especies errantes grandes.

on the conservative colonization behavior of mountain sheep. The result has been an emphasis on conservation of mountainous habitats for wild sheep, with little concern for intermountain areas. For example, the 21 specific plans to conserve habitat for desert-dwelling mountain sheep called for in the California Desert Conservation Area Plan (Bureau of Land Management 1980:35–36) are restricted to specific mountainous areas totaling only 4,800 km². It is not our purpose to criticize these attempts to protect and enhance habitat; instead, we cite that document as an example of "traditional" thinking with respect to the protection of "traditional" habitat.

In addition to the behavioral conservatism of mountain sheep that Geist (1971) emphasized relative to dispersal, he documented some interpopulation movements, mostly by rams, in which they crossed "nontraditional" sheep habitat. Desert ecosystems differ markedly from the northern systems studied by Geist (1971), in that the relatively flat terrain separating "traditional" habitat islands lacks dense vegetation. Such terrain should represent less of a barrier to dispersal than the forests of more northern ecosystems. Additionally, many desert mountain ranges lack large carnivores such as mountain lions (*Felis concolor*) and wolves (*Canis lupus*), which may be more common in intermountain habitats of the north. Consequently, one might expect less conservative dispersal behavior of mountain sheep in desert ecosystems compared with northern systems.

Early researchers (e.g., Russo 1956) were aware of intermountain movements by desert-dwelling mountain sheep. Recent technology has resulted in a vastly expanded knowledge of patterns of habitat utilization by these animals. In Arizona, occasional intermountain movements by ewes were documented, in addition to extensive intermountain movements by rams (Witham & Smith 1979; Cochran & Smith 1983; Ough & deVos 1984; Krausman & Leopold 1986). In Nevada, McQuivey (1978) noted the presence of rams and ewes in ranges not known to have resident populations. Similarly, Elenowitz (1982) and King & Workman (1983) documented movements of mountain sheep across highways, fences, and intermountain flats in New Mexico and Utah, respectively. Extensive ongoing telemetry studies in the Mojave Desert of California also confirm

intermountain movement by both rams and ewes (Bersbach 1987; V. C. Bleich, A. M. Pauli, R. L. Vernoy, J. D. Wehausen, unpublished data).

Wilson et al. (1980) noted that, "all areas utilized by desert bighorn are essential to their continued survival". This has become an increasingly common concept in recent years, as more and more investigators have considered the role of habitats separating desert mountain ranges (e.g., Ough & deVos 1984; Cooperrider 1985; Krausman & Leopold 1986; Schwartz et al. 1986). These authors also considered the importance of small populations and began to incorporate concepts of population genetics relative to questions of wild sheep management.

Genetic Considerations

The concern about genetic health of desert-dwelling mountain sheep arose from (1) a popular (Seton 1929; Buechner 1960; DeForge et al. 1979), but probably greatly exaggerated (Welles 1962; V. C. Bleich and S. A. Holl, unpublished data) assumption that mountain sheep in general have declined to approximately 2% of their historical population level in North America; (2) their relatively isolated natural habitat, the rugged peaks of desert mountain ranges (Hansen 1980); (3) their polygynous mating system (Geist 1971); and (4) the assumption that cultural features developed in the last century prevent dispersal across the relatively flat ground between desert mountain ranges (Bailey 1980). Geist (1975) raised the general question of genetic effects on mountain sheep populations when interpopulation movements could no longer occur.

Schwartz et al. (1986) looked at this question through applying population genetics theory to a "metapopulation" of mountain sheep in the Mojave Desert of California and Nevada that was bounded by two major fenced highways and the Colorado River, and included about 1,600 sheep distributed in 15 subpopulations (demes). Their analyses suggested that relatively low levels of gene migration were necessary to prevent loss of genetic diversity in small populations. While migration of genes is difficult to document, the increasing evidence of intermountain movement by rams in the breeding season suggests that the low levels of gene migration considered necessary probably are met. Their study area would satisfy the requirements for a preserve of a size consistent with (1) the long-term genetic health of populations, (2) the possibility of establishing additional subpopulations, and (3) the possibility of continued divergence and long-term evolution (level 7 or 8 preserve; Schonewald-Cox 1983). Also, mounting evidence (Festa-Bianchet 1986; Geist 1971; J. D. Wehausen, V. C. Bleich, A. M. Pauli, and R. L. Vernoy, un-

published data) indicates substructuring within traditionally defined populations that would minimize inbreeding. Many populations appear to consist of a number of distinct but overlapping female home ranges. Although female offspring generally appear to adopt the home range of their mother, mature males appear to spend the rut outside of their maternal home range.

Both dispersal and social structure potentially are important determinants of effective population size (Chepko-Sade et al. 1987). Dispersal, coupled with substructuring of populations, probably acts to maintain genetic variation within populations of mountain sheep. Maintaining such variation presumably is important in preserving the evolutionary potential of metapopulations and, as such, should be of concern to managers.

Ecological Considerations

In addition to corridors necessary to facilitate gene flow, the ecological value of mountainous habitats not permanently occupied should be recognized. Recent work in California has documented further the use of areas not traditionally considered to be mountain sheep habitat. For example, Cowhole Mountain, located approximately 5 km across a broad, sandy area west of Old Dad Peak, has been found to be a lambing area for the Old Dad Peak population and is used at other times of the year by different cohorts of the population as well. Similarly, in 1987 two telemetered ewes from the Old Woman Mountains visited the neighboring Iron Mountains in winter and the Ship Mountains in spring. One of these bore a lamb in the Iron Mountains and returned to the Old Woman Mountains three months later. Her disappearance from the Old Woman Mountains in the winter of 1986 suggests that this may be a regular pattern. This view is supported by a native of Milligan (personal communication 1987), a town at the southern tip of the Old Woman Mountains, who reported regularly seeing sheep tracks crossing between the Old Woman and Iron mountains in winter and spring. Both the Ship and Iron mountains are separated from the Old Woman Mountains by 6–8 km of desert flats and blow sand. The potential ecological importance of these and similar areas should not be underestimated. The sheep population in the Old Woman Mountains has been depressed during the 1980s, possibly because of a high prevalence of cattle diseases (Clark et al. 1985; Wehausen 1988). The observed intermountain movements by ewes may be remnants of movements that formerly occurred on a larger scale and that could be in danger of being lost as a regular pattern. No land management plan even considers the potential importance of the Ship and Iron mountains to the Old Woman Mountains population.

Although the Iron Mountains have been identified as

a potential reintroduction site (see below), such action has been delayed by the potential that animals moving from the Old Woman Mountains will transmit disease to the Iron Mountains. Dobson and May (1986) have cautioned against such scenarios. Indeed, intermountain movements are a double-edged sword — necessary for gene flow, but potentially deleterious due to disease transmission (Simberloff & Cox 1987). Such movements may have been a major factor in the current widespread distribution of parainfluenza-III virus in desert populations of mountain sheep (Clark et al. 1985; Wehausen 1987).

Conclusions

The notion that the habitat of desert-dwelling mountain sheep is restricted to those mountain masses that provide food, cover, and water and that support permanent populations of the species is no longer adequate. Although habitat within mountain ranges can be enhanced (e.g., Bleich et al. 1982a, 1982b; Werner 1985), such activities must be conducted with the awareness that all areas used by mountain sheep may be essential for their long-term survival. For viable populations of mountain sheep to persist, more than “mountain islands within desert seas” must be protected. Although natural forces such as precipitation may drive the dynamics of populations within these “islands” (Monson 1960; Bleich 1986; Douglas & Leslie 1986; Wehausen et al. 1987), and disjunct populations may simultaneously experience “boom” or “bust” phenomena, the actions of humans will determine the ultimate fate of this species.

Wilcox and Murphy (1985) concluded that the risk of fragmentation is threefold (1) demographic units may be destroyed outright, reduced in size, or subdivided; (2) potential sources of emigrants may be lost; and (3) immigration may be impeded by conversion of natural habitat. All of these are applicable to the conservation of mountain sheep in desert ecosystems. Nonetheless, it is important to recognize that a *naturally* fragmented distribution, as found among populations of desert-dwelling mountain sheep, can minimize the probability of extinction where catastrophic population losses are a factor (Quinn & Hastings 1987). This is the fundamental concept underlying the Recovery and Conservation Plan for mountain sheep in the Sierra Nevada of California (Sierra Bighorn Interagency Advisory Group 1984). The history of mountain sheep is replete with examples of decimation and extinction of local populations due to diseases, mostly contracted from domestic livestock (Buechner 1960; Robinson et al. 1967; Stelfox 1971; Sandoval 1980; Foreyt & Jessup 1982; Goodson 1982; Onderka & Wishart 1984; Jessup 1985). Although such demographic impacts may far outweigh long-term genetic considerations from a conservation standpoint

(Lande 1988), migration between disjunct subpopulations remains critically important, not only for genetic reasons, but also for natural recolonization of habitat that may become vacant. Berger (1990) has recently demonstrated the high probability of extinctions of small populations of mountain sheep in this century. If even a fraction of these extinctions would have occurred in the absence of influences related to the white man, natural extinction and recolonization may be considerably more common than previously thought.

To ensure the long-term conservation of these animals in a wild state, future management strategies for mountain sheep in the desert must take more factors into account in a larger-scale approach. Management documents should begin to seriously consider intermountain travel corridors for sheep, taking steps to minimize potential barriers such as range fences and motorized recreational activities. Managers should also recognize that if domestic livestock graze along such corridors, diseases may be transmitted to mountain sheep populations via migrating animals. Domestic sheep are particularly dangerous in this regard because they carry fatal respiratory bacterial strains (Onderka & Wishart 1988; Onderka et al. 1988; Foreyt 1989). Small, isolated tracts of “traditional” habitat that is not permanently occupied should be recognized as potential seasonal habitat and as “stepping stones” within migration corridors. Translocation programs should give priority to reestablishing populations on ranges that will decrease interdeme distances so as to facilitate gene migration.

The Bureau of Land Management recently prepared a management plan for mountain sheep on all applicable desert ranges in the southwestern United States. The plan incorporates the concept of metapopulations (BLM 1988). It sets as its goal the recovery of 115 “populations” to “viable” status (≥ 100 sheep). However, there remains a need to map all potential metapopulations of mountain sheep as well as known and potential intermountain corridors throughout their desert range, and to develop conservation strategies on that geographic scale.

Figure 1 is an example of a metapopulation from southeastern California. It is bounded on the north, south, and west by major, fenced interstate highways, and on the east by the Colorado River. Relatively few unfenced, paved roads exist within this metapopulation; thus, with the exception of the Twenty-Nine Palms and Lucerne Valley areas, and an aqueduct partially separating the Coxcomb Mountains from the Granite/Palen and southern Iron mountains to the east and the Turtle Mountains from the unoccupied ranges to the south, there are few physical obstructions to intermountain movements by mountain sheep. Approximately 1,000 mountain sheep permanently inhabit 15 of 31 mountain ranges in this region. Two of the 15 inhabited ranges



Figure 1. Map of a metapopulation of mountain sheep in southeastern California. Stippled mountain ranges currently have resident populations of the approximate size listed. Mountain ranges with $N = 0$ are extirpated populations; ranges with no N value listed are not known ever to have had resident populations. Arrows indicate documented intermountain movements by mountain sheep.

have been reestablished by translocation (Whipple and Sheephole). Only 8 of the 15 ranges support populations of 50 or more sheep. We have documented movements of mountain sheep between 11 pairs of mountain ranges depicted in Figure 1; the mean distance between those ranges is about 9 km (range = 6–20).

From the standpoint of fragmentation, the population in the Newberry Mountains in the NW corner of Figure 1 is particularly isolated. In fact, as recently as 1982 this population was not known to exist (Weaver 1982). Reestablishing populations along the link between the Rodman and Bullion mountains should be a high priority within this metapopulation. The entire Bullion and Lava Bed Mountains, however, are within the Twenty-Nine Palms Marine Corps Training Center. The Department of Defense is currently pursuing a reintroduction of mountain sheep in the Bullion Mountains in cooperation with the California Department of Fish and Game.

Geographically, the second most notable fragmentation within this metapopulation is the separation of the three populations in the SW corner from the others.

This constitutes a much less serious situation than the Newberry Mountains in that the combined population in this area totals about 275 sheep (Fig. 1). Nevertheless, reestablishing a population in the Pinto Mountains would facilitate migration between these three populations and the remainder of the metapopulation.

Within the eastern portion of this metapopulation, reestablishing a population in the Iron Mountains would provide an important connection between the Sheephole/Eagle/Coxcomb/Granite-Palen mountains complex and the occupied ranges to the NE. Given that the former complex contains only about 100 total sheep, reestablishing a population in the Iron Mountains should have priority over such an effort in the Pinto Mountains. The aforementioned disease question, however, will play an important role in the decision to reestablish a permanent population in the Iron Mountains.

Of the ranges not known previously to have had resident mountain sheep populations, the Stepladder Mountains are particularly important as a central "stepping stone" potentially connecting four surrounding

populations. The Piute, Little Piute, Ship, and Calumet mountains are only somewhat less central, and three of these are known to have been visited by sheep from adjacent ranges. Similarly, the Lava Bed Mountains have the potential to serve as an important link between the Bullion and Rodman mountains, if populations become established there.

Our discussion has centered around the importance to mountain sheep of unimpeded movement. A similar concern can be extended to other terrestrial species whose primary habitat naturally occurs in disjunct patches but that cross expanses of less desirable habitat between such patches to some extent. Both mule deer (*Odocoileus hemionus eremicus*, *O. h. crooki*) and mountain lions, where they occur in deserts, probably fit these criteria. Previous discussions of habitat corridors (Simberloff & Cox 1987; Noss 1987) have referred to maintaining or creating corridors of habitats similar to those being connected. The situation considered here differs somewhat in that the disjunct nature of primary habitat patches is natural and the corridor habitat is clearly less desirable to the species involved but is nevertheless used in moving between suitable patches.

Schwartz et al. (1986) concluded, "In general, desert-dwelling mountain sheep populations are sufficiently abundant and juxtaposed, and areas of habitat are still sufficiently large to allow the continued existence of this species throughout much of its historic range." We still have the raw materials; what is needed is a commitment to protect and manage them properly. Only with the recognition that stewardship responsibilities extend beyond areas of "traditional" habitat and what are perceived to be "viable" populations will we assure the long-term stability of desert-dwelling mountain sheep and other vagile species that similarly inhabit naturally fragmented habitat.

Acknowledgments

We thank R. T. Bowyer, A. Y. Cooperrider, D. Ehrenfeld, V. Geist, R. R. Ramey II, O. A. Schwartz, and an anonymous reviewer for critical comments and helpful suggestions. C. Tiernan and K. Quinlan helped prepare the figure, and V. Blankinship translated the abstract into Spanish. This paper was originally presented as an invited paper at the 24th Annual Meeting of the Western Section of the Wildlife Society, during which productive interchange with M. E. Soulé occurred.

Literature Cited

Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57–76 in M. E. Soulé, editor. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts.

Bailey, J. A. 1980. Desert bighorn, forage competition, and zoogeography. *Wildlife Society Bulletin* 8:208–216.

Berbach, M. W. 1987. The behavior, nutrition, and ecology of a population of reintroduced desert mountain sheep in the Whipple Mountains, San Bernardino County, California. M.S. thesis, California Polytechnic State University, Pomona, California.

Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of recent extinctions in bighorn sheep. *Conservation Biology* 4:91–98.

Bleich, V. C. 1986. Early breeding in free-ranging mountain sheep. *Southwestern Naturalist* 31:530–531.

Bleich, V. C., L. J. Coombes, and J. H. Davis. 1982a. Horizontal wells as a wildlife habitat improvement technique. *Wildlife Society Bulletin* 10:324–328.

Bleich, V. C., L. J. Coombes, and G. W. Sudmeier. 1982b. Volunteer participation in California wildlife habitat management projects. *Transactions of the Desert Bighorn Council* 26:56–58.

Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. *Wildlife Monographs* 4:1–174.

Bureau of Land Management. 1980. Final environmental impact statement and proposed plan. USDI, Bureau of Land Management, Desert District, Riverside, California.

Bureau of Land Management. 1988. Rangewide plan for managing habitat of desert bighorn sheep on public lands. USDI, Bureau of Land Management, Washington, D.C.

Chepko-Sade, B. D., W. M. Shields, J. Berger, et al. 1987. The effects of dispersal and social structure on effective population size. Pages 287–321 in B. D. Chepko-Sade and Z. T. Halpin, editors. *Mammalian dispersal patterns. The effects of social structure on population genetics*. University of Chicago Press, Chicago, Illinois.

Clark, R. K., D. A. Jessup, M. D. Kock, and R. A. Weaver. 1985. Survey of desert bighorn sheep in California for exposure to selected infectious diseases. *Journal of the American Veterinary Medical Association* 187:1175–1179.

Cochran, M. H., and E. L. Smith. 1983. Intermountain movements by a desert bighorn ram in western Arizona. *Transactions of the Desert Bighorn Council* 27:1–2.

Cooperrider, A. Y. 1985. The desert bighorn. Pages 473–485 in R. L. DiSilvestro, editor. *Audubon wildlife report 1985*. National Audubon Society, New York.

DeForge, J. R., C. W. Jenner, A. J. Plechner, and G. W. Sudmeier. 1979. Decline of bighorn sheep (*Ovis canadensis*), the genetic implications. *Transactions of the Desert Bighorn Council* 23:63–66.

Dobson, A. P., and R. M. May. 1986. Disease and conservation. Pages 345–365 in M. E. Soulé, editor. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts.

Douglas, C. L., and D. M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. *Journal of Wildlife Management* 50:153–156.

- Elenowitz, A. 1982. Preliminary results of a desert bighorn transplant in the Peloncillo Mountains, New Mexico. *Transactions of the Desert Bighorn Council* 26:8–11.
- Festa-Bianchet, M. 1986. Seasonal dispersion of overlapping mountain sheep ewe groups. *Journal of Wildlife Management* 50:325–330.
- Foreyt, W. J. 1989. Fatal *Pasteurella haemolytica* pneumonia in bighorn sheep after direct contact with clinically normal domestic sheep. *American Journal of Veterinary Research* 50:341–344.
- Foreyt, W. J., and D. A. Jessup. 1982. Fatal pneumonia of bighorn sheep following association with domestic sheep. *Journal of Wildlife Diseases* 18:163–168.
- Frankel, O. H. 1983. The place of management in conservation. Pages 1–14 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, editors. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, California.
- Geist, V. 1967. A consequence of togetherness. *Natural History* 76(8):24, 29–30.
- Geist, V. 1971. *Mountain sheep, a study in behavior and evolution*. University of Chicago Press, Chicago, Illinois.
- Geist, V. 1975. On the management of mountain sheep: theoretical considerations. Pages 77–98 in J. B. Trefethen, editor. *The wild sheep in modern North America*. Winchester Press, New York, N.Y.
- Goodson, N. J. 1982. Effects of domestic sheep grazing on bighorn sheep populations: a review. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 3:287–313.
- Hansen, C. G. 1980. Habitat. Pages 64–79 in G. Monson and L. Sumner, editors. *The desert bighorn*. University of Arizona Press, Tucson, Arizona.
- Harris, L. D. 1984. *The fragmented forest: island biogeographic theory and the preservation of biotic diversity*. University of Chicago Press, Chicago, Illinois.
- Jessup, D. A. 1985. Diseases of domestic livestock which threaten bighorn sheep populations. *Transactions of the Desert Bighorn Council* 29:29–33.
- King, M. M., and G. W. Workman. 1983. Preliminary report on desert bighorn movements on public lands in southeastern Utah. *Transactions of the Desert Bighorn Council* 27:4–6.
- Krausman, P. R., and B. D. Leopold. 1986. The importance of small populations of desert bighorn sheep. *Transactions of the North American Wildlife and Natural Resources Conference* 51:52–61.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455–1460.
- Lehmkuhl, J. F. 1984. Determining size and dispersion of minimum viable populations for land management planning and species conservation. *Environmental Management* 8:167–176.
- McQuivey, R. P. 1978. The desert bighorn sheep of Nevada. Nevada Department of Fish and Game Biological Bulletin 6:1–81.
- Monson, G. 1960. Effects of climate on desert bighorn numbers. *Transactions of the Desert Bighorn Council* 4:12–14.
- Noss, R. F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. *Conservation Biology* 1:159–164.
- Onderka, D. K., and W. D. Wishart. 1984. A major bighorn sheep die-off from pneumonia in southern Alberta. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 4:356–363.
- Onderka, D. K., and W. D. Wishart. 1988. Experimental contact transmission of *Pasteurella haemolytica* from clinically normal domestic sheep causing pneumonia in Rocky Mountain bighorn sheep. *Journal of Wildlife Diseases* 24:663–667.
- Onderka, D. K., S. A. Rawluk, and W. D. Wishart. 1988. Susceptibility of Rocky Mountain bighorn sheep and domestic sheep to pneumonia induced by bighorn and domestic livestock strains of *Pasteurella haemolytica*. *Canadian Journal of Veterinary Research* 52:439–444.
- Ough, W. D., and J. C. deVos, Jr. 1984. Intermountain travel corridors and their management implications for bighorn sheep. *Transactions of the Desert Bighorn Council* 28:32–36.
- Quinn, J. F., and A. Hastings. 1987. Extinction in subdivided habitats. *Conservation Biology* 1:198–208.
- Ralls, K. P., H. Harvey, and A. M. Lyles. 1986. Inbreeding in natural populations of birds and mammals. Pages 35–56 in M. E. Soulé, editor. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Robinson, R. M., T. L. Hailey, C. W. Livingston, and J. W. Thomas. 1967. Bluetongue in the desert bighorn sheep. *Journal of Wildlife Management* 31:165–168.
- Russo, J. P. 1956. The desert bighorn in Arizona. *Arizona Game and Fish Department Wildlife Bulletin* 1:1–153.
- Sandoval, A. V. 1980. Management of a psoroptic scabies epizootic in bighorn sheep (*Ovis canadensis mexicana*) in New Mexico. *Transactions of the Desert Bighorn Council* 24:21–28.
- Schonewald-Cox, C. M. 1983. Conclusions: guidelines to management: a beginning attempt. Pages 414–445 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, editors. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, California.
- Schonewald-Cox, C. M., S. M. Chambers, B. MacBryde, and W. L. Thomas, editors. 1983. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, California.
- Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation* 37:179–190.
- Seton, E. T. 1929. *Lives of game animals*. Volume III, Part II. Hoofed Animals. Doubleday Page and Co., New York, N.Y.

Sierra Bighorn Interagency Advisory Group. 1984. Sierra Nevada bighorn sheep recovery and conservation plan. Inyo National Forest, Bishop, California.

Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1:63-71.

Soulé, M. E., editor. 1986. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.

Soulé, M. E., and B. A. Wilcox, editors. 1980. *Conservation biology. An evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts.

Stelfox, J. G. 1971. Bighorn sheep in the Canadian Rockies: a history 1800-1970. *Canadian Field-Naturalist* 85:101-122.

Weaver, R. A. 1982. Bighorn in California: a plan to determine current status and trends. Administrative Report, California Department of Fish and Game, Sacramento, California.

Wehausen, J. D. 1987. Some probabilities associated with sampling for diseases in bighorn sheep. *Transactions of the Desert Bighorn Council* 31:8-10.

Wehausen, J. D. 1988. Cattle impacts on mountain sheep in the Mojave Desert: report II. Unpublished report, California Department of Fish and Game, Bishop, California.

Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California mountain sheep population. *Journal of Wildlife Management* 51:86-98.

Welles, R. E. 1962. What makes a valid observation? *Transactions of the Desert Bighorn Council* 7:29-40.

Werner, W. E. 1985. Philosophies of water development for bighorn sheep in southwestern Arizona. *Transactions of the Desert Bighorn Council* 29:13-14.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-256 in M. E. Soulé, editor. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125:879-887.

Wilson, L. O., J. Blaisdell, G. Welsh, et al. 1980. Desert bighorn habitat requirements and management recommendations. *Transactions of the Desert Bighorn Council* 24:1-7.

Witham, J. H., and E. L. Smith. 1979. Desert bighorn movements in a southwestern Arizona mountain complex. *Transactions of the Desert Bighorn Council* 23:20-23.

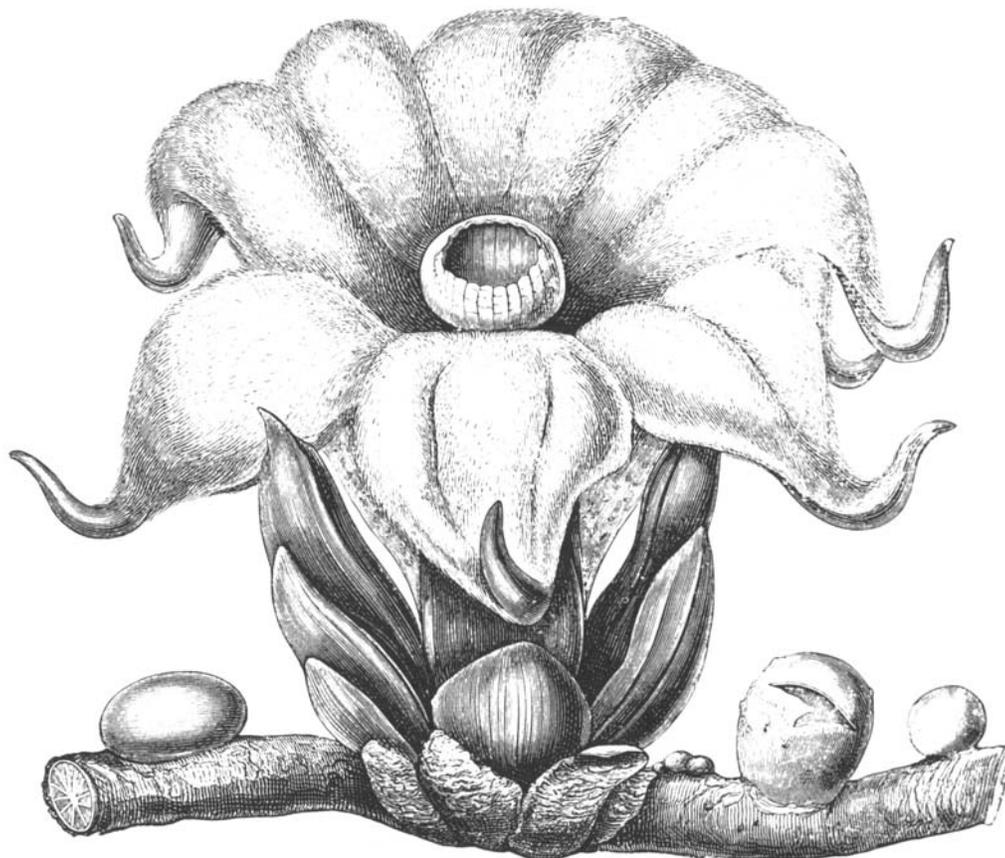


EXHIBIT 421



Sexual Segregation in Mountain Sheep: Resources or Predation?

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Wildlife Monographs, No. 134, Sexual Segregation in Mountain Sheep: Resources or Predation?. (Jan., 1997), pp. 3-50.

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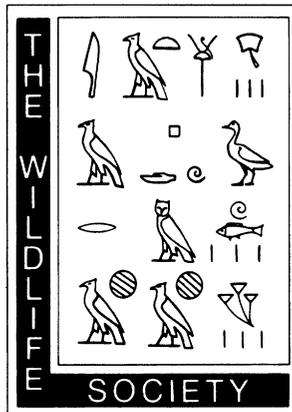
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WILDLIFE MONOGRAPHS

(ISSN:0084-0173)

A Publication of The Wildlife Society



SEXUAL SEGREGATION IN MOUNTAIN SHEEP: RESOURCES OR PREDATION?

by

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AND JOHN D. WEHAUSEN



FRONTISPIECE. Mountain sheep exhibit extreme sexual dimorphism, which is thought to play an essential role in sexual segregation (photograph© by David McNew).

SEXUAL SEGREGATION IN MOUNTAIN SHEEP: RESOURCES OR PREDATION?

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Abstract: We studied mountain sheep (*Ovis canadensis nelsoni*) at Old Dad Mountain, in the Kelso Mountains, and in the Marl Mountains in the eastern Mojave Desert, San Bernardino County, California during 1981–90 to determine causes of sexual segregation. Forty-four mountain sheep were captured, fitted with radio collars, and located systematically from a fixed-wing aircraft to determine differences in habitats used by males and females. In addition, diet composition and forage quality and availability along with information on diets and distribution of predators were obtained to test 4 hypotheses potentially explaining sexual segregation in ungulates.

Mature males and females were segregated from December to July and were aggregated from August to November. Mature males obtained higher quality diets than did females (based on values for fecal crude protein) during 2 of the 3 years for which data were available. Indices of predator abundance were substantially lower on ranges used by females and juveniles than on those used by mature males. Females occurred closer to permanent sources of water and in steeper, more rugged, and more open habitats than did mature males. Moreover, forage was more abundant in habitats used primarily by mature male sheep. Females with and without lambs did not differ in their distance from water during aggregation or segregation, and females did not visit water more often during the period of peak lactation when compared with other times of the year. Female groups with lambs, however, occurred on steeper slopes and in more rugged and open habitats during segregation, when lambs were very young.

Based on our results, we refute the hypotheses (1) that females outcompete males for available resources, and allometric differences between the sexes lead to sexual segregation; (2) that the constraints of lactation may be important in explaining sexual segregation in this desert-adapted ungulate; and (3) that males segregate to avoid competition with their mates, potential mates, and offspring, at least in desert ecosystems. In contrast, our findings strongly support the hypothesis that, because of their smaller body size and potentially greater vulnerability to predation, and the need to minimize risk to their offspring, female ungulates and their young use habitats with fewer predators and greater opportunities to evade predation than do mature males, but that males are able to, and do, exploit nutritionally superior areas.

We conclude that sexual segregation likely results from differing reproductive strategies of males and females among sexually dimorphic ungulates. Males may enhance their fitness by exploiting habitats with superior forage and thereby enhance body condition and horn growth while simultaneously incurring greater risks than do females. In contrast, females appear to enhance their fitness by minimizing risks to their offspring, albeit at the expense of nutrient quality. Further, we suggest that how food and risk of predation are arrayed in the environment may affect whether males or females inhabit better quality ranges, as well as which sex moves to produce spatial separation.

WILDL. MONOGR. 134, 1–50

Key words: behavior, California, forage, habitat use, Mojave Desert, mountain sheep, *Ovis canadensis*, predation, sexual segregation.

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INTRODUCTION

Large mammals that exhibit sexual segregation frequently are sexually dimorphic. Darwin (1871:511–567) postulated that such morphological differences were a mechanism to reduce intersexual competition. The importance of sexual dimorphism in sexual segregation has been investigated for an array of organisms (Schoener 1966; Selander 1966, 1972; Storer 1966; Feduccia and Slaughter 1974; Freeman et al. 1976; Keast 1977; Hill and Ridley 1987; Klimley 1987; Smallwood 1987), including mammals (Bowers and Smith 1979, Gautier-Hion 1980, Fay 1982, Morris 1987, Bailey and Anger 1989, Litvaitis 1990). The prevailing notion has been that the resultant resource-partitioning reduces intersexual competition and, thereby, enhances reproductive success. Because critical tests of hypotheses related to sexual segregation are few, Bierzychudek and Eckhart (1988) suggested that future studies avoid inferring that sexual segregation is adaptive, or represents an evolved response to competition between the sexes, until supporting evidence is ob-

tained. We believe that the causes of sexual segregation in large mammals have not been investigated adequately. Hence, the notion that sexual segregation evolved as an adaptation (Williams 1966) remains speculative.

In contrast to intersexual competition, an alternative explanation for sexual segregation and sexual dimorphism involves sexual selection. In this explanation, sexual dimorphism is the result of intrasexual competition among males (Alexander et al. 1979), and sexual dimorphism underlies differential uses of resources and, ultimately, sexual segregation (McCullough 1979). Thus, sexual segregation may result from sexual dimorphism, a phenomenon that is most readily explained as a result of sexual selection.

Ungulates offer a unique opportunity to study the ecological consequences of sexual segregation because of the extreme sexual dimorphism exhibited by many of these mammals (Ralls 1977). Studies have documented spatial separation of the sexes for a variety of ungulates, including caribou and reindeer (*Rangifer tarandus*) (Cameron and Whitten 1979, Skogland

1989), red deer and elk (*Cervus elaphus*) (Peek and Lovaas 1968, Clutton-Brock et al. 1982), mule deer (*Odocoileus hemionus*) (Bowyer 1984, Scarbrough and Krausman 1988, Weckerly 1993, Bowyer et al. 1996, Main and Coblenz 1996), white-tailed deer (*O. virginianus*) (McCullough et al. 1989, LaGory et al. 1991, Jenks et al. 1994), moose (*Alces alces*) (Miquelle et al. 1992), giraffe (*Giraffa camelopardalis*) (Young and Isbell 1991), bison (*Bos bison*) (Guthrie 1990), Cape buffalo (*Syncerus caffer*) (Sinclair 1977, Prins 1989), Tibetan antelope (*Pantholops hodgsoni*) (Schaller and Junrang 1988), pronghorn (*Antilocapra americana*) (Kitchen 1974), waterbuck (*Kobus ellipsiprymnus*) (Wirtz and Kaiser 1988), chamois (*Rupicapra rupicapra*) (Shank 1985), mountain goat (*Oreamnos americanus*) (Holmes 1988), mouflon (*Ovis ammon*) (Bon and Campan 1989), muskox (*Ovibos moschatus*) (Oakes et al. 1992), and mountain sheep (*Ovis canadensis*) (Geist 1971, Wehausen 1980). Only recently, however, has research been designed specifically to address the causes of sexual segregation (e.g., Shank 1982, Bowyer 1984, Beier 1987, Clutton-Brock et al. 1987, Miquelle et al. 1992).

Because of allometric differences among mammals (Clutton-Brock and Harvey 1983, Peters 1983), it is unlikely that the ecological determinants of spatial separation of the sexes will be the same for small- and large-bodied species. Thus, hypotheses or models that explain the population characteristics of small mammals may not suffice for large ones (Caughley and Krebs 1983, Millar and Zammuto 1983). Also, the existing models of sexual selection and dimorphism, derived largely from passerines, simply are not applicable to many mammals (Ralls 1977), although Geist (1977) discussed parallels between the evolution of sexual dimorphism in ungulates and gallinaceous birds.

Biology of Mountain Sheep in Desert Environments

Mountain sheep are ideal for studying sexual segregation because they (1) exhibit

extreme sexual dimorphism, (2) are easily distinguishable as adult males or females throughout the year, even from great distances, and (3) commonly show pronounced and prolonged spatial separation of the sexes. They generally are associated with mountain ranges having precipitous areas for use as escape terrain (Bleich and Holl 1982) and permanent water (Shackleton 1985). Frequently, these mountain ranges are isolated from each other (Schwartz et al. 1986, Bleich et al. 1990a). Mountain sheep inhabiting desert environments are physiologically specialized in terms of water metabolism (Turner 1973, 1979); these ungulates maintain their water balance despite high heat loads and widely dispersed and limited free water (Turner and Weaver 1980, Krausman et al. 1985a).

Mountain sheep are gregarious, but, for much of the year, males ≥ 3 years old live apart from females (i.e., they sexually segregate). Males and females aggregate during rut, which may extend for numerous months in desert environments (Welles and Welles 1961, Bunnell 1982). Mountain sheep have a corresponding protracted birthing season relative to their more northern congeners (Bunnell 1982, Thompson and Turner 1982, Rachlow and Bowyer 1991). Seegmiller and Ohmart (1982) demonstrated dietary differences between juvenile and adult female mountain sheep.

Wolves (*Canis lupus*) may have been present in low numbers in desert habitats (Young and Goldman 1944), but extirpation of this canid from southeastern California (Johnson et al. 1948) has eliminated its potential effects on wild sheep there. Coyotes (*Canis latrans*), mountain lions (*Felis concolor*), and bobcats (*F. rufus*) are the most important predators of mountain sheep in desert environments (Kelly 1980). Berger (1978) reported attempts of coyotes to kill mountain sheep, and Bowyer (1987) noted that coyotes in southern California are effective predators of adult mule deer. Therefore, coyote predation on mountain sheep may be widespread, given the wide distribution of coyotes. Mountain

sheep primarily evade predation on young by inhabiting steep, rugged terrain (Geist 1981).

Hypothesized Explanations for Sexual Segregation

Numerous hypotheses have been forwarded to account for sexual segregation in polygynous ungulates (Main and Coblenz 1990, Miquelle et al. 1992). Miquelle et al. (1992) eliminated several hypotheses because they were not consistent with existing data and were deemed unlikely explanations for sexual segregation. They cautioned that there may be no single, universal explanation for sexual segregation in ungulates. We agree that there are some hypotheses that are sufficiently incompatible with observed patterns of sexual segregation in ungulates in general, and mountain sheep in particular, to render them unlikely explanations. Therefore, researching these notions is unlikely to yield fruitful results.

The first such hypothesis is that males may avoid areas heavily contaminated by feces because they are more likely to suffer from increased parasite loads than are females (Clutton-Brock et al. 1987). Clutton-Brock et al. (1987) refuted this hypothesis for red deer. Although mountain sheep in some areas may be severely affected by lungworms (*Protostrongylus* spp.) (Forrester 1971), this parasite is absent from most desert ranges, as are other fecal-borne diseases of potential importance to the health of wild sheep (Clark et al. 1985). Consequently, avoidance of fecal-contaminated areas is an unlikely explanation for sexual segregation for desert-dwelling mountain sheep.

A second unlikely hypothesis is that segregation of the sexes results from males avoiding aggressive interactions provoked by the presence of females (Shank 1985). Geist (1971) reported low-intensity interactions between male sheep outside rut, but this does not mean that the presence of females would precipitate serious clashes. Main and Coblenz (1990) noted that rutting behaviors (including aggression) of

temperate and Arctic ungulates were regulated by hormones that are highly seasonal. If this hypothesis is correct, young males, many of which remain with females outside rut (Geist 1971) and may be sexually mature (Turner 1976), should continue to engage in serious fights and other rut-related behaviors; intense interactions have not been reported among mountain sheep outside the mating season.

Verme (1988) speculated that male cervids might segregate because they require more open areas (to prevent damage to growing antlers) than do females. Although this hypothesis is not applicable to bovids, which do not cast their horns (Main and Coblenz 1990), it also is not supported by data from species of deer. Mule deer living year-round in exceptionally open habitats still exhibited sexual segregation (Scarborough and Krausman 1988). Moreover, male mule deer inhabiting vegetation types varying from dense brush to open meadows did not use habitats differently during periods of segregation and aggregation (Bowyer 1984, 1986a). These findings make this hypothesis an unlikely explanation even for segregation by cervids.

McCullough (1979) and Verme (1988) suggested that males might segregate to more open areas where they could maintain visual contact and thereby evaluate the dominance of other males. This hypothesis infers that ungulates inhabiting open habitats should not segregate. Contrary evidence is available from a number of cervids (Main and Coblenz 1990). Additionally, this hypothesis will not explain why some young males remain with females (Geist and Petocz 1977). Moreover, ungulates possess means of recognizing conspecifics and their status other than vision (e.g., olfaction [Coblenz 1976, Bowyer and Kitchen 1987]). The size of horn-like organs is often an indication of the hierarchical status of males (Geist 1971, Hirth 1977, Kucera 1978, Bowyer 1986b, and many others). This assessment of dominance does not require especially open areas, and this hypothesis does not explain why males should remain segre-

gated for such an extended period. Indeed, sparring, in which males assess dominance, is most often focused around rut when the sexes are at least partially aggregated (Geist 1971, Bowyer 1986*b*). Although males may have opportunities to assess the dominance of potential rivals during segregation, there is no compelling evidence that this leads to or causes segregation.

Geist and Bromley (1978) proposed 2 hypotheses about sexual segregation. First, male cervids may spatially separate from females following mating, but then return after antler casting because mimicry of females allows males to rejoin such groups without being conspicuous to predators. As with other hypotheses related to the casting of antlers (or horn sheaths), this idea applies only to cervids and perhaps antilocaprids and may not be invoked as a general explanation for ungulates. Moreover, this hypothesis does not explain segregation beyond the time of antler casting or where segregation is more pronounced during spring, when antler regrowth is obvious (Bowyer 1984, McCullough et al. 1989). Miquelle et al. (1992) concluded that the presence of antlers did not appear to be an important factor influencing the distribution of the sexes for moose following rut. Too much contrary evidence exists to make this a viable hypothesis.

Geist and Bromley (1978) also suggested that males that retain their horn-like organs through winter should segregate from females to avoid being conspicuous because of their increased vulnerability to predation resulting from strenuous rutting activities. Indeed, rutting activities among ungulates can decrease physical condition and thereby increase mortality of large, dominant males (Geist 1971; Bowyer 1981, 1991; Miquelle 1990*a*). This hypothesis may be applicable to both cervids and bovids, because both horns and antlers would be conspicuous for at least some period following rut. Moreover, male ungulates sometimes predominate among kills of predators (McCullough 1979:204, Harrison and Hebert 1988). This hypothesis, however, poorly explains the timing of seg-

regation for some cervids. For instance, mule deer remain segregated following antler casting and well into the period of antler regrowth (Bowyer 1984), and male mountain sheep can remain with females on restrictive winter ranges following the mating season (Wehausen 1980). Horns and antlers may offer a cue to predators in identifying vulnerable males exhausted from rut, but this hypothesis will not explain the observed patterns of sexual segregation among most ungulates.

Another possible explanation for sexual segregation is that males seek habitats with cover that helps minimize energy losses following rut (Staines 1976, Watson and Staines 1978). Clutton-Brock et al. (1987) and Miquelle et al. (1992), however, observed contradictory behavior in red deer and moose, respectively. A harsh winter climate is an improbable explanation for segregation by ungulates inhabiting desert environments. Indeed, the period of segregation in desert-dwelling mountain sheep encompasses a wide variety of climatic conditions (Leslie and Douglas 1979), suggesting this is not the cause of segregation in these ungulates. Additionally, sheep aggregated when temperatures were high and the climate was most stressful (Leslie and Douglas 1979). Climate may play an important role in habitat selection by ungulates, but evidence that it causes sexual segregation is not compelling.

Four remaining hypotheses provide potentially useful explanations for sexual segregation in artiodactyls (Table 1). We use the approach of multiple working hypotheses (Platt 1964) because multiple causations of ecological events are common (Hilborn and Stearns 1982). Predictions for each hypothesis in Table 1 will be compared with the results from this research; thus, each is potentially falsifiable. Nonetheless, critical tests of these hypotheses are difficult to obtain because they are not mutually exclusive (Quinn and Dunham 1983).

H₁: Sexual segregation in mountain sheep occurs because males avoid areas occupied by females and young to decrease

Table 1. Summary of hypotheses, predicted outcomes, and means of differentiating among hypotheses related to sexual segregation in mountain sheep.

Outcome	Hypotheses	Differentiation
Males on a lower quality diet than females.	H ₁ : Males avoid competition with females to enhance their own fitness. H ₂ : Allometric differences lead to segregation. Males use low quality resources inadequate for females. Females outcompete males for high quality resources.	Primarily Class ^a III and IV males segregate from females. Class II-IV males segregate from females. Female movements result in sexual segregation. Primarily male movements result in sexual segregation.
Male diets either of higher or lower quality than females.	H ₃ : Differential water requirements cause spatial segregation.	From H ₁ : Class II-IV males occur farther from water than females. From H ₂ : Regardless of range quality, females, and particularly females with young, will be closer to water than Class II-IV males.
Males on a higher quality diet than females.	H ₄ : Females avoid predation by segregating from males.	Females inhabit areas with more rugged terrain, or with fewer predators than do males.

^a Males are categorized according to age and size following Geist (1966, 1968).

competition with their offspring and potential mates. This hypothesis was proposed initially by Geist and Petocz (1977) to explain sexual segregation by male mountain sheep in northern environments with small winter ranges with extreme snow cover. Geist and Petocz (1977) provided empirical data in support of this hypothesis, but under limited and very specialized conditions. Other investigators (McCullough 1979, Bowyer 1984, Verme 1988, Miquelle et al. 1992) have challenged the hypothesis on theoretical grounds and have argued that it is difficult to explain why young males that typically have not mated should avoid competition with unrelated young without invoking group selection. Moreover, Morgantini and Hudson (1981) argued that such behavior would result in males potentially reducing their own reproductive fitness. Group selection is unlikely to have affected the evolution or ecology of ungulates because of the unusual conditions necessary for it to operate (Williams 1966). Nevertheless, large, dominant males, which account for most mating in mountain sheep (Geist 1971), might incur some fitness benefits if their absence from ranges occupied by their mates resulted in en-

hanced nutrient availability for those females.

Female mountain sheep and offspring foraging on the tiny, wind-swept winter ranges described by Geist and Petocz (1977) could incur nutritional benefits if fathers of the offspring did not forage on the same ranges, assuming that the diets of the 2 sexes would have been similar; males also could incur indirect benefits in the form of enhanced nutrient availability for their mates and offspring, and potentially direct benefits to themselves in the form of increased nutrient availability.

If the hypothesis of Geist and Petocz (1977) has applicability beyond the specialized conditions for which it was developed, then male mountain sheep from different environments must have a high fidelity to rutting ranges, similar to that reported by Geist (1971), where the annual probability of males encountering and breeding with the same females is great. Additionally, mature males must arrive on rutting ranges later than young males, and mature males must depart from those ranges earlier than young males (Geist 1971), because shorter periods of aggregation between breeding males and their mates would minimize competition for re-

sources. Assuming these conditions are met, the hypothesis of Geist and Petocz has potential application in areas aside from the limited conditions for which it was developed and can be tested with sheep inhabiting a desert environment. If males segregate from females to enhance their own fitness, we predict during sexual segregation that

1. Females will inhabit ranges with better quality forage than do males.
2. Large dominant males will spatially separate from females and young; but smaller subordinate males are less likely to do so, because there would be limited reproductive advantages incurred by them.

H₂: Allometric differences between male and female mountain sheep lead to differential uses of food that result in segregation. Because energy requirements per unit body weight scale to a power less than unity, the energy requirements of smaller animals are greater proportionally to body weight than those of large animals (Van Soest 1982). Nonetheless, the absolute energy requirements of large animals are greater than those of small ones. A larger ruminant may require a larger quantity of forage to meet this need, but also may be able to subsist on a lower quality diet than a smaller one due to greater metabolic efficiency. Because most ungulates exhibit extreme sexual dimorphism in body size, males may be able to occupy habitats having poorer quality forage, yet do as well nutritionally as females on higher quality ranges (McCullough 1979, Bowyer 1984, Beier 1987), as long as the amount of forage is adequate. Among mountain sheep, males are notably larger than females (Remington 1982) and are expected to have larger rumens than females; thus, males may be able to subsist on lower quality diets. Indeed, Illius and Gordon (1987) suggested that the differential scaling of metabolic requirements to body weight may underlie ecological segregation of the sexes among grazing ungulates.

Because of differential scaling of metabolic requirements and incisor breadth,

Seegmiller and Ohmart (1982) hypothesized that lambs would forage more selectively than adult females. Moreover, they concluded that adults, having higher energy and nutrient requirements per unit time, were precluded from consuming the smaller and more widely scattered food items of highest quality (forbs and annual grasses) that were used by lambs. Seegmiller and Ohmart (1982) further suggested that adult male and female mountain sheep may have different diets, thereby explaining the spatial segregation observed between the sexes during particular seasons.

The supposed ability of larger animals to tolerate lower quality food, however, does not provide a rationale for seeking such foods, unless the supply of superior foods is limited. Where habitat segregation occurs between the sexes of ruminants, males often occupy habitats with poorer quality forage than females (e.g., Illius and Gordon 1987). Male red deer are less tolerant of low plant biomass than are females and may be excluded from mutually preferred communities by indirect (passive) competition (Clutton-Brock et al. 1987). Thus, Clutton-Brock et al. (1987) suggested that smaller grazing animals might tolerate lower levels of food availability than larger ones and may progressively exclude larger conspecifics (i.e., males) from mutually preferred areas by reducing standing crops to levels inadequate for larger animals to graze economically.

If allometric differences allow males on forage of poorer quality to maintain themselves as well as females, then, where ranges are inadequate for females, we predict that segregation will result primarily from the movement of female sheep to areas with greater availability of nutrients. This situation would be exacerbated late in gestation because of nutritional demands. Alternatively, if female ranges support forage of adequate quality but insufficient quantity for males, females will have a competitive advantage over males and segregation will result from males leaving female ranges.

H₃: Females spatially segregate from males because of greater water requirements associated with lactation or their smaller body size. Water requirements of lactating female ungulates are high (Short 1981), and this may be especially important in desert ecosystems. Bowyer (1984) ascribed sexual segregation of mule deer in a semiarid environment, in part, to the dependence of females and their young on free water. The physiological burden of lactation may constrain females from venturing far from sources of free water. Moreover, the relatively low water requirements of males compared with smaller-bodied females may allow them to occupy areas farther from summer sources of water and thereby exploit resources unavailable to females. Inherent in the predictions for this hypothesis is the assumption that the distance an animal occurs from water provides an index to the importance of water to that animal.

If the constraints of lactation and body size on water needs contribute to sexual segregation, then we predict that

1. Sexual segregation should be most pronounced during the birthing and early lamb-rearing periods and females with lambs should use water sources regularly at this time.
2. Females with young should occur closer to water than do males or females without young.
3. Because of their lower water requirements, mature males should occur farther from free water than females or young males during hot summer months.

H₄: Spatial separation of the sexes occurs because mature males, owing to their larger body size and strength, are less susceptible to predators than smaller-bodied females and young, thereby allowing these males to exploit resources unavailable to smaller individuals. This hypothesis infers that mature males are able to use different ranges than females and immature animals, because adult males are larger and presumably less vulnerable to predators. Numerous authors have argued that pre-

dition is at least partially related to segregation. For instance, by differential use of ranges, mature males are thought to maximize nutrient intake, whereas females and young minimize predation risk (Ober 1931, King and Smith 1980, Geist 1982, Festa-Bianchet 1988, McCullough et al. 1989, Main and Coblentz 1990).

Strategies of predator evasion might influence the distribution of the sexes. Because of their smaller body size, females and especially juveniles are particularly susceptible to predation (Curio 1976) and often inhabit precipitous terrain, where forage quantity or quality may be lower than nearby less-precipitous habitats, but where their ability to evade predators is enhanced (Geist 1981). On the other hand, males may take more risks to obtain nutrients to ensure growth and large body size necessary for successful competition for mates (Trivers 1972). McCullough (1979) suggested that the preponderance of adult male ungulates in the diet of many predators reflected the greater risks associated with sexual competition. Consistent with this notion, several investigators (Wehausen 1980, Shank 1982, Festa-Bianchet 1986) reported that male mountain sheep occurred on higher quality sites than did females, but others (Charles et al. 1977, Watson and Staines 1978, Staines et al. 1982, Beier 1987, Clutton-Brock et al. 1987) noted the opposite to be true among other species of ungulates.

This hypothesis of predator evasion holds the potential to explain sexual segregation for species in which adult females occur on areas of either higher or lower quality than do adult males. For instance, if females are relegated to areas of precipitous terrain necessary to evade predators, males might be able to exploit areas too risky to be used regularly by females, especially ranges with high quality forage. Conversely, if areas with escape cover also possessed high quality forage, then females could occur on higher quality ranges than do males. Likewise, where high quality areas allow the formation of large groups of females, that sex may be able to reduce its risk of predation through group

advantages (Hamilton 1971) while occupying good quality range. These last 2 scenarios do not explain why males should occupy lower quality sites during segregation; however, predation coupled with size differences between the sexes and differing population densities on male and female ranges might produce this pattern.

If females and young segregate from males principally to minimize risk of predation, we predict that

1. Females will occupy more rugged areas, with greater opportunities to evade predators than do males.
2. Relative numbers of predators will be lower on ranges primarily occupied by females than on ranges inhabited by mature males.
3. Females may obtain a lower quality diet than do mature males.

Predictions from these 4 basic hypotheses were subdivided into a limited number of categories relative to data required to test them. Hence, we concentrated our effort on (1) physical differences in the habitats used by the sexes, (2) the availability of forages of differing nutrient value, (3) resulting differences in diet quality, (4) availability and use of water, and (5) predator abundance.

Objectives and Implications of the Research

Our objectives were to (1) describe and quantify sexual segregation in a population of mountain sheep inhabiting a desert ecosystem and (2) test 4 hypotheses (Table 1) to explain sexual segregation among polygynous ungulates. Hypotheses potentially explaining sexual segregation in ungulates have been the subject of some controversy (Main and Coblentz 1990, Main et al. 1996). Information from a large number of ungulates existing under diverse conditions is necessary to explain any general adaptive significance of sexual segregation (Miquelle 1990*b*); perhaps, however, no universal, single explanation for this phenomenon exists (Main and Coblentz 1990, Miquelle et al. 1992).

Understanding how male and female mountain sheep partition space and resources, and the demographic consequences thereof, expands our knowledge of sexual selection in polygynous ungulates and may be important in the conservation of this species. Likewise, knowledge of why the sexes remain apart outside the mating season is necessary to the understanding of habitat use and may advance modeling of population dynamics. Information for mountain sheep inhabiting desert environments is especially important to understand the complex habitat and nutritional relationships exhibited by these large mammals. Results from our research will have important implications for habitat conservation (e.g., Bleich et al. 1990*a*) and for the persistence of these large, unique ungulates. Moreover, these results will be useful when selecting sites to re-establish populations of mountain sheep (Bleich et al. 1991, 1992*a*).

Acknowledgments.—We thank the California Department of Fish and Game for providing V. C. Bleich (senior author) a leave of absence to pursue graduate work at the University of Alaska Fairbanks (UAF). At UAF, F. H. Fay, R. D. Guthrie, D. R. Klein, and V. Van Ballenberghe provided reviews of the manuscript, numerous editorial suggestions, and many hours of stimulating discussion. Others at UAF who contributed to the success of this project include C. J. Button, L. R. Burleigh, F. S. Chapin, J. F. Fox, M. Klingensmith, M. E. Laursen, S. F. MacLean, L. Morisky, N. Mosso, T. Picolo, P. X. Quang, R. G. White, and J. A. Yarie.

M. A. Charpentier, M. C. Nicholson, and D. Pearson provided training and support in the use of a Geographical Information System, and B. D. Bowyer prepared the graphics. D. J. Clark, J. R. Jaeger, T. Manning, and W. D. McIntyre served as capable field assistants. At the California Department of Fish and Game, R. K. Clark, W. E. Clark, J. L. Clark, L. J. Coombes, J. K. Fischer, D. R. Hunter, D. A. Jessup, K. R. Jones, R. A. Teagle, J. R. Thompson, S. G. Torres, and R. A. Weaver contributed substantially to the success of

this project, and we especially thank R. W. Anthes, A. M. Pauli, and R. L. Vernoy for conducting the telemetry flights.

Helicopter pilots S. DeJesus, B. K. Novak, and the late J. D. "Don" Landells are recognized for their skill and professionalism in survey and capture operations, and we extend special thanks to the entire crew at Landells Aviation for their support in meeting research objectives. Others who contributed in meaningful ways include the late J. C. Bickett, T. Eskey, L. D. Foreman, J. G. Kie, L. M. Lesicka, A. Pfister, B. M. Pierce, R. R. Ramey II, and G. W. Sudmeier. Finally, Teresa, Theron, and Anastasia Bleich warrant special recognition for their sacrifices on behalf of this project.

All aspects of this research complied with acceptable field methods adopted by the American Society of Mammalogists (Am. Soc. Mammal. 1987) and were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks. This is a contribution from the California Department of Fish and Game Mountain Sheep Management Program.

STUDY AREA

The study area encompassed Old Dad Mountain, Cowhole Mountain, the Kelso Mountains, and the Marl Mountains in San Bernardino County, California (Fig. 1). This is part of a larger metapopulation of mountain sheep described by Schwartz et al. (1986). The immediate surrounding area includes expansive lava beds located north of the Kelso Mountains and a large area of relatively stable sand dunes (the Devils Playground) west of Old Dad Mountain. The study area encompasses 1,265 km².

Nearby ranges include the Bristol, Soda, and Providence mountains. We documented movements of mountain sheep among all ranges in the study area except the Bristol Mountains. Old Dad Mountain reaches an elevation of 1,308 m, and the maximum elevation of the Marl Mountains is 1,387 m; Kelso Peak has an elevation of

1,466 m. Within the study area, the desert floor gradually gains elevation from west to east, and intermountain areas range in elevation from approximately 300 m at the base of Cowhole Mountain to about 1,750 m near the Providence Mountains, southeast of the Marl Mountains. Old Dad and Cowhole mountains are composed mostly of limestone, and the Kelso and Marl mountains are primarily of granitic origin. South and east of Old Dad Mountain, major ridges of volcanic origin occur. The geology of Old Dad Mountain and vicinity has been described in detail by Barca (1966), Dunne (1977), and Curry and Resigh (1983).

Daytime maxima in summer normally exceed 38 C, and winter low temperatures below freezing are not uncommon (R. A. Weaver, J. L. Mensch, and R. D. Thomas, A report on bighorn sheep in northeastern San Bernardino County, California, Fed. Aid in Wildl. Restor. Final Rep., Proj. W-51-R-14, Calif. Dep. Fish and Game, Sacramento, 26pp., 1969). Annual precipitation in the vicinity of the study area averaged 8 cm, with about 50% falling as localized summer thundershowers (Fig. 2) (Freiwald 1984). A pronounced drought occurred in 1990 with only 3 cm of precipitation.

Ten sources of water used by mountain sheep were present in the study area (Fig. 1) and availability of water at most of the natural springs was unpredictable. Four artificial sources provided water on a year-round basis (Bleich and Pauli 1990) and were used heavily by mountain sheep, particularly during summer (Bleich 1983a, Jaeger et al. 1991). Two ephemeral springs in the volcanic badlands receive only occasional use by mountain sheep.

Martens and Baldwin (1983) and Bleich (1993:appendix A) described 6 primary vegetation communities in the study area (Fig. 3):

1. creosote bush (*Larrea tridentata*) scrub (CBS),
2. wash scrub (Wash),
3. *Yucca-Ephedra* scrub (YES),
4. partially stabilized dunes,

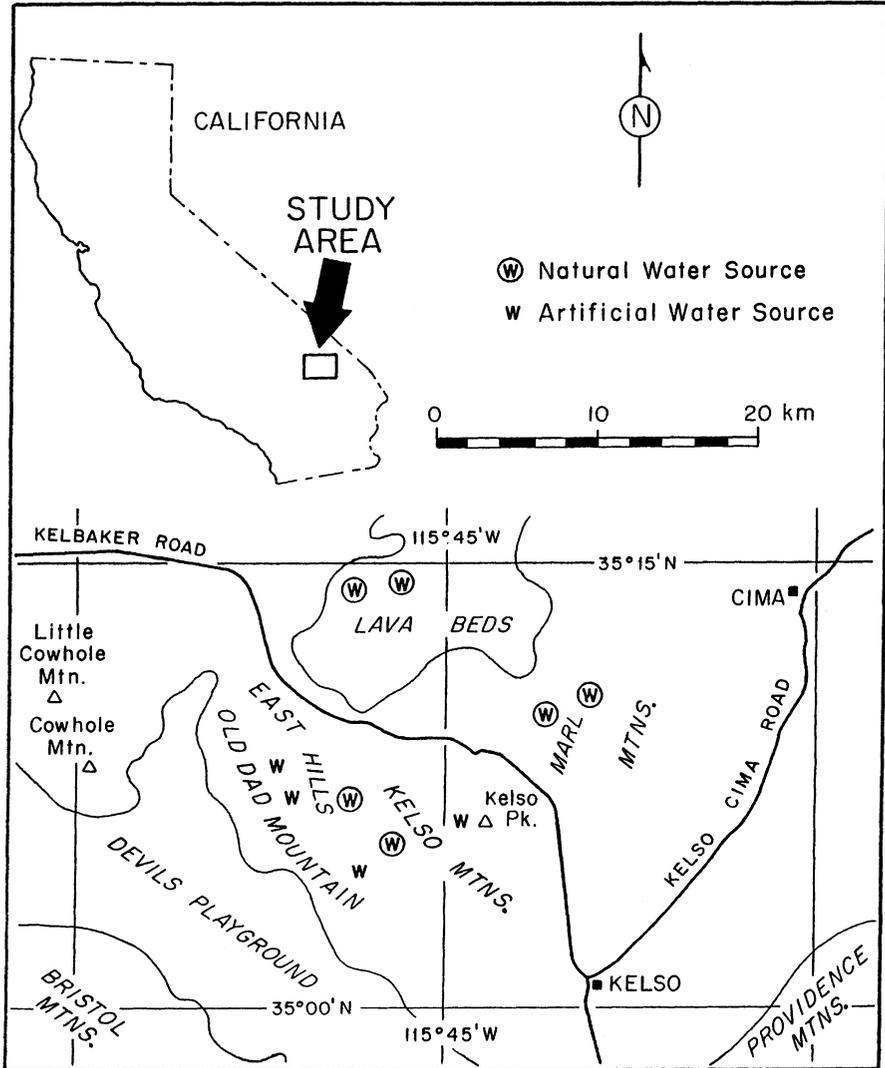


Fig. 1. Study area in San Bernardino County, California, showing the desert mountain ranges inhabited by mountain sheep.

5. stabilized dunes, and
6. rupicolous scrub (RS).

A seventh vegetation type, intermediate in characteristics between CBS and YES, which occurred between the upper limits of CBS and the lower limits of YES, is the transition zone (TZ). A primary characteristic of the TZ was its remarkably dissimilar vegetation on different slope aspects. In general, north-facing slopes supported vegetation similar to YES; all other aspects

within the TZ have vegetation typical of CBS (Martens and Baldwin 1983).

In the eastern portion of the study area, YES, CBS, and TZ vegetation associated with lava flows were identified as such (Fig. 3). Areas almost devoid of vegetation also occurred east of Old Dad Mountain; these areas were identified as "cinder" for descriptive purposes. We grouped stabilized dunes and partially stabilized dunes into a single vegetation category termed Dune.

With the exception of wolves, the study

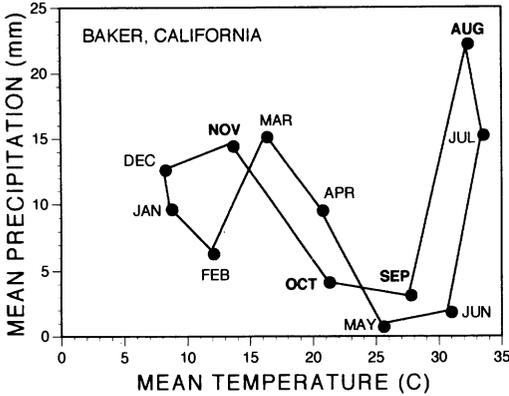


Fig. 2. Thermograph of monthly precipitation and temperature 30 km northwest of Old Dad Mountain, San Bernardino County, California, 1983–89.

area contained a full complement of native large carnivores, including bobcats, mountain lions, and coyotes (the most common predator) (Johnson et al. 1948). Mountain lions were not reported in the eastern Mojave Desert by Johnson et al. (1948); these

large felids apparently colonized the study area following the introduction of mule deer in 1948 (Longhurst et al. 1952).

Mule deer occurred only infrequently in the study area; other sympatric ungulates include domestic cattle and feral asses (>100 animals). Three livestock allotments overlapped the study area. Cattle were grazed during spring, autumn, and winter in the Kelso and Marl mountains and on sandy areas south of Old Dad Mountain. Approximately 160 female and 205 male mountain sheep inhabited the study area (Jaeger et al. 1991). Based on the estimates of Jaeger et al. (1991) and the distribution of mountain sheep (this paper), males occurred at a slightly higher overall density (0.32/km²) than did females (0.27/km²). This difference in density is a bias resulting from the translocation of more female than male sheep from the study area (Bleich et al. 1990b). Nonetheless, a high density of females occurred in the RS vegetation type during periods of segre-

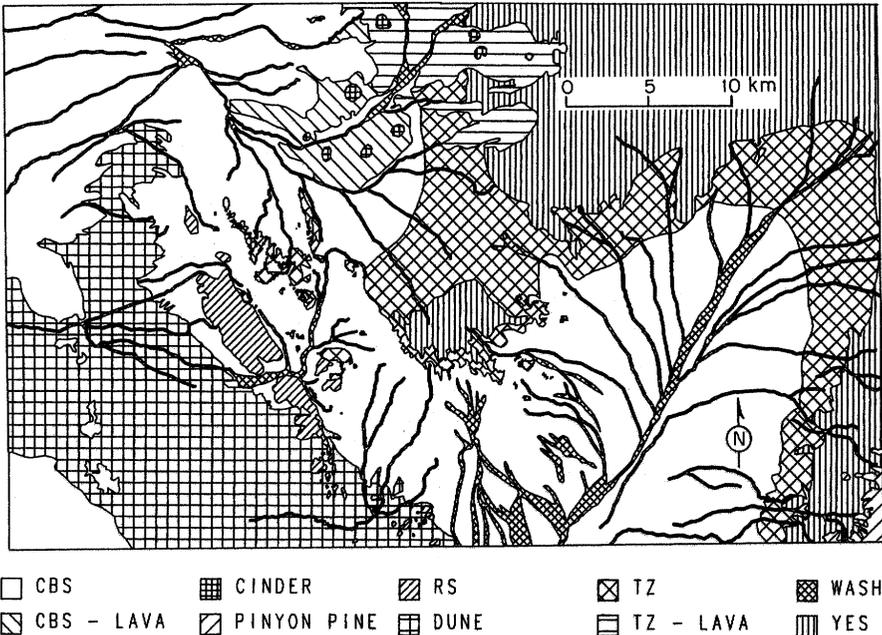


Fig. 3. Distribution of vegetation types in the Old Dad Mountain–Kelso Mountains study area, San Bernardino County, California. Vegetation types are as follows: CBS = creosote bush scrub; Cinder = creosote bush scrub on cinder cones; CBS–Lava = creosote bush scrub on lava flows; RS = rupicolous scrub vegetation; TZ = transition zone vegetation; TZ–Lava = transition zone vegetation on lava flows; Wash = wash vegetation; Dune = dune vegetation; YES = *Yucca-Ephedra* scrub vegetation; Pinyon Pine = pinyon pine vegetation.

gation compared with ranges used by males at that time.

The study area has been open to limited hunting of mountain sheep since 1987, with 25 mature males harvested through the 1991 hunting season (Bleich et al. 1992a). From 1983 to 1989, 172 mountain sheep (46 males, 126 females) were removed from the study area for translocation to other historical ranges (Bleich et al. 1990b).

METHODS

Capture and Measurement of Mountain Sheep

From September 1986 to June 1990, we captured 44 mountain sheep (27 males, 17 females) and fitted them with radio collars incorporating mortality sensors (Telonics, Inc., Mesa, Ariz.) (Bleich et al. 1990c). Most individuals were captured using a hand-held net gun (Krausman et al. 1985b) fired from a Bell 206B-III helicopter flown by a pilot experienced in that procedure (Bleich 1983b); 2 animals were captured by driving them into a net (Beasom et al. 1980).

We estimated the age of each radio-collared animal using patterns of incisor replacement (Deming 1952) and horn-growth rings (Geist 1966). We also determined body weight (to the nearest 0.5 kg) using a platform scale and chest girth (to the nearest 1.0 cm) for 172 mountain sheep in the study area during 1983–89 to evaluate the degree of sexual dimorphism in this population.

Radiotelemetry

We relied on telemetry data for intersexual comparisons of habitat use and movement patterns and to determine the home ranges and range fidelity of rutting males on an annual basis. We attempted to locate radio-collared animals once each week from 1 October 1986 to 31 December 1990 using a fixed-winged aircraft (Cessna 185) flown by an experienced pilot, but inclement weather precluded strict

adherence to that schedule. The aircraft was equipped with a directional "H-antenna" (Telonics, Inc., Mesa, Ariz.) on each wing strut. Locations of radio-collared animals were determined in a manner similar to that described by Krausman et al. (1984), and geographic positions were estimated using LORAN-C (Boer et al. 1989). Some locations of radio-collared mountain sheep were confirmed visually during 14 flights, and each coincided with the location of the strongest telemetry signal on those occasions.

To evaluate the bias of the LORAN-C navigation system, we used the airplane to obtain 16 sets of geographic coordinates for each of 6 easily recognized ground features in the study area. We estimated the geographic coordinates of each of these features by digitizing them from USGS 7.5-minute (1:24,000) topographic maps. On average, LORAN-C coordinates indicated the aircraft was 161 m east and 104 m north of ground features. We corrected all geographic coordinates recorded by LORAN-C by these values prior to initiating any analyses (Patric et al. 1988).

Errors associated with telemetry locations estimated using LORAN-C (Jaeger et al. 1993) were small relative to the home ranges of sheep (≥ 5 km²). Such accuracy was adequate for this investigation because categories of vegetation and slope occurred over relatively large, homogeneous areas. We chose to not consider aspect as a variable in our analyses because of its potentially greater sensitivity to resolution problems resulting from the small size of aspect polygons relative to potential location error.

Aerial Surveys

Data from 20 helicopter surveys conducted from May 1981 to December 1990 were used to determine periods of sexual segregation and aggregation as well as for intrasexual comparisons where group composition was important. A pilot and 3 observers experienced in those procedures (Bleich 1983b) participated in all surveys. The study area was partitioned into 5 sur-

vey polygons (26–83 km²), and each was searched systematically (Bleich et al. 1990*d*) at an average intensity of 2.5 minutes/km². During helicopter surveys, vertical and lateral distances to the ground varied considerably because of high topographic diversity within survey polygons (Bleich et al. 1990*d*, 1994). Each observation of a mountain sheep was plotted on USGS 15-minute (1:62,500) topographic maps, and these locations were digitized and converted to Universal Transverse Mercator (UTM) Grid coordinates (Monmonier and Schnell 1988). Marked animals seen during these surveys also were recorded as were other ungulates and predators. Although helicopter overflights of mountain sheep disturbed them, these animals did not become sensitized or habituated to this aerial sampling (Bleich et al. 1994). Moreover, sheep did not begin moving until they were directly overflown (Bleich et al. 1994). Consequently, we believe this sampling method provided unbiased data on habitat use by sheep.

Ground Observations

Ground observations were made from June 1987 to December 1990, and these data also were used to define periods of sexual segregation and aggregation. Because the intent of ground surveys was to obtain data on the female and lamb cohorts of the population, these efforts were concentrated in areas used primarily by females and lambs and, thus, were not appropriate for other analyses. Observations were recorded on USGS 15-minute topographic maps and later digitized and converted to UTM coordinates.

Time-lapse Photography

We used time-lapse photography (Jaeger et al. 1991) to record sheep at water sources. Photographs were taken every 60 seconds during adequate daylight, and cameras were positioned to facilitate the correct classification of sheep (Jaeger et al. 1991). Cameras operated almost constantly during June through September 1988

and again during June through September 1989, 4 days/month during October 1989 through May 1990, and on 4 days during July 1990.

We analyzed each frame of film using the “groups-per-frame” method of Jaeger et al. (1991) to help ensure that samples were independent. These data supplemented those obtained during ground and aerial sampling to determine periods of sexual segregation, to evaluate seasonal use of water sources by sheep, and to assess the relative abundance of carnivores.

Group Composition

For statistical purposes, a group consisted of ≥ 1 mountain sheep. During aerial surveys, animals ≤ 100 m from each other were considered to be in the same group because the noise associated with the aircraft may have caused groups to begin fragmenting as they were observed. During ground sampling, undisturbed animals were placed in the same group if they were ≤ 50 m from one another (Siegfried 1979) or appeared to be aware of the presence of other nearby conspecifics and moved cohesively. Sheep in the same photograph were considered to be a social group.

Each sheep was classified (Geist 1968) as a Class I, II, III, or IV male; yearling female; adult female (≥ 2 yrs old); or lamb (individuals of either sex, < 1 yr old). Class I males were < 2 years old and are referred to as yearling males. Class II males generally were 2–3 years old and are referred to as young males. Class III and IV males were ≥ 4 years old and were termed mature males. All males \geq Class II were considered to be adults.

We recognized 5 major social groups (Hirth 1977) of sheep. Female groups contained ≥ 1 adult female, but could include yearlings or lambs. Male groups contained ≥ 1 Class II, III, or IV males and also could include Class I males, but contained no females or lambs. Mixed groups contained ≥ 1 adult male and 1 female and any other group members. Yearling groups consisted of yearlings of either sex and

rarely included lambs. Lamb groups contained only young-of-the-year.

Vegetation Sampling

During April 1990, we quantified vegetation using 92 randomly located step-point transects (Evens and Love 1957, as modified by Bowyer and Bleich [1984]). We recorded a cover "hit" if the point (<1 mm in diameter) fell within the canopy of a shrub or on a stem or leaf of a plant; a frequency hit was recorded if the point contacted the stem of any plant where it entered the ground. Points not recorded as frequency or cover for plants were tallied as bare ground (including rocky substrates). Each transect contained about 300 step-points (recorded every other step; approx 2 m apart) that were used to calculate percent cover and frequency for that transect. Adequate sample size for each vegetation type was determined by cumulatively summing the percent cover of the 5 most common plant species across transects until the means stabilized (Kershaw 1964:29). We also sampled annual vegetation during April 1991 and April 1992. Plant nomenclature follows Munz (1974).

At the beginning, middle, and end of each step-point transect, we estimated horizontal cover using a cover-pole (Griffith and Youtie 1988). Cover-poles were 2 m long, and divided into 8 bands, each 25 cm in length. An observer recorded cover of the pole from 4 directions from a distance of 15 m. These directions were at right angles to one another, and the initial direction was selected randomly. The percentage of each band not visible from the 4 directions was estimated. The average cover for each 1-m length of the cover pole was then calculated, using the 16 values estimated for that increment of the pole. Horizontal cover for each vegetation type is expressed as the mean percent of the pole not visible from >1 m and from ≤ 1 m above the ground. To quantify the role of geomorphic features in determining horizontal cover, we recorded those instances in which rocks or changes in slope

affected cover as measured by the pole; these were expressed as the mean number of occurrences/1-m increment of the cover-pole for each vegetation type.

Habitat Characteristics

We used a Geographic Information System (GIS) to create a coverage of vegetation types. We used commercially available digital-elevation models (SoftWright, Inc., Aurora, Colo.) with the triangulated irregular network (TIN) module of ARC/INFO (Environmental Systems Research Institute, Inc., Redlands, Calif.) to create a 3-dimensional surface model of the study area and later converted this to a 2-dimensional polygon coverage. From the TIN, the elevation and slope of ground, aerial, and telemetry locations of mountain sheep were determined (Bleich et al. 1992*b*). Additionally, we calculated the distance from each sheep location to the nearest available source of water to serve as an index of the importance of this resource to sheep.

We created an index of terrain ruggedness by converting the 3-dimensional surface model into a coverage of 12-m contour lines. Grids, each 1 km by 1 km, were overlaid on the study area, and the number of arcs forming the contour lines within each square was tallied. Using the GIS, this index of ruggedness was associated with each sheep location according to its grid square. Because of the large size of the grid cells, the total number of contour lines occurring within each cell provided an indirect measure of overall topography; the more rugged the terrain, the greater the number of contour lines that occurred in that cell.

We developed separate coverages for vegetation type and slope based on minimum-convex polygons created from telemetry data for periods when the sexes were segregated and aggregated and for year-round distributions of sheep. Each of these polygons then was enlarged with a buffer of 1,000 m, and the resulting polygons were used to determine the availability of 9 categories of slope steepness

within each buffered area. Using the GIS, new coverages containing information on slope were created, and summary information concerning the availability of these slope classes was generated. In a similar manner, new vegetation coverages were produced for each buffered minimum-convex polygon. We generated summary statistics concerning the availability of vegetation types from these coverages. We used these data, in combination with plant cover on ranges used by males and females, to develop an index of forage availability for each sex.

Diets of Mountain Sheep

Whenever possible, we collected fresh fecal pellets ($n \geq 25$) each month from July 1987 to June 1990 from individuals of known sex and age; otherwise, feces were obtained from female or male groups. During sexual segregation, sampling was concentrated in parts of the study area used predominantly by males or females. During rut, male sheep regularly occurred in areas otherwise used by females, and fecal samples were collected from males when encountered. As samples were collected, we placed them in paper bags and air-dried them until further processing.

Fecal samples were analyzed by a technician familiar with diets of desert sheep (Krausman et al. 1989) at the Forage Analysis Laboratory, University of Arizona, using the method of Sparks and Malechek (1968). Three slides per pellet group were prepared (Holechek and Vavra 1981), the frequency of a species appearing in each of 20 randomly selected microscope fields per slide was determined (i.e., 60 fields/pellet group), and these data were used to estimate percent diet composition of feces. We used Schoener's (1968) value to compare overlap in diets of males and females.

To avoid artificial inflation of sample sizes (Hurlbert 1984), we calculated the average frequency with which a forage species appeared on each slide and converted these values to relative particle density (Sparks and Malechek 1968) for each sample (pellet group). Thus, the number

of monthly samples for each sex was equal to the number of pellet groups examined. Mean particle density was then calculated by summing the relative density for each forage species and dividing the result by the total number of samples. We categorized plants as annuals (forbs and grasses combined), perennial forbs, perennial grasses, woody perennials, and succulents (cacti).

Absolute determination of sheep diets from microhistological analysis may be problematical because of differential digestibility of some forages (Fitzgerald and Waddington 1979). We assume, however, that this technique provides an index to diets of male and female sheep.

Diet Quality

Fecal crude protein (FCP = fecal nitrogen $\times 6.25$) usually was determined for ≥ 5 individual pellet groups/sex/month using micro-Kjeldahl digestion at the Wildlife Habitat Laboratory, Washington State University or the University of Alaska Agricultural Experiment Station, Palmer. To investigate overall differences between sexes in diet quality during segregation, we integrated the curve of monthly mean FCP above a baseline of 5% (< the minimum value recorded) for the segregation period, divided this area by the number of days between end points, and multiplied it by 100. This measure indexed average diet quality over the entire period of segregation in lieu of emphasizing monthly differences in mean FCP (J. D. Wehausen, Demographic studies of mountain sheep in the Mojave Desert: report IV, Calif. Dep. Fish and Game, Sacramento, Final Rep. FG9239, 54pp., 1992).

Although FCP frequently correlates with nitrogen level of the diet, Wehausen (1995) showed that FCP primarily indexes apparent digestibility. Moreover, this index varies with the quality of habitat for ungulates (Hodgman and Bowyer 1986). The ability of this measure to index diet quality can be confounded if the diet contains sufficient levels of forage species high in protein-complexing phenolics (Robbins et al.

1987). We tested the relationship between FCP and the shrub component of the diet (considered to be the primary source of phenolics) to determine the potential effects of phenolics on our results.

Forage Quality

Percent *in vitro* dry matter digestibility (IVDMD), percent crude protein (CP), and percent moisture content were determined on a monthly basis for 20 plant species eaten by mountain sheep. Samples were collected from portions of the study area inhabited almost exclusively by either sex during the nonrutting period. Data from Bleich et al. (1992c) were combined by forage class and reanalyzed to evaluate potential differences in IVDMD, CP, and moisture content. These analyses were conducted at the Wildlife Habitat Laboratory, Washington State University.

Relative Abundance of Predators

We indexed relative abundance of potential predators using 3 independent measures: (1) predator feces on transects, (2) time-lapse photography at water sources, and (3) aerial surveys. Data were recorded from areas used predominantly by mature males or females.

Belt transects ($n = 93$) were sampled coincident with the routes hiked ($\bar{x} \pm SE$; 8.0 ± 0.31 km) when conducting surveys of sheep during 1987–88. We tallied all fresh (unbleached) predator feces within 1 m either side of a line of travel (Pelton 1972, Hone 1988); no transects were re-sampled. Predator feces (scats) were identified according to characteristics described by Murie (1954) and Danner and Dodd (1982). Sparse ground cover in this arid environment reduced the likelihood that scats were overlooked. Relative abundance is expressed as scats per hectare.

We used time-lapse photography to record daytime visits to water sources by coyotes, bobcats, gray foxes (*Urocyon cinereoargenteus*), and kit foxes (*Vulpes macrotis*); no mountain lions were recorded. Because foxes and juvenile coyotes some-

times were not distinguishable, these carnivores were pooled in a category termed "other." Bobcats and adult coyotes occasionally may have been placed in this category.

Time-lapse cameras at 2 water sources (Kelso Guzzler and Jackass Spring) were located in areas used predominantly by male mountain sheep; 2 others (Old Dad and Kerr guzzlers) were in areas used predominantly by females. Relative abundance of predators at water sources was expressed as the number of predators (by species)/10,000 frames of film.

We also recorded predators observed in sampling polygons (Bleich et al. 1990d) during >100 hours of helicopter surveys ($n = 20$). Abundance was expressed as predators/survey hour/km² $\times 1,000$.

Predator Diets

We collected predator scats from the aforementioned transects ($n = 60$) and when they were encountered during other field activities ($n = 60$). These were analyzed for prey remains following the procedures of Bowyer et al. (1983) based on the identification of ungulate hairs by their characteristic morphology (Mayer 1952). In the field, we carefully examined carcasses of mountain sheep and, if evidence was adequate, the predator was identified according to the criteria of Shaw (1983) or Woolsey (1985).

Data Analyses

Statistics used in this study include multivariate and univariate tests. We examined assumptions of each test and transformed data (\log , SIN, COS, SIN⁻¹, rank) as necessary to meet these assumptions. In some instances, we substituted the appropriate nonparametric test (e.g., Mann-Whitney, Kruskal-Wallis and Friedman tests, and Spearman correlation; Zar 1984) for t tests, analysis of variance, or regression. Proportions were examined with the Z test; the G test was used for most categorical analyses (Zar 1984). We used SYSTAT (Wilkinson 1988) or BMDP software (Dix-

Table 2. Degree of sexual dimorphism as reflected in body mass and girth for sex and age classes of mountain sheep, San Bernardino County, California, 1983–89.

	Males ^a						Females							
	Class III & IV (n = 16)		Class II (n = 8)		Yearling (n = 12)		Lamb (n = 11)		Adult (n = 90)		Yearling (n = 22)		Lamb (n = 14)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Body mass (kg)	70.2	3.0	58.5	2.9	40.7	2.7	27.8	8.5	47.9	2.6	35.0	1.2	26.4	1.6
Girth (cm)	98.0	2.1	92.2	1.8	83.9	2.0	75.3	11.4	89.0	1.3	78.3	1.2	72.5	1.8
Age (yrs)	5.3	0.4	2.8	0.2	1.0	0.0	<1.0 ^b		5.1	0.7	1.0	0.0	<1.0 ^b	

^a Class II males were 2–3 years old; Class III and IV males were ≥ 4 years old.

^b Most lambs were captured in December and were approximately 8–10 months old.

on 1985) for most analyses. In all instances, an $\alpha = 0.05$ was adopted.

We corrected telemetry locations for each animal for autocorrelation (Solow 1989) using BLOSSOM statistical software (Slauson et al. 1991) to generate a subset of statistically independent data points. The resulting point locations were used in subsequent analyses of habitat selection (Neu et al. 1974, Heisey 1985); each animal contributed a near equal number of observations for these analyses.

We plotted home ranges (minimum-convex polygon) of mature males that inhabited the study area during ≥ 2 consecutive periods of sexual aggregation using CALHOME software (Kie et al. 1994). Home ranges of individual males during aggregation were overlaid on each other, and those overlapping by $\geq 50\%$ were considered to demonstrate home range fidelity.

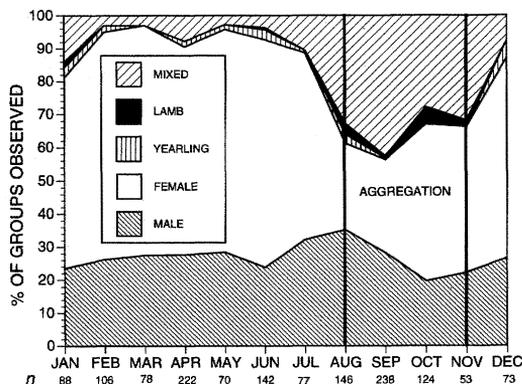


Fig. 4. Percent of social groups of mountain sheep based on ground and aerial sampling, San Bernardino County, California, 1981–90. The period of sexual aggregation is the rut.

RESULTS

Sexual Dimorphism

Desert-dwelling mountain sheep exhibited extreme sexual dimorphism in body weight (Table 2). Class III and IV males were about 1.5 times heavier than adult females, and Class II males were about 1.2 times heavier; yearling males and male lambs also were slightly larger than their female counterparts.

Social Aggregation and Segregation

There was a significant positive correlation ($r_s = 0.68$, $P < 0.05$, $n = 11$) between the percent of mixed groups per month in aerial ($n = 869$ total groups) and ground ($n = 548$) sampling, suggesting these 2 sampling methods yielded similar results; consequently, both data sets were combined (Fig. 4).

A difference ($Z = 2.6$, $P = 0.004$) was evident between the proportion of mixed groups occurring August–November ($\bar{x} = 18.4 \pm 1.8\%$) and December–July ($\bar{x} = 3.3 \pm 0.5\%$). Indeed, most mixed groups (73.5%) occurred during August–November (Fig. 4); consequently, the season of sexual aggregation was defined as that period, and sexual segregation as December–July. Likewise, 221,854 frames of time-lapse camera film at water sources used by both sexes indicated that mountain sheep ($n = 361$ groups) occurred twice as often in mixed groups during aggregation (14%) as during segregation (7%). Significant differences in the proportion of mixed groups between these periods occurred from July

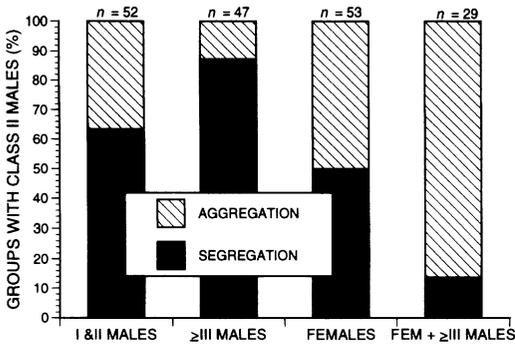


Fig. 5. Associations of Class II males (as determined by ground and aerial observation) in other social groups of mountain sheep during periods of aggregation and segregation, San Bernardino County, California, 1981–90.

1988 to June 1989 ($G = 9.13$, 3 df, $P = 0.03$) and from July 1989 to June 1990 ($G = 18.26$, 3 df, $P = 0.002$).

Because some mixed groups (Fig. 4) contained males no larger than Class II, and these males are important in testing hypotheses concerning sexual segregation (Table 1), we further examined how these males associated with other sheep (Fig. 5). Significant differences existed in the percent of Class II males associating with groups containing females, other young males (Class I and II), mixed groups with mature males (Class III and IV), and groups containing only mature males ($G = 22.44$, 3 df, $P < 0.001$). During segregation, groups containing Class II males and males \geq Class III occurred more frequently than those containing Class II males and females (Fig. 5). During aggregation, Class II males were observed often with females and, especially, in groups containing both females and mature males (Fig. 5).

During July through December, we observed 711 groups of sheep, of which 189 groups contained adult females and males \geq Class I. We observed a total of 640 males (75 Class I, 120 Class II, 285 Class III, 160 Class IV) during that period, and 308 of these individuals occurred in mixed groups. Yearling and young males associated with female sheep earlier in the year than did mature males; conversely, following the period of sexual aggregation, mature males disassociated with females

more rapidly than did yearling and young males (Fig. 6).

Group Size

A 3-way ANOVA (1, 1,358 df) indicated that group size of mountain sheep varied by survey type ($F = 24.10$, $P < 0.001$), periods of segregation and aggregation ($F = 99.00$, $P < 0.001$), and type of social group ($F = 26.60$, $P < 0.001$) (Fig. 7). Overall, mixed groups ($\bar{x} = 5.3 \pm 0.25$, $n = 207$) were larger than female ($\bar{x} = 3.4 \pm 0.11$, $n = 738$), male ($\bar{x} = 1.9 \pm 0.07$, $n = 424$), yearling ($\bar{x} = 1.9 \pm 0.07$, $n = 31$) and lamb ($\bar{x} = 1.9 \pm 0.36$, $n = 17$) groups.

Spatial Distribution

Whether males joined females during sexual aggregation or vice versa is an important consideration (Table 1). On an annual basis, approximately 70% of the observations of radio-collared female mountain sheep occurred at Old Dad Mountain (Fig. 8). No significant difference ($G = 4.06$, 3 df, $P = 0.26$) existed in the distribution of females between segregation and aggregation. Female mountain sheep remained primarily in those areas typified by steep, open terrain. In contrast, significant differences ($G = 34.82$, 3 df, $P < 0.001$) occurred in the distribution of males between segregation and aggregation (Fig. 8). Males moved to areas of concentrated use by females during aggregation and then returned to the East Hills and the Kelso and Marl mountains during segregation (Figs. 1, 8).

Range Fidelity of Male Mountain Sheep

To evaluate the hypothesis of Geist and Petocz (1977), male mountain sheep must demonstrate a high fidelity to rutting ranges from year to year. Of 27 radio-collared males in our study population, 9 mature individuals were alive during 2 consecutive periods of sexual aggregation, and 2 other mature males lived through 3 consecutive

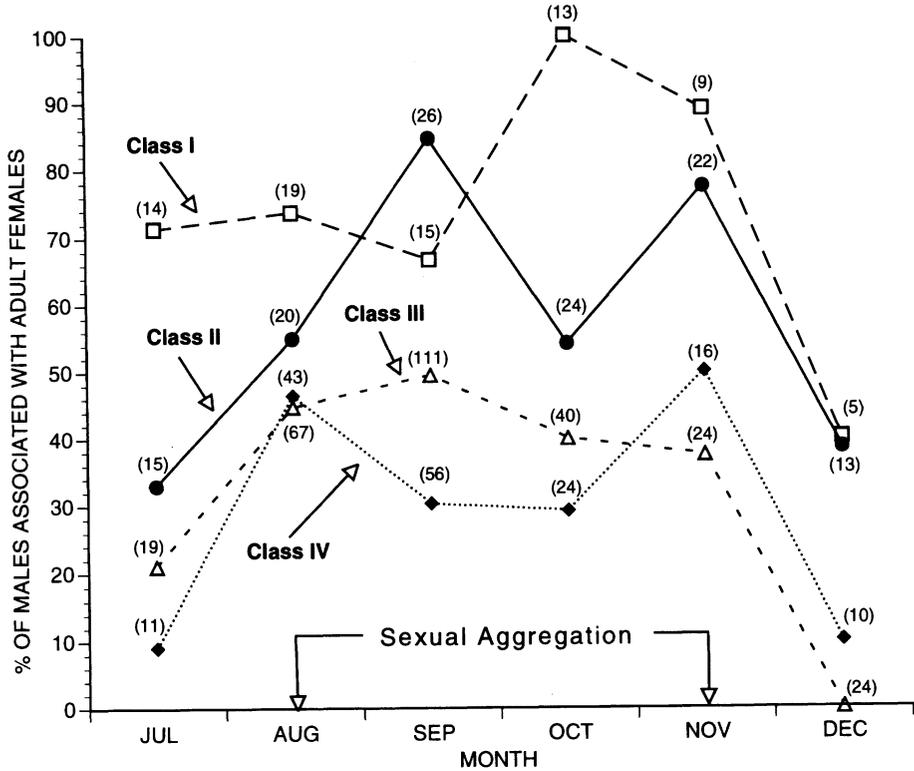


Fig. 6. Percent of males in each of 4 size categories (Geist 1968) associated with adult females during July–December, San Bernardino County, California, 1987–90. Numbers in parentheses are total number of males observed in each size class during each month.

periods of aggregation. Ten of 13 of these ranges were the same (as defined by $\geq 50\%$ overlap in home range) during consecutive years, and 3 differed during consecutive years. There was no difference ($Z = 0.177$, $P = 0.84$) in the proportion of male home ranges that were the same during sexual aggregation in the consecutive years of this study (77%) and the proportion of the rutting ranges of individual males reported to be the same by Geist (1971:table 21) during consecutive years (81%).

Composition of Plant Communities

To examine the potential role of vegetation in the way males and females used habitat, we analyzed the composition of 6 vegetation types (Fig. 9; Bleich 1993:appendix A). Percent ground cover of non-

woody vegetation (annual plants, perennial forbs, perennial grasses), succulents, and perennial shrubs was significantly different among vegetation types (Friedman's Test, $\chi_r^2 = 6.78$, 2 df, $P < 0.05$). Percent ground cover of nonwoody vegetation was greater in *Yucca-Ephedra* scrub (YES) and transition zone (TZ) (Fig. 9) than in rupicolous scrub (RS) (a vegetation type used predominantly by female mountain sheep). These data indicate greater availability of annual plants, perennial forbs, and grasses in areas used by males than those inhabited by females. Similarly, percent ground cover of woody shrubs was greater in YES and TZ than in RS, suggesting that shrub-by forages also were more abundant in areas used predominantly by males (Fig. 9).

Annual vegetation potentially is an important source of high quality forage when mountain sheep are segregated by sex. We

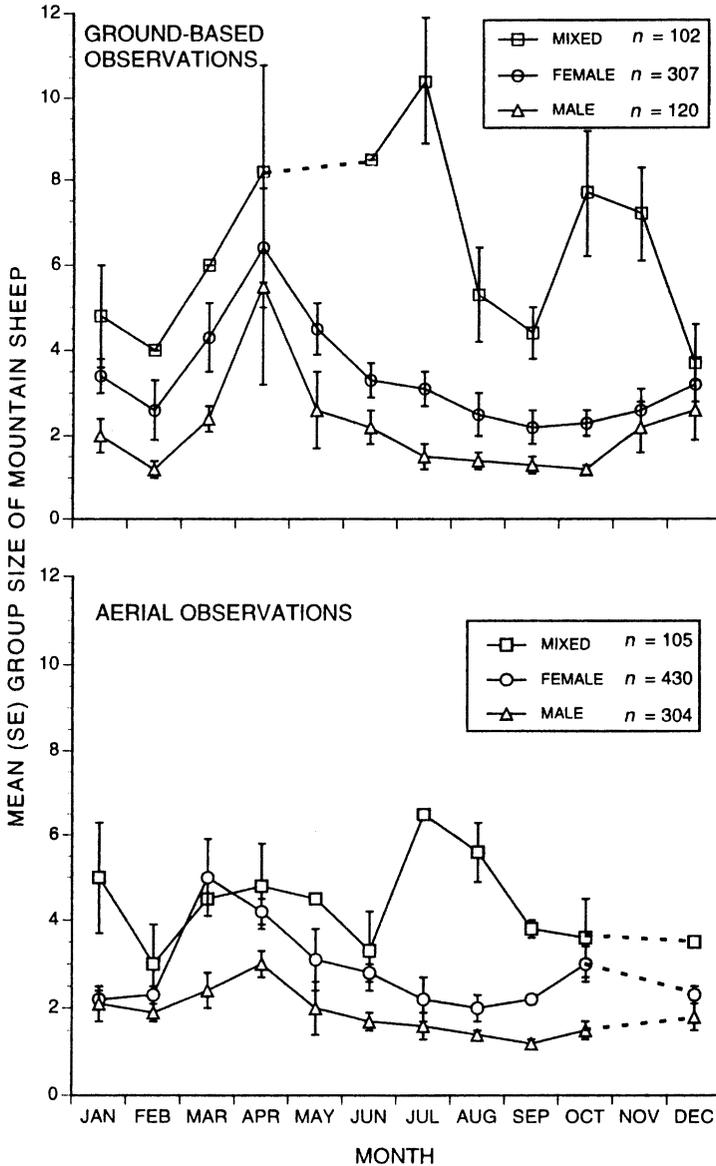


Fig. 7. Mean size of mixed, female, and male groups of mountain sheep, San Bernardino County, California, 1981–90.

compared the cover and frequency of annual plants in creosote bush scrub (CBS), YES, and RS during April for 3 consecutive years (Fig. 10). No significant differences existed in mean cover of annual plants (Kruskal-Wallis test, $\chi^2 = 5.23$, 2 df, $P = 0.15$) among these vegetative types during the drought of 1990, but differences did exist in 1991 ($\chi^2 = 12.90$, 2 df,

$P = 0.002$) and 1992 ($\chi^2 = 29.10$, 2 df, $P < 0.001$; Fig. 10).

Horizontal cover may affect visibility and be important in explaining why male and female sheep use habitats differently. Within vegetation types, horizontal cover was least from 1 to 2 m in height and greatest at ≤ 1 m above the ground (Fig. 9). Friedman's test indicated significant

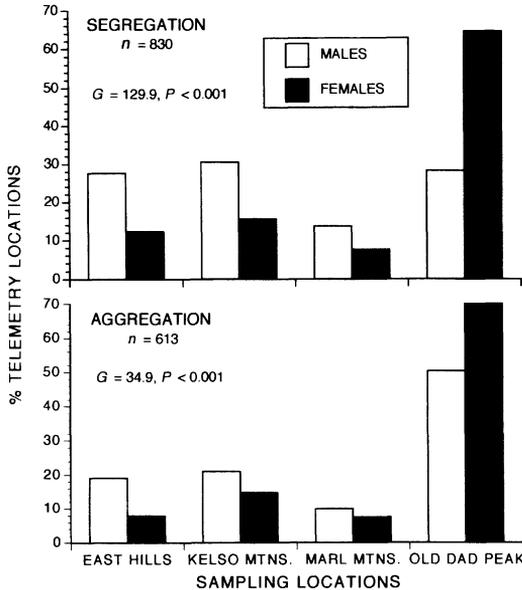


Fig. 8. Percent of telemetry locations of male and female mountain sheep on various ranges, San Bernardino County, California, 1986–90.

differences among the 6 vegetation types ($\chi_r^2 = 16.14, 5 \text{ df}, P < 0.01$). We noted a positive correlation between percent horizontal cover and the number of times geomorphic features (e.g., rocks or slope) contributed to that measure for CBS ($r_s = 0.38, P < 0.01$), YES ($r_s = 0.34, P < 0.01$), TZ ($r_s = 0.25, P < 0.01$), RS ($r_s = 0.79, P < 0.001$), and Dune ($r_s = 0.25, P < 0.001$) vegetation, but not for Wash vegetation ($r_s = 0.00, P = 1.00$). For all vegetation types, ground cover was significantly correlated with cover ≤ 1 m above the ground ($r_s = 0.89, P < 0.03$) but not for > 1 m in height ($r_s = 0.37, P > 0.25$).

Habitat Use

Radio-collared males and females used vegetation types differently between periods of segregation and aggregation ($G = 175.21, 16 \text{ df}, P < 0.001$). Females used RS more and CBS less often than did males, while use of Dune, Wash, TZ, and YES was approximately equal (Fig. 11). We noted no difference in the occurrence of females in vegetation types between

segregation and aggregation ($G = 3.88, 5 \text{ df}, P = 0.57$), but differential occurrence of males among vegetation types was evident ($G = 13.80, 5 \text{ df}, P = 0.02$), reflecting the movement of males to female ranges for rut.

To test for differences in physical characteristics of habitat in which males and females occurred, we examined a suite of variables, including distance to water, elevation, slope, ruggedness, and openness of terrain. Data from aerial telemetry and those obtained during helicopter observations were examined separately; because ground-based samples were not distributed throughout the study area, we restricted our analyses to aerial samples. For females, a 1-way MANOVA indicated no significant overall difference in the physical characteristics of habitats used between periods of sexual segregation and aggregation based on telemetry locations ($F = 1.46; 5, 704 \text{ df}, P = 0.20$). Females used similar habitats throughout the year (Table 3). When males were considered separately, a 1-way MANOVA indicated a significant overall difference in habitats used between periods of sexual segregation and aggregation ($F = 8.86; 5, 772 \text{ df}, P < 0.001$). Males occurred at lower elevations, on steeper slopes, in more rugged terrain, and in more open habitats during aggregation compared with segregation (Table 3).

A 1-way MANOVA indicated significant overall differences in use of physical characteristics of habitat between males and females during segregation ($F = 47.87; 5, 853 \text{ df}, P < 0.001$). Females occurred closer to water, at lower elevations, on steeper slopes, in more rugged terrain, and in more open habitats than did males (Table 3). Elevation was significant in this model probably because the study area increased in elevation from west to east, and males moved eastward during segregation. Consequently, males occurred at higher elevations largely independent of other habitat characteristics.

Similarly, when habitat variables were examined during aggregation, a 1-way MANOVA indicated significant overall dif-

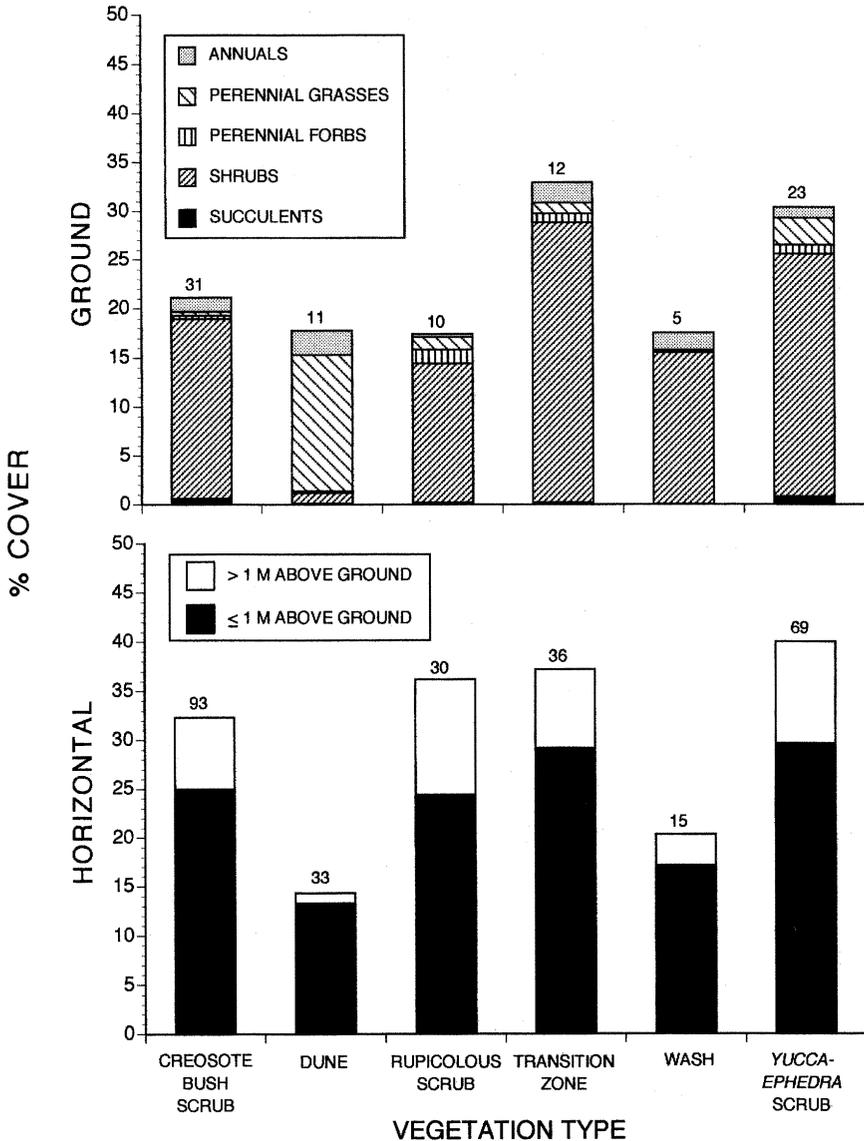


Fig. 9. Percent ground cover of vegetation classes composing habitat types and percent horizontal cover (which obscures visibility) in those types, San Bernardino County, California, April 1990.

ferences in habitat characteristics between the sexes ($F = 10.64$; 5, 623 df; $P < 0.001$). Females again occurred closer to water, on steeper slopes, in more rugged terrain, and in more open habitats, but no difference existed in the mean elevation at which females and males occurred (Table 3).

Helicopter surveys showed that female groups without lambs ($\bar{x} = 2,145 \pm 201$ m,

$n = 64$) and female groups with lambs ($\bar{x} = 2,234 \pm 214$ m, $n = 68$) occurred at similar distances to water during aggregation. Likewise, there was little difference in distance to water for these same groups during sexual segregation (without lambs, $\bar{x} = 2,553 \pm 139$ m, $n = 165$; with lambs, $\bar{x} = 2,533 \pm 171$ m, $n = 133$). ANOVA (3, 426 df) demonstrated no effect of the

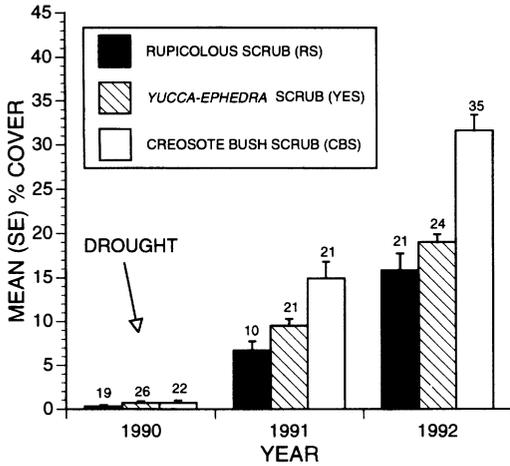


Fig. 10. Percent ground cover of annual plants during April in 3 vegetation types important to mountain sheep, San Bernardino County, California, 1990–92. Sample sizes (no. of transects in each vegetation type) appear above each bar.

presence of a lamb on distance to water ($F = 0.64$, $P = 0.42$), a marginally nonsignificant effect of period (segregation and aggregation) ($F = 3.19$, $P = 0.08$), and no lamb-by-period interaction ($F = 0.27$, $P = 0.60$). When steepness of slope and ruggedness of terrain were included as covariates (ANCOVA, 5, 424 df), there was a highly significant effect of period ($F = 6.83$, $P = 0.01$), but no effect of the presence of a lamb ($F = 0.83$, $P = 0.36$) or an interaction between these variables ($F = 0.80$, $P = 0.37$). Thus, when effects of potential escape terrain were held constant, females occurred closer to water during the hot months that composed the period of aggregation (especially Aug and Sep; Fig. 2) and occurred farther from water during segregation. This outcome suggests that suitable terrain constrained the distance that females occurred from water. There was, however, no effect of whether a female group contained a lamb, nor did we detect any small lambs with ewes at water during February–April, the period of peak lactation. Additionally, adult females visited water sources less often during this period than the remainder of the year ($\chi^2 = 5.727$, 1 df, $P = 0.017$; Fig. 12).

Like females, males occurred closer to water during aggregation than segregation

(ANOVA, $F = 3.78$; 1, 405 df; $P = 0.05$). No such difference occurred, however, between size classes of males ($F = 0.01$, $P = 0.93$), and there was no period-by-size-class interaction ($F = 0.01$, $P = 0.93$). Indeed, mature and young males occurred at similar distances from water during aggregation (Class II, $\bar{x} = 2,642 \pm 656$ m; Class III and IV, $\bar{x} = 2,500 \pm 178$ m) and segregation (Class II, $\bar{x} = 3,332 \pm 425$ m; Class III and IV, $\bar{x} = 3,050 \pm 153$ m), even though Class II males were substantially smaller than Class III and IV males (Table 2).

During segregation, females with lambs were observed on steeper slopes in more open areas than those without lambs; they also tended to inhabit more rugged terrain, but not significantly so (Table 4). Such differences were not observed during aggregation, when lambs were older (approx 6 months of age). With periods (segregation and aggregation) combined, female groups with lambs occurred in habitat similar to that used by female groups not containing young (MANOVA, $F = 1.430$; 5, 424 df; $P = 0.212$).

Mature males (Class III and IV) were observed in areas with different terrain characteristics than were groups containing only younger males (Class II) during segregation, but not during aggregation (Table 5). With periods combined, mature males used terrain characteristics differently than young ones (MANOVA, $F = 2.77$; 5, 298 df; $P = 0.018$); such differences were pronounced, with mature males occurring in less open and less rugged terrain.

Habitat Selection

Because females used the same range year-round and no difference occurred in use of vegetation types between periods of segregation and aggregation (Fig. 11), we determined habitat selection for females on a year-round basis. Females strongly selected (use > availability) RS and avoided (use < availability) other vegetation types, except YES, which was used in proportion to its availability ($\chi^2 = 3,698.5$, 5 df, $P <$

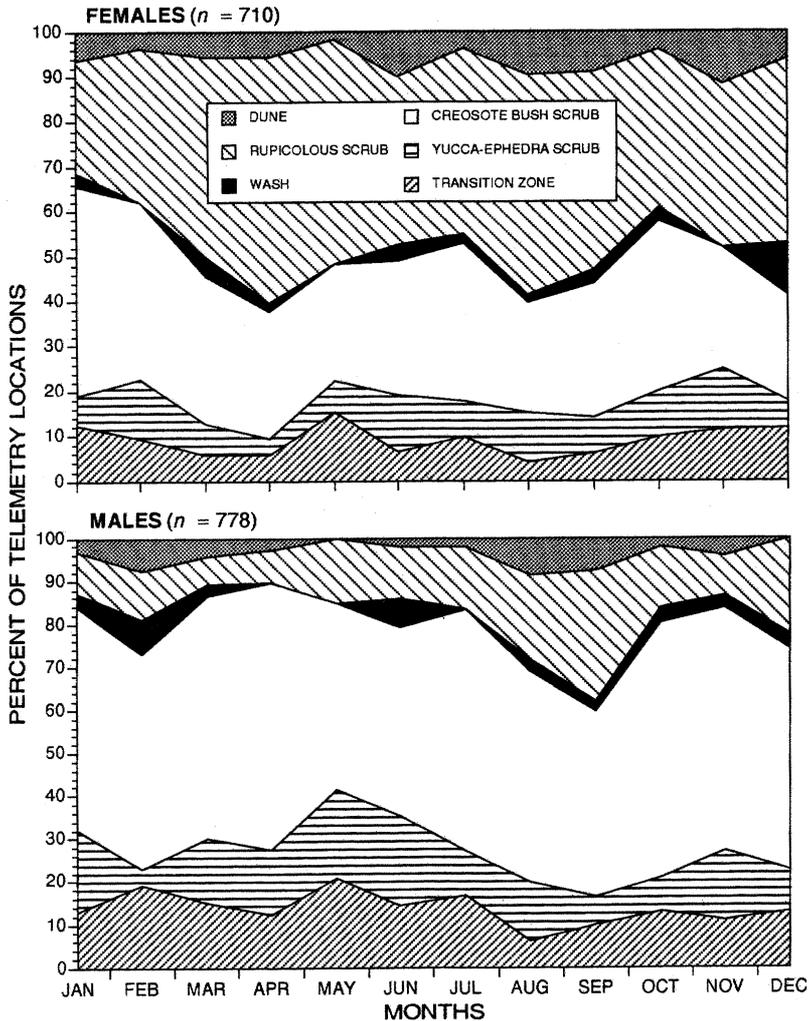


Fig. 11. Percent of telemetry locations for male and female mountain sheep in various vegetation types, San Bernardino County, California, 1986–90.

0.001; Fig. 13). Unlike females, males showed pronounced differences in use of vegetation types during aggregation and segregation (Fig. 11). Nevertheless, males selected CBS and RS and used YES in proportion to its availability during sexual segregation ($\chi^2 = 242.8$, 5 df, $P < 0.001$) and aggregation ($\chi^2 = 389.4$, 5 df, $P < 0.001$); males avoided other vegetation types during both segregation and aggregation (Fig. 13).

Log-likelihood models indicated that mature males selected vegetation types

differently than did females during segregation ($\chi^2 = 109.7$, 5 df, $P < 0.001$) and aggregation ($\chi^2 = 32.3$, 5 df, $P < 0.001$). Differential selection between the sexes occurred for CBS; females selected RS more strongly than did males (Fig. 13).

Year-round differences existed in the selection of categories of slope steepness by females ($\chi^2 = 2,313.7$, 8 df, $P < 0.001$). Generally, females avoided slopes of 0–10 and 41–50%; they selected slopes >10 and <41% and slopes >70% (Fig. 13).

During segregation, males avoided

Table 3. Habitat characteristics and distance to water for male and female mountain sheep during periods of segregation (Dec-Jul) and aggregation (Aug-Nov) based on telemetry locations, San Bernardino County, California, 1986-90.

Habitat characteristics	Males						Females			
	Segregation (<i>n</i> = 445)			Aggregation (<i>n</i> = 333)			Segregation (<i>n</i> = 414)		Aggregation (<i>n</i> = 296)	
	\bar{x}	SE	<i>P</i> ^a	\bar{x}	SE	\bar{x}	SE	<i>P</i> ^a	\bar{x}	SE
Distance to water (m)	3,091 ^b	83	*	3,087 ^c	120	2,449	108	*	2,481	117
Elevation (m)	1,012 ^b	8	**	957	10	961	9.7	*	943	12
Slope (%)	14 ^b	0.6	**	17 ^c	0.8	25	0.5	*	24	0.9
Ruggedness (index)	13 ^b	0.4	**	16 ^c	0.5	24	0.6	*	22	0.7
Openness (ranked 1-6; 1 = most open)	3.9 ^b	0.05	**	3.6 ^c	0.06	3.2	0.06	*	3.1	0.08

^a *P* values are from within sex ANOVAs with Bonferroni corrections; * = *P* > 0.05; ** = *P* ≤ 0.05.

^b Males differed (*P* ≤ 0.05) from females during segregation.

^c Males differed (*P* ≤ 0.05) from females during aggregation.

slopes of 0-10%, 41-50%, and >70% and selected slopes of 11-40% ($\chi^2 = 348.8$, 8 df, *P* < 0.001) (Fig. 13). During aggregation, males used the steepest slopes (>70%) in proportion to their availability, whereas they avoided this same slope category during segregation ($\chi^2 = 461.7$, 8 df, *P* < 0.001) (Fig. 13). For both sexes, there was no significant selection for, or against, slopes of 51-70%.

Log-likelihood models indicated significant differences in the selection of slope steepness by males and females during segregation ($\chi^2 = 121.2$, 5 df, *P* < 0.001) and aggregation ($\chi^2 = 35.6$, 5 df, *P* < 0.001). These tests required that the 4 categories reflecting extremely steep slopes

(>40%) be combined. In general, females avoided more level terrain and selected steeper slopes more strongly than did males, especially during segregation, which included the birthing season (Fig. 13).

Because the distribution of water on ranges occupied by males and females could be a factor explaining the distance that the sexes occurred from water, it was necessary to control for that possibility. To do so, we determined the mean difference between the distances that radio-collared male (*n* = 445) and female (*n* = 414) sheep and equal numbers of random points occurred from water. A 1-way ANOVA indicated that females ($\bar{x} = -3,244 \pm 186$ m) occurred significantly closer to water than did males ($\bar{x} = -1,648 \pm 151$ m) when compared with random points (*F* = 44.94; 1, 857 df; *P* < 0.001). When the relative availability of water on male and female ranges was taken into account, females still selected areas closer to water than did males during segregation.

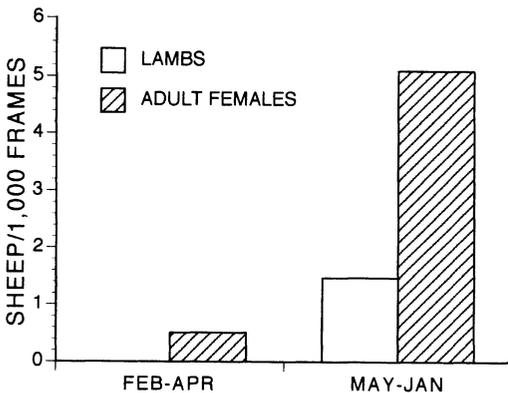


Fig. 12. Relative numbers of females and lambs recorded by time-lapse photography at water sources used by female mountain sheep during the period of peak lactation (Feb-Apr) in comparison to the rest of the year, San Bernardino County, California, 1989-90.

Forage Availability and Quality

The distribution and diet of sheep may be influenced, in part, by availability of forage within vegetation types. Forage available to sheep is a function of vegetative cover within a habitat and the relative size of that vegetation type. In our study area, the availability of vegetation types differed markedly (Fig. 3). Within these

Table 4. Characteristics of terrain in which female groups without lambs and female groups with lambs were observed from a helicopter during segregation and aggregation, San Bernardino County, California, 1981–90.

Terrain characteristics	Female groups									
	Segregation						Aggregation			
	With lambs (n = 133)			Without lambs (n = 165)			With lambs (n = 68)		Without lambs (n = 64)	
	\bar{x}	SE	P^a	\bar{x}	SE	\bar{x}	SE	P^a	\bar{x}	SE
Elevation (m)	910	15	*	935	13	884	20	*	865	22
Slope (%)	34	1.6	**	27	1.4	28	2.0	*	28	2
Ruggedness (index)	27	1.1	*	24	1.0	23	1.5	*	26	1.5
Openness (rank; 1 = most open)	2.6	0.1	**	3.0	0.1	2.8	0.1	*	2.6	0.1

^a P values are corrected Bonferroni comparisons within periods of segregation and aggregation; * = $P > 0.05$, ** = $P \leq 0.05$. Significant differences occurred overall between segregation and aggregation (MANOVA, $F = 3.27$; 5, 424 df; $P = 0.007$).

vegetation types, there are considerable differences in forage availability, as indexed by percent cover (Fig. 9). Mature males moved to ranges used by few females during segregation (Fig. 8). As a result, the use of vegetation types differed between the sexes during segregation; mature males occurred predominantly in CBS and YES, and females in RS (Fig. 11). When the cover of vegetation and the size of vegetation types were considered, males clearly used areas with more forage than did females (Fig. 14).

To examine the potential role of forage quality in explaining sexual segregation, we used data from Bleich et al. (1992c) to test for overall differences in food quality (moisture content, CP, and IVDMD) of 20 plant species eaten by mountain sheep. One-way MANOVA's indicated significant monthly effects on quality for grasses ($F = 4.23$; 33, 266 df; $P < 0.001$), perennial

forbs ($F = 2.50$; 33, 26 df; $P = 0.009$), and shrubs ($F = 5.02$; 33, 659 df; $P < 0.001$) (Fig. 15). Inadequate samples of succulents precluded their use in this analysis, and data for perennial and deciduous shrubs were pooled. On an annual basis, perennial forbs had the highest levels of CP ($\bar{x} = 14.2 \pm 1.0\%$), IVDMD ($\bar{x} = 52.5 \pm 2.1\%$), and moisture content ($\bar{x} = 55.8 \pm 3.3\%$), and grasses had the lowest levels of CP ($\bar{x} = 6.9 \pm 0.8\%$), IVDMD ($\bar{x} = 40.3 \pm 2.0\%$), and moisture content ($\bar{x} = 32.5 \pm 4.9\%$). Shrubs were intermediate in CP ($\bar{x} = 10.3 \pm 1.2\%$), IVDMD ($\bar{x} = 43.4 \pm 4.6\%$), and moisture content ($\bar{x} = 44.4 \pm 4.1\%$). There were clear increases in the overall quality of these forage classes during January–April (Fig. 15).

When an overall model considered quality of forage classes during segregation and aggregation on ranges inhabited primarily by mature males or females and

Table 5. Characteristics of terrain in which groups of mature males (Class III and IV) and groups of only young males (Class II) were observed during helicopter surveys, San Bernardino County, California, 1981–90.

Terrain characteristics	Male groups									
	Segregation						Aggregation			
	Class II (n = 23)			Class III & IV (n = 161)			Class II (n = 13)		Class III & IV (n = 107)	
	\bar{x}	SE	P^a	\bar{x}	SE	\bar{x}	SE	P^a	\bar{x}	SE
Elevation (m)	897	46	**	1,018	15	958	29	*	968	16
Slope (%)	21	4	**	13	0.9	23	4	*	22	1.5
Ruggedness (index)	21	3	**	13	0.6	22	4	*	19	1
Openness (rank; 1 = most open)	3.5	0.25	**	4.1	0.08	2.8	0.30	*	3.4	0.13

^a P values are corrected Bonferroni comparisons within periods of segregation and aggregation; * = $P > 0.05$, ** = $P \leq 0.05$.

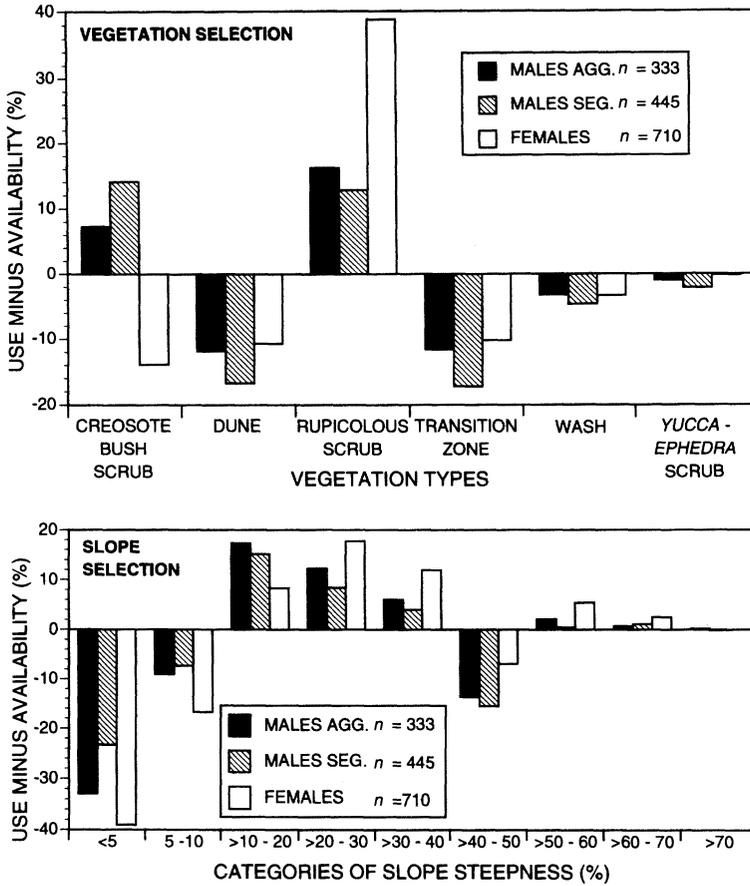


Fig. 13. Selection (% use minus % available) of vegetation types and slope categories by male and female mountain sheep, San Bernardino County, California, 1986-90. The period that males aggregated (AGG.) with females was August-November. The period of sexual segregation (SEG.) was December-July.

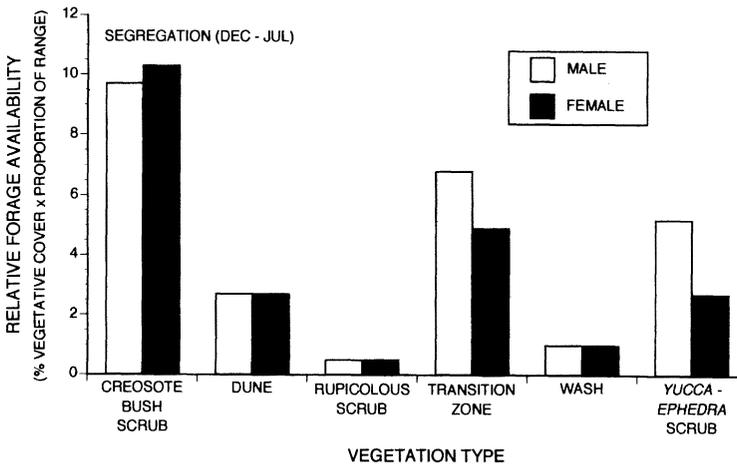


Fig. 14. Availability of potential forage in 6 vegetation types used by mountain sheep during sexual segregation, San Bernardino County, California, 1990.

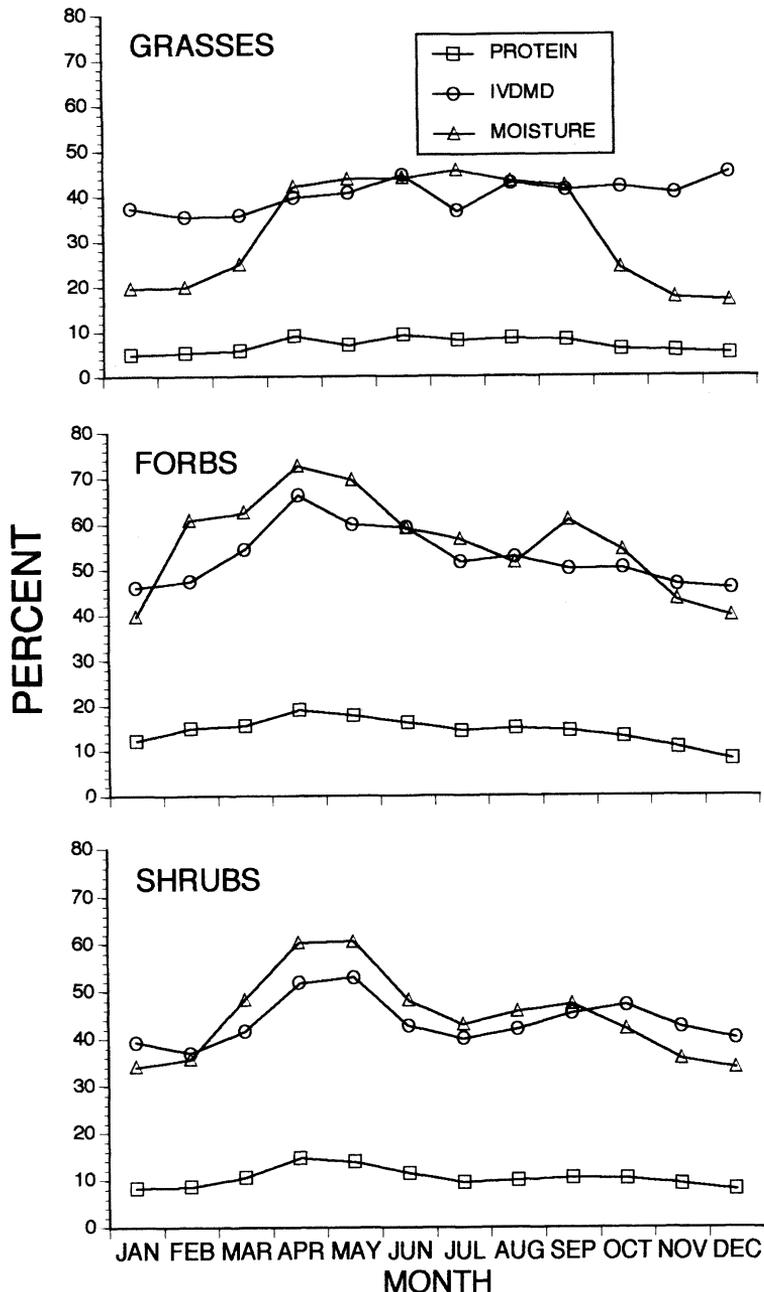


Fig. 15. Percent protein, *in vitro* dry matter digestibility (IVDMD), and moisture of forage classes eaten by mountain sheep in San Bernardino County, California, 1990–91.

their interaction term (period of segregation–aggregation by sex), the outcome was highly significant ($F = 6.46$; 3, 357 df; $P < 0.001$). Examination of univariate F sta-

tistics, however, indicated this result was due mostly to moisture content ($F = 9.04$, $P = 0.03$) and not CP ($F = 0.15$, $P = 0.70$) or IVDMD ($F = 0.14$, $P = 0.71$). In-

creased moisture content on areas inhabited primarily by females probably was not a good measure of overall forage quality because similar increases in CP and IVDM were not evident.

Diets of Mountain Sheep

Fecal analysis indicated both within and among year variation in the consumption of annual plants, perennial grasses, perennial forbs, shrubs, and succulents by female and male mountain sheep (Fig. 16, Table 6). During sexual segregation in 1987–88, male sheep fed more extensively on annuals, shrubs, and succulents than did females, whereas females ate more grasses and perennial forbs than did males. During aggregation, females fed more extensively on perennial forbs, shrubs, and succulents than did males, whereas males ate more annuals and perennial grasses.

During the 1988–89 segregation period, males consumed more shrubs and succulents than did females, whereas females consumed more annuals, perennial forbs, and perennial grasses. During aggregation, males fed more extensively on shrubs and succulents than did females, and females ate more annuals, perennial grasses, and perennial forbs (Fig. 16, Table 6).

Overlap in forage classes consumed by the sexes was similar during periods of sexual aggregation (Aug–Nov) during the first ($70.6 \pm 7.1\%$ [SD]) and second ($75.8 \pm 13.1\%$ [SD]) years of study (Fig. 16). Likewise, dietary overlap as determined by fecal analysis during segregation (Dec–Jul) was similar during the first ($74.4 \pm 10.0\%$ [SD]) and second ($61.1 \pm 16.6\%$ [SD]) years. The lower value for the second year was produced largely by males consuming more shrubs and females eating more perennial grasses during segregation (Fig. 16).

Diet Quality

Integrated values of fecal crude protein (FCP) for males were higher than for females during segregation in 1988 and 1988–89, but the pattern was reversed in

the extreme drought year of 1989–90 (Table 7). That FCP indexed diet quality for mountain sheep is indicated by the correspondence between crude protein levels in the feces (Fig. 17) and measures of forage quality (Fig. 15); both these indices were elevated during spring. Males consumed more shrubs than did females (Table 6), and tannins possibly increased levels of FCP at that time. This is unlikely, however, because there was no relationship between the percent of shrubs in the diet and FCP for males ($r^2 < 0.01$; 1, 88 df; $P = 0.44$) or females ($r^2 < 0.001$; 1, 120 df; $P = 0.91$).

Abundance of Predators

From June 1987 to August 1990, 740 km of transects ($n = 93$) were sampled in 2 areas occupied predominantly by mature male sheep during sexual segregation (East Hills and Kelso Mountains) and in 2 areas inhabited mostly by females (Old Dad Mountain and Cowhole Mountain). When we pooled feces from all predators within each area, there were significant differences in the densities among these 4 sampling areas ($F = 26.15$; 3, 89 df; $P < 0.001$); predator feces occurred at higher densities in those areas used predominantly by males (Fig. 18). No scats of mountain lions were located.

Predators recorded by time-lapse photography at water sources were more frequent (animals/10,000 frames of film) on ranges of mature males than those used by females ($Z = 6.18$, $P < 0.001$). This pattern was especially pronounced for coyotes (Fig. 18). No mountain lions were photographed.

During aerial surveys, bobcats and coyotes were observed more often in areas used predominantly by males. This pattern was consistent with results from scat transects and photography (Fig. 18); however, a 1-way ranked ANOVA failed to detect significant differences in rates of aerial observation for all predators ($F = 0.39$; 4, 71 df; $P = 0.81$) because of the low numbers of observations. No mountain lions were observed during aerial surveys.

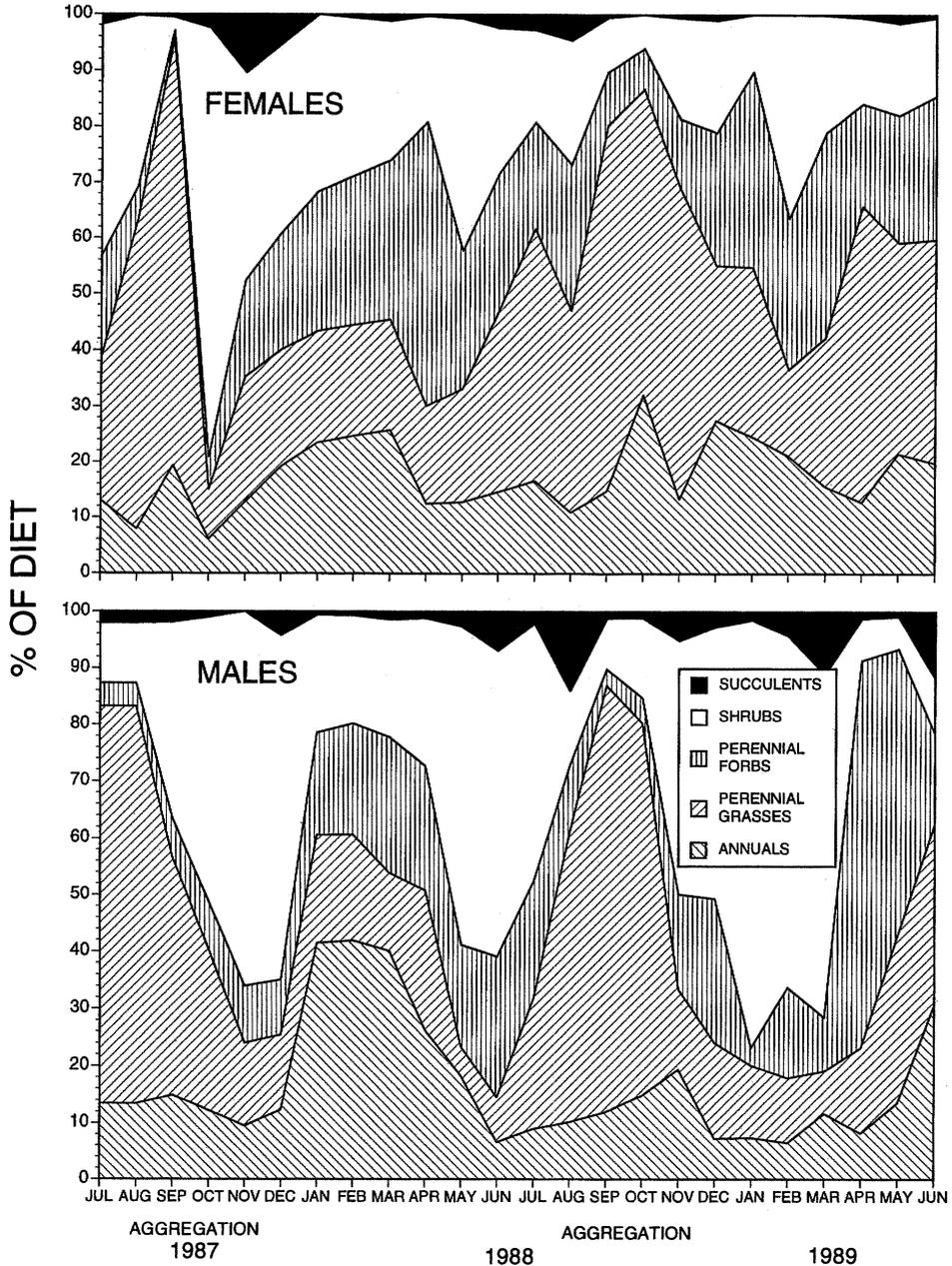


Fig. 16. Percent of various forages in the diets of female and male mountain sheep, indexed from microhistological analysis of their feces, San Bernardino County, California, 1987–89.

Causes of Mortality and Evidence of Sheep in Carnivore Diets

Of radio-collared sheep, at least 4 males were killed by mountain lions, and 1 male

drowned in a steep-sided tinaja (Bleich 1993:appendix B). Three other males and 1 female in relatively flat terrain had been scavenged by coyotes, but cause of death could not be ascertained.

Table 6. Percent of forage classes in the diets of male and female mountain sheep as indexed by microhistological examination of the feces, San Bernardino County, California, 1987–89.

Season	Sex	Percent of forage class ^a									
		Annual		Perennial grass		Perennial forb		Shrub		Succulent	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
1987–88											
Segregation	F	17.1	2.0	22.5*	2.1	28.6	3.1	30.8	3.7	1.0*	0.1
	M	24.3	3.0	14.3*	1.8	19.6	1.7	39.0	4.0	2.8*	0.8
Aggregation	F	9.6	1.9	31.0*	6.3	8.0	1.9	47.9	6.9	3.5	1.6
	M	13.8	2.0	50.3*	6.6	6.1	1.2	28.1	6.4	1.8	0.6
1988–89											
Segregation	F	19.4*	1.3	35.4*	2.0	25.5	1.4	18.3*	1.6	0.8*	0.2
	M	11.6*	1.8	16.7*	1.6	24.6	4.1	42.0*	5.2	5.3*	2.3
Aggregation	F	16.8	2.2	54.1	4.8	13.7	3.2	14.0	2.8	1.4*	0.9
	M	13.5	1.7	52.9	6.7	8.8	2.1	18.5	5.1	6.3*	2.6

^a Data presented for each season, period, and sex. Statistical comparisons are between males and females within seasons and periods. MANOVA's for year ($F = 6.17$; 5, 118 df; $P < 0.001$), month ($F = 10.99$; 35, 582 df; $P < 0.001$), and sex ($F = 12.04$; 5, 118 df; $P < 0.001$) were significant. * $P \leq 0.05$.

Remains (hair) of mountain sheep were detected in only 3.1% of 97 coyote scats. No other evidence of ungulates (e.g., bones, hooves) was present in the 120 total predator scats analyzed. None of the scats examined contained remains of other ungulates.

bility to predation (Williams 1975, Berger 1991), and result in strong allometric differences, especially for ruminants (Dement and Van Soest 1985). Among desert ecotypes of mountain sheep, adult males are 50% heavier than adult females; hence, male and female mountain sheep exhibit

DISCUSSION

Sexual Dimorphism and Hypotheses Explaining Sexual Segregation

Sexual dimorphism in body size and secondary sexual characteristics are pronounced in North American wild sheep (Shackleton 1985, Bowyer and Leslie 1992); we also observed this pattern for desert-dwelling mountain sheep (Table 2). Differences in body weight may be important in understanding why the sexes segregate, because they are associated with social behavior (Geist 1971) and suscepti-

Table 7. Fecal crude protein (FCP) values integrated above 5% FCP for male and female mountain sheep during sexual segregation, San Bernardino County, California, 1988–90.

Year	Months	Integrated FCP >5%/100 days		
		Male	Female	Ratio
1988	Jan–Jul	88.28	82.61	1.07
1988–89	Dec–Jul	66.43	55.85	1.19
1989–90	Dec–Jul	55.69	63.69	0.87

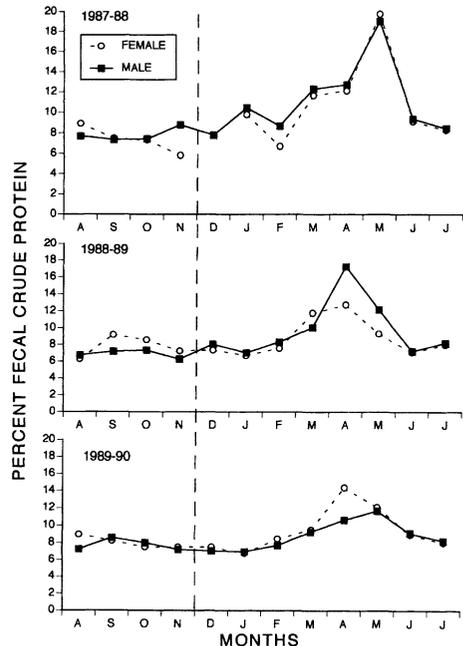


Fig. 17. Fecal crude protein of male and female mountain sheep over 3 years, San Bernardino County, California, 1987–90.

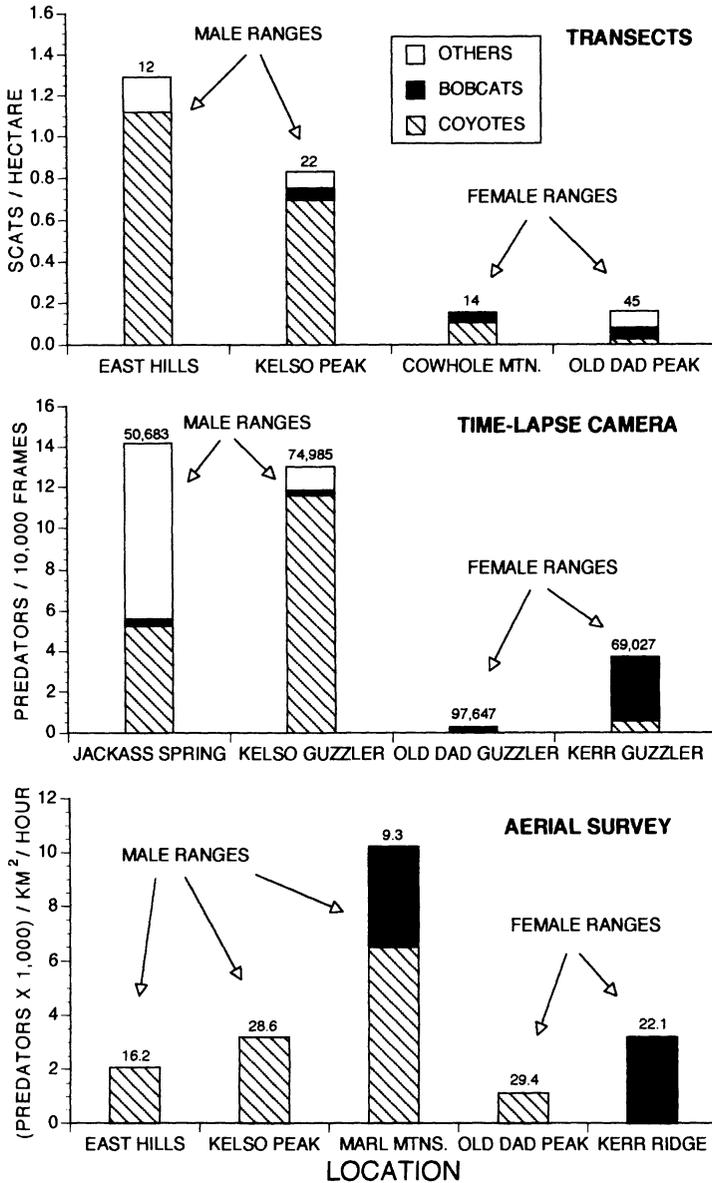


Fig. 18. Relative abundance of predators on ranges occupied primarily by mature male or female mountain sheep, San Bernardino County, California, 1987–90. Sample sizes appear above bars and represent the number of transects, frames of time-lapse camera film evaluated, and hours of helicopter time.

morphological differences that are necessary to postulate allometric explanations for sexual segregation. Indeed, most hypotheses forwarded to explain sexual segregation are based on morphological differences between the sexes (Main and

Coblentz 1990, Miquelle et al. 1992, Main et al. 1996).

An additional consideration that sometimes has been overlooked is that hypotheses forwarded to explain sexual segregation must account for the spatial separa-

tion of the sexes, and not merely changes in group composition and association of the sexes (Bowyer 1984, Main et al. 1996). Four hypotheses (Table 1) met this criterion and have some promise as general explanations for sexual segregation among ungulates.

Predictions of Hypotheses Versus Empirical Observations

H₁: Sexual segregation in mountain sheep occurs because mature males avoid areas occupied by females and young to decrease competition with their offspring and potential mates. Geist and Petocz (1977) proposed this hypothesis to explain sexual segregation between male and female sheep wintering on small, snow-covered areas in the northern Rocky Mountains. In our study, mature males aggregated with females later than did immature or young males (Fig. 6) in a pattern nearly identical to that reported by Geist (1971:fig. 24). Moreover, the proportion of congruent male home ranges during sexual aggregation in consecutive years (77%) did not differ from that (81%) reported by Geist (1971). Meeting both of these conditions was necessary to evaluate the applicability of this hypothesis to mountain sheep in general and, potentially, to other ungulates inhabiting areas with less-constrained ranges in winter than those experienced by mountain sheep at northern latitudes.

Contrary to the expectations of this hypothesis, diet quality of mature male sheep (as indexed by fecal crude protein, FCP) was better than that of females during sexual segregation during 2 of 3 study years (Table 7). Cover of potential forage, likewise, was greater in vegetation types inhabited primarily by mature males (CBS, YES, TZ) compared with vegetation (RS) used mostly by females (Fig. 9). This trend was especially evident for the cover of annual plants during nondrought years (Fig. 10). Moreover, when the area of available vegetation types was considered, the pattern was even more evident because the RS type used by females composed but a

small proportion of sheep range (Figs. 3, 14). This relationship is further exacerbated by population density; although males occurred in greater numbers, 42% of females occurred in RS, a vegetation type that composed only 3% of the study area. This concentration of sheep further reduced the availability of forage per individual female. None of these observed outcomes is consistent with males moving to lower quality ranges.

Although large males (Class III and IV) spatially segregated from females, so did many Class II males (Fig. 5). Class II males seldom copulate with females (Geist 1971, Hogg 1987) because they are subordinate to large males during rut. Based on the occurrence of mixed groups (Fig. 4) and a prolonged lambing period, rut for these desert-dwelling sheep occurs over ≥ 4 months. Consequently, it is unlikely that most Class II males ever obtain copulations (even from females that underwent a second estrus) because of the extended association of mature males with females through the period of sexual aggregation (Fig. 6).

Young male mountain sheep may associate with females and lambs until they are no longer subordinate to adult females (Geist 1971). Because young males are intermediate in body size between mature males and females (Table 2) and possess horns similar in morphology to females (Geist 1971), they may be able to continue to interact socially with adult females. The finding that some young males remain with female groups while others of the same relative age join male bands is likely a function of relative body size and horn development (Nievergelt 1967). The protracted lambing season of desert-dwelling mountain sheep (Bunnell 1982, Thompson and Turner 1982) results in considerable variation in body size among animals from the same lamb cohort. Such differences in age may explain the propensity of some young males to remain with females, while others do not. Whatever the reason underlying this phenomenon, the observation that some Class II males segregated from the females and moved to higher quality

ranges than those used by females is inconsistent with the notion that breeding males segregate from females solely to decrease competition for forage. Moreover, if Class II males that did not mate segregated from females to benefit the offspring of unrelated, large males, then group selection must be invoked to explain this phenomenon.

There may be other benefits that accrue to young males that join old, large males during segregation (Geist 1971, McCullough 1979), but such advantages are unrelated to avoiding competition with their offspring. In snowbound northern systems, segregation by large or immature males could result in decreased competition with females and young, but resources must be limited for such an outcome to be realized. In the desert system we studied, an equally plausible and more parsimonious explanation for segregation of males from females is that males simply moved to ranges with better quality and more abundant forage.

Although segregation by large males from females results in decreased competition with those females and young inhabiting small, snow-free winter ranges (Geist and Petocz 1977), males in our study area moved to ranges with high quality and ample forage availability. In our system, reduced competition with females could occur *if* resources were limiting; however, any reduction in competition would clearly be a consequence, rather than a cause, of sexual segregation. The finding that males moved to ranges that allowed them to ingest better quality forage (and with more forage available per male than per female) is inconsistent with the notion that males segregated to enhance their reproductive fitness by decreasing competition with females and young. We conclude that the hypothesis of Geist and Petocz (1977) cannot explain *why* the sexes segregate in the population of mountain sheep we studied, although decreased competition could occur under circumstances of low forage availability on female ranges. Because this hypothesis cannot explain sexual segregation by mountain sheep occurring in des-

erts, it should not be invoked as a general explanation for sexual segregation in sexually dimorphic ungulates.

H₂: Allometric differences between male and female mountain sheep lead to differential uses of food that result in segregation. Dietary differences between the sexes have been reported for a variety of ruminants, and these observations support the notion of allometric differences allowing males to inhabit lower quality ranges than could females, given sufficient biomass of forage available to males (Watson and Staines 1978, McCullough 1979, Staines et al. 1982, Bowyer 1984, Beier 1987, Clutton-Brock et al. 1987). We also noted dietary differences between sexes, with only 71–76% overlap in diet even during sexual aggregation. Male mountain sheep in our study, however, obtained higher quality diets than did females during segregation in 2 of 3 years (Table 7). Also, in nondrought years, annual plants were more abundant in spring on ranges occupied by mature male sheep than on ranges occupied by females (Fig. 10), and forage availability was generally higher on ranges occupied by males (Figs. 9, 14). Moreover, these differences in availability are greater per capita, given differences in density between the sexes.

Differences in diet composition and quality between the sexes of some ungulates may be present, but difficult to detect. For instance, Bowyer (1984) reported that the major difference in ranges used by male and female mule deer during segregation was the phenological stage of a preferred forage. Likewise, Beier (1987) noted slight, but significant, differences in foods eaten by the sexes of white-tailed deer during segregation. Even small differences in diet quality may have a profound effect on the productivity of ruminants (White 1983) and could underlie sexual segregation.

Our finding that males obtained better quality diets than did females during the 2 nondrought years is not consistent with the hypothesis that allometric differences result in sexual segregation. This hypothesis still may be viable for ungulates where fe-

males obtain higher quality diets, but appears not to be a general explanation for sexual segregation.

Our finding that mature male sheep moved from areas selected by females during sexual segregation (Fig. 8) is consistent with the hypothesis that segregation might be caused by females outcompeting males where forage was of high quality but of low biomass (Clutton-Brock et al. 1987). Additionally, the percent of shrub cover was greater in CBS, an area selected by males during segregation, but avoided by females (Fig. 13). The substantially higher densities of females than males during sexual segregation also is consistent with this hypothesis. Nevertheless, our findings that males had higher diet quality (Fig. 17) and greater availability of annual plants (Fig. 9) are not consistent with this hypothesis; therefore, we reject it.

Low population density and high availability of forage led Miquelle et al. (1992) and du Toit (1995) to conclude that competition was not the primary factor responsible for sexual segregation. An expectation from this hypothesis would be that populations at low density with respect to carrying capacity should not sexually segregate because of reduced competition with conspecifics. Conversely, segregation of the sexes should be pronounced at high density. Although this hypothesis cannot be entirely ruled out for ungulates in which females occur on higher quality ranges, the lack of confirmatory evidence for this notion leads us to question it. We believe that differential risk of predation and allometric differences offer more likely alternatives than competition between the sexes as an explanation for sexual segregation.

H₃: Females spatially segregate from males because of greater water requirements associated with lactation or their smaller body size. Mountain sheep living in desert environments are physiologically specialized in terms of their water metabolism (Turner 1973, 1979). These sheep drink about 4% of their body weight in water each day to maintain water balance during extreme temperatures in summer;

however, during winter, forage with 1.5–3.0 μl of preformed water per gram dry weight may preclude the need for free water (Turner 1973). Some desert populations of mountain sheep persist year-round in areas lacking free water (Krausman et al. 1985b). During segregation, the moisture content of forage on areas occupied by females in this study was higher than for ranges used mostly by mature males (Fig. 15).

Females occurred significantly closer to sources of free water during sexual segregation than did males, and this difference was maintained even when we controlled for water availability. Although males in our study did occur on ranges with a lower moisture content of forage during segregation, females with lambs did not occur closer to water than those without lambs. Adequate escape cover (steep, rugged terrain) may limit the distribution of female sheep whether or not they have lambs at heel. Indeed, when we controlled for terrain characteristics with ANCOVA, the importance of free water to females was further highlighted. Most importantly, few females visited water sources during the early period of lamb-rearing (Feb–Apr; Fig. 12), and none of these was accompanied by small lambs.

Differences in the distances males and females occurred from water were even more pronounced during aggregation, ostensibly because temperatures were extremely high for about one-half of this period (Fig. 2). We noted no differences in distances from water for females with lambs versus females without young during either segregation or aggregation. Likewise, there was no difference in distance from water between smaller-bodied Class II and larger Class III and IV males during either period.

Whatever the cause of females being closer to water than males, it cannot be invoked to explain sexual segregation in this population, because the same general pattern with respect to distance from water occurred during both segregation and aggregation. Lactational requirements for free water in these desert-adapted sheep

can be rejected as an explanation for sexual segregation. This hypothesis, however, may explain segregation in other species (especially those less adapted to arid environments) and warrants further consideration.

H₄: Spatial separation of the sexes occurs because mature males, owing to their larger body size and strength, are less susceptible to predators than smaller-bodied females and young, thereby allowing these males to exploit resources unavailable to smaller individuals. Geist (1981) postulated for mountain sheep that spatial separation of the sexes occurs because males must regularly forage in areas that promote horn growth and maximize fitness. Conversely, females maximize fitness by choosing the best escape terrain for their young. Hence, females should compromise forage quality in favor of security, whereas males should compromise security in favor of forage quality. Geist (1982) also applied this hypothesis to elk. This idea, however, cannot apply to ungulates in general because it does not explain why some females occur on better ranges during segregation.

In our study, male mountain sheep occurred on ranges with greater forage availability, and they obtained a higher quality diet during the 2 nondrought years than did females during sexual segregation. These findings are consistent with this hypothesis; however, the opposite relationship during the dry third year suggests that more years of data are necessary to determine if males generally obtain diets of higher quality than females during segregation, especially during years of poor forage production.

Females selected steeper, more open habitats than did males, and females with lambs occurred in steeper, more rugged terrain than females without young (Table 4). Such areas apparently facilitate evasion of predators by females and their offspring. Likewise, young males used areas that were more rugged and open than areas used by large males during segregation (Table 5). These smaller-bodied sheep also apparently used habitats that enhanced

their ability to evade predators. Three indices indicated that predators were less common on areas inhabited by females than males (Fig. 18), and mature males (despite their larger body size) predominated among kills made by predators during this study (Bleich 1993:appendix B). Wehausen (1980) also noted that females with young lambs traded off nutrition for apparently safer habitats. Likewise, caribou may "space away" from areas where predators are abundant during parturition (Bergerud et al. 1984, Bergerud and Page 1987). These observations strongly support the hypothesis that risk of predation plays a major role in sexual segregation.

Increased risks of predation to males could be a function of their using areas with higher nutritional quality or greater abundance of forage and less-rugged terrain (Wehausen 1980, Berger 1991, this study), but with higher densities of predators. Male tule elk (*Cervus elaphus nannodes*) foraged in better habitats with a higher likelihood of predation by mountain lions than did females (Berbach 1991), and female moose with calves foraged less efficiently than females without young, or adult males, in a predator-rich environment (Molvar and Bowyer 1994). Likewise, male Asian elephants (*Elephas maximus*) incurred risks while obtaining higher quality diets than females (Sukumar and Gadgil 1988). Main and Coblenz (1990) argued generally that males and females select areas according to different criteria, with females selecting those most suitable for successful gestation and rearing of offspring and males selecting areas where they can maximize body condition.

Some studies of sexual segregation, however, have reported that females obtained a higher quality diet and occurred on better areas than males (Watson and Staines 1978, Staines et al. 1982, Beier 1987, Clutton-Brock et al. 1987, Illius and Gordon 1987), and Weckerly and Nelson (1990) concluded that both males and females obtained diets high in essential nutrients. Measuring just range quality could be misleading because variation in population density of ungulates on areas occu-

pied by males and females may affect per capita consumption of nutrients. For instance, Bowyer (1984) reported that female mule deer were segregated onto areas with a greater abundance of preferred forage than ranges inhabited by males. However, when the higher density of females was considered, no significant difference in forage availability per individual was noted. Nonetheless, several studies have corrected for differential densities of the sexes and still concluded that females obtained higher quality forage than males during segregation (Watson and Staines 1978, Clutton-Brock et al. 1987).

Perhaps females of some species in particular environments can maximize intake of high quality forage and simultaneously minimize risk of predation (Eastland et al. 1989). If this is correct, then how forage and risk of predation are arrayed in the environment would have a profound effect upon the pattern of sexual segregation and quality of forage obtained by males and females. It remains unclear, however, why males would segregate when females maximize forage quality and simultaneously minimize risk of predation. Such an outcome probably would require invoking *Hypothesis 2*—that allometric differences contribute to sexual segregation under these circumstances.

The behavior of mountain sheep undoubtedly has been influenced by predation throughout their evolutionary history. Indeed, in the absence of serious competition from other ungulates, evolution has resulted in a propensity for North American wild sheep to use rocky terrain when faced with dangerous situations (Geist 1971). Mountain sheep appear to evade predation through their exceptional eyesight, climbing ability, and use of open areas adjacent to and within rugged terrain (Wishart 1978).

Berger's (1991) review reported that female mountain sheep and lambs using shallow slopes were more vulnerable to predation than when in escape terrain. Despite the extensive use of rugged terrain, particularly by females, Murie (1944) and Sumanik (1987) described wolves suc-

cessfully hunting mountain sheep by attacking from above and forcing them to flee from steep cliffs to less precipitous terrain. Sumanik (1987) concluded, however, that in 4 of 6 hunts, proximity to escape terrain was the deciding factor that allowed sheep to evade wolves.

Among mountain sheep, sexual selection (Trivers 1972) has favored large, powerful males with huge horns (Geist 1971). Adequate forage is an important factor limiting body and horn size in these ungulates (Bunnell 1978, Geist 1981, Guthrie 1990). Indeed, the importance of maximizing body condition and size may exceed the increased risk of predation associated with foraging on high quality ranges; such risks may be undertaken to enhance reproductive success of males (Kurt 1974, Geist 1981, Poole and Moss 1981, Poole 1987, Prins 1989). Among females, selection has been for behaviors that reduce the risk of predation on individuals and their offspring, sometimes at the expense of nutrient intake. As long as nutrition is sufficient for ovulation, gestation, and lactation, individual females may maximize their fitness by enhancing their survival and that of their young. Females do this by occupying areas with lower densities of predators and terrain that allows greater opportunities to evade these carnivores. Findings from this study are consistent with the hypothesis that female mountain sheep occupy habitats in which they and their young are less susceptible to predation, but simultaneously sacrifice nutrient quality as a trade off for security, as reported by Wehausen (1980) and Berger (1991). Indeed, such trade offs may affect foraging efficiency and reproduction for an array of organisms (Lima et al. 1985, Magnhagen 1991, Molvar and Bowyer 1994).

CONCLUSIONS

The evolutionary significance of sexual segregation in mountain sheep is, in all probability, best understood as the result of differing life-history strategies of males and females (Geist 1981, Main and Co-

blentz 1990, Main et al. 1996). Our findings support the hypothesis that females maximize their Darwinian fitness by minimizing risks of predation, albeit by potentially compromising nutrient intake.

Among males, reproductive fitness is strongly influenced by body size and condition (Clutton-Brock et al. 1982, Prins 1989, Guthrie 1990), and the larger body size of mature males and lack of parental care may reduce susceptibility to predation (Berger 1991), especially by small predators such as coyotes and bobcats. Hence, risks associated with foraging in high quality habitats, which enhance body condition, may increase the probability of fathering offspring. Miquelle et al. (1992) proposed that sexual dimorphism may lead to differences between the sexes that relate to risk of predation, constraints on foraging, habitat use, and even competition. Nonetheless, their model for sexual segregation requires a heterogeneous environment where the sexes can select resources to meet differential costs and constraints. We extend their model and suggest that the manner in which forage and predation risk are arrayed in such a heterogeneous environment is an important factor in determining how and why the sexes segregate, including which sex moves and which obtains a better diet. During sexual segregation, males and females may be adapted differently for foraging and evading predators in their preferred habitats (Lopez Ornat and Greenberg 1990). Thus, sexual segregation might best be viewed as a compromise between optimal foraging and decreasing predation risk (Skogland 1987).

Main and Coblentz (1990) argued that the strategy of maximizing body condition, and its resultant increased fitness in males of sexually dimorphic species, appears to be widespread, if not universal. Females of such species likely concentrate on reducing the risks of predation on themselves and their offspring, albeit at the expense of nutrient intake in some species (Main and Coblentz 1996). We believe such life-history strategies are best viewed from the perspective of how predation risk, forage

abundance, and forage quality are distributed in a heterogeneous environment. We further suggest that this relationship may yet provide a general understanding of sexual segregation among ungulates.

MANAGEMENT IMPLICATIONS

Ecological differences between male and female mountain sheep have important implications for conservation. Management of mountain sheep in desert ecosystems has centered on the construction of artificial watering devices (Bleich 1983a, Bleich and Pauli 1990) in the belief that both sexes will benefit (Turner and Weaver 1980). Females occurred significantly closer to water (an index to its importance) than males during segregation and aggregation, even when we controlled for the availability of water. This observation suggests that water developments may be of greatest value if they are constructed in areas used predominantly by females and their offspring (Seegmiller and Ohmart 1982).

During sexual segregation, males and females used habitats that were distinctively different. Generally, females used areas that were characterized by steep, open, and rugged terrain with low availabilities of annual and perennial vegetation. In contrast, males used areas that were less steep, less rugged, and with greater availabilities of such vegetation. Areas used by males during sexual segregation were associated with rolling hills (and sometimes flats) and not the steep terrain traditionally considered to be habitat for mountain sheep. These less steep habitats must be recognized as important to mountain sheep populations, as emphasized previously by Schwartz et al. (1986) and Bleich et al. (1990a). During segregation, such areas provide better opportunities for mature males to obtain high quality forage than do the steep, rugged terrain used primarily by females.

Grazing by cattle occurs throughout much of the Southwest. Although distributional overlap and resultant competition between cattle and mountain sheep may

not be an important limiting factor in some areas (Dodd and Brady 1986, Dodd 1987), cattle may alter vegetation (particularly cover of grasses) in habitats used by mountain sheep (J. D. Wehausen, Demographic studies of mountain sheep in the Mojave Desert: report IV, Calif. Dep. Fish and Game, Sacramento, Final Rep. FG9239, 54pp., 1992). Allocations for livestock often are based on the amount of ephemeral vegetation occurring on less rugged areas under the assumption that mountain sheep seldom use areas away from steep slopes. Male mountain sheep, however, often make extensive use of areas that are grazed heavily by cattle. Moreover, ephemeral plants are important in the diets of male sheep. If grazing by cattle results in competition with mountain sheep for forage, there may be a reduction in suitable habitat for males and possibly the population.

In the eastern Mojave Desert, mountain sheep may be prone to predation by mountain lions. In the Granite Mountains, located approximately 40 km south of our study area, heavy predation on females has had severe consequences for that population (J. D. Wehausen, Demographic studies of mountain sheep in the Mojave Desert: report IV, Calif. Dep. Fish and Game, Sacramento, Final Rep. FG9239, 54pp., 1992). During our study, however, confirmed losses of sheep to mountain lions were restricted to males because such predation occurred only in habitats used predominantly by that sex. Consequently, lion predation has not significantly affected the reproductive base of our study population. Predation by mountain lions may not have generalized demographic implications for mountain sheep, unless females are preyed upon heavily.

Aerial surveys are an important method of obtaining demographic data for populations of large ungulates, particularly mountain sheep (Bleich et al. 1990*d*, 1994). Because of the pronounced differences in the ways that males and females use habitats and space, demographic surveys conducted during sexual segregation may lead to biased conclusions if survey

effort is not properly distributed. Aerial surveys to estimate population size and composition should coincide with the period of sexual aggregation when adult males and females are most likely to be in close proximity to each other. Surveys conducted during sexual segregation must encompass large areas and incorporate the range of habitats used by males and females during that period (Schaller and Junrang 1988) to decrease the possibility of biased demographic data.

Finally, mountain sheep may use widely separated parts of their home ranges on a seasonal basis. These animals, particularly the males, move from some mountain ranges to others within our study area; males join females during periods of aggregation and cross Kelbaker Road to do so. Movement to and from female ranges located west of Kelbaker Road (Fig. 1) necessitates that those males cross that right-of-way at least twice annually. Kelbaker Road currently receives little use, but traffic is expected to increase substantially with the anticipated National Park Service administration of our study area. Proposals to fence this thoroughfare to decrease the likelihood of vehicle collisions with livestock or feral asses are probable. If Kelbaker Road is fenced, an important intermountain corridor (Bleich et al. 1990*a*) will be eliminated, with potential landscape-level implications (Schwartz et al. 1986) for mountain sheep. Movements resulting from sexual segregation, as males travel to and from female ranges, will be impeded and negative effects will occur at both the population and metapopulation level (Bleich et al. 1996).

LITERATURE CITED

- ALEXANDER, P. D., J. L. HOOGLAND, R. D. HOWARD, M. NOONAN, AND P. W. SHERMAN. 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates, and humans. Pages 402-435 in N. A. Chagnon and W. Irons, eds. *Evolutionary biology and human social behavior: an anthropological perspective*. Duxbury Press, North Scituate, Mass.
- AMERICAN SOCIETY OF MAMMALOGISTS. 1987. Acceptable field methods in mammalogy. *J. Mammal.* 68(4, suppl.). 18pp.

- BAILEY, R. C., AND R. AUNGER, JR. 1989. Net hunters vs. archers: variation in women's subsistence strategies in the Ituri Forest. *Human Ecol.* 17: 273–297.
- BARCA, R. A. 1966. Geology of the northern part of the Old Dad Mountain quadrangle, San Bernardino County, California. Calif. Div. Mines and Geol., Sacramento, Map Sheet 7.
- BEASOM, S. L., W. EVANS, AND L. TEMPLE. 1980. The drive net for capturing western big game. *J. Wildl. Manage.* 44:478–480.
- BEIER, P. 1987. Sex differences in quality of white-tailed deer diets. *J. Mammal.* 68:323–329.
- BERBACH, M. W. 1991. Activity patterns and range relationships of tule elk and mule deer in Owens Valley. Ph.D. Thesis, Univ. California, Berkeley. 154pp.
- BERGER, J. 1978. Maternal defensive behavior in bighorn sheep. *J. Mammal.* 59:620–621.
- . 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Anim. Behav.* 41:61–77.
- BERGERUD, A. T., H. E. BUTLER, AND D. R. MILLER. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Can. J. Zool.* 62:1566–1575.
- , AND R. E. PAGE. 1987. Displacement and dispersion of parturient caribou as antipredator tactics. *Can. J. Zool.* 65:1597–1606.
- BIERZYCHUDEK, P., AND V. ECKHART. 1988. Spatial segregation of the sexes of dioecious plants. *Am. Nat.* 132:34–43.
- BLEICH, V. C. 1983a. Big game guzzlers and mountain sheep. *Outdoor Calif.* 44(6):10.
- . 1983b. Comments on helicopter use by wildlife agencies. *Wildl. Soc. Bull.* 11:304–306.
- . 1993. Sexual segregation in desert-dwelling mountain sheep. Ph.D. Thesis, Univ. Alaska, Fairbanks. 126pp.
- , R. T. BOWYER, D. J. CLARK, AND T. O. CLARK. 1992c. Analyses of forage eaten by mountain sheep in the Mojave Desert, California. *Desert Bighorn Council. Trans.* 36:41–47.
- , ———, A. M. PAULI, M. C. NICHOLSON, AND R. W. ANTHES. 1994. Mountain sheep (*Ovis canadensis*) and helicopter surveys: ramifications for the conservation of large mammals. *Biol. Conserv.* 45:1–7.
- , ———, ———, R. L. VERNON, AND R. W. ANTHES. 1990d. Responses of mountain sheep to helicopter surveys. *Calif. Fish and Game* 76: 197–204.
- , C. D. HARGIS, J. A. KEAY, AND J. D. WEHAUSEN. 1991. Interagency coordination and the restoration of wildlife populations. Pages 277–284 in J. Edelbrock and S. Carpenter, eds. *Natural areas and Yosemite: prospects for the future.* U.S. Natl. Park Serv., Denver Serv. Center, Colo.
- , AND S. A. HOLL. 1982. Management of chaparral habitat for mule deer and mountain sheep in southern California. Pages 247–254 in C. E. Conrad and W. C. Oechel, tech. coords. *Proc. of the symposium on dynamics and management of Mediterranean-type ecosystems.* U.S. For. Serv. Gen. Tech. Rep. PSW-58.
- , M. C. NICHOLSON, A. T. LOMBARD, AND P. V. AUGUST. 1992b. Using a geographic information system to test mountain sheep habitat models. *Bienn. Symp. North. Wild Sheep and Goat Council. Proc.* 8:256–263.
- , AND A. M. PAULI. 1990. Mechanical evaluation of artificial watering devices built for mountain sheep in California. Pages 65–72 in G. K. Tsukamoto and S. J. Stiver, eds. *Wildlife water development.* Nev. Dep. Wildl., Reno.
- , S. G. TORRES, D. A. JESSUP, AND G. P. MULCAHY. 1992a. Status of bighorn sheep in California, 1991. *Desert Bighorn Council. Trans.* 36: 76–77.
- , J. D. WEHAUSEN, AND S. A. HOLL. 1990a. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conserv. Biol.* 4:383–390.
- , ———, K. R. JONES, AND R. A. WEAVER. 1990b. Status of bighorn sheep in California, 1989 and translocations from 1971 through 1989. *Desert Bighorn Council. Trans.* 34:24–26.
- , ———, J. A. KEAY, J. G. STAHPMANN, AND M. W. BERBACH. 1990c. Radiotelemetry collars and mountain sheep: a cautionary note. *Desert Bighorn Council. Trans.* 34:6–8.
- , ———, R. R. RAMEY, II, AND J. L. RECHEL. 1996. Metapopulation theory and mountain sheep: implications for conservation. Pages 353–373 in D. R. McCullough, ed. *Metapopulations and wildlife conservation.* Island Press, Covelo, Calif.
- BOER, A. H., G. REDMOND, AND T. J. PETTIGREW. 1989. LORAN-C: a navigation aid for aerial surveys. *J. Wildl. Manage.* 53:228–230.
- BON, R., AND R. CAMPAN. 1989. Social tendencies of the Corsican mouflon (*Ovis ammon musimon*) in the Caroux-Espinouse Massif (south of France). *Behav. Proc.* 19:57–78.
- BOWERS, M. A., AND H. D. SMITH. 1979. Differential habitat utilization by sexes of the deer mouse, *Peromyscus maniculatus*. *Ecology* 50:869–875.
- BOWYER, R. T. 1981. Activity, movement, and distribution of Roosevelt elk during rut. *J. Mammal.* 62:572–584.
- . 1984. Sexual segregation in southern mule deer. *J. Mammal.* 65:410–417.
- . 1986a. Habitat selection by southern mule deer. *Calif. Fish and Game* 72:153–169.
- . 1986b. Antler characteristics as related to social status of southern mule deer. *Southwest. Nat.* 31:289–298.
- . 1987. Coyote group size relative to predation on mule deer. *Mammalia* 51:515–526.
- . 1991. Timing of parturition and lactation in southern mule deer. *J. Mammal.* 72:138–145.
- , AND V. C. BLEICH. 1984. Effects of cattle grazing on selected habitats of southern mule deer. *Calif. Fish and Game* 70:240–247.

- , J. G. KIE, AND V. VAN BALLEMBERGHE. 1996. Sexual segregation in black-tailed deer: effects of scale. *J. Wildl. Manage.* 60:10–17.
- , AND D. W. KITCHEN. 1987. Behavioral significance of scent-marking by Roosevelt elk. *J. Mammal.* 68:418–423.
- , AND D. M. LESLIE, JR. 1992. *Ovis dalli*. *Mamm. Species* 393:1–7.
- , S. A. MCKENNA, AND M. E. SHEA. 1983. Seasonal changes in coyote food habits as determined by fecal analysis. *Am. Midland Nat.* 109: 266–273.
- BUNNELL, F. L. 1978. Horn growth and population quality in Dall sheep. *J. Wildl. Manage.* 42:764–775.
- . 1982. The lambing period of mountain sheep: synthesis, hypotheses, and tests. *Can. J. Zool.* 60:1–14.
- CAMERON, R. D., AND K. R. WHITTEN. 1979. Seasonal movements and sexual segregation of caribou determined by aerial survey. *J. Wildl. Manage.* 43:626–633.
- CAUGHLEY, G., AND C. KREBS. 1983. Are big mammals simply little mammals writ large? *Oecologia* (Berlin) 59:7–17.
- CHARLES, W. N., D. MCCOWAN, AND K. EAST. 1977. Selection of upland swards by red deer (*Cervus elaphus* L.) on Rhum. *J. Appl. Ecol.* 14:55–64.
- CLARK, R. K., D. A. JESSUP, M. D. KOCK, AND R. A. WEAVER. 1985. Survey of desert bighorn sheep in California for exposure to selected infectious diseases. *J. Am. Vet. Med. Assoc.* 187:1175–1179.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. Univ. Chicago Press, Chicago, Ill. 378pp.
- , AND P. H. HARVEY. 1983. The functional significance of variation in body size among mammals. Pages 632–697 in J. F. Eisenberg and D. G. Kleiman, eds. *Advances in the study of mammalian behavior*. Am. Soc. Mammal., Spec. Publ. 7.
- , G. R. IASON, AND F. E. GUINNESS. 1987. Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). *J. Zool., Lond.* 211:275–289.
- COBLENTZ, B. E. 1976. Functions of scent-urination in ungulates with special reference to feral goats (*Capra hircus*). *Am. Nat.* 110:549–557.
- CURIO, E. 1976. The ethology of predation. *Zoophysiol. Ecol.* 7. Springer-Verlag, Berlin, Germany; New York, N.Y. 250pp.
- CURRY, B. B., AND D. RESIGH. 1983. Geology. Pages 2.1–2.92 in B. B. Curry, ed. *Old Dad–Kelso Mountains resource survey*. Environ. Stud. Prog., Univ. California, Santa Barbara.
- DANNER, D. A., AND N. DODD. 1982. Comparison of coyote and gray fox scat diameters. *J. Wildl. Manage.* 46:240–241.
- DARWIN, C. 1871. The descent of man and selection in relation to sex. Murray, London, U.K. 409pp.
- DEMING, O. V. 1952. Tooth development of the Nelson bighorn sheep. *Calif. Fish and Game* 38: 523–529.
- DEMMENT, M. W., AND P. J. VAN SOEST. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125:641–672.
- DIXON, W. J. 1985. BMDP statistical software. Univ. California Press, Berkeley. 733pp.
- DODD, N. L. 1987. Ecological relationships of sympatric bighorn sheep and cattle at Aravaipa Canyon, Arizona. M.S. Thesis, Arizona State Univ., Tempe. 129pp.
- , AND W. W. BRADY. 1986. Cattle grazing influences on vegetation of sympatric desert bighorn range in Arizona. *Desert Bighorn Counc. Trans.* 30:8–13.
- DUNNE, G. C. 1977. Geology and structural evolution of Old Dad Mountain, Mojave Desert, California. *Geol. Soc. Am. Bull.* 88:737–748.
- DU TOIT, J. 1995. Sexual segregation in kudu: sex differences in competitive ability, predation risk, or nutritional needs? *S. Afr. J. Wildl. Res.* 25: 127–132.
- EASTLAND, W. G., R. T. BOWYER, AND S. G. FANCY. 1989. Effects of snow cover on selection of calving sites by caribou. *J. Mammal.* 70:824–828.
- EVENS, R. A., AND R. M. LOVE. 1957. The step-point method of sampling—a practical tool in range management. *J. Range Manage.* 10:208–212.
- FAY, F. H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *North Am. Fauna* 74:1–279.
- FEDUCCIA, A., AND B. H. SLAUGHTER. 1974. Sexual dimorphism in skates (Rajidae) and its possible role in differential niche utilization. *Evolution* 28:164–168.
- FESTA-BIANCHET, M. 1986. Site fidelity and seasonal range use by bighorn rams. *Can. J. Zool.* 64: 2126–2132.
- . 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* (Berlin) 75:500–506.
- FITZGERALD, A. E., AND D. C. WADDINGTON. 1979. Comparison of two methods of fecal analysis of herbivore diet. *J. Wildl. Manage.* 43:468–473.
- FORRESTER, D. J. 1971. Bighorn sheep lungworm-pneumonia complex. Pages 158–173 in J. W. Davis and R. C. Anderson, eds. *Parasitic diseases of wild mammals*. Iowa State Univ. Press, Ames.
- FREEMAN, D. C., L. G. KLIKOFF, AND K. T. HARPER. 1976. Differential resource utilization by the sexes of dioecious plants. *Science* 193:597–599.
- FREIWALD, D. A. 1984. Groundwater resources of Lanfair and Fenner valleys and vicinity, San Bernardino County, California. U.S. Geol. Surv. Water Res. Invest. Rep. 83-4082.
- GAUTIER-HION, A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *J. Anim. Ecol.* 49:237–269.
- GEIST, V. 1966. Validity of horn segment counts in aging bighorn sheep. *J. Wildl. Manage.* 30:634–635.

- . 1968. On the interrelation of external appearance, social behavior and social structure of mountain sheep. *Z. Tierpsychol.* 25:199–215.
- . 1971. Mountain sheep: a study in behavior and evolution. Univ. Chicago Press, Chicago, Ill. 383pp.
- . 1977. A comparison of social adaptations in relation to ecology in gallinaceous bird and ungulate societies. *Annu. Rev. Ecol. Syst.* 8:193–207.
- . 1981. On the reproductive strategies in ungulates and some problems of adaptation. Pages 111–132 in G. G. E. Scudder and J. L. Reveal, eds. *Evolution today*. Proc. Second Int. Congr. Syst. Evol. Biol., Carnegie Mellon Univ., Pittsburgh, Pa.
- . 1982. Adaptive behavioral strategies. Pages 219–277 in J. W. Thomas and D. E. Towell, eds. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Penn.
- , AND P. T. BROMLEY. 1978. Why deer shed antlers. *Z. Saugtierkd.* 43:223–231.
- , AND R. G. PETOCZ. 1977. Bighorn sheep in winter: do rams maximize reproductive fitness by spatial and habitat segregation from ewes? *Can. J. Zool.* 55:1802–1810.
- GRIFFITH, B., AND B. A. YOUTIE. 1988. Two devices for estimating foliage density and deer hiding cover. *Wildl. Soc. Bull.* 16:206–210.
- GUTHRIE, R. D. 1990. Frozen fauna of the mammoth steppe: the story of Blue Babe. Univ. Chicago Press, Chicago, Ill. 323pp.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31:295–311.
- HARRISON, S., AND D. HEBERT. 1988. Selective predation by cougar within the Junction Wildlife Management Area. *Bienn. Symp. North. Wild Sheep and Goat Council. Proc.* 6:292–306.
- HEISEY, D. M. 1985. Analyzing selection experiments with log-linear models. *Ecology* 66:1744–1748.
- HILBORN, R., AND S. C. STEARNS. 1982. On inference in ecology and evolutionary biology: the problem of multiple causation. *Acta Biotheor.* 31:145–164.
- HILL, D. A., AND M. W. RIDLEY. 1987. Sexual segregation in winter, spring dispersal and habitat use in the pheasant (*Phasianus colchicus*). *J. Zool., Lond.* 212:657–668.
- HIRTH, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. *Wildl. Monogr.* 53. 55pp.
- HODGMAN, T. P., AND R. T. BOWYER. 1986. Fecal crude protein relative to browsing intensity by white-tailed deer on wintering areas in Maine. *Acta Theriol.* 31:347–353.
- HOGG, J. T. 1987. Intrasexual competition and mate choice in Rocky Mountain bighorn sheep. *Ethology* 75:119–144.
- HOLECHEK, J. L., AND M. VAVRA. 1981. The effect of slide and frequency observation numbers on the precision of microhistological analysis. *J. Range Manage.* 34:337–338.
- HOLMES, E. 1988. Foraging behaviors among different age and sex classes of Rocky Mountain goats. *Bienn. Symp. North. Wild Sheep and Goat Council. Proc.* 6:13–25.
- HONE, J. 1988. Evaluation of methods for ground survey of feral pigs and their sign. *Acta Theriol.* 33:451–465.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187–211.
- ILLIUS, A. W., AND I. J. GORDON. 1987. The allometry of food intake in grazing ruminants. *J. Anim. Ecol.* 56:989–999.
- JAEGER, J. R., J. D. WEHAUSEN, AND V. C. BLEICH. 1991. Evaluation of time-lapse photography to estimate population parameters. *Desert Bighorn Council. Trans.* 35:5–8.
- , ———, ———, AND C. L. DOUGLAS. 1993. Limits in the resolution of LORAN-C for aerial telemetry studies. *Desert Bighorn Council. Trans.* 37:20–23.
- JENKS, J. A., D. M. LESLIE, JR., R. L. LOCHMILLER, AND M. A. MELCHIORI. 1994. Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. *J. Mammal.* 75:1045–1053.
- JOHNSON, D. H., M. D. BRYANT, AND A. H. MILLER. 1948. Vertebrate animals of the Providence Mountains area of California. *Univ. Calif. Publ. Zool.* 48:221–376.
- KEAST, A. 1977. Mechanisms expanding niche width and minimizing intraspecific competition in two centrarchid fishes. Pages 333–395 in M. K. Hecht, W. C. Steere, and B. Wallace, eds. *Evolutionary biology*. Plenum Press, New York, N.Y.
- KELLY, W. E. 1980. Predator relationships. Pages 186–196 in G. Monson and L. Sumner, eds. *The desert bighorn: its life history, ecology, and management*. Univ. Arizona Press, Tucson.
- KERSHAW, K. K. 1964. Quantitative and dynamic ecology. Edward Arnold, London, U.K. 183pp.
- KIE, J. G., J. A. BALDWIN, AND C. J. EVANS. 1994. CALHOME: home range analysis program. U.S. For. Serv., Pac. Southwest Res. Stn., Fresno, Calif. 19pp.
- KING, M. M., AND H. D. SMITH. 1980. Differential habitat utilization by the sexes of mule deer. *Great Basin Nat.* 40:273–281.
- KITCHEN, D. W. 1974. Social behavior and ecology of the pronghorn. *Wildl. Monogr.* 38. 96pp.
- KLIMLEY, A. P. 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environ. Biol. Fishes* 18:27–40.
- KRAUSMAN, P. R., J. J. HERVERT, AND L. L. ORDWAY. 1984. Radio tracking desert mule deer and bighorn sheep with light aircraft. Pages 115–118 in P. R. Krausman and N. Smith, eds. *Deer in the southwest: a workshop*. Sch. of Renewable Nat. Resour., Univ. Arizona, Tucson.
- , ———, AND ———. 1985b. Capturing deer and mountain sheep with a net-gun. *Wildl. Soc. Bull.* 13:71–73.
- , B. D. LEOPOLD, R. F. SEEGMILLER, AND S.

- G. TORRES. 1989. Relationships between desert bighorn sheep and habitat in western Arizona. *Wildl. Monogr.* 102. 66pp.
- , S. TORRES, L. L. ORDWAY, J. J. HERVERT, AND M. BROWN. 1985a. Diel activity of ewes in the Little Harquahala Mountains, Arizona. *Desert Bighorn Council Trans.* 29:24–26.
- KUCERA, T. E. 1978. Social behavior and breeding system of the desert mule deer. *J. Mammal.* 59: 463–476.
- KURT, F. 1974. Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. Pages 618–634 in V. Geist and F. Walther, eds. *The behaviour of ungulates and its relation to management*. Vol. 2. International symposium held at University of Calgary, Alberta, Canada, 2–4 November 1971. *Int. Union Conserv. Nat. and Natur. Resour., Publ. New Ser.* 24. Morges, Switzerland.
- LAGORY, K. E., C. BAGSHAW, III, AND I. L. BRISBIN, JR. 1991. Niche differences between male and female white-tailed deer on Ossabaw Island, Georgia. *Appl. Anim. Behav. Sci.* 29:205–214.
- LESLIE, D. M., JR., AND C. L. DOUGLAS. 1979. Desert bighorn sheep of the River Mountains, Nevada. *Wildl. Monogr.* 66. 56pp.
- LIMA, S. L., T. J. VALONE, AND T. CARACO. 1985. Foraging-efficiency predation-risk trade-off in the grey squirrel. *Anim. Behav.* 33:155–165.
- LITVAITIS, J. A. 1990. Differential habitat use by sexes of snowshoe hares (*Lepus americanus*). *J. Mammal.* 71:520–523.
- LONGHURST, W. M., A. S. LEOPOLD, AND R. F. DASMANN. 1952. A survey of California deer herds, their ranges and management problems. *Calif. Dep. Fish and Game, Game Bull.* 6:1–136.
- LOPEZ ORNAT, A., AND R. GREENBERG. 1990. Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. *Auk* 107:539–543.
- MAGNHAGEN, C. 1991. Predation risk as a cost of reproduction. *Trends Ecol. and Evol.* 6:183–186.
- MAIN, M. B., AND B. E. COBLENTZ. 1990. Sexual segregation among ungulates: a critique. *Wildl. Soc. Bull.* 18:204–210.
- , AND ———. 1996. Sexual segregation in Rocky Mountain mule deer. *J. Wildl. Manage.* 60:497–507.
- , F. W. WECKERLY, AND V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. *J. Mammal.* 77:449–461.
- MARTENS, S., AND B. BALDWIN. 1983. Vegetation and flora. Pages 3.1–3.43 in B. B. Curry, ed. *Old Dad—Kelso Mountains resource survey*. *Environ. Stud. Prog.*, Univ. California, Santa Barbara.
- MAYER, V. W. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. *Am. Midland Nat.* 48:480–512.
- MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. Univ. Michigan Press, Ann Arbor. 271pp.
- , D. H. HIRTH, AND S. J. NEWHOUSE. 1989. Resource partitioning between sexes in white-tailed deer. *J. Wildl. Manage.* 53:277–283.
- MILLAR, J. S., AND R. M. ZAMMUTO. 1983. Life histories of mammals: an analysis of life tables. *Ecology* 64:631–635.
- MIQUELLE, D. G. 1990a. Why don't bull moose eat during the rut? *Behav. Ecol. Sociobiol.* 27:145–151.
- . 1990b. Behavioral ecology of moose in Denali National Park and Preserve, Alaska. Ph.D. Thesis, Univ. Idaho, Moscow. 141pp.
- , J. M. PEEK, AND V. VAN BALLEMBERGHE. 1992. Sexual segregation in Alaskan moose. *Wildl. Monogr.* 122. 57pp.
- MOLVAR, E. M., AND R. T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *J. Mammal.* 75:621–630.
- MONMONIER, M., AND G. A. SCHNELL. 1988. Map appreciation. Prentice Hall, Englewood Cliffs, N.J. 431pp.
- MORGANTINI, L. E., AND R. J. HUDSON. 1981. Sex differential in use of the physical environment by bighorn sheep (*Ovis canadensis*). *Can. Field-Nat.* 95:69–74.
- MORRIS, D. W. 1987. Sexual differences in habitat use by small mammals: evolutionary strategy or reproductive constraint? *Oecologia (Berlin)* 65: 51–57.
- MUNZ, P. A. 1974. A flora of southern California. Univ. California Press, Berkeley. 1086pp.
- MURIE, A. 1944. The wolves of Mount McKinley. *U.S. Natl. Park Serv., Fauna Ser.* 5:1–238.
- MURIE, O. J. 1954. A field guide to animal tracks. Houghton Mifflin Co., Boston, Mass. 374pp.
- NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541–545.
- NIEVERGELT, B. 1967. Die Zusammensetzung der Gruppen beim Alpensteinbock. *Z. Saugetierkd.* 82:129–144.
- OAKES, E. J., R. HARMSSEN, AND C. EBERL. 1992. Sex, age, and seasonal differences in the diets and activity budgets of muskoxen (*Ovibos moschatus*). *Can. J. Zool.* 70:605–616.
- OBER, E. H. 1931. The mountain sheep of California. *Calif. Fish and Game* 17:27–39.
- PATRIC, E. F., T. P. HUSBAND, C. G. MCKIEL, AND W. M. SULLIVAN. 1988. Potential of LORAN-C for wildlife research along coastal landscapes. *J. Wildl. Manage.* 48:474–478.
- PEEK, J. M., AND A. L. LOVAAS. 1968. Differential distribution of elk by sex and age on the Gallatin winter range, Montana. *J. Wildl. Manage.* 32: 553–557.
- PELTON, M. R. 1972. Use of foot trail travelers in the Great Smokey Mountains National Park to estimate black bear (*Ursus americanus*) activity. *Int. Conf. Bear Res. and Manage.* 2:36–42.
- PETERS, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, London, U.K. 329pp.

- PLATT, J. R. 1964. Strong inference. *Science* 146: 347–353.
- POOLE, J. H. 1987. Rutting behaviour in African elephants: the phenomenon of musth. *Behaviour* 102:283–316.
- , AND C. J. MOSS. 1981. Musth in the African elephant. *Nature (London)* 292:830–831.
- PRINS, H. H. T. 1989. Condition changes and choice of social environment in African buffalo bulls. *Behaviour* 108:297–324.
- QUINN, J. F., AND A. E. DUNHAM. 1983. On hypothesis testing in ecology and evolution. *Am. Nat.* 122:602–617.
- RACHLOW, J. L., AND R. T. BOWYER. 1991. Inter-annual variation in timing and synchrony of parturition in Dall's sheep. *J. Mammal.* 72:487–492.
- RALLS, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.* 111:917–938.
- REMINGTON, R. A. 1982. Age and weight relationships of desert bighorn sheep captured in Arizona during 1981–82. *Desert Bighorn Council Trans.* 26:38–42.
- ROBBINS, C. T., T. A. HANLEY, A. E. HAGERMAN, O. HJELJORD, D. L. BAKER, C. C. SCHWARTZ, AND W. W. MAUTZ. 1987. Role of tannins in defending plants against ruminants. *Ecology* 68:98–107.
- SCARBROUGH, D. L., AND P. R. KRAUSMAN. 1988. Sexual segregation by desert mule deer. *Southwest. Nat.* 33:157–165.
- SCHALLER, G. B., AND B. JUNRANG. 1988. Effects of a snowstorm on Tibetan antelope. *J. Mammal.* 69:631–634.
- SCHOENER, T. W. 1966. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155:474–477.
- . 1968. The anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704–726.
- SCHWARTZ, O. A., V. C. BLEICH, AND S. A. HOLL. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biol. Conserv.* 37:179–190.
- SEEGMILLER, R. F., AND R. D. OHMART. 1982. Desert bighorn lamb and adult-yearling diets from western Arizona. *Desert Bighorn Council Trans.* 26:34–38.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68: 113–151.
- . 1972. Sexual selection and dimorphism in birds. Pages 180–230 in B. Campbell, ed. *Sexual selection and the descent of man, 1871–1971*. Aldine Press, Chicago, Ill.
- SHACKLETON, D. M. 1985. *Ovis canadensis*. *Mamm. Species* 230:1–9.
- SHANK, C. C. 1982. Age and sex differences in the diets of wintering Rocky Mountain bighorn sheep. *Ecology* 63:627–633.
- . 1985. Inter- and intra-sexual segregation of chamois (*Rupicapra rupicapra*) by altitude and habitat during summer. *Z. Säugetierkd.* 50:117–125.
- SHAW, H. G. 1983. Mountain lion field guide. *Ariz. Game and Fish Dep., Spec. Rep.* 9:1–27.
- SHORT, H. L. 1981. Nutrition and metabolism. Pages 99–127 in O. C. Wallmo, ed. *Mule deer and black-tailed deer of North America*. Univ. Nebraska Press, Lincoln.
- SIEGFRIED, W. R. 1979. Vigilance and group size in springbok. *Madoqua* 12:151–154.
- SINCLAIR, A. R. E. 1977. The African buffalo: a study of resource limitation of populations. Univ. Chicago Press, Chicago, Ill. 355pp.
- SKOGLAND, T. 1987. Ungulate foraging strategies: optimization for predator avoidance or competition for limiting resources? *Trans. Congr. Int. Union Game Biol.* 18:186.
- . 1989. Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Adv. Ethology* 29:1–74.
- SLAUSON, W. L., B. S. CADE, AND J. D. RICHARDS. 1991. User manual for BLOSSOM statistical software. U.S. Ecol. Res. Cent., Fort Collins, Colo. 61pp.
- SMALLWOOD, J. A. 1987. Sexual segregation by habitat in American kestrels wintering in southcentral Florida: vegetative structure and responses to differential prey availability. *Condor* 89:842–849.
- SOLOW, A. R. 1989. A randomization test for independence of animal locations. *Ecology* 70:1546–1549.
- SPARKS, D. R., AND J. C. MALECHEK. 1968. Estimating percentage dry weight in diets using a microscope technique. *J. Range Manage.* 21: 264–265.
- STAINES, B. W. 1976. The use of natural shelter by red deer (*Cervus elaphus*) in relation to weather in N-E Scotland. *J. Zool., Lond.* 180:1–8.
- , J. M. CRISP, AND T. PARISH. 1982. Differences in the quality of food eaten by red deer (*Cervus elaphus*) stags and hinds in winter. *J. Appl. Ecol.* 19:65–77.
- STORER, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. *Auk* 83:423–436.
- SUKUMAR, R., AND M. GADGIL. 1988. Male–female differences in foraging on crops by Asian elephants. *Anim. Behav.* 36:1233–1235.
- SUMANIK, R. S. 1987. Wolf ecology in the Kluanne Region, Yukon Territory. M.S.F. Thesis, Michigan Tech. Univ., Houghton. 102pp.
- THOMPSON, R. W., AND J. C. TURNER. 1982. Temporal geographic variation in the lambing season of bighorn sheep. *Can. J. Zool.* 60:1781–1793.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, ed. *Sexual selection and the descent of man*. Aldine Press, Chicago, Ill.
- TURNER, J. C. 1973. Water, energy and electrolyte balance in the desert bighorn sheep, *Ovis canadensis*. Ph.D. Thesis, Univ. California, Riverside. 138pp.
- . 1976. Initial investigations into the reproductive biology of the desert bighorn ram, *Ovis*

- canadensis nelsoni*, *O. c. cremnobates*. Bienn. Symp. North. Wild Sheep and Goat Counc. Proc. 2:22-25.
- . 1979. Osmotic fragility of desert bighorn sheep red blood cells. *Comp. Biochem. Physiol.* 64A:167-175.
- , AND R. A. WEAVER. 1980. Water. Pages 100-112 in G. Monson and L. Sumner, eds. *The desert bighorn: its life history, ecology and management*. Univ. Arizona Press, Tucson.
- VAN SOEST, P. J. 1982. *Nutritional ecology of the ruminant*. O & B Books, Inc., Corvallis, Ore. 374pp.
- VERME, L. J. 1988. Niche selection by male white-tailed deer: an alternative hypothesis. *Wildl. Soc. Bull.* 16:448-451.
- WATSON, A., AND B. W. STAINES. 1978. Differences in the quality of wintering areas used by male and female red deer (*Cervus elaphus*) in Aberdeenshire. *J. Zool., Lond.* 186:544-550.
- WECKERLY, F. W. 1993. Intersexual resource partitioning in black-tailed deer: a test of the body size hypothesis. *J. Wildl. Manage.* 57:475-494.
- , AND J. P. NELSON. 1990. Age and sex differences of white-tailed deer diet composition, quality, and calcium. *J. Wildl. Manage.* 54:532-538.
- WEHAUSEN, J. D. 1980. *Sierra Nevada bighorn sheep: history and population ecology*. Ph.D. Thesis, Univ. Michigan, Ann Arbor. 240pp.
- . 1995. Fecal measures of diet quality in wild and domestic ruminants. *J. Wildl. Manage.* 59: 816-823.
- WELLES, R. E., AND F. B. WELLES. 1961. The big-horn of Death Valley. U.S. Natl. Park Serv., Fauna Ser. 6. 242pp.
- WHITE, R. G. 1983. Foraging patterns and their multiplier effect on productivity of northern ungulates. *Oikos* 40:377-384.
- WILKINSON, L. 1988. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Ill. 822pp.
- WILLIAMS, G. C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton Univ. Press, Princeton, N.J. 307pp.
- . 1975. *Sex and evolution*. Princeton Univ. Press, Princeton, N.J. 200pp.
- WIRTZ, P., AND P. KAISER. 1988. Sex differences and seasonal variation in habitat choice in a high density population of waterbuck, *Kobus ellipsipyrmus* (Bovidae). *Z. Säugetierkd.* 53:162-169.
- WISHART, W. 1978. Bighorn sheep. Pages 161-171 in J. L. Schmidt and D. L. Gilbert, eds. *Big game of North America: ecology and management*. Stackpole Books, Harrisburg, Pa.
- WOOLSEY, N. G. 1985. *Coyote field guide*. Ariz. Game and Fish Dep., Spec. Rep. 15:1-39.
- YOUNG, S. P., AND E. A. GOLDMAN. 1944. *The wolves of North America*. Am. Wildl. Inst., Washington, D.C. 636pp.
- YOUNG, T. P., AND L. A. ISBELL. 1991. Sex differences in giraffe feeding ecology: energetic and social constraints. *Ethology* 87:79-89.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, N.J. 718pp.

Received 25 May 1993.

Accepted 27 August 1996.

EXHIBIT 422



Tools and Technology Article

Using Genetic Tools to Track Desert Bighorn Sheep Colonizations

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ABSTRACT Understanding colonization is vital for managing fragmented populations. We employed mitochondrial DNA haplotypes and 14 microsatellite (nuclear DNA) markers to infer the origins of newly established populations of desert bighorn sheep (*Ovis canadensis nelsoni*) and to assess loss of genetic diversity during natural colonizations. We used haplotype distribution, *F*-statistics, Bayesian population clustering, and assignment tests to infer source populations for 3 recent colonies and identified a previously undetected colonization from multiple source populations. Allelic richness declined in 3 of 4 colonies in comparison to the primary source populations, but not as much as has been reported for translocated populations. Heterozygosity declined in only one colony. We also demonstrated that both native and translocated desert bighorn sheep have naturally recolonized empty habitats and suggest that colonization may partially offset population extinction in the region as long as connectivity is maintained. Genetic techniques and mitochondrial DNA haplotypes we described will allow managers to determine the origins of future colonizations by bighorn sheep in California, USA, and prioritize protection of linkages between known sources and colonies.

KEY WORDS assignment test, California, colonization, metapopulation, microsatellites, mitochondrial DNA, *Ovis canadensis*, translocation.

Colonization of empty habitat is required to offset high population extinction rates for species with fragmented distributions (Levins 1970). Understanding colonization could help wildlife managers identify and protect key linkages between habitat patches, prioritize translocations when natural colonization rates are thought to be inadequate, predict range expansions, and respond appropriately to newly discovered populations of unknown origins. Colonization processes also can affect loss or retention of genetic diversity, which has been linked to individual fitness and population performance (Vila et al. 2003, Hogg et al. 2006). However, studying colonization usually requires either repeated surveys in all potential habitat patches or long-term monitoring of many individuals (Ims and Yoccoz 1997).

Population genetic data offer alternative means to track or identify recent colonizations (e.g., Eldridge et al. 2001, Scribner et al. 2003, Latch et al. 2006b). Emigration of a few individuals to new habitat results in a founder event that is analogous to a population bottleneck and, therefore, is predicted to affect genetic structure and diversity in 2 ways. First, because of the underrepresentation of rarer alleles in emigrants, genetic diversity is expected to be lower in the colony than in the source population (Nei et al. 1975). Second, although allele frequencies in colony and source(s) are expected to diverge after a founder event (e.g., Mock et al. 2004, Hawley et al. 2006), the identity and frequency of

alleles in a recent colony should be more similar to those in the source population(s) than to other nearby populations. The largest changes in allele frequencies and genetic diversity are expected when there are few founders, the colony remains small, and if there is no subsequent gene flow between colony and source (Nei et al. 1975, Keller et al. 2001). Those changes are also influenced by time since the founder event (see Cornuet and Luikart 1996). Changes in genetic structure and loss of genetic diversity resulting from population reintroductions or translocations (e.g., Mock et al. 2004, Whittaker et al. 2004), invasions (e.g., Hufbauer et al. 2004, Hawley et al. 2006), or rare long-distance natural recolonizations (e.g., Onorato et al. 2004, Hedmark and Ellegren 2007) have been well-described. Effects of local-scale colonizations on genetic structure and diversity in a metapopulation may be less predictable because the size of the founding population is rarely known and gene flow between source and colony may continue after colonization.

Bighorn sheep favor mountainous habitat that is often naturally discontinuous, resulting in natural metapopulations (Schwartz et al. 1986; Bleich et al. 1990, 1996; Epps et al. 2003). In the 19th and 20th centuries bighorn sheep suffered dramatic range reductions, many of which were attributed to disease and human exploitation (Buechner 1960). In the California, USA, deserts, however, extinctions were a more recent phenomenon of the mid-20th century (Wehausen et al. 1987, Wehausen 1999, Epps et al. 2004). In part because colonization was considered unlikely, bighorn sheep have been translocated extensively throughout the western United States (Ramey 1993). However, unaided colonization of empty habitat patches has now been well-documented (Bleich et al. 1996, Singer et al. 2000,

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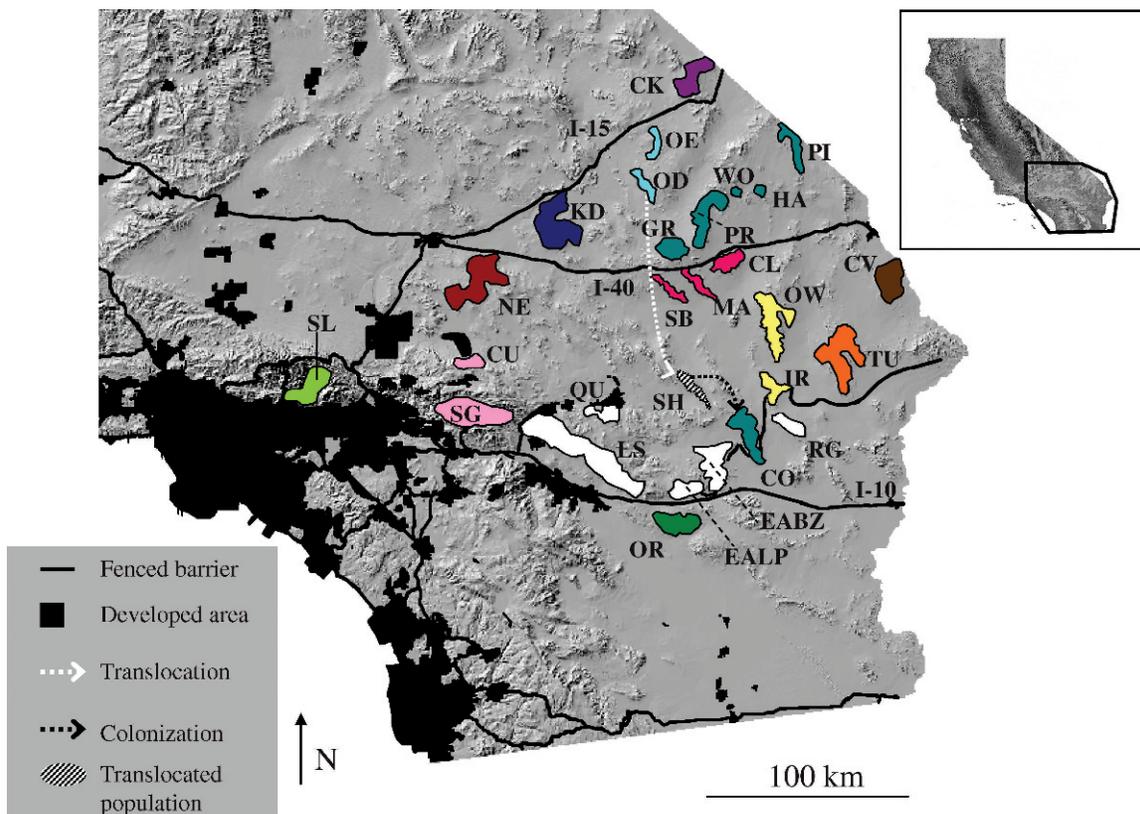


Figure 1. Relief map of southeastern California, USA, showing the 27 populations of desert bighorn sheep we sampled in 2000–2004, as well as the translocated population in the Sheephole Mountains (SH). Population polygon coloring represents results of BAPS clustering analysis; we clustered like-colored populations by genetic similarity, indicative of recent or current gene flow. We defined population identification codes in Appendix A; human-made dispersal barriers including fenced highways, fenced canals, and urban areas are mapped in black with interstate highways indicated as, for example, “I-15.” We inferred colonization of the Coxcomb Range (CO; dashed black arrow) from SH because CO individuals were assigned genetically to the Old Dad (OD) population. Old Dad was the source of the bighorn sheep translocated to SH (dashed white arrow).

Epps et al. 2003). We define colonization as emigration of individuals of both sexes to an empty habitat patch, with subsequent reproduction. We examined recent colonizations by desert bighorn sheep (*Ovis canadensis nelsoni*) in California to determine 1) whether source populations could be confidently identified using standard tests for genetic structure and population assignment, and 2) whether significant reductions in genetic diversity (i.e., allelic richness) and heterozygosity occurred during natural colonizations.

STUDY AREA

We conducted our study in the Mojave and Sonoran Desert regions of California (Fig. 1), where desert bighorn sheep typically inhabited small mountain ranges isolated by flat desert with little water and limited forage. More than 50 native and reintroduced populations totaled approximately 4,200 bighorn sheep (*O. c. nelsoni*), but about half of those populations contained <50 individuals (Epps et al. 2003), making them vulnerable to genetic drift and loss of genetic diversity. Gene flow among those populations was affected by distance, topography, and human-made barriers such as fenced interstate highways (Epps et al. 2005, 2007). Due to frequent extinction of bighorn sheep populations in the 20th century, uninhabited mountain ranges occur

throughout the study area (Wehausen et al. 1987, Wehausen 1999).

Although population monitoring often was sporadic (Wehausen 1999), radiotelemetry and population surveys identified 3 recent colonizations (or recolonizations). The South Bristol Mountains (SB; Fig. 1) were uninhabited (Torres et al. 1994) until 3 females radiocollared in the nearby (5 km) Marble Mountains (MA; Fig. 1) traveled to SB in 1993. By the late 1990s, a small but rapidly increasing population was established; a 2007 survey resulted in a mark-resight estimate of 68 individuals (J. D. Wehausen, White Mountain Research Station, personal communication). The second colonization occurred in the Iron Mountains (IR; Fig. 1). Observations at the sole known water source in IR indicated no resident sheep in 1993 (G. Sudmeier, Society for the Conservation of Bighorn Sheep, personal communication) but we observed males, females, and juveniles in 2001–2003. Historical evidence of movement by male and female bighorn sheep between the Old Woman Mountains (OW; Fig. 1) and IR, as well as movements between those ranges by radiocollared males, suggested OW was the likely source (Bleich et al. 1990; A. Pauli, California Department of Fish and Game, personal communication). The third apparent colonization occurred when emigrants from an unknown source founded the

Cushenbury population (CU; Fig. 1) in the 1980s (J. Davis, California Department of Fish and Game, personal communication), which at the time of our study was estimated at 25–50 individuals (Epps et al. 2003).

METHODS

Genetic Data Collection

We used previously published microsatellite genotypes and mitochondrial DNA (mtDNA) sequence data for 397 individuals from 27 populations of desert bighorn sheep in southeastern California (Fig. 1), collected from fecal and blood samples obtained during 2000–2004 (Epps et al. 2005). We restricted analyses to unique individuals that were successfully genotyped at all 14 microsatellite loci; 515 nucleotides near the beginning of the mtDNA control region were sequenced for 394 of these samples. Mean sample size per population was 15 individuals (range = 6–29).

Where sex identification was necessary, we determined sex of each individual sampled using the SE47 and SE48 sex identification primers (Yamamoto et al. 2002), which amplify fragments of different sizes on the X and Y chromosomes. We used 20 μ L PCR (Polymerase Chain Reaction) with the following reaction conditions: 1 \times PCR Buffer I (Applied BioSystems, Foster City, CA), 0.16 mM dNTPs, 10 μ g bovine serum albumin (New England BioLabs, Ipswich, MA), 2.25 mM MgCl₂, 80 nM each primer, 0.7 units of Amplitaq Gold™ DNA polymerase (Applied BioSystems), and 1 μ L of extracted DNA. We used an initial heating cycle of 95° C for 7 minutes and 30 seconds, followed by 40 cycles of 95° C for 30 seconds, 54° C for 45 seconds, and 72° C for 30 seconds. We visualized the SE47 and SE48 amplification products on 2% agarose gels, prestained with ethidium bromide. We repeated amplifications until we observed the male-specific PCR fragment or we observed the single female band in 3 replicates.

Analyses

We applied common analytical techniques for describing genetic structure and diversity among populations to confirm (SB and IR) or infer (CU and other) source populations for recent colonizations and to test for population bottlenecks and decreased genetic diversity in colonies. Because most gene flow in this system occurred between populations <15 km apart (Epps et al. 2005), we evaluated potential source populations <30 km from each colonized population. To infer the source of females for each colony, we mapped distribution of mtDNA haplotypes (maternally inherited) in potential source populations. Female movements probably limited colonization because female bighorn are more philopatric than males (Festa-Bianchet 1986, Singer et al. 2000).

We evaluated whether genetic distance (F_{ST} ; Wright 1921, Weir and Cockerham 1984) was significantly lower between colony and source in comparison to other nearby populations. Interpreting gene flow from F_{ST} is problematic unless populations are assumed to be in drift–migration–

mutation equilibrium, which is unlikely in recent colonizations, but F_{ST} provides a useful relative estimate of population similarity (Neigel 2002). We used FSTAT (Goudet 1995) to calculate F_{ST} with bootstrap 95% confidence intervals from the microsatellite data between all population pairs. We also estimated F_{ST} from the mtDNA sequence variation and haplotype frequency (ARLEQUIN Version 3.11, <http://cmpg.unibe.ch/software/arlequin3/>; accessed 30 Jun 2008).

To distinguish clusters of populations linked by high gene flow, we grouped all 27 study populations by genetic similarity using Bayesian clustering methods employed by BAPS (Corander et al. 2003). We set burn-in time to 10,000, chain length to 50,000, thinning to 5, and ensured these values were sufficient to achieve convergence of estimates (Corander et al. 2003). We reported only clusters with posterior probabilities >0.95.

Individual-based assignment tests such as STRUCTURE (Pritchard et al. 2000) are often used to identify migrants or determine population origins (e.g., Mock et al. 2004). We used STRUCTURE to evaluate whether colonies had single or multiple origins. We combined all individuals from all 27 populations into one data set with no information on sample origin and estimated the likely number of clusters (k) of genetically similar individuals by running 10 simulations for each k from 1 and 30, using a burn-in of 500,000 chains followed by 1,000,000 chains for each run. We assumed that individuals were of admixed ancestry and allele frequencies were correlated (λ set at 1), and we allowed STRUCTURE to infer the degree of admixture. We identified the best value of k (k_{best}) as that where the second-order rate of change in the log-likelihood values for different k was maximized (Evanno et al. 2005). Program STRUCTURE fractionally assigns each individual to each cluster based on an assignment index (q) that sums to 1 across all clusters; we assigned individuals to the single most likely cluster based on the maximum value of q (q_{max}) estimated at k_{best} and defined individual assignments at $q_{max} > 0.5$ as high confidence.

Methods that assign individuals to a priori populations (e.g., mountain ranges) with high gene flow may split assignment probabilities among those populations. Alternatively, methods that assign individuals to clusters determined post hoc from genetic structure (e.g., STRUCTURE) may be hard to interpret or evaluate statistically, especially if assignment indices are low. To address both of those problems, we used GENECLASS2 (Piry et al. 2004) to assign 1) recently colonized populations to potential source populations (all other populations sampled) by ranked likelihood scores using the Bayesian classification method of Rannala and Mountain (1997) and an assignment threshold of 0.01, and 2) individuals from recently colonized populations to potential source populations (all other populations sampled) based on ranked likelihood scores. We then interpreted assignments to individual populations in the context of population clusters with high gene flow as identified by BAPS.

After identifying the most likely sources for each colony, we tested whether genetic diversity declined sharply during natural colonizations. We estimated allelic richness (A ; average allelic diversity corrected for differences in sample size) at each locus for source and colony with FSTAT (Goudet 1995) and estimated unbiased heterozygosity (H_e ; Nei 1987). After examining distribution of differences for normality, we used a 1-tailed paired sample t -test across loci to determine whether A and H_e in each colony were lower than in the respective sources (Zar 1999). For populations with clear evidence of mixed origins (see Results), we tested for differences in A and H_e via 2-tailed paired sample t -tests. We checked for population bottlenecks by testing for shifted modes in allele frequencies in each population (Luikart et al. 1998) using BOTTLENECK (Cornuet and Luikart 1996) because Mock et al. (2004) found that test to be most effective in detecting founder events.

RESULTS

We detected 19 mtDNA haplotypes in 27 populations (Appendix A; GenBank accession no. AY903993-AY904012, AF076912). The SB and IR colonies contained a subset of mtDNA haplotypes detected in their respective source populations (MA and OW; Appendix A). However, NE (>80 km W of SB; Fig. 1) also contained the 2 haplotypes found in SB (Appendix A). The CU colony (unknown source) contained only one haplotype (N), also found in SG, and found elsewhere only in the more distant QU, LS, EALP, and RG complex of populations (Appendix A; Fig. 1). We detected none of the NE haplotypes in CU, implying that SG was the most likely source of colonizing females. Genetic distance values calculated from mtDNA values accurately linked IR-OW and supported CU-SG (Table 1) but conflicted with other data in one case: $F_{ST-mtDNA} = 0$ for NE-SB, whereas $F_{ST-mtDNA} = 0.11$ for MA-SB (the likely source-colony pair based on radiotelemetry and microsatellite analyses; Table 1). Genetic distance estimates (F_{ST}) from microsatellite data generally corroborated known source-colony pairs, although wide confidence intervals precluded confident distinction of the source population for SB (Table 1). Despite identical mtDNA haplotypes in NE and SB, microsatellite markers did not support NE as a population of origin (Table 1). Genetic distance between CU and NE was 5 times higher than that between CU and SG, implying that male as well as female colonizers originated in SG (Table 1).

Bayesian population (not individual) clustering via BAPS from the microsatellite data resulted in 13 population clusters (Fig. 1). Although BAPS may overestimate cluster number (Latch et al. 2006a), the observed number of clusters was less than determined by STRUCTURE (below). Program BAPS grouped MA with SB and grouped OW with IR (Fig. 1). The CU population was linked to SG rather than NE. A population previously considered to be native (CO) was grouped with PR, HA, WO, and PI >95 km north rather than with other nearby populations (Fig. 1).

Table 1. Genetic distance (F_{ST}) values for microsatellite (with 95% CIs) and mitochondrial DNA (mtDNA) markers for 4 recently colonized populations and potential source populations of desert bighorn sheep we sampled in 2000–2004 in California, USA. See Appendix A for explanation of population codes.

Population pair	F_{ST} (microsatellite markers)			F_{ST} (mtDNA)
	Point estimate	95% CI (lower lim)	95% CI (upper lim)	
SB-MA ^a	0.039	0.019	0.061	0.112
SB-GR	0.111	0.057	0.171	0.336
SB-NE	0.189	0.110	0.274	-0.005
SB-KD	0.118	0.079	0.157	0.802
SB-OD	0.152	0.091	0.220	0.767
SB-PR	0.140	0.093	0.196	0.384
SB-CL	0.069	0.046	0.097	0.589
IR-OW ^a	0.048	0.023	0.075	0.0346
IR-TU	0.212	0.161	0.273	0.946
IR-RG	0.212	0.105	0.237	0.872
IR-CO	0.157	0.094	0.214	0.596
CU-SG ^a	0.069	0.035	0.102	0
CU-SL	0.374	0.274	0.471	1
CU-LS	0.197	0.133	0.260	0.768
CU-QU	0.233	0.169	0.301	0.387
CU-NE	0.372	0.276	0.459	0.850
CO-OD ^a	0.059	0.026	0.096	0.320
CO-EABZ	0.110	0.042	0.191	0.686
CO-IR	0.157	0.092	0.214	0.596
CO-RG	0.103	0.051	0.160	0.470

^a Known or inferred comparison between source population and colony.

Using the Evanno et al. (2005) method for identifying cluster number with STRUCTURE, all 397 individuals were grouped into 14 genetic clusters ($k_{best} = 14$) from the microsatellite data. Individual assignments across replicate runs at same k were consistent, although q for each individual varied slightly; therefore, we present only the results of the first run at $k = 14$. Most individuals were grouped in clusters that matched source-colony pairings determined by other methods (Appendix B). Previously known colonies appeared to be of single origin with one possible exception: 13 of 14 individuals from SB were assigned to the same cluster as 23 of 29 individuals from MA (cluster c5; Appendix B), but the 14th individual, determined via SE47 and SE48 to be female, was assigned at low confidence ($q < 0.5$) to cluster c4, which included mostly individuals from other populations to the north (Appendix B; Fig. 1). All 11 individuals from the IR were assigned to cluster c8 at high confidence ($q > 0.5$), which also included 23 of 26 individuals from the OW population (22 at $q > 0.5$) but only one individual from TU ($q > 0.5$) and none from the CO, EABZ, and RG populations. Finally, all 15 of the CU individuals were assigned at $q > 0.5$ to cluster c9, to which none of the NE but all 17 of the SG individuals were also assigned at $q > 0.5$ (Appendix B).

Because of the counterintuitive clustering of CO with populations >95 km away by BAPS, we also examined individual assignments for CO after determining their sex with SE47 and SE48. Four males and one female were assigned (4 of 5 at $q > 0.5$) to the same cluster as 25 bighorn sheep sampled at OD (c4; Appendix B); those 5 sheep also had OD-type mtDNA haplotypes D or I (Appendix A).

Table 2. Sample size (n), differences in average allelic richness at 14 loci (A , corrected for the smaller sample size within each comparison) and average unbiased heterozygosity (H_e) as inferred from 1-tailed Wilcoxon paired-sample tests (except where noted), and shifted mode in allele frequencies test for population bottlenecks in source populations and colonies of desert bighorn sheep in California, USA, 2000–2004.

Source-colony	n		A		H_e		Bottleneck	
	Source	Colony	Source	Colony	Source	Colony	Source	Colony
MA-SB	27	14	4.1	3.6*	0.65	0.60	yes	yes
OW-IR	26	11	3.5	3.1*	0.51	0.46	no	no
SG-CU	17	15	3.1	2.7*	0.54	0.45*	no	yes
OD-CO	25	7	3.1	3.6 ^a	0.52	0.58 ^a	no	no ^b
EABZ-CO	17	7	3.8	3.6 ^a	0.65	0.58 ^a	no	no ^b

^a 2-tailed Wilcoxon paired-sample test.

^b Sample size below recommended min. of 10 individuals.

* $P < 0.05$.

The remaining 2 males were assigned at $q > 0.5$ to the same cluster as many of the bighorn sheep from the nearby EABZ, EALP, LS, QU, and RG populations (c12; Appendix B); those 2 individuals had mtDNA haplotype F, which was commonly found in those nearby populations but unknown at OD (Appendix A).

At the population level, GENECLASS2 grouped SB with MA, IR with OW, and CU with SG at likelihood scores of 100%. CO was grouped with GR (a population N of Interstate 40 and connected to OD with moderate gene flow; likelihood score = 91%) and OD (source of the translocated individuals in the SH population N of CO, likelihood score = 9%). At the individual level, GENECLASS2 assigned 12 of 14 individuals from SB to MA at likelihood scores $>96\%$, one to CL (61%) and MA (39%), and the same female distinguished by STRUCTURE to OD north of Interstate 40 (90%). Ten of 11 individuals from IR were assigned to OW at scores $>95\%$, and the 11th was assigned to OW at 51% with remaining assignment score percentage apportioned among the closely linked EALP, EABZ, LS, and QU populations (Fig. 1). All 15 individuals from CU were assigned to SG (13 at $>99\%$, 1 at 93%, and 1 at 89%). Lastly, the 2 male individuals in CO with Haplotype F were assigned to QU with scores $>99\%$ (part of a BAPS cluster including the more likely EABZ; Fig. 1), whereas the other 5 individuals with OD-type mtDNA were assigned to OD (3 at $>96\%$, 1 at 93%) and GR (1 at 89%).

In comparison with each inferred source, allelic richness (A) was lower for all 3 colonies primarily of single origin (Table 2; MA-SB $t_{1,13} = 3.10$, $P = 0.004$; OW-IR $t_{1,13} = 1.83$, $P = 0.045$; SG-CU $t_{1,13} = 2.06$, $P = 0.030$). Estimates of A in CO did not differ from OD (Table 2; $t_{2,13} = 1.79$, $P = 0.097$) or EABZ (Table 2; $t_{2,13} = 0.58$, $P = 0.284$). Heterozygosity in CU was 17% lower than in SG (Table 2; SG-CU $t_{1,13} = 3.15$, $P = 0.004$) but H_e did not decline for any other single-origin colony (Table 2; MA-SB $t_{1,13} = 1.48$, $P = 0.081$; OW-IR $t_{1,13} = 1.35$, $P = 0.100$). Estimated H_e for CO did not differ from OD (Table 2; $t_{2,13} = 1.05$, $P = 0.273$) or EABZ ($t_{2,13} = 1.51$, $P = 0.170$). We detected shifted modes in distribution of allele frequencies, indicative of recent population bottlenecks (Luikart et al. 1998), in MA and SB and CU but not SG. We did not detect shifted modes in IR, OW, CO, OD, or EABZ,

although the sample size for CO was less than the recommended minimum (Table 2).

DISCUSSION

As expected given the philopatric and social nature of female bighorn sheep in particular (Festa-Bianchet 1986, Singer et al. 2000), the 3 previously known colonies (SB, IR, and CU) appear to have originated primarily from single source populations (MA, OW, and SG). Nearly all analyses agreed, although we detected 2 ambiguities: 2 possible source populations for SB had identical mtDNA haplotypes (Fig. 1; Appendix A), and one female in SB was assigned by STRUCTURE and GENECLASS2 to populations north of Interstate 40 rather than MA. Because that assignment was not at high confidence, that individual could be, rather than a migrant, the offspring of a migrant.

We also identified a possible cryptic colonization (CO; Fig. 1) with males originating in multiple source populations. Population clustering (BAPS) demonstrated that bighorn in CO were closer genetically to populations north of Interstate 40 (Fig. 1). Population CO is near the SH population, which was reestablished or augmented by translocation of desert bighorn sheep from population OD in 1984 and 1985 (Bleich et al. 1990, 1996). The F_{ST} estimate between CO and OD was 50% lower than the lowest estimate between CO and any other population (Table 1). Because the 1 female and 4 of 6 males sampled in CO had OD-type mtDNA haplotypes that could only have originated in SH, and because those same individuals were also assigned using nuclear DNA markers by both STRUCTURE and GENECLASS2 to OD or other distant northern populations, we hypothesize that females and males from SH recently recolonized CO after an unobserved extinction and were then joined by males from other nearby populations. Although neither mtDNA data, F_{ST} values, nor population assignments clearly indicated whether the 2 males with local haplotypes originated in EABZ, RG, or even QU to the west of EABZ (Table 1; Appendices A, B), the close proximity of the EABZ to CO and the presence of a fenced canal between the CO and RG imply that EABZ was the likely origin (Fig. 1). Because mtDNA and nuclear DNA assignments matched, little interbreeding appears to have occurred yet between the SH

(OD-derived) individuals and EALP–EABZ–RG-derived individuals present in CO.

The genetic structure and loss of genetic diversity that we detected for these colonizations demonstrate that bighorn sheep of both sexes will move substantial distances across unsuitable habitat, but only occasionally (Tables 1, 2). Although founding population sizes and the degree of subsequent gene flow between colony and source are still unclear, decreased A in the colonies (Table 2) implied that founder effects occurred and, thus, the size of the founding population was small. However, we did not observe declines in H_e except in CU (Table 2). Studies of translocated populations and long-distance colonizations have typically detected declines in A (e.g., Mock et al. 2004) but not always in H_e (e.g., Hicks et al. 2007), especially when founder numbers are high (e.g., Hufbauer et al. 2004). Expected heterozygosity is predicted to decline more slowly than A after a bottleneck, particularly if the colony or bottlenecked population grows rapidly (Allendorf 1986).

Direct comparisons of genetic diversity between source and colony were more informative than results of the bottleneck test; although we detected a bottleneck in CU but not SG, as might be expected after a founder event, we did not detect a bottleneck in IR or OW. Because we detected a bottleneck in MA, it is unclear whether the bottleneck detected in SB resulted from the founder event or reflects the bottleneck in the source population. Divergence (Table 1) and loss of genetic diversity (Table 2) was greatest in the SG–CU colonization, which also occurred over the greatest distance. Thus, ongoing gene flow may be an important mechanism for maintaining higher genetic diversity in the other less isolated colonies (i.e., OW–IR and MA–SB). For instance, radiocollared males made repeated movements between IR and OW during monitoring in 2001–2003, but no radiocollared individual in CU has returned to SG (J. Davis, personal communication).

Employing multiple analytical approaches strengthened inferences about source populations. Although F_{ST} estimates from mtDNA could not always determine population of origin (Table 1), mapping mtDNA haplotypes provided useful inferences on female dispersal and may provide sufficient resolution if strong genetic structure is suspected (e.g., Latch et al. 2006b). Comparing F_{ST} estimates from microsatellite markers identified the same source populations as other analyses but did not completely exclude one nearby nonsource population (Table 1; SB–GR) and did not distinguish multiple source populations for CO. Population clustering methods using BAPS (Fig. 1) and GENECLASS2 demonstrated isolating effects of both distance and human-made dispersal barriers such as fenced canals, interstate highways, and urban areas (Fig. 1) and identified the cryptic colonization of CO from SH.

Individual-based assignment tests (STRUCTURE, GENECLASS2) were useful for evaluating whether colonies had multiple origins but are difficult to summarize and interpret for large data sets. Counterintuitive results are common, such as an assignment at $q > 0.5$ for one individual in OW to the same cluster as SL (Appendix B,

c3), which is >250 km distant. Therefore, we stress that interpreting assignment tests for individual animals requires great caution. Nonsensical assignments may result from homologous mutations, genotyping errors, or poor ability to distinguish clusters among areas of high gene flow (e.g., Worley et al. 2004). We had greater confidence in assignments of CO individuals to different populations because mtDNA haplotype matching to sources corresponded exactly. The weak assignment of one individual in SB to OD is more difficult to interpret.

Wildlife managers are sometimes confronted by newly discovered populations or stray individuals of unknown origin (e.g., Onorato et al. 2004, Latch et al. 2006b). Determining the origin may be critical to identifying the appropriate response. For instance, did the strays originate from a population of high conservation value? In California, where an Endangered Species Act (ESA)–listed subspecies (Sierra Nevada bighorn sheep [*O. c. sierrae*]) and an ESA-listed distinct population segment of desert bighorn sheep in the Peninsular Ranges occur in close proximity to unlisted populations of desert bighorn sheep, population genetic data may provide the best means for determining origin quickly. For instance, 2 small groups of bighorn sheep were documented in 2005 at the western edge of the Coso Range, where they have been absent for half a century (Wehausen 1999). Using DNA from fecal pellets collected in the vicinity of those sheep, microsatellites to distinguish individuals, and sequencing of mtDNA control region, 2 individuals with mtDNA haplotype E were identified (J. D. Wehausen, unpublished data). Haplotype E is common in the OD population (Fig. 1; Appendix A), which was the source of a reintroduction to the Argus Range immediately east of the Coso Range in 1986 (Bleich et al. 1990). Clearly, the newly detected individuals in the Coso Range were descendants of animals introduced into the Argus, rather than endangered Sierra Nevada bighorn. Similarly, Latch et al. (2006b) applied the mtDNA protocols we described here to determine that a newly detected population of bighorn sheep in Arizona originated from Rocky Mountain bighorn (*O. c. canadensis*) rather than desert bighorn populations.

Our findings demonstrate that translocations of bighorn sheep into habitat within 10–15 km of established populations may not always be necessary in the absence of other dispersal barriers. Translocation is expensive, sometimes unsuccessful, and comes at the biological cost of the individuals removed from the source population (Bleich et al. 1996). However, colonizations of CO and the Coso Range (above) suggest that translocated individuals may help maintain populations in nearby habitat patches and could help offset high population extinction rates.

Natural colonizations in this system have lower genetic diversity, like translocations described elsewhere (e.g., Hedrick et al. 2001, Whittaker et al. 2004). However, although A decreased in 3 of 4 and H_e declined in 1 of 4 colonizations that we examined (Table 2), genetic diversity still exceeded values reported in translocated populations of bighorn sheep in other locations (Gutierrez-Espeleta et al. 2000, Hedrick et al. 2001). For instance, using a different

set of 11 loci and samples sizes of 10–23 individuals/population, Whittaker et al. (2004) reported 2.2–2.4 alleles/locus and much lower H_e estimates (0.32–0.39) in translocated populations in Oregon but comparable estimates of 3.8 alleles/locus and $H_e = 0.57$ in one native population in Nevada, USA. Because natural colonization can result in continued interaction, genetic diversity may not decline as severely as after a translocation. For instance, we did not detect declines in H_e in the 2 cases where we observed radiocollared individuals traveling repeatedly between the source and colony (SB and IR). Thus, when human-made barriers threaten to block bighorn sheep dispersal (e.g., Flesch et al. 2010), translocation is less likely to be a successful strategy for mitigating loss of genetic diversity than maintaining natural connectivity.

MANAGEMENT IMPLICATIONS

Our data and data from Boyce et al. (1999) and recent extensive sampling in the northern desert from Death Valley to the Sierra Nevada (J. D. Wehausen, unpublished data) describe 42 unique mtDNA control region haplotypes among nearly all known bighorn sheep populations in California. These, coupled with microsatellite data, could be used to determine populations or regions of origin for future bighorn sheep colonizations. The colonizations we described and detected demonstrate that natural recolonization still helps maintain bighorn sheep across this region despite high rates of population extinctions (Epps et al. 2004). We recommend that populations described as extinct in previous surveys be resurveyed more frequently to determine whether recolonization has occurred. Populations reestablished by translocation served as sources for natural recolonizations of other nearby mountain ranges in 2 cases (SH and Argus), implying that translocation is an important tool for metapopulation management. However, because genetic diversity in colonizations did not decline as severely as has been reported for population translocations (e.g., Hedrick et al. 2001), we recommend maintaining connectivity and the potential for recolonization by avoiding disruption of natural dispersal routes and bridging anthropogenic barriers rather than relying solely on translocation. Known linkages between source populations and colonies should be protected.

ACKNOWLEDGMENTS

We thank Associate Editor E. Latch and 2 anonymous reviewers for suggestions on improving this manuscript. We thank T. Anderson, J. Andre, N. Andrew, J. Ashdown, W. Baczkowski, V. Bleich, B. Campbell, J. Davis, R. Dodd, M. Fan, C. Gallinger, B. Gonzales, L. Kimura, L. Lessicka, J. Novembre, A. Pauli, M. B. Rew, G. Roderick, J. Sexton, G. Sudmeier, S. Torres, R. Tran, D. Weaver, and G. Weiss for their assistance, advice, and guidance. Our research was supported by the National Science Foundation Graduate Fellowship, the Bighorn Global Warming Project funded by the Agricultural Experiment Station of California, the Golden Gate Chapter of Safari Club International, Resources Assessment Program of the California Depart-

ment of Fish and Game, and Sigma Xi. Publication of this paper was supported, in part, by the Thomas G. Scott Publication Fund.

LITERATURE CITED

- Allendorf, F. W. 1986. Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology* 5:181–190.
- Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conservation Biology* 4:383–390.
- Bleich, V. C., J. D. Wehausen, R. R. Ramey II, and J. L. Rechel. 1996. Metapopulation theory and mountain sheep: implications for conservation. Pages 353–373 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Covelo, California, USA.
- Boyce, W. M., R. R. Ramey II, T. C. Rodwell, E. S. Rubin, and R. S. Singer. 1999. Population subdivision among desert bighorn sheep (*Ovis canadensis*) revealed by mitochondrial DNA analysis. *Molecular Ecology* 8:99–106.
- Buechner, H. K. 1960. The bighorn sheep in the United States: its past, present, and future. *Wildlife Monographs* 4.
- Corander, J., P. Waldmann, and M. J. Sillanpaa. 2003. Bayesian analysis of genetic differentiation between populations. *Genetics* 163:367–374.
- Cornuet, J. M., and G. Luikart. 1996. Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics* 144:2001–2014.
- Eldridge, M. D. B., J. E. Kinnear, and M. L. Onus. 2001. Source population of dispersing rock-wallabies (*Petrogale lateralis*) identified by assignment tests on multilocus genotypic data. *Molecular Ecology* 10:2867–2876.
- Epps, C. W., V. C. Bleich, J. D. Wehausen, and S. G. Torres. 2003. Status of bighorn sheep in California, 2004. *Desert Bighorn Council Transactions* 47:20–35.
- Epps, C. W., D. R. McCullough, J. D. Wehausen, V. C. Bleich, and J. L. Rechel. 2004. Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conservation Biology* 18:102–113.
- Epps, C. W., P. J. Palsbøll, J. D. Wehausen, G. K. Roderick, R. R. Ramey II, and D. R. McCullough. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters* 8:1029–1038.
- Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology* 44:714–724.
- Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* 14:2611–2620.
- Festa-Bianchet, M. 1986. Seasonal dispersion of overlapping mountain sheep ewe groups. *Journal of Wildlife Management* 50:325–330.
- Flesch, A. D., C. W. Epps, J. W. Cain III, M. Clark, P. R. Krausman, and J. R. Morgart. 2010. Potential effects of the United States–Mexico border fence on wildlife. *Conservation Biology* 24:171–181.
- Goudet, J. 1995. FSTAT (version 1.2): a computer program to calculate F -statistics. *Journal of Heredity* 86:485–486.
- Gutierrez-Espeleta, G. A., S. T. Kalinowski, W. M. Boyce, and P. W. Hedrick. 2000. Genetic variation and population structure in desert bighorn sheep: implications for conservation. *Conservation Genetics* 1:3–15.
- Hawley, D. M., D. Hanley, A. A. Dhondt, and I. J. Lovette. 2006. Molecular evidence for a founder effect in invasive house finch (*Carpodacus mexicanus*) populations experiencing an emergent disease epidemic. *Molecular Ecology* 15:263–275.
- Hedmark, E., and H. Ellegren. 2007. DNA-based monitoring of two newly founded Scandinavian wolverine populations. *Conservation Genetics* 8:843–852.
- Hedrick, P. W., G. A. Gutierrez-Espeleta, and R. N. Lee. 2001. Founder effect in an island population of bighorn sheep. *Molecular Ecology* 10:851–857.
- Hicks, J. F., J. L. Rachlow, O. E. Rhodes, C. L. Williams, and L. P. Waits. 2007. Reintroduction and genetic structure: Rocky Mountain elk in Yellowstone and the western states. *Journal of Mammalogy* 88:129–138.

- Hogg, J. T., S. H. Forbes, B. M. Steele, and G. Luikart. 2006. Genetic rescue of an insular population of large mammals. *Proceedings of the Royal Society B-Biological Sciences* 273:1491–1500.
- Hufbauer, R. A., S. M. Bogdanowicz, and R. G. Harrison. 2004. The population genetics of a biological control introduction: mitochondrial DNA and microsatellite variation in native and introduced populations of *Apidius ervi*, a parasitoid wasp. *Molecular Ecology* 13:337–348.
- Ims, R. A., and N. G. Yoccoz. 1997. Studying transfer processes in metapopulations: emigration, migration, and colonization. Pages 247–265 in I. A. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Keller, L. F., K. J. Jeffery, P. Arcese, M. A. Beaumont, W. M. Hochachka, J. N. M. Smith, and M. W. Bruford. 2001. Immigration and the ephemerality of a natural population bottleneck: evidence from molecular markers. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268:1387–1394.
- Latch, E. K., G. Dharmarajan, J. C. Glaubitz, and O. E. Rhodes. 2006a. Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. *Conservation Genetics* 7:295–302.
- Latch, E. K., J. R. Heffelfinger, B. F. Wakeling, J. Hanna, D. Conrad, and O. E. Rhodes, Jr. 2006b. Genetic subspecies identification of a recently colonized bighorn sheep population in central Arizona. Pages 1–9 in J. W. Cain, III and P. R. Krausman, editors. *Managing wildlife in the Southwest: proceedings of the symposium*. Southwest Section of the Wildlife Society, Tucson, Arizona, USA.
- Levins, R. A. 1970. Extinction. Pages 75–107 in M. Gerstenhaber, editor. *Lectures on mathematics in the life sciences*. Volume 2. American Mathematical Society, Providence, Massachusetts, USA.
- Luikart, G., F. W. Allendorf, J. M. Cornuet, and W. B. Sherwin. 1998. Distortion of allele frequency distributions provides a test for recent population bottlenecks. *Journal of Heredity* 89:238–247.
- Mock, K. E., E. K. Latch, and O. E. Rhodes. 2004. Assessing losses of genetic diversity due to translocation: long-term case histories in Merriam's turkey (*Meleagris gallopavo merriami*). *Conservation Genetics* 5:631–645.
- Nei, M. 1987. *Molecular evolutionary genetics*. Columbia University Press, New York, New York, USA.
- Nei, M., T. Maruyama, and R. Chakraborty. 1975. Bottleneck effect and genetic variability in populations. *Evolution* 29:1–10.
- Neigel, J. E. 2002. Is F–ST obsolete? *Conservation Genetics* 3: 167–173.
- Onorato, D. P., E. C. Hellgren, R. A. Van Den Bussche, and D. L. Doan-Crider. 2004. Phylogeographic patterns within a metapopulation of black bears (*Ursus americanus*) in the American Southwest. *Journal of Mammalogy* 85:140–147.
- Piry, S., A. Alapetite, J. M. Cornuet, D. Paetkau, L. Baudouin, and A. Estoup. 2004. GeneClass2: a software for genetic assignment and first-generation migrant detection. *Journal of Heredity* 95:536–539.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- Ramey, II, R. R. 1993. *Evolutionary genetics and systematics of North American mountain sheep: implications for conservation*. Dissertation, Cornell University, Ithaca, New York, USA.
- Rannala, B., and J. L. Mountain. 1997. Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences of the United States of America* 94:9197–9201.
- Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation* 37:179–190.
- Scribner, K. T., R. A. Malecki, B. D. Batt, R. L. Inman, S. Libants, and H. H. Prince. 2003. Identification of source population for Greenland Canada geese: genetic assessment of a recent colonization. *Condor* 105:771–782.
- Singer, F. J., M. E. Moses, S. Bellew, and W. Sloan. 2000. Correlates to colonizations of new patches by translocated populations of bighorn sheep. *Restoration Ecology* 8:66–74.
- Torres, S. G., V. C. Bleich, and J. D. Wehausen. 1994. Status of bighorn sheep in California, 1993. *Desert Bighorn Council Transactions* 38:17–28.
- Vila, C., A. K. Sundqvist, O. Flagstad, J. Seddon, S. Bjørnerfeldt, I. Kojola, A. Casulli, H. Sand, P. Wabakken, and H. Ellegren. 2003. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:91–97.
- Wehausen, J. D. 1999. Rapid extinction of mountain sheep populations revisited. *Conservation Biology* 13:378–384.
- Wehausen, J. D., V. C. Bleich, and R. A. Weaver. 1987. Mountain sheep in California: a historical perspective on 108 years of full protection. *Western Section Wildlife Society Transactions* 23:65–74.
- Weir, B. S., and C. C. Cockerham. 1984. Estimating *F* statistics for the analysis of population structure. *Evolution* 38:1358–1370.
- Whittaker, D. G., S. D. Ostermann, and W. M. Boyce. 2004. Genetic variability of reintroduced California bighorn sheep in Oregon. *Journal of Wildlife Management* 68:850–859.
- Worley, K., C. Strobeck, S. Arthur, J. Carey, H. Schwantje, A. Veitch, and D. W. Coltman. 2004. Population genetic structure of North American thornhorn sheep (*Ovis dalli*). *Molecular Ecology* 13:2545–2556.
- Wright, S. 1921. Systems of mating. *Genetics* 6:111–178.
- Yamamoto, K., T. Tsubota, T. Komatsu, A. Katayama, T. Murase, I. Kita, and T. Kudo. 2002. Sex identification of Japanese black bear, *Ursus thibetanus japonicus*, by PCR based on the *amelogenin* gene. *Journal of Veterinary Medical Science* 64:505–508.
- Zar, J. H. 1999. *Biostatistical analysis*. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Associate Editor: Latch.

Appendix A. Mitochondrial DNA haplotypes (515 base pairs) from 394 bighorn sheep we sampled in 2000–2004 in 27 populations in southeastern California, USA. Haplotype 5 was first described by Boyce et al. (1999) in the Peninsular Ranges of California.

Code	Population	5	A	A2	B	C	D	E	F	G	H	I	J	K	M	N	O	P	Q	R	S	Total	
CK	Clark					9																12	
CL	Clipper		4			7	4		2					3									16
CO	Coxcomb								2			1											7
CU	Cushenbury								2							15							15
CV	Chemhuevi		7																				7
EABZ	Eagle-Buzzard								18														18
	Spring																						
EALP	Eagle-Lost Palms	3							10							1							14
GR	Granite		1			2	2	6	9		1												21
HA	Hackberry								13														13
IR	Iron				10	1																	11
KD	Cady						4	1			5						2						12
LS	Little San Bernardino	1							9						2								12
MA	Marble					1			24	3													28
NE	Newberry								10	4													14
OD	Old Dad						7	12				6											25
OE	Indian Spring						1	10				1											12
OR	Orocopia								14									1	3				18
OW	Old Woman		3		18	5																	26
PI	Piute Range					3														3			13
PR	Providence		8		3			2	6				1										20
QU	Queen								4										1				11
RG	Riverside Granite	3							5							6							8
SB	South Bristol								8	6													14
SG	San Gorgonio															17							17
SL	San Gabriel																				6		6
TU	Turtle		13	1																			14
WO	Wood	7	36	1	31	31	18	31	140	13	13	9	1	3	3	41	2	1	4	3	6	10	394
Total																							

Appendix B. Individual assignments of desert bighorn sheep sampled in 2000–2004 from 27 populations (rows) in California, USA, to genetic clusters (columns) using STRUCTURE (Pritchard et al. 2000). First number of each entry is number of assignments with assignment index >0.5 and the second number reflects total number of assignments to that cluster based on the highest assignment probability for each individual.

Code	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10	c11	c12	c13	c14
CK	1/1		10/11											
CL	8/8				8/8									
CO				4/5								2/2		
CU									15/15					
CV	7/7								0/1		10/12	3/4		
EABZ											7/7	5/7		
EALP													1/2	
GR	1/1	0/1		4/4		6/6	8/12 5/6		0/1					
HA			0/1					11/11						
IR													10/10	
KD				1/1	0/1						8/11	1/1		
LS														
MA	1/1	2/2			23/26									
NE		15/15												
OD				25/25										
OE				7/7									5/5	
OR										18/18				
OW														0/1
PI		0/2	1/1					22/23				1/1		
PR						9/10	0/1							
QU						2/4	16/16							
RG											6/6	4/5		
SB					0/2						2/2	4/6		
SG				0/1	12/13									
SL									17/17					
TU			6/6											
WO						5/6	4/4	1/1			1/1			10/12

EXHIBIT 423

2000 DESERT BIGHORN COUNCIL TRANSACTIONS

Basin, there were several groups of bighorn sheep that comprised a metapopulation and, in all likelihood, in a short period of time, all of these groups will be extirpated

HUMAN INDUCED MIGRATION AND HOMING BEHAVIOR OF A DESERT BIGHORN RAM IN THE WHIPPLE MOUNTAINS, CALIFORNIA: OR HERMAN THE TRAILER PARK RAM

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On 7/12/99, a mature desert bighorn ram (9+years old) was reported causing a disturbance at a resort property located approximately 1 mile south of Parker Dam, on the Colorado River, San Bernardino County, California. This animal was subsequently monitored and the decision was made to capture, examine, and move the animal to an area approximately 10 miles northwest in the Whipple Mountains. The animal returned to the original capture site within 4 days. A second capture was made on 8/20/99 and the ram was examined and then transported (via helicopter) approximately 110 air miles northwest to Old Dad Peak. This ram was last recorded in the Old Dad Peak area on 9/27/99. On 11/4/99, the animal was confirmed to have returned to have returned to the original capture area along the Colorado River. The potential movement path of this animal will be reviewed, and management policies and conservation implication will be discussed.