CALIFORNIA FISH AND GAME

"Conservation of Wild Life Through Education"

Volume 100 Summer 2014 Number 3

Special Wildlife Issue


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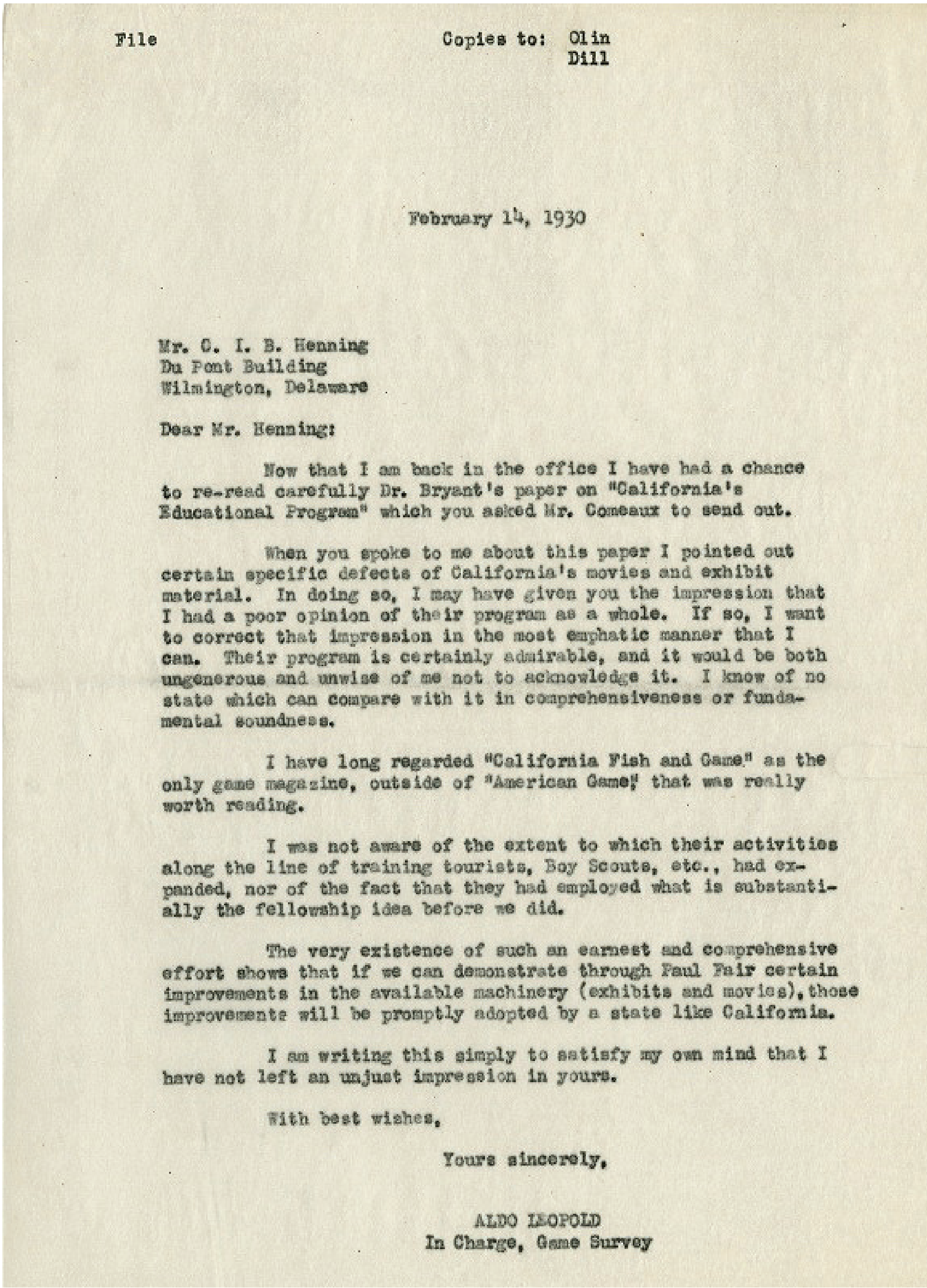

File

Copies to: Olin
Dill

February 14, 1930

Mr. C. I. B. Henning
Du Pont Building
Wilmington, Delaware

Dear Mr. Henning:

Now that I am back in the office I have had a chance to re-read carefully Dr. Bryant's paper on "California's Educational Program" which you asked Mr. Comeaux to send out.

When you spoke to me about this paper I pointed out certain specific defects of California's movies and exhibit material. In doing so, I may have given you the impression that I had a poor opinion of their program as a whole. If so, I want to correct that impression in the most emphatic manner that I can. Their program is certainly admirable, and it would be both ungenerous and unwise of me not to acknowledge it. I know of no state which can compare with it in comprehensiveness or fundamental soundness.

I have long regarded "California Fish and Game" as the only game magazine, outside of "American Game," that was really worth reading.

I was not aware of the extent to which their activities along the line of training tourists, Boy Scouts, etc., had expanded, nor of the fact that they had employed what is substantially the fellowship idea before we did.

The very existence of such an earnest and comprehensive effort shows that if we can demonstrate through Paul Fair certain improvements in the available machinery (exhibits and movies), those improvements will be promptly adopted by a state like California.

I am writing this simply to satisfy my own mind that I have not left an unjust impression in yours.

With best wishes,

Yours sincerely,

ALDO LEOPOLD
In Charge, Game Survey

Frontispiece.—This letter, dated some 85 years ago and retrieved from Aldo Leopold's archives, notes Leopold's appreciation for *California Fish and Game* as a leading journal (image courtesy of E. Loft).

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California Fish and Game 100(2):351-352; 2014

Notes from the Editor

Readers of this column will note that Volume 100(3), originally scheduled to be a special issue addressing fresh water ecology and fisheries, has become the Special Wildlife Issue. This change occurred as a result of the extremely heavy workload experienced by California Department of Wildlife inland fisheries staff as a result of the ongoing, historic drought. Fisheries Branch personnel were to be the primary contributors to the Special Fisheries Issue, and other staff were to serve as Corresponding Editors. It remains my intent to produce the Special Fisheries Issue in tribute to this journal's centennial year, but it is uncertain as to the publication date given the drought-related challenges that Fisheries Branch personnel continue to address.

This Special Wildlife Issue is comprised of the largest number of pages ever published in a single issue of *California Fish and Game*, and is the now third in the series of four special issues originally planned to comprise the centennial volume of the journal. Production of these special issues has not been without its challenges, many of which have been overcome or are in the process of being resolved. Among these challenges were the continuing transition to electronic publication; development of a mailing list of those libraries, universities, and other institutions that wish to continue to receive a print edition of the journal; preparation and approval of a contract for transitioning from the Office of State Printing to a private contractor for the production of the print edition of Volume 100; and changes in publishing software, among others.

As has been the case with the earlier special issues, Chuck Bonham—Director of the California Department of Fish and Wildlife—and a scientist of his choice have contributed an introduction to this issue, and Anthony Rendon—Member of the State Assembly and Chair of the Assembly Water, Parks, and Wildlife Committee—provides additional recognition regarding the 100-year publication history of *California Fish and Game*.

Among the papers in the Special Wildlife Issue are reviews addressing the historical distribution of Sierra Nevada bighorn sheep (an endangered taxon); the historical terminology as it relates to the conservation of mule deer habitat; the evolution of wildlife capture techniques; contributions of CDFW biologists to the conservation of waterfowl in the Pacific Flyway; and a primer describing the field of ecoimmunology and its potential applications to wildlife conservation. An additional contribution centers on a discussion of density dependence in ungulate populations, and provides a review of causes and concepts, as well as offering clarifications regarding the interpretation of density dependence and its application to management.

Papers reporting results of original research consist of those addressing the nest-site ecology of desert tortoise (a threatened species); a technique that can be used to index use of specific geographic areas by mountain lions (California's only specially protected mammal); compositional changes in vegetation nearly thirty years following removal of feral ruminants from Santa Cruz Island; and the use of water developments by female elk in an arid ecosystem. Results of additional original research reported herein centers on the application modern statistical methods to a foundational approach used to explore species diversity among bird communities, and an updated evaluation of the dynamics and social issues of overpopulated deer ranges throughout the United States. Natural history observations have provided the basis for many of the hypotheses that have been posited and tested by wildlife scientists, and included in this issue is an example of such an observation. This issue is rounded out with a tribute to a dedicated and productive employee of the Department that recently passed on.

I want to acknowledge those Associate Editors that took on an extra burden and served as Corresponding Editor for several of the papers included in this issue: Scott Osborn, Cherilyn Burton, and Laura Patterson. Additionally, Scott Osborn, Jeff Villepique, and Jack Connelly willingly stepped forward and served in the necessary, albeit awkward, capacity of Guest Editor for several contributions to this issue.

Vernon C. Bleich, Ph.D.
Editor-in-Chief
California Fish and Game

California Fish and Game 100(3):353-354; 2014

Introduction to the special wildlife issue

California Fish and Game has been and will continue to be an important resource for scientists around the world. The Frontispiece for this issue is a February 14, 1930 letter found in Also Leopold's archives in which he noted, "I have long regarded 'California Fish and Game' as the only game magazine, outside of 'American Game,' that was worth reading." Leopold, the author of *A Sand County Almanac*, was a pioneer of wildlife science, conservation, and ecology.

Following its humble beginnings in 1914, *California Fish and Game* has become California's longest continuously running in-state scientific publication. Over the last century, there have been a number of special issues produced. As you know, we are now publishing volume 100 of the journal, which is planned to consist of four special issues averaging about 200 pages in length.

This special issue of Volume 100 focuses on the conservation and management of terrestrial wildlife. Although "evolution" appears in the title of one contribution, many of the papers included in this issue are based on the evolution of thoughts, statistical techniques, physiology, and methods of spatial analyses. Further, a number of papers germane to the current status or management of several species of wildlife are included.

Over this incredible period as California's longest-running, continuously published scientific journal, great leaders in wildlife science and conservation ecology have written in the journal or praised its prominence and usefulness for science. Joseph Grinnell was a regular and prominent contributor to *California Fish and Game* in the early days. Grinnell was the first director of the University of California, Berkeley's Museum of Vertebrate Zoology. He surveyed and recorded much of California's fauna, along the way creating a detailed field observation protocol still employed today by a majority of professional biologists and field naturalists, named in his honor as the Grinnell System. Joseph Grinnell's work fed into seminal works such as *Game Birds of California* (1918) and *Fur-bearing Mammals of California* (1937).

This third issue of volume 100 will continue the tradition of leading scientists publishing in the journal, as Grinnell did in his day, and will further bolster the journal's stature, as confirmed by Leopold eighty-five years ago. For example, Brett Furnas and Reginald Barrett open this issue by revisiting a foundational approach to evaluating species diversity in bird communities, and apply modern statistical techniques to that question. Dirk VanVuren describes the regeneration of shrubs on Santa Cruz Island nearly thirty years following the removal of feral sheep and feral goats from that isolated location off the coast of California. This kind of before and after analysis is incredibly valuable for today's resource managers. Dan Yparraguirre and coauthors have nicely described the contributions of the California Department of Fish and Wildlife scientists and collaborators to the conservation of waterfowl in California, and the Pacific Flyway in general. John Wehausen and Fred Jones have produced a succinct summary of the historical records of bighorn sheep in the Sierra Nevada, and Jeff Lovich and his coauthors provide detailed information on nest-site fidelity in desert tortoises. David Jessup and his coauthors present a detailed narrative on the evolution of ungulate capture techniques in California, and nicely summarized the literature on that subject. Eric Loft is the senior author of a sorely needed history of the origin and application of terminologies applicable to deer ranges, and Becky Pierce and her coauthor developed a novel method of estimating the number of mountain lions within predefined study areas. All of these contributions relate directly to wildlife conservation within the state of California.

Contributions from several other authors address issues related to wildlife conservation in general, but that are not particularly restricted to California. For example, Paul Krausman and his coauthors reviewed the status of overpopulated deer ranges throughout the United States; this is a follow-up to an early (1947) paper published by Aldo Leopold and his colleagues, as well as work published more than 20 years ago in this journal by Krausman and his coauthors. Cynthia Downs and Kelley Stewart present new information on the utility of ecoimmunology and its application to the conservation and management of wildlife. Glen Sargeant and his coauthors raise the question of the utility of artificial water developments in a northern plains ecosystem, and their benefit to elk in that semi-arid environment. And, a group that includes the co-author of this introduction, Terry Bowyer, and some of his former students at the University of Alaska or Idaho State University, present a discussion to clarify many concepts and interpretations regarding density dependence among ungulates.

Natural history observations form the basis for many of the hypotheses that wildlife scientists have formulated and tested over the decades. In recognition of the importance of natural history to the science of wildlife ecology—and its effects on wildlife conservation and management—the final paper in this issue addresses novel feeding habits of a common species of waterfowl, and summarizes the existing, albeit sparse, literature on that subject. Collectively, all of the papers in this issue represent a wide and broad-based approach to wildlife ecology and wildlife conservation. Finally, former Deputy Director Terry Mansfield pays tribute to Bill Clark—who passed away last year—and the important role he played in wildlife conservation in California over a period of more than 30 years.

The future is replete with many challenges to the conservation of wildlife, particularly with respect to the western United States. Solar energy projects threaten to further fragment habitat for a number of desert species, among which are bighorn sheep and desert tortoise, as do development of gas and oil resources across the nation. In California, drought continues to be an issue not only for fisheries resources but, in many instances, also for terrestrial wildlife. The ever-present prospect of climate change provides challenges that have important implications for the conservation of wildlife and wildlife habitat. Those challenges are being addressed by scientists throughout the world. We are proud that *California Fish and Game* is again ascending to the heights of relevance, and that scientists from across the nation, as well as internationally, are again publishing the results of their research in this journal. To all the contributors to this journal, the readers of this journal, and all those who may follow in their footsteps, we ask that you never stop seeking to understand and manage the many current challenges—as well as those not yet imagined—that wildlife and wildlife habitat in California and the world face. We salute *California Fish and Game* in its centennial year, and recognize the important role it can play in the forthcoming hundred years.

Charlton H. Bonham, Director
California Department of Fish and Wildlife

R. Terry Bowyer, Professor
Idaho State University, Pocatello

California Fish and Game 100(3):355; 2014

California Fish and Game 100(3): the special wildlife issue

Welcome to issue 3 of the 100th Anniversary volume of *California Fish and Game.* As Chair of the Assembly Water, Parks and Wildlife Committee, I am pleased to introduce this special issue devoted to terrestrial wildlife and ecosystems. The fact that this is California's longest-running, continuously published scientific journal is a testament to the commitment of our state scientists, their pursuit of knowledge, and their dedication to our exceptionally diverse wildlife populations. It also reflects the increasing interest of world-renowned scientists in publishing in *California Fish and Game*.

The work of scientists at the Department of Fish and Wildlife and elsewhere has helped guide decisions and the direction of natural resource conservation and management programs for more than a century. It has also helped educate the public, with the result that they are able to provide better informed comments to their elected representatives regarding legislation or regulations.

As a result of careful research by scientists throughout the world—some of which has been published in *California Fish and Game*—we have learned how to prevent, mitigate, or correct some ecological challenges. The recent expansion of the 24-year-old California Oil Spill Prevention and Response Act is a good example of this. The law enabling the state to prevent, prepare for, respond to, and mitigate oil spills in our *marine* waterways now protects *all* of California's waters. Another example is the recent state-wide requirement for use of non-lead ammunition for hunting, which will reduce wildlife exposure to lead as that law is phased in by the Department and Commission.

In 1914 the human population in California was around 2.5 million. Today 15 times as many people live in our state, and the development that made that level of population increase possible has destroyed a tremendous amount of wildlife habitat. An educated public's concerns and positive attitudes toward wildlife have led to mitigation for some impacts to ecosystems, but there is much more work to do, and new challenges to address.

One hundred years ago most people had never heard of invasive species, but now we are painfully aware of them and the devastating effects they can have on native ecosystems. As a result of research published in *California Fish and Game*, we now have programs designed to minimize the potential for new non-natives from being transported into the state. Climate change and cyclical droughts also affect our wildlife by changing habitat conditions. Our scientists are on the cutting edge of coping with those forces. At the same time, we know we have much more work to do, particularly with regard to climate change adaptation, and time is of the essence in addressing these needs. Meeting these and other challenges requires, and will continue to require, decisions founded in solid science.

The Department of Fish and Wildlife is a leader in the conservation of natural resources and the scientific papers published in *California Fish and Game* demonstrate that admirably. Congratulations to Director Charlton H. Bonham, and all the managers and employees of the Department, for your excellent work. "Conservation of Wildlife Through Education" is more than a motto; it is your way of life. Thank you and much continued success to you all.

Anthony Rendon, Chair
Assembly Water, Parks and Wildlife Committee

California Fish and Game 100(3):356-370; 2014

Comparisons of intermediately ranked species in avian rank-abundance distributions from four California forests

Brett J. Furnas* and Reginald H. Barrett

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Biodiversity indices, such as those that measure species richness or evenness, provide limited information about ecological communities. The species abundance distributions from which these indices are derived contain greater detail about community structure. For this reason conservation planners and land managers would benefit from methods that allow more informative comparisons of these distributions than offered by traditional indices. We used bird survey data from four research forests in California to construct rank-abundance distributions. Using bootstrap re-sampling, we created uncertainty bands associated with the empirical shapes of these curves, allowing identification of significant (P<0.05) differences between distributions over a portion of their ranks. We found higher abundances of intermediately ranked species on two of the forests, and ascribe this result to differences in forest productivity and habitat complexity leading to greater niche partitioning of resources. Diversity indices derived from these data were less informative.

Key words: bootstrap re-sampling, California, community ecology, diversity indices, forest birds, rank-abundance distributions, resource partitioning

Many researchers have advocated diversity indices for quantifying and evaluating biodiversity. The simplest index, species richness, formed the basis of MacArthur and Wilson's (1967) landmark theory of island biogeography. Other indices (Simpson 1949, Shannon and Weaver 1963) furnish relative abundance-derived information on evenness (or dominance) among species in a community. These measures remain central to biodiversity assessment for conservation planning (Margules and Pressey 2000, Moilanen et al. 2009, Zipkin et al. 2009, Chandler et al. 2013, Iknayan et al. 2014).

Species abundance distributions (Motomura 1932, Fisher et al. 1943, Preston

1948, Hubbell 2001, Harte 2011) provide a richer source of information than indices for quantifying biodiversity. One way of displaying these data, known as a rank-abundance distribution (RAD), is to plot species abundances in rank order. Whittaker (1965) was one the first to use the RAD to connect concepts of resource competition and ecological niche to differences in abundance for dominant, intermediately abundant, and rare species. Beedy (1981) applied this method to compare bird communities and forest structure in California. He drew RADs for different forest types, and concluded that the lognormal form (Preston 1948) of the associated species abundance distribution in structurally complex habitats was indicative of greater resource partitioning (and food availability) supporting greater numbers of intermediately ranked species. One shortcoming of Beedy's (1981) results was the lack of a formal test of differences in abundances for these ranks.

We modified Beedy's approach, comparing the avian communities from four montane conifer forest locations in California. Rather than using indices, we evaluated empirical shapes of RADs and their sampling errors by means of bootstrap re-sampling (Efron 1982). Instead of evaluating entire curves, we focused attention on intermediate ranks because the amount of niche partitioning among these species may be demonstrative of differences between avian communities and the habitats that support them (Whittaker 1965, Beedy 1981, Lennon et al. 2004). Comparing pairs of forests, we estimated the percentage of intermediate ranks that supported higher abundances for one forest versus another. We compared these results with diversity indices of the data pertaining to species richness (alpha and gamma diversity) and evenness. To ascertain whether higher abundances in the intermediate ranks were associated with niche partitioning, we compared abundances of wood warblers (Parulidae) with the abundances of other species, because warblers provide a good avian example of niche differentiation in feeding habits (MacArthur 1958, Morse 1989, Lovette and Bermingham 1999).

The methods developed here offer an alternative to traditional diversity indices to assess differences among ecological communities. Bootstrap comparisons of RADs may be more useful than parametric approaches for estimating species diversity because they allow one to focus on a portion of ranks. Our evaluation of intermediately abundant species facilitates understanding of how niche partitioning differs among locations, habitats, and guilds of species, and this information may be of use to conservation planners and wildlife managers.

MATERIALS AND METHODS

Study areas.— The avian survey data were from four research forests owned and managed by the University of California at Berkeley or the California Department of Forestry and Fire Protection (Figure 1). Management objectives for these forests included timber production and research.

The 3,650-ha Latour State Demonstration Forest (40° 38' N, 121° 42' W) is located 70 km east of Redding in the southern Cascade Mountains; elevations range from 1,200 to 2,050 m. Average annual precipitation was 117 cm on volcanic soils. The forest was predominantly mixed conifer and true fir (*Abies spp.*) forest punctuated by a few wet meadows and some post-fire brush fields. The forest was generally even-aged with sparse understory vegetation except along creeks and in brush fields. Average forest productivity was characterized as a low Dunning Site Class II (Dunning 1942, Ronald 1992, Barrett and Bise 1993).

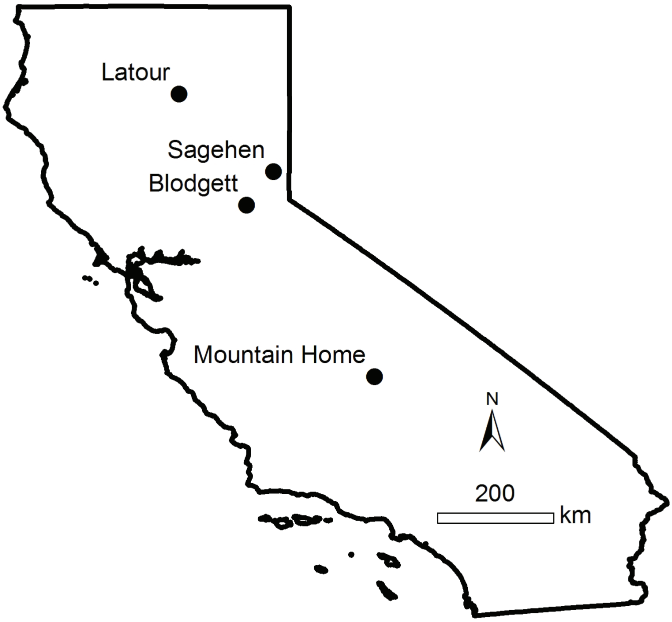

FIGURE 1.— California research forests where birds surveys occurred over the course of two breeding seasons at approximately 80 sites on each forest from 1979 to 1996.

The 1,175-ha Blodgett Forest (38° 54’ N, 120° 39’W) is located 18 km east of Georgetown in the central Sierra Nevada. Elevations range from 1,200 m to 1,500 m across gently rolling, highly productive terrain. Average annual precipitation was 166 cm. The forest was primarily mixed conifer with some oak (*Quercus spp.*) stands and brush fields. Average forest productivity was characterized as a high Dunning Site Class I (R. York, UC Berkeley, personal communication).

The 3,280-ha Sagehen Experimental Forest (39° 35’ N, 120° 14’ W) is located 16 km north of Truckee in the central Sierra Nevada. Elevations range from 1,450 to 2,300 m. Average annual precipitation was 85 cm. The forest was a mosaic of mixed conifer and white fir (*Abies concolor*) stands, post-fire plantations, grassy meadows, and rocky shrublands. Average forest productivity was characterized as Dunning Site Class III or IV (S. Conway, US Forest Service, personal communication).

The 1,870-ha Mountain Home State Demonstration Forest (36° 14’ N, 118° 41’ N) is located 35 km northeast of Porterville in the southern Sierra Nevada. Elevations range from 1,450 to 2,300 m. Average annual precipitation was 102 cm. The forest was predominantly mixed conifer forest with approximately 5,000 giant sequoia (*Sequoiadendron giganteum*) trees in excess of 1 m in diameter spread across half of the property. The forest was generally uneven-aged with more understory vegetation than at Latour. Springs supporting wet meadows occurred at numerous locations. Average forest productivity was characterized as a high Dunning Site Class II (Ronald 1992, Barrett and Bise 1993).

Bird surveys.— Breeding bird surveys were part of a comprehensive wildlife and wildlife habitat inventory undertaken by the University of California throughout the State beginning in 1977 (Dedon and Barrett 1982). We limited this study to those locations from this inventory that occurred in coniferous forests and for which approximately 80 sites were surveyed at each forest over the course of more than one year. At Sagehen, 80 sites were surveyed in 1979 or 1981. At Latour and Mountain Home, 80 sites and 79 sites, respectively, were surveyed in 1993 or 1994. At Blodgett, 81 sites were surveyed in 1996 or 1997. Those sites were distributed evenly across each forest using a systematic design (Thompson 2002), and they were generally spaced at least 400 m apart. Each survey consisted of 20 consecutive 10-minute point counts (Ralph et al. 1995, Bibby et al. 2000) beginning 30 minutes after sunrise on a single morning, by a single surveyor during the breeding season, from the middle of May through the middle of July (Dedon and Barrett 1982, Barrett and Bise 1993).

Abundance estimation.—For analyses we limited detections to those birds the surveyor judged to have breeding territories intersecting at least half of the 30-m radial area surrounding the point count site. As surveys at each site occurred on a single day, we did not attempt to address detection probability via a model-based approach (Royle 2004). Instead, we used the highest count from the 20 consecutive survey replicates to approximate the true abundance of each species at the site. Counts were converted into densities (birds/ha) by dividing by area of the 30-m circle to which surveys applied. We assumed each naïve estimate of density to represent an index of abundance for use in our RADs.

Rank-abundance distributions.— We rank-sorted and then plotted point estimates of species densities in descending order. Considering the small survey area (0.28 ha) of the point counts and because most counts were unitary, we did not log-transform our densities as is usually done for these distributions (Whittaker 1965). We constructed RAD curves for each forest. As an exact distinction between dominant, intermediate and rare species is arbitrary, we chose a conservative definition of intermediate ranks that was less likely to unintentionally include species that might be considered dominant or rare. For the four forests we evaluated we defined intermediate species as ranks 6 to 20. Following the same reasoning we defined rare species at ranks > 25.

To assess differences between RADs we used bootstrap re-sampling (Efron 1982). We randomly sampled with replacement from the set of ~80 sites where surveys occurred at each forest and calculated an average density for each species. By repeating this process 10,000 times and rank-sorting the abundances each time, we created a sampling distribution for our index of abundance for each rank for each forest. By disregarding changing species identities within these ranks, we took a neutral theory (Hubbell 2001, Harte 2011) approach to evaluate ranks within RADs. Lastly, we estimated the uncertainty of the RAD curves using the 2.5th and 97.5th percentiles for each rank corresponding to a 95% confidence interval. Each upper confidence interval bound was connected by rank for graphing an uncertainty band associated with each RAD. Each lower confidence band was connected similarly. Pairs of forest-level RADs were considered significantly ($P<0.05$) different over a portion of their ranks as indicated by the bootstrapped uncertainty bands. We rejected the null hypothesis that both forests had the same avian abundance at a particular rank if each point estimate was outside of the confidence interval of the other forest.

To evaluate differences among the avian communities for pairs of forests, we calculated the percentage of intermediate ranks that had significantly ($P<0.05$) higher abundances for one forest versus the other. We repeated these comparisons for all 6 combinations of forest pairs. We applied hierarchical cluster analysis (Sharma 1996, McCune et al. 2002) to these results because the sample size of forest pairs was too small for a parametric test, and we used this technique to assign the forests to two groups representing higher and lower abundances in the intermediate ranks.

To evaluate how well the uncertainty band technique worked with respect to traditional diversity indices, we computed average site-level species richness (alpha diversity; Whittaker 1960), forest-level species richness (gamma diversity; Whittaker 1960), and Simpson's measure of evenness (Smith and Wilson 1996). We used the same bootstrap re-samples to create 95% confidence intervals for these indices.

Our *a priori* hypotheses about differences in RADs for intermediately abundant species were based on niche and resource partitioning concepts (Grinnell 1917, MacArthur 1958, Hutchinson 1959, Whittaker et al. 1973, Schoener 1974, Chesson 2000). We hypothesized that higher forest productivity at the Blodgett and Mountain Home would lead to higher abundances of intermediately ranked species than at Sagehen and Latour, because larger trees, taller forests and greater structural complexity should lead to an increased potential for resource partitioning with respect to nesting and foraging habitat. We also believed that wood warblers (Parulidae) would rise to higher abundances in the intermediate ranks with respect to other species, because this taxon is well known to partition foraging resources in forests (MacArthur 1958, Morse 1989, Lovette and Bermingham 1999). Our expectation was that the percentage of individual birds within a community that was warblers would be higher for intermediate versus rare ranks and that this pattern would be more pronounced on higher productivity forests (Blodgett and Mountain Home). We estimated these percentages as the total densities of warblers in either the intermediate or rare ranks multiplied by 100 divided by the total densities of all birds in these ranks. We used the bootstrap samples to construct 95% confidence intervals about those percentages.

RESULTS

Abundance estimation.—A total of 47 species was detected at least once at Latour, 57 at Blodgett, 62 at Sagehen, and 62 at Mountain Home. A total of 91 species was detected at least once for at least one of the forests. Species in the top five abundance ranks for at least one of the forests were American robin (*Turdus migratorius*), black-headed grosbeak (*Pheucticus melanocephalus*), dark-eyed junco (*Junco hyemalis*), golden-crowned kinglet (*Regulus satrapa*), mountain chickadee (*Poecile gambeli*), Nashville warbler (*Oreothlypis ruficapilla*), pine siskin (*Spinus pinus*), red-breasted nuthatch (*Sitta canadensis*), red crossbill (*Loxia curvirostra*), spotted towhee (*Pipilo maculatus*), Steller's jay (*Cyanocitta stelleri*), western tanager (*Piranga ludoviciana*), and yellow-rumped warbler (*Setophaga coronata*). Dark-eyed junco was the only species in the top five ranks for all forests.

Species in the intermediate ranks (6 to 20) for at least one of the forests were American robin, band-tailed pigeon (*Patagioenas fasciata*), black-headed grosbeak, brown-headed cowbird (*Molothrus ater*), Brewer's blackbird (*Euphagus cyanocephalus*), brown creeper (*Certhia americana*), Calliope hummingbird (*Selasphorus calliope*), Cassin's finch (*Haemorhous cassinii*), Cassin's vireo (*Vireo cassinii*), chipping sparrow (*Spizella passerina*), common raven (*Corvus corax*), dusky flycatcher (*Empidonax oberholseri*), fox sparrow (*Passerella iliaca*), golden-crowned kinglet, hairy woodpecker (*Picoides villosus*), Hammond's flycatcher (*Empidonax hammondii*), hermit thrush (*Catharus guttatus*), hermit warbler (*Setophaga occidentalis*), house wren (*Troglodytes aedon*), MacGillivray's warbler (*Geothlypis tolmiei*), mountain chickadee, Nashville warbler, northern flicker (*Colaptes *auratus*), purple finch (*Haemorhous purpureus*), red-breasted nuthatch, red-breasted sapsucker (*Sphyrapicus ruber*), Steller's jay, warbling vireo (*Vireo gilvus*), western tanager, white-headed woodpecker (*Picoides albolarvatus*), Wilson's warbler (*Cardellina pusilla*), yellow warbler (*Setophaga petechia*), and yellow-rumped warbler. Brown creeper and fox sparrow were the only species in the intermediate ranks of all forests, despite the fact that 24 of the 33 intermediately ranked species listed above were detected at least once at every forest. A full reporting of densities by forest is provided in Appendix I.

Rank-abundance distributions.— Visual inspection of RADs without the aid of uncertainty bands suggested differences in abundances among the four research forests we studied (Figure 2). The bootstrap method provided a quantitative description of those differences for pairs of forests (see Figures 3 and 4 as examples). In summary, we demonstrated significant ($P<0.05$) differentiation between a majority of intermediate ranks (6 to 20) for the Blodgett and Mountain Home forests versus Latour and Sagehen (Figure 5).

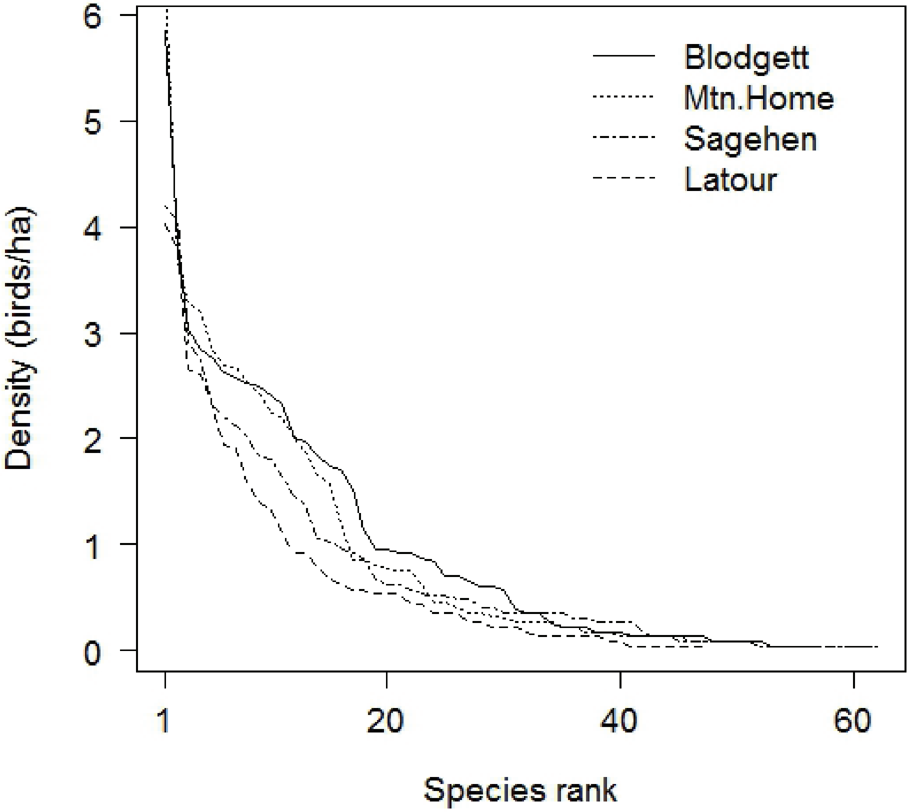

Figure 2.—Avian rank-abundance distributions from four research forests in Califonia based on point count surveys.

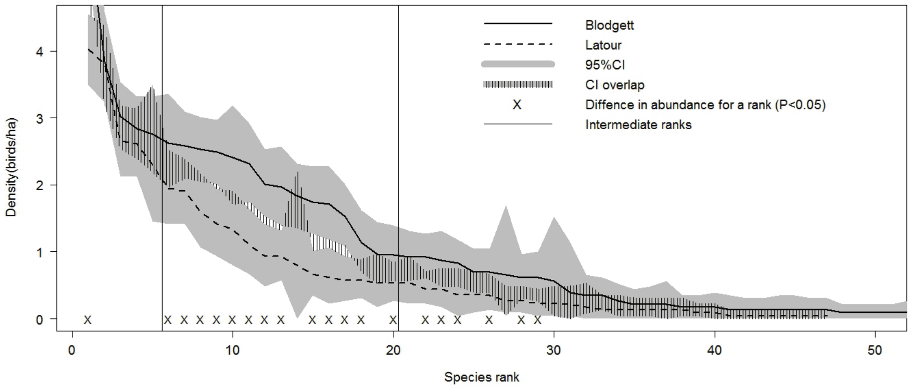

Figure 3.—Pairwise of comparison of avian rank-abundance distributions from the Blodgett and Latour research forests in California. Using bootstrap re-sampling we created 95% confidence intervals for each rank. We identifed differences in abundance for intermediate ranks (6-20) in cases where the point estimates for each forest lay beyond the confidence interval of the other. For this comparison 13 of 15 intermediate ranks had higher abundances at Blodgett than at Latour.

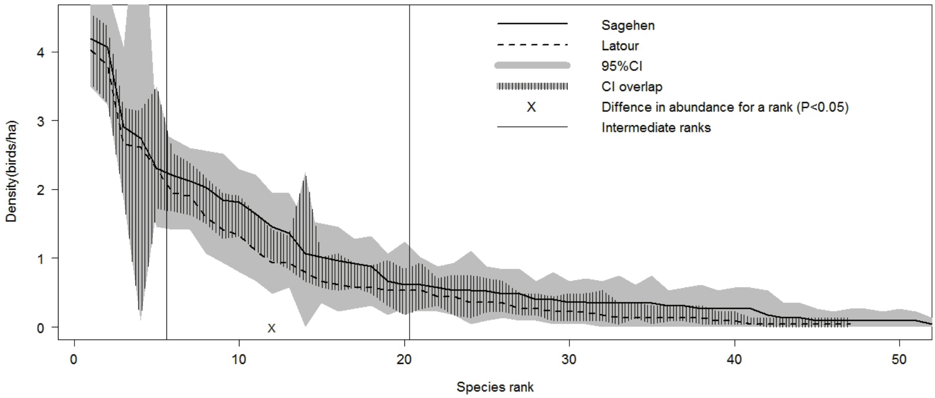

Figure 4.—Pairwise of comparison of avian rank-abundance distributions from the Sagehen and Latour research forests in California. Using bootstrap re-sampling we created 95% confidence intervals for each rank. We identifed differences in abundance for intermediate ranks (6-20) in cases where the point estimates for each forest lay beyond the confidence interval of the other. For this comparison only 1 of 15 intermediate ranks had higher abundances at Sagehen than at Latour.

The exception to this pattern was the comparison between Mountain Home and Sagehen. Nevertheless, hierarchical cluster analysis split the forests into two groups (Blodgett and Mountain Home versus Latour and Sagehen) based on their differences in abundances in the intermediate ranks. These groups coincide with differences in soil productivity (Dunning Site Classification) among the forests.

Diversity indices.—Differences in diversity indices for the six pairwise combinations of forests varied considerably and this result did not appear to be associated with results of the bootstrap method (Figure 5). There was always a difference (*P*<0.05) in alpha diversity between forests. All three indices were different (*P*<0.05) for two of the four comparisons

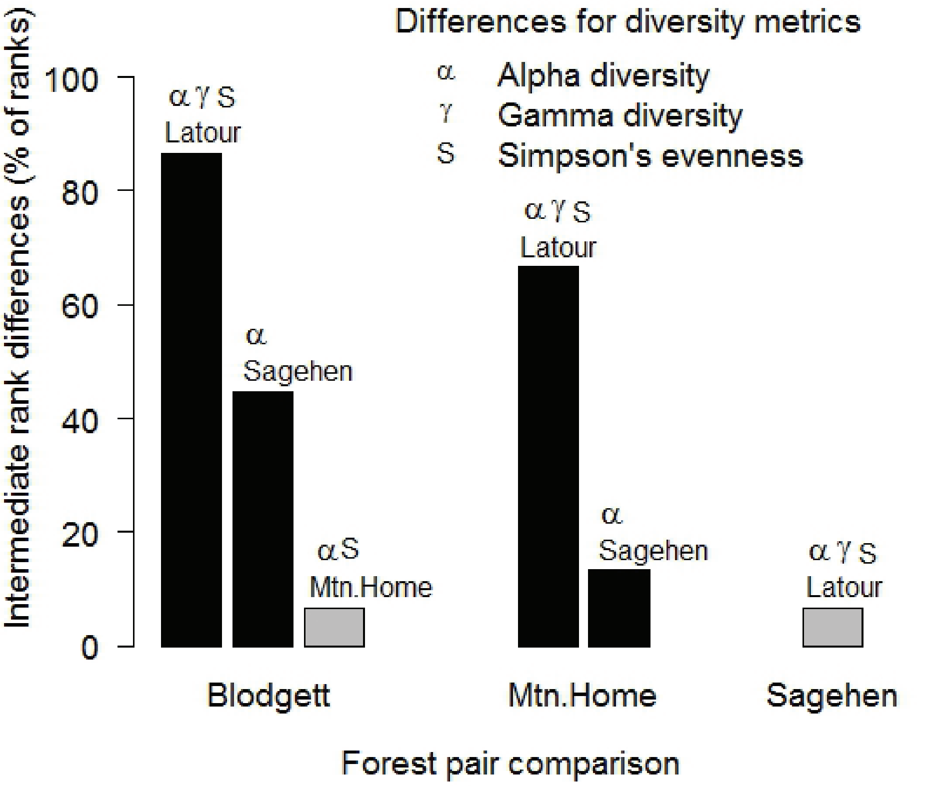

Figure 5.—Summary of all pairwise comparisons of avian rank-abundance distributions among four research forests in California. Forests listed at the bottom represent those that had higher abundances of intermediately ranked species compared to the forests listed above. Using bootstrap re-sampling we created 95% confidence intervals for each rank. For each pair of forests we identifed differences in abundance for intermediate ranks (6-20) in cases where the point estimates for each forest lay beyond the confidence interval of the other. The dark colored bars represent comparisons between high and low abudance forests as confirmed by hierarchical cluster analysis. There was no consitency between the percentage of intermediate rank differences between forests and significant ($P<0.05$) differences in diversity indices between forests.

between the higher and lower abundance forests we identified, but they were also all different ($P<0.05$) for one of the two comparisons between lower abundance forests.

Wood warblers.—As expected, our estimates of the percentages of individual birds that were warblers were higher ($P<0.05$) for intermediate versus rare ranks on the more productive forests (Blodgett and Mountain Home, Figure 6). In contrast, our estimates of the percentages of individual birds that were warblers were not higher ($P>0.05$) for intermediate versus rare ranks on the less productive forests (Sagehen and Latour).

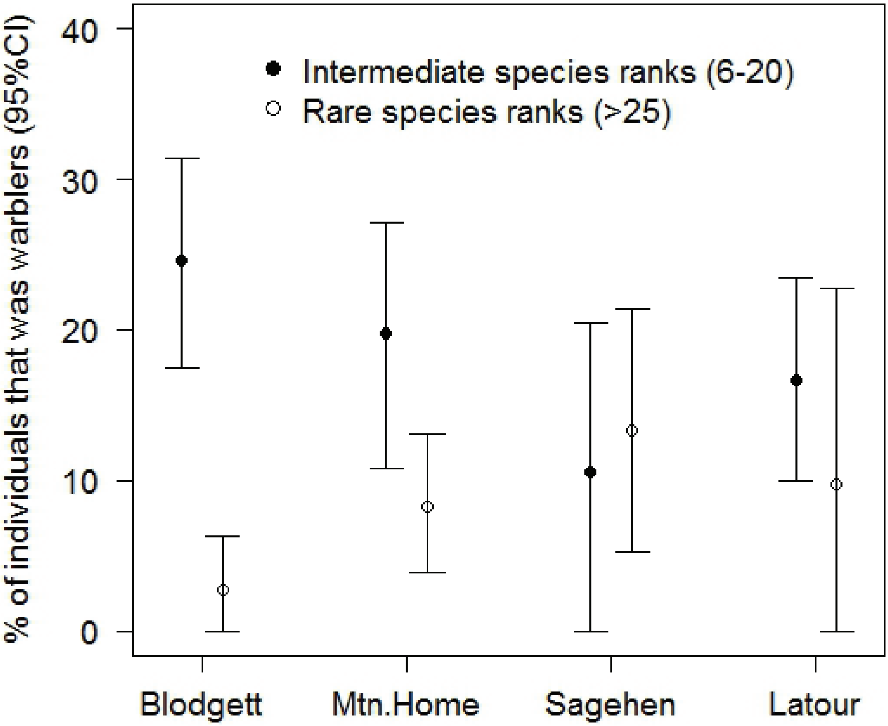

FIGURE 6.—Warblers abundances at four research forests in California. To identify evidence of resource partitioning within this taxon, we calculated the percentage of indviduals of all birds surveyed that were wood warblers (Parulidae). We made this calculation separately with respect to intermediately abundant and rare species. The results show that warblers rose to higher abundances in the intermediate ranks at two of the forests. This finding supports the idea that higher productivity forests with greater structural complexity of habitats provide more opportunities for niche partioning among avian species.

DISCUSSION

Ecologists have proposed a confusing variety of biodiversity indices over the past century (Magurran and McGill 2011), and those indices have been accompanied by some criticism of their usefulness (Hurlbert 1971, Schwartz et al. 2000). Others have focused on the mathematical forms of species abundance distributions (Fisher et al. 1943, MacArthur 1957, Wilson 1991, Flather 1996). Rather than computing indices or fitting mathematical forms, we directly compared the empirical shapes of RADs using a bootstrap method to differentiate pairwise combinations of avian communities. This method provided greater information than indices about how abundances varied for dominant, intermediate, and rare species, a distinction that allowed us to explain results in terms of competition among species. Instead of making a measure of the entire RAD, we directly evaluated those intermediate ranks believed by plant and bird ecologists to be strongly associated with resource partitioning and the structural complexity of habitats (Whittaker 1965, Beedy 1981). In this regard, our method is similar to the approach taken by those researchers; however, we did so without needing to make complicated assumptions about the mathematical properties of different classes of RADs.

Our results suggest that the avian communities at Blodgett and Mountain Home had higher abundances of intermediately ranked species than at Sagehen and Latour. These findings are consistent with the hypothesis that higher productivity forests provide the potential for greater structural diversity and enable more intermediately common species to rise to higher abundances, because niche partitioning reduces interspecies competition for resources. Blodgett and Mountain Home occurred on more productive soils (Dunning Site Class I and high II) than the other forests.

There was no consistency between the values of 3 commonly used diversity indices and our findings on how middle ranks were differentiated among forests. This discrepancy suggests that our bootstrap method may illuminate different community properties than traditional diversity indices do. These indices might not be optimal for isolating competitive effects over a portion of ranks or for a guild of species within a community. This distinction is important because resource partitioning does not occur to the same extent for all species in a community. For example, we used a comparison of abundances between intermediate and rare species to show how warblers rose to higher relative abundances on forests with more productive soils.

Results from this study are qualified by some limitations related to study design. First, these data reflected avian community structure over 2-year timeframes, and the survey years were different by forest. However, only one of the survey years was preceded by a strong El Niño or La Niña event that might have confounded results (Sillett et al. 2000). Second, we used raw survey data to which we were unable to apply hierarchical modeling to address heterogeneity in survey detection probability (Royle 2004) beyond taking the maximum count during a single day. It is possible that systematic differences in detectability (e.g., different surveyors, years, habitat conditions) confounded the conclusion that apparent differences in RADs were due to differences in forest productivity. This problem was compounded by the small sample size (n=4) of the comparison among forests. Despite these study limitations, the RAD bootstrapping has diverse applications for evaluating and comparing communities.

Scale is another issue to be considered. The point counts used for estimating density covered a small area (0.28 ha), leading to generally small survey counts. In particular, 89% of non-zero counts per species per survey period were = 1, and 99% were ≤ 2. It is unclear whether the rank differences reported here would have been the same for larger survey units. Nevertheless, the methodological advantages of bootstrapping, as discussed above for comparing a portion of ranks, are not especially related to scale. Furthermore, considering the dominance of ones and zeros in the data we used, the RAD bootstrap approach may also be appropriate for application to rank-occupancy distributions derived from presence-absence data.

In conclusion, methods that look at differences in abundances for individual ranks within RADs have advantages over diversity indices. By evaluating finer distinctions between dominant, intermediate, and rare species, there is greater potential for drawing ecological inferences, particularly with respect to resource partitioning. This approach may be especially relevant to biodiversity monitoring and conservation planning. Declines of individual species may be better understood in context of their relationship to other species, or niches, within the community. Segments of RADs could be monitored for changes in composition over time (Collins et al. 2008).

Multi-species abundance models (MSAMs; Yamaura et al. 2012, Chandler et al. 2013, Iknayan et al. 2014) that address heterogeneity in detection probability may offer a more sophisticated means of evaluating niche partitioning using RADs than provided by our bootstrapping method. We would have taken this approach if our surveys had been repeated on different days for estimating detectability of point counts. The hierarchical structure of MSAMs could be used to keep track of abundances of dominant, intermediate, and rare species separately as derived quantities in the model. The Bayesian algorithm for solving this model generates posterior distributions for all parameters (Link et al. 2002) which eliminates the need for additional bootstrapping to describe the uncertainty of abundance estimates for each rank. However, all of the other elements of our approach for quantifying and contrasting the intermediate ranks of RADs could be readily incorporated into a MSAM.

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APPENDIX I. DENSITY ESTIMATES FOR AVIAN SPECIES SURVEYED AT FOUR RESEARCH FORESTS IN CALIFORNIA

		Density (birds/ha)			
Common Name	Scientific Name	Latour	Blodgett	Sagehen	Mt. Home
Acorn Woodpecker	*Melanerpes formicivorus*	0.000	0.217	0.000	0.000
American Dipper	*Cinclus mexicanus*	0.000	0.000	0.044	0.000
American Kestrel	*Falco sparverius*	0.000	0.131	0.089	0.000
American Robin	*Turdus migratorius*	0.221	3.843	2.032	2.013
Anna's Hummingbird	*Calypte anna*	0.044	0.176	0.000	0.268
Ash-throated Flycatcher	*Myiarchus cinerascens*	0.000	0.000	0.045	0.091
Band-tailed Pigeon	*Patagioenas fasciata*	0.533	0.218	0.355	0.756
Bewick's Wren	*Thryomanes bewickii*	0.000	0.351	0.000	0.045
Black-headed Grosbeak	*Pheucticus melanocephalus*	0.044	2.836	0.000	2.688
Black-backed Woodpecker	*Picoides arcticus*	0.000	0.000	0.089	0.000
Brown-headed Cowbird	*Molothrus ater*	0.220	0.698	1.367	0.179
Brewer's Blackbird	*Euphagus cyanocephalus*	0.000	0.000	0.000	1.664
Brewer's Sparrow	*Spizella breweri*	0.000	0.000	0.353	0.000
Brown Creeper	*Certhia americana*	1.902	2.011	1.809	2.195
Blk.-throated Gray Warbler	*Setophaga nigrescens*	0.000	0.133	0.000	0.044
Bullock's Oriole	*Icterus bullockii*	0.000	0.000	0.000	0.447
Bushtit	*Psaltriparus minimus*	0.000	0.390	0.000	0.178
Calliope Hummingbird	*Selasphorus calliope*	0.000	0.000	2.123	0.000
California Towhee	*Melozone crissalis*	0.000	0.000	0.000	0.045
Cassin's Finch	*Haemorhous cassinii*	0.356	0.131	1.849	1.566
Cassin's Vireo	*Vireo cassinii*	0.223	2.579	0.000	0.000
Chestnut-backed Chickadee	*Poecile rufescens*	0.000	0.660	0.000	0.000
Chipping Sparrow	*Spizella passerine*	0.000	0.831	0.665	0.314
Clark’s Nutcracker	*Nucifraga columbiana*	0.089	0.000	0.528	0.000
Common Nighthawk	*Chordeiles minor*	0.132	0.000	0.000	0.045
Common Raven	*Corvus corax*	0.440	0.000	0.000	0.849
Cooper’s Hawk	*Accipiter cooperii*	0.132	0.043	0.044	0.000
Dark-eyed Junco	*Junco hyemalis*	4.022	5.844	4.068	6.309
Downy Woodpecker	*Picoides pubescens*	0.132	0.131	0.000	0.089
Dusky Flycatcher	*Empidonax oberholseri*	1.594	0.918	0.881	0.764
Evening Grosbeak	*Coccothraustes vespertinus*	0.134	0.350	0.616	0.357
Forster's Tern	*Sterna forsteri*	0.044	0.000	0.000	0.000
Fox Sparrow	*Passerella iliaca*	0.930	1.137	1.637	2.548
Green-tailed Towhee	*Ardea herodias*	0.045	0.000	0.308	0.224
Golden-crowned Kinglet	*Pipilo chlorurus*	2.610	2.489	2.204	3.673
Great Blue Heron	*Regulus satrapa*	0.000	0.088	0.000	0.000
Hairy Woodpecker	*Picoides villosus*	0.531	0.955	0.967	0.629
Hammond's Flycatcher	*Empidonax hammondii*	1.108	0.612	0.926	0.312
Hermit Thrush	*Catharus guttatus*	0.929	0.611	0.576	0.267
Hermit Warbler	*Setophaga occidentalis*	1.413	1.832	0.044	1.211
House Wren	*Troglodytes aedon*	0.000	0.173	0.000	0.807
Hutton's Vireo	*Vireo huttoni*	0.044	0.130	0.000	0.045
Lazuli Bunting	*Passerina amoena*	0.000	0.000	0.132	0.136
Lincoln’s Sparrow	*Melospiza lincolnii*	0.000	0.000	0.044	0.134
MacGillivray's Warbler	*Geothlypis tolmiei*	0.265	2.317	0.132	1.880
Mountain Bluebird	*Sialia currucoides*	0.133	0.000	0.351	0.000
Mountain Chickadee	*Poecile gambeli*	3.798	2.405	4.194	2.683
Mourning Dove	*Oreortyx pictus*	0.000	0.087	0.000	0.090
Mountain Quail	*Zenaida macroura*	0.089	0.088	0.043	0.045
Nashville Warbler	*Oreothlypis ruficapilla*	0.577	1.746	0.353	2.824
Northern Flicker	*Colaptes auratus*	0.531	1.528	0.309	0.762
Northern Goshawk	*Accipiter gentilis*	0.000	0.000	0.045	0.000
Olive-sided Flycatcher	*Contopus cooperi*	0.264	0.918	0.088	0.134
Orange-crowned Warbler	*Oreothlypis celata*	0.000	0.000	0.267	0.178
Pacific-slope Flycatcher	*Empidonax difficilis*	0.000	0.000	0.000	0.135
Pileated Woodpecker	*Dryocopus pileatus*	0.045	0.263	0.045	0.045
Pine Grosbeak	*Pinicola enucleator*	0.000	0.000	0.089	0.000
Pine Siskin	*Carduelis pinus*	0.000	0.087	2.913	0.000
Plumbeous Vireo	*Vireo plumbeus*	0.000	0.000	0.088	0.000
Purple Finch	*Haemorhous purpureus*	0.796	0.000	0.000	0.449
Pygmy Nuthatch	*Sitta pygmaea*	0.000	0.000	0.176	0.000
Red-breasted Nuthatch	*Sitta canadensis*	2.298	1.967	1.062	2.416
Red-breasted Sapsucker	*Sphyrapicus ruber*	0.354	0.962	0.484	0.401
Red Crossbill	*Loxia curvirostra*	0.177	0.000	2.746	0.000

APPENDIX I (CONTINUED). DENSITY ESTIMATES FOR AVIAN SPECIES SURVEYED AT FOUR RESEARCH FORESTS IN CALIFORNIA

Red-tailed Hawk	*Buteo jamaicensis*	0.000	0.044	0.000	0.224
Rock Wren	*Salpinctes obsoletus*	0.000	0.000	0.089	0.000
Ruby-crowned Kinglet	*Regulus calendula*	0.000	0.000	0.267	0.000
Rufous Hummingbird	*Selasphorus rufus*	0.000	0.000	0.268	0.000
Sharp-shinned Hawk	*Accipiter striatus*	0.000	0.000	0.088	0.000
Song Sparrow	*Melospiza melodia*	0.000	0.000	0.266	0.000
Sooty Grouse	*Dendragapus fuliginosus*	0.000	0.088	0.000	0.088
Spotted Towhee	*Pipilo maculatus*	0.133	3.018	0.000	0.044
Steller's Jay	*Cyanocitta stelleri*	1.327	2.620	0.616	3.187
Swainson’s Thrush	*Catharus ustulatus*	0.000	0.131	0.044	0.000
Townsend's Solitaire	*Myadestes townsendi*	0.443	0.131	0.485	0.090
Townsend's Warbler	*Setophaga townsendi*	0.000	0.044	0.000	0.045
Tree Swallow	*Tachycineta bicolor*	0.000	0.000	0.044	0.000
Warbling Vireo	*Vireo gilvus*	0.618	1.709	0.399	0.357
Western Bluebird	*Sialia mexicana*	0.000	0.000	0.000	0.091
Western Tanager	*Piranga ludoviciana*	1.946	2.531	1.457	3.272
Western Wood-Pewee	*Contopus sordidulus*	0.000	0.174	0.355	0.270
White-breasted Nuthatch	*Sitta carolinensis*	0.045	0.000	0.526	0.134
White-crowned Sparrow	*Zonotrichia leucophrys*	0.000	0.044	0.044	0.000
White-headed Woodpecker	*Picoides albolarvatus*	0.573	0.699	0.352	2.241
Willow Flycatcher	*Empidonax traillii*	0.000	0.219	0.000	0.045
Williamson's Sapsucker	*Sphyrapicus thyroideus*	0.000	0.000	0.400	0.000
Winter Wren	*Troglodytes hiemalis*	0.000	0.872	0.000	0.270
Wilson’s Warbler	*Cardellina pusilla*	0.664	0.044	0.533	0.135
Wrentit	*Chamaea fasciata*	0.000	0.566	0.000	0.000
Yellow Warbler	*Setophaga petechia*	0.353	0.000	1.016	0.089
Yellow-rumped Warbler	*Setophaga coronata*	2.653	2.755	2.301	0.851

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A primer in ecoimmunology and immunology for wildlife research and management

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Two predictions of changing climate are the emergence of new diseases and the expansion of the ranges of existing parasites. Variation among individuals, especially in response to parasites, directly affects population dynamics and how populations respond to management. Immune function, therefore is a key individual-level trait that influences demographic characteristics and life-history traits because it directly affects the survival outcome of a parasitic challenge. Mounting an immune response is expensive in energy and resources and, thus, the principle of allocation predicts that trade-offs will occur with other energetically demanding tasks, such as survival or reproduction. Therefore, understanding immune function in wild animals is important for predicting how animal populations will respond to management, and we recommend that managers integrate data on immune function into larger studies of population dynamics and management of populations. In this review, we introduce how types of immune function are classified within traditional immunology and the emerging field of ecological immunology (ecoimmunology). We also review the resources available to wildlife managers for learning about techniques in ecoimmunology, and provide guidance for developing studies of immune function within larger projects on demography among populations.

Key words: adaptive immunity, constitutive immunity, ecoimmunology, immune function, innate immunity, individual variation, induced immunity, life history, parasite, population regulation

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Models of population dynamics and management plans are based on estimates of life-history parameters, such as survival and reproduction. Those life-history parameters directly affect how species or populations respond to management. Because individuals within a population vary greatly in survival and reproductive success (Clutton-Brock 1988), population managers and ecologists have become increasingly interested in how variation among individuals affects demographics at the level of the population (Sheldon and Verhulst 1996, Hayes and Jenkins 1997). Although studies at the population level are important for conservation and management, these studies are substantially limited because of difficulty distinguishing among proximate causes of changes in population size, such as breeding success, survival, immigration, and emigration (Clutton-Brock and Sheldon 2010). Recently, individual-based studies have advanced our understanding of population ecology considerably (Clutton-Brock and Sheldon 2010). Data collection and analyses at the individual level are complementary to those at the population level, but individual-based studies provide further insight into the mechanisms of population change and selection for life-history traits (Stearns 1992, Lindstrom 1999, Testa 2004, Benton et al. 2006, Monteith et al. 2014b). An improved understanding of how individual heterogeneity affects population dynamics will continue to improve models of population dynamics and inform management decisions. To accomplish this task, one needs to answer the question: what mechanisms underlie heterogeneity among individuals in their life histories (Flatt et al. 2011)?

WHY MEASURE IMMUNE FUNCTION AND PARASITE LOAD?

A major component of the expanding field of ecological immunology (ecoimmunology) is understanding how ecology and evolution have shaped immune responses, and how immune responses, in turn, have shaped the ecology and evolution of wild organisms (Downs et al. 2014). Hypotheses developed to explain variation in life histories emphasize the role of physiology as an integrator between genetics and environmental effects on expressed phenotypes (Sibly and Calow 1986, Ricklefs and Wikelski 2002, Martin et al. 2011b, Cohen et al. 2012). Immune responses have received particular emphasis because of their integral role regulating physiology of animals (Ricklefs and Wikelski 2002, Martin et al. 2008, Demas et al. 2011a, Martin et al. 2011b, Cohen et al. 2012, Demas and Nelson 2012). For example, the same signaling molecules (e.g., growth hormones, sex hormones) are involved in the regulation of both immune function and reproduction (Downs et al. 2014 and references therein).

Immune responses are also integrated with other systems because they are costly in energy and nutrients (Demas et al. 1997, Lochmiller and Deerenberg 2000, Iseri and Klasing 2013). When resources are limited, the principle of allocation predicts that a trade-off will occur between competing processes, such as investment in immune function and investment in reproduction. Indeed, the immune system has been proposed as a mediator of long-term trade-offs between reproduction and survival (Sheldon and Verhulst 1996), and experimental work has shown that energetic and nutritional limitations result in trade-offs between immune responses with reproduction or growth rates (Lochmiller et al. 1993a, French et al. 2007a, French et al. 2007b).

Finally, immune responses are an important component of survival because of their role in regulating parasites (Alizon and van Baalen 2008, Day et al. 2011, Hawley and Altizer 2011, Downs et al. 2014, Klein et al. 2014). For the purposes of this discussion, we define parasite to include micro-parasites that cause disease (i.e., pathogens, including viruses, bacteria, and fungi) as well as macro-parasites (i.e., intestinal worms, ticks, and fleas) (Anderson and May 1979). Parasites are ubiquitous in the environment, and their role in regulating population size was recognized by Leopold (1933). The optimal intensity of immune response to a parasite infection, however, depends on a complex balance of costs and benefits. If responses are too weak, animals succumb to disease or parasites but, if too vigorous, responses might damage the individual's own tissues or use resources that could otherwise be invested elsewhere (Raberg et al. 1998, Schmid-Hempel 2003, Viney et al. 2005, Zimmerman et al. 2014). Thus, natural selection should select for individuals that mount an appropriate intensity of immune response to parasites, making the immune system a focus for natural selection (Ardia et al. 2011). Immune responses, therefore, are important for understanding individual heterogeneity in survival and reproduction and the regulation of animal populations because they provide a mechanistic link between disease dynamics and consequences in host populations (Krebs 1995, Lochmiller 1996).

Implications of Studies of Immune Function for Management

Two predicted effects of climate change are the emergence of new parasites and the expansion of ranges of known parasites (Harvell et al. 2002). Diseases such as chronic wasting disease are already having adverse effects on populations of wildlife (Monello et al. 2014), and emerging fungi are contributing to the decline of amphibian populations worldwide (Blehert et al. 2009, Frick et al. 2010) and bat populations in North America (Daszak et al. 1999, Daszak et al. 2003, Stuart et al. 2004). In addition, macroparasites including winter ticks and lice are expanding their ranges and having decimating effects on populations of moose (*Alces alces*) (Drew and Samuel 1985, Samuel 2007) and black-tailed deer (*Odocoileus hemionus* ssp.) (Bildfell et al. 2004), respectively. In general, effects of parasites often are difficult to assess in free-ranging wildlife because of predation or scavenging of dead individuals (Wobeser 2007). Effects of parasites in populations of wildlife also may result in decreased productivity or recruitment, which are much more difficult to quantify than adult mortality but may have a stronger effect on population dynamics.

Models of disease spread in populations traditionally assume random variation in organismal responses to infections (Anderson and May 1979); however members of the population are not homogenous and variability exists among portions of the population as well as among individuals. Differences among individuals in immunocompetence also determine whether an individual resists or tolerates an infection. Resistance involves reducing parasite numbers, and thus reflects the ability of the host to kill an invading parasite, while tolerance involves minimizing fitness losses in responses to a particular parasite load (Caldwell et al. 1958, Simms 2000, Raberg et al. 2009, Downs et al. 2014). An individual with a high tolerance can maintain higher fitness during an infection despite having a high parasite loads. As a consequence, whether an individual is tolerant or resistant to a parasite will affect transmission rates within a population because a tolerant individual has the potential to infect many other individuals (Boots et al. 2009, Arsnoe et al. 2011). Understanding variation among individuals in immune function will provide a mechanistic understanding of whether an individual will adopt a strategy of tolerance or resistance, which will in turn inform disease dynamics (Hawley and Altizer 2011).

Effects of parasites may be more difficult to detect if a small portion of the population is affected or if individuals in poor nutritional condition are disproportionately affected (Caron et al. 2013). Given those difficulties in identification and detection, parasites may become established in wildlife populations with relatively few obvious indicators of the presence of that parasite (see, for example, Bleich et al. 2014). From a management perspective, a stronger understanding of how physiology correlates with, and potentially mediates, life-history traits will lead to the development of biomarkers that indicate animal health and condition. These biomarkers may replace traditionally measured traits that often are difficult to quantify without repeated capture and sampling of individuals, which is often prohibited by cost, time, and the risk to the animals. Thus, biomarkers that are relatively easy to quantify and more cost effective may be more useful indices for large numbers of free-ranging animals, particularly if they provide insights into disease dynamics and factors affecting population regulation. Investigations into immune responses have the potential to yield biomarkers of this type (Sild and Hörak 2009).

In this review, we start by discussing briefly the importance of understanding nutritional condition when interpreting immunological assays (Arsnoe et al. 2011). We then review how the immune system is classified in traditional immunological and ecoimmunology studies. Finally, we introduce general techniques that help address questions about the immunological state of vertebrate animals, and we provide guidance for implementing those techniques. We do not attempt a complete review of all possible techniques. Rather, we provide references of key review papers and other resources that provide further information about immunological techniques currently being used in the field so that the reader may locate additional resources.

The Importance of Understanding Nutritional Condition

Nutritional condition (generally described as percent body fat) functions as the mechanism through which intraspecific competition for resources is mediated, and provides the most direct and sensitive measure of resource limitation for the organism (Parker et al. 2009, Monteith et al. 2013, Monteith et al. 2014b). Body fat is strongly related to survival and reproduction in animals because energy from fat is used during winter fasts, thermoregulation, migration, incubation, and lactation (Barboza et al. 2009). Moreover, fat reserves also are tied directly to productivity in adult females (Testa and Adams 1998, Keech et al. 2000, Cook et al. 2001, Stephenson et al. 2002, Stewart et al. 2005). Indeed, vital rates of large herbivores, in particular, generally respond to resource limitation in a predictable sequence beginning with decreased survival of young (corresponding to decreased recruitment), increased age at first reproduction, decreased reproduction by adults, and decreased adult survival (Gaillard et al. 1998, Gaillard et al. 2000, Eberhardt 2002, Monteith et al. 2014b). Processes such as reproduction or mounting an immune response demand resources above those necessary for maintenance (Wobeser 2007, Monteith et al. 2014a), and large herbivores have been shown to favor their own survival over reproduction (Stearns 1992, Morano et al. 2013, Monteith et al. 2014b). Changes in life-history characteristics operate through changes in nutritional condition, which is an integrator of both intake of forage and physiological demands of that organism (Monteith et al. 2014b). Because of our clear understanding that nutritional condition of animals directly influences survival and reproduction, indices of nutritional condition are useful for managers especially when fecundity and survival cannot be measured directly (Bishop et al. 2009). Body fat and protein reserves are a direct indication of nutritional status of animals and are often used to make predictions about survival and reproduction (Hobbs 1989, Moen et al. 1997, Stephenson et al. 2002). How fat reserves are tied to immune function and thus affect tradeoffs with reproduction and survival are still in need of further studies, especially with free-ranging species of wildlife.

Limitations in body protein and other macronutrients also are documented to lead to immunosuppression (Klasing 1998, Klasing and Leshchinsky 1999, Lochmiller and Deerenberg 2000, Brunner et al. 2014). For example, protein reserves were critical for maintaining immunocompetence in juvenile cotton rats and bobwhite quail chicks (Lochmiller et al. 1993b, Vestey et al. 1993, Lochmiller et al. 1994). We recommend acquiring measures of nutritional condition, specifically protein and fat reserves, of individuals in studies investigating immune function in wild animals to better understand the relationship between nutritional condition and immunocompetence.

Finally, micronutrients, including trace minerals, also play an important rule in regulating immune responses (Chandra and Dayton 1982, Suttle and Jones 1989, Bhaskaram 2002). A detailed review these relationships is beyond the scope of this paper, but blood samples can also be used to quantify micronutrient levels in wildlife (Duffy et al. 2009) and we recommend investigating these levels in populations that are exhibiting signs of disease.

CLASSIFICATION OF IMMUNE RESPONSES

General classification of immune function.—The front line of defense against infection is behavioral (Nelson et al. 1975, Murphy et al. 2007; Figure 1). The second line of defense against infection, and the first layer of the architecture of the immune system, is the epidermal layer that provides a physical barrier to invasion (Hofmeyr 2001, Murphy et al. 2007; Figure 1). The third line of defense is the physical barrier created by physiological conditions within the body, such as pH, which determine whether the internal environment is appropriate for the parasite (Hofmeyr 2001; Figure 1). The fourth line of defense is physiological. Traditionally the immune system is partitioned into two types of responses: innate and adaptive (Figure 1). Both systems consist of a multitude of cells and molecules

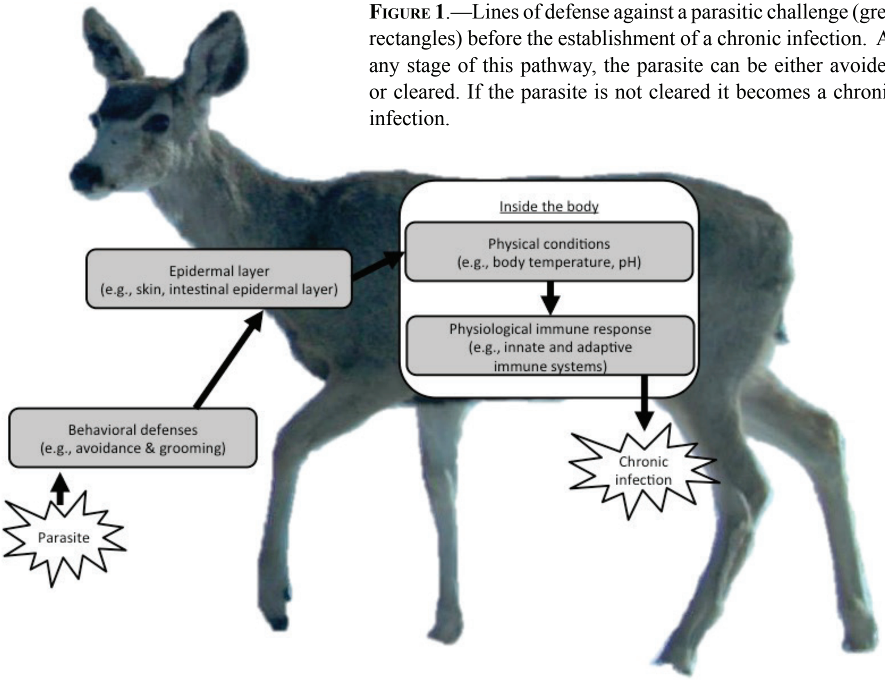

FIGURE 1.—Lines of defense against a parasitic challenge (grey rectangles) before the establishment of a chronic infection. At any stage of this pathway, the parasite can be either avoided or cleared. If the parasite is not cleared it becomes a chronic infection.

that interact in a complex manner to detect and eliminate parasites (Hofmeyr 2001). We focus on the physiological defense against infection and Appendix I includes a glossary of terms for aspects of the immune system.

Traditional immunological classification.—Innate immunity includes immediate responses following detection of a parasite and responses during the early stage of infection. Innate responses include the complement activity, cytokine cascades, the acute phase response, and the phagocytic system, which involves scavenger cells (e.g., macrophages) that detect and engulf extracellular molecules and material (Murphy et al. 2007). Some portions of the innate immune system are constitutive (always present), such as complement proteins, whereas some are induced, such as acute phase responses (Figure 2).

In contrast, adaptive immunity is the response of antigen-specific lymphocytes to an antigen, and includes the development of immunological memory (Murphy et al. 2007). Adaptive immunity includes responses of B cells involved in humoral immunity and responses of T cells involved in cellular immunity (Figure 2). Note that processes that are part of innate immunity induce adaptive responses. For example, macrophages recognize parasites and initiate innate immune responses, but macrophages also initiate an adaptive immune response by recruiting T cells to the site of infection and presenting antigens to initiate T-cell mediated killing of infected cells (Murphy et al. 2007).

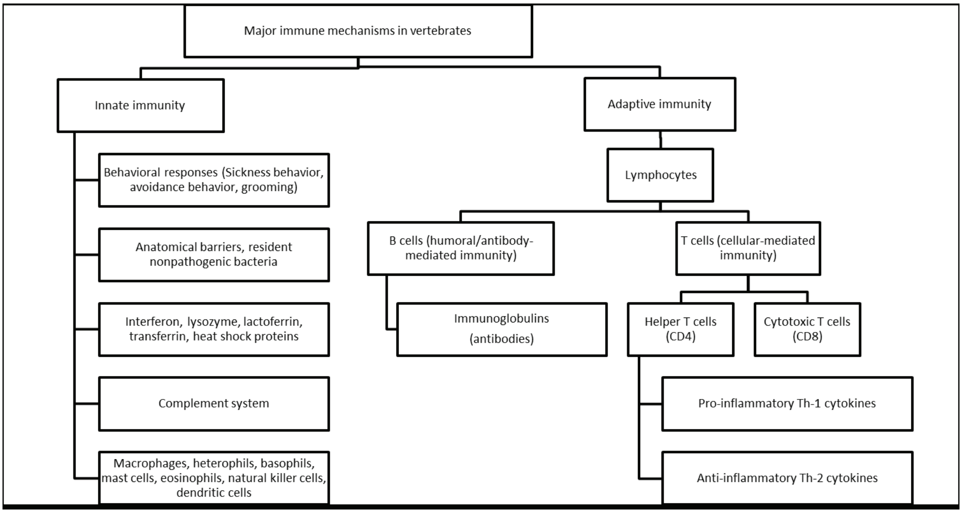

Figure 2.—Traditional classification of the immune system. Terms used in the figure are defined in Appendix I. This figure is modified from Demas et al. (2011) and Muehlenbein (2010).

Functional classification from ecoimmunology.—A helpful classification of immune function used in ecoimmunological studies involves classifying immune responses along two axes, which are not mutually exclusive: (1) a readiness axis ranging from constitutive to induced responses, and (2) a specificity axis ranging from non-specific to specific responses (Schmid-Hempel and Ebert 2003; Figure 3). Constitutive immune responses are always present, are capable of immediate physiological defense, and include defenses such as complement activity and phagocytosis (Schmid-Hempel and Ebert 2003). Induced immune responses are activated when a parasite is recognized, and include responses such

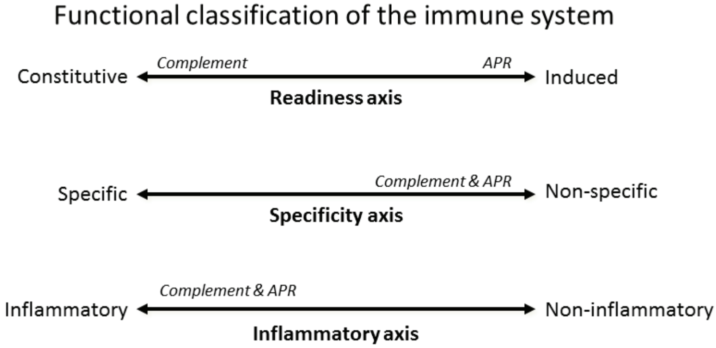

Figure 3.—Three functional axes are often used to describe immune responses in ecoimmunology studies: readiness, specificity, and inflammatory. Traditionally, immune responses are partitioned into innate and adaptive responses. No combination of functional axes describes all responses classified as innate or adaptive under the traditional classification; rather, each innate or adaptive response can be described as a combination of these three functional axes. This figure depicts the placement of two innate immune responses, the acute phase response (APR) and complement activity (complement), on the three functional axes.

as antibody production and the acute phase response (Schmid-Hempel and Ebert 2003). Non-specific immunity is characterized by responses that are not specific to an antigen and are used against numerous types of parasites and includes the complement pathway, local inflammation, and the acute phase response (Schmid-Hempel and Ebert 2003, Lee 2006). In contrast, specific immunity is characterized by responses that target specific antigens, and include toll-like receptors, antibody responses, and T-cell mediated killing (Schmid-Hempel and Ebert 2003, Lee 2006). Specific responses tend to cause less damage to the host than non-specific responses because they are specific to a parasite. An inflammatory axis, ranging non-inflammatory to inflammatory, is a commonly used third axis (Lee 2006; Figure 3).

Ecoimmunological classifications are helpful for hypothesis development because they divide the immune system into functional groups that have different relative costs of energy, resources, and immunopathology. Immunopathology is damage to the host caused by the actual immune responses rather than the parasite. For example, the release of reactive oxygen species during an inflammatory response can damage host tissues (Mates and Sanchez-Jimenez 1999). Note that these axes of ecoimmunological classification include both innate and adaptive immune responses, and no single ecoimmunological axis describes innate versus adaptive immune responses. For example, the acute phase response is part of the innate immune system, but is classified as inflammatory on the inflammation axis, induced on the readiness axis, and non-specific on the specificity axis (Figure 3). Likewise, complement activity is also traditionally classified as part of the innate immune system, but it is classified as constitutive, non-specific, and inflammatory under the ecoimmunological classification scheme (Figure 3). The type and strength of the immune response will determine the energetic, resource, and immunopathology costs associated with mounting an immune response. The type and strength of the immune response will therefore determine the selective pressures on that immune response and will inform predictions about how an individual will respond to endogenous and environmental forces.

REVIEW PAPERS AND RESOURCES AVAILABLE FOR FINDING AN IMMUNE ASSAY

Demas et al. (2011b) and Boughton et al. (2011) provide broad and comprehensive reviews of techniques that are commonly used by ecoimmunologists. These reviews include tables describing the type of immune function measured by each assay, the pros and cons of each assay, and references of key papers that describe each assay. In addition to these broad reviews, numerous reviews of more specific topics have been published recently, including a review of developing serological assays to quantify antibody responses to specific parasites (Garnier and Graham 2014), molecular techniques to quantify gene expression and circulating protein levels in non-model species (Fassbinder-Orth 2014), and remote biomonitoring techniques that can be used to quantify heterogeneity in immune responses and disease dynamics in small, free-living animals (Adelman et al. 2014). In addition, Zimmerman et al. (2014) reviewed the role of specific cytokines, important signaling molecules that regulate the strength and type of immune response. Cytokines also integrate immune responses with responses of other physiological systems (e.g., endocrine) making them important in integrated, whole-animal responses to infection (Zimmerman et al. 2014). Cytokine expression can be measured using numerous molecular techniques reviewed by Frassbinder-Orth (2014). Finally, the National Science Foundation sponsored the Research Coordination Network in Ecoimmunology, which compiled laboratory protocols for many immune response assays on their website (www.ecoimmunology.org) in an effort to standardize techniques across laboratory groups.

CAVEATS AND CONSIDERATIONS WHEN PICKING AN ASSAY

The immune system is clearly complex and cannot be described with a single assay (Adamo 2004, Boughton et al. 2011, Demas et al. 2011b). This complexity leads to numerous methodological considerations and caveats when choosing an assay. First, choose an assay that measures the immune pathway of interest. This advice may seem obvious, but it is easy to pick an inappropriate assay because the immune system is complex. Second, we recommend functional assays, such as a bactericidal assay, over morphometric assays, such as counts of white blood cells. While morphometric assays provide information about the immune system (e.g., Nunn 2002, Nunn et al. 2003, Matson et al. 2006a), extrapolating from morphology to functionality, such as clearance of a parasite, is difficult (Demas et al. 2011b). Third, if interested in the immune system in general (e.g., immunocompetence), then measure many different parts of the immune system. Results for different parts likely will differ and it is difficult to extrapolate from single assays to overall immunocompetence. Fourth, a general limitation to the application of immunological techniques to new species is the lack of species-specific reagents (Demas et al. 2011b, Downs et al. 2014). Three general solutions exist: (1) develop species-specific reagents (e.g., Hibma and Griffin 1990, Hunter et al. 2008); (2) adapt reagents from a closely related species and calibrate the assay for the new species (e.g., Svensson et al. 1998, Graham et al. 2010, Brock et al. 2013); or (3) use assays that do not require species-specific reagents (e.g., Matson et al. 2006a, Sparkman and Palacios 2009). Finally, different types of samples yield different information. For example, samples of whole blood include white blood cells, but plasma and serum samples do not. As a result, only bactericidal assays using samples of whole blood include measurements of phagocytic activity, because white blood cells are required.

Choosing between induced and constitutive immune responses.—If the goal of the study is to understand overall immunocompetence, then a researcher should measure aspects of both induced and constitutive immunity because both contribute to the outcome of an immune challenge. If animals are sampled only once, constitutive immune responses can be quantified, but induced immune responses can also be measured only if individuals can be held for at least a couple of hours or if using remote biomonitoring techniques (Boughton et al. 2011, Adelman et al. 2014). Similarly if animals cannot be handled, techniques are restricted to behavioral observations. Regardless of the approach, single samples of immune function conflate within-individual and between-individual variation, and animals should be sampled multiple times if possible to disentangle these types of variation (Downs and Dochtermann 2014).

Considerations for constitutive immune responses.—Almost by definition, studies are restricted to constitutive immune responses if a single sample is taken from an individual upon capture. As described previously, constitutive responses are present without being induced by a parasite. A complication of measuring constitutive immunity is that parasite status of the individual is often unknown. Concentrations of constitutive components of immune function change during an induced response making it difficult to determine if concentrations are due to a parasitic challenge or differences in investment (Gabay and Kushner 1999, Tieleman et al. 2005). For example, the bactericidal assay is a functional assay that measures levels of complement, natural antibodies, and phagocytosis, and it is predictive of the ability of an individual to clear a microbial parasite when challenged (Tieleman et al. 2005, French et al. 2010). Aspects of the immune system involved in bactericidal capacity increase in blood when an individual is challenged by a parasite (Gabay and Kushner 1999, Tieleman et al. 2005). In a study of 12 species of wild passerine birds, Tieleman et al. (2005) found a negative correlation between bactericidal capacity and metabolic rates, but it was unclear whether this correlation was caused by differences in life histories or by differences in parasite load that elevated both metabolic rates and bactericidal capacity. This particular example is also an example of the broader caveat that correlation does not equal causation, something that should be considered carefully when interpreting correlative studies. This example also highlights the need to obtain measurements of parasite loads or disease environment to provide context for interpreting measures of immune function (Horrocks et al. 2011).

Considerations for induced immune responses.—Induced immune responses are activated by constitutive components of the immune system; therefore, measurements of induced responses measure a part of the integrated network that encompasses a full pathway (Boughton et al. 2011). An advantage of measuring induced responses is that they can provide a direct measure of the intensity of an immune response and the related fitness consequences. Induced responses can be experimentally stimulated with a living parasite (e.g., avian influenza virus (Arsnoe et al. 2011) or *Trichinella spiralis* (Dlugosz et al. 2013) or a non-parasitic stimulant. Examples of non-parasitic stimulants include heat-killed *Escherichia coli* (Tieleman et al. 2005, Lee et al. 2008), lipopolysaccharide (Downs et al. 2012), sheep red blood cells (Ardia et al. 2003), or a vaccine (Ilmonen et al. 2000). The information that can be gleaned from a study will depend on type of stimulant used and response measured. If a living parasite is used, then the physiological, behavioral, and fitness consequences of tolerating, resisting, or clearing an infection can be measured. For example, Allenby's gerbils (*Gerbillus andersoni allenhbyi*) experimentally challenged with fleas (*Synosternus cleopatrae* *pyramidis*) experienced increased predation risk because of changes in foraging behavior (Raveh et al. 2011), but whether effects on physiology, behavior, and fitness were attributable to immune responses or to parasites could not be separated because a live parasite was used. Similarly, experimentally removing warble flies (*Hypoderma tarandi*) from female reindeer (*Rangifer tarandus tarandus*) had a positive effect on body mass (Ballesteros et al. 2012), but it is unclear whether this effect was caused directly by a reduction in the parasite load or caused indirectly by decreased immune responses. In contrast, non-parasitic stimulants do not have the ability to replicate or establish an infection, and are advantageous because it is clear that changes in physiology and behavior associated with the immune response rather than the parasite (Elin and Wolff 1976). Ideally, connections between immune responses to parasitic and non-parasitic challenges should be tested directly to confirm the degree of correlation between those two measurements.

Measuring induced immune responses requires holding the animal until a measureable response occurs or recapturing the individual numerous times. One way to quantify induced responses is to measure cytokines that are involved with initiating that response (Zimmerman et al. 2014). Depending on the species under investigation and which cytokine is chosen as the biomarker, it can take hours to days for cytokines to peak in blood (Dantzer 2001, Demas et al. 2011b). Animals have to be held for multiple days or recaptured to quantify these responses, which is possible for some species but may be logistically infeasible for others (e.g., Tieleman et al. 2005, Owen-Ashley and Wingfield 2007). Alternatively, scientists are making use of remote biomonitoring techniques, such as radio transmitters, to measure some immune responses, which eliminate the need for holding individuals of some species (Adelman et al 2014).

If interested in quantifying adaptive immunity, a way around the constraint of multiple capture events is to measure responses for a known disease using serological techniques (Garnier and Graham 2014). An advantage of this approach is the ability to measure a response to a natural infection and an ecologically relevant disease; a disadvantage, however, is that the initial infection load and date of infection are unknown. Nevertheless, information about the intensity of infection can be paired with information about the level of immune response to create a more complete picture about the dynamics of both the parasite and immune responses (Nussey et al. 2014).

Handling times and stress.—The interaction between stress responses and immune function must be considered when collecting samples from wild animals (Boughton et al. 2011). Stress hormones, such as glucocorticoids, are involved in the regulation of immune function and increase in the blood during capture, handling, and captivity (Sapolsky et al. 2000, Jacobson 2005). Acute stress increases glucocorticoids and often stimulates immune responses, whereas chronic stress increases glucocorticoids and suppresses immune responses (Martin et al 2009), but how stress affects immunity is specific to the type of response (Sapolsky et al. 2000). Indeed, zebra finches (*Taeniopygia guttata*) held in captivity had lower white blood cell counts and decreased skin swelling in responses to phytohaemagglutinin challenge (Ewenson et al. 2001), but house sparrows (*Passer domesticus*) held in captivity had increased inflammatory responses (Martin et al. 2011a). Thus, caution must be used when interpreting results from animals held for a long duration.

Even when animals are not held in captivity, the time between capture and processing can be sufficient enough to alter immune responses (Matson et al. 2006b, Buehler et al. 2008). Glucocorticoids begin to increase within 1–3 minutes in many species (Romero and Romero 2002). Immune markers generally change at a slower pace but responses vary by species (Matson et al. 2006b, Buehler et al. 2008). For example, handling times of 1 hour reduced bactericidal capacity in three bird species, but not in two other bird species (Matson et al. 2006b). Buehler et al. (2008) recommended taking samples within 30 minutes of capture to avoid changes in immune measures caused by stress of capture. If recorded, handling times can be controlled for statistically and used to test for trends. Sometimes, especially when working with animals that are passively trapped, it is not possible to obtain blood samples quickly or to record handling times. Immune function can still be quantified, but the result will be an integrated measure of the individual's response that includes the intensity of the baseline immune response before capture and stress of capture and handling.

Notes on logistics.—When collecting samples in the field, a number of precautions must be considered. Owens (2011) reviewed blood collection techniques for birds and Boughton et al. (2011) reviewed some logistical considerations more thoroughly. Briefly, sterilize skin at the collection site, and ensure sterility of collection materials (e.g., cryovials, pipette tips). Also, take precautions to ensure viability of samples: e.g., dilute in appropriate media, reduce exposure to oxygen, cool or freeze rapidly (Boughton et al. 2011). If assays require living white blood cells, the assay must be run shortly after blood is collected and the sample cannot be frozen. Regardless of the assay, minimize time between collection of sample and performing the assay, and once in the laboratory, ensure sterility of media and buffers (Boughton et al. 2011). In addition, assays must be calibrated for each new species, and calibrating assays makes it difficult to compare results among species.

SOAY SHEEP: A CASE STUDY

Despite the cautionary notes above, the mechanistic insights gained by investigating immune responses in wildlife are worth the effort. A study of the unmanaged population of Soay sheep (*Ovis aries*) in Village Bay on Hirta, St. Kilda off the northwest coast of Scotland provides an excellent case study. The population has been monitored since 1985, and experiences periodic crashes caused by high mortality (Clutton-Brock and Pemberton 2003). Gut parasites were one factor contributing to these crashes; parasite loads increased during crash years (Clutton-Brock and Pemberton 2003). Individuals that invested in high levels of antibodies that were specific to the predominate gut parasite had lower parasite loads, and higher over-winter survival (Nussey et al. 2014). Nevertheless, Graham et al. (2010) found that although an indicator of investment in immunocompetence was positively associated with survival probability in crash years, it was always negatively associated with female fecundity and probability of a male siring an offspring. This research provides direct evidence of trade-offs between immune function and survival, which suggests a reason why more individuals do not mount a more intense immune response to gut parasites despite the positive association with survival (Graham et al. 2010, Nussey et al. 2014). This case study reveals the complexity of the interactions among types of immune responses, as well as between immune responses and life history traits, but it also highlights the importance of understanding immune function when investigating population dynamics.

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APPENDIX I: GLOSSARY OF TERMS RELATED TO THE IMMUNE SYSTEM

The immune system is multifaceted and complex. Herein we present a glossary of terms related to functions of the immune system (also see Figure 1).

Acute phase response: An evolutionary conserved innate defense that is activated at the beginning of an infection. It is triggered by pro-inflammatory cytokines which orchestrate a cascade of immunological recruitment and inflammation, behavioral responses (e.g., sickness behavior), hormonal responses, and metabolic responses (e.g., febrile response) (Hart 1988, Kent et al. 1992, Owen-Ashley and Wingfield 2007). During the acute phase response, acute phase proteins are released from the liver, and these proteins are involved in antimicrobial activities including opsonization of bacteria, activation of complement, enhancement of phagocytosis, and scavenging minerals from the blood stream that are limiting for bacterial growth and replication (Weinberg 1974, Baumann and Gauldie 1994, Owen-Ashley and Wingfield 2007).

Adaptive immunity: The response of antigen-specific lymphocytes to antigen that includes development of immunological memory (Murphy et al. 2007). Adaptive immunity is distinct from the innate or non-adaptive phases of immunity, which are not mediated by antigen-specific lymphocytes (Murphy et al. 2007). Adaptive immunity includes responses of B cells that are involved in humoral immunity and T cells that are involved in cellular immunity.

Antibody: A protein that binds specifically to a particular substance—that is its antigen (Murphy et al. 2007). Antibodies are produced in plasma cells (terminally differentiated B cells) in response to infection and they bind to and neutralize parasites or prepare parasites for uptake and destruction by phagocytes (Murphy et al. 2007). Natural antibodies are present in small concentrations and bind to parasites that the individual has not encountered previously. Antibodies are known collectively as immunoglobulins, but there are six major classes of antibodies; IgA, IgD, IgE, IgG, IgM and IgY. **IgA** is the main antibody class secreted by mucosal lymphoid tissues; **IgD** appears on the surface of mature naïve B cells and are involved in mucosal immunology and stimulating basophiles to release proinflammatory and antimicrobial mediators; **IgE** is involved in the defense against macro-parasite infections (e.g., tape worms) and in allergic reactions; **IgM** is the first immunoglobulin to appear on the surface of B cells and the first to be secreted; **IgY** is found in birds and transferred to hatchlings from mothers (Murphy et al. 2007, Chen and Cerutti 2011, Edholm et al. 2011). In mammals, IgG, IgA, and IgM are part of the maternal immunity passed to offspring through milk (Carlier and Truyens 1995, Boulinier and Staszewski 2008)

Antigen: Any molecule that can bind specifically to an antibody; some antigens do not elicit antibody responses, rather they produce cellular immune responses (Murphy et al. 2007). Thus, an antigen is any molecule that can produce an adaptive immune response that is specific to that antigen. Antibodies bind directly to antigens in responses by B cells. In contrast, in responses involving T cells antigens are presented as peptide fragments bound to major histocompatibility complex (MHC) molecules on the surface of antigen presenting cells where they are recognized by T cells (Murphy et al. 2007).

Anti-inflammatory cytokines: Cytokines including interleukin-4 (IL-4), interleukin-5 (IL-5), and interleukin-10 (IL-10) that inhibit inflammatory responses and cellular immunity (Muehlenbein 2010, Demas et al. 2011b). These cytokines are secreted by Type 2 helper T cells (Th-2) and are involved in humoral immunity (i.e., the production of antibodies by B cells); they suppress Type 1 helper T-cells (Th-1) (Delves and Roitt 2000, Zimmerman et al. 2014). Zimmerman et al. (2014) review the function of anti-inflammatory cytokines.

B cells: A lymphocyte that produces antibodies upon activation by an antigen (Murphy et al. 2007). Antibodies neutralize parasites and their products, block binding of parasites to host cells, induce complement activation, promote cellular migration to sites of infections, and enhance phagocytosis, among other actions (Demas et al. 2011b). B cells can recognize native or free antigens, in contrast to T cells that recognize antigens that have been processed by antigen-presenting cells (Muehlenbein 2010).

Basophils: White-blood cells that are part of the innate immune system and contain large granules that store a variety of proteins such as toxins, prostaglandins, and histamine that are secreted upon activation (Demas et al. 2011b). When activated by IgG, basophils cause a local or systemic immediate hypersensitivity reaction. This response is part of the immune response to parasites that are too large to be engulfed by macrophages and phagocytic cells including ectoparasites such as ticks and fleas (Wakelin 1996). Basophils play a role in allergy reactions (Delves and Roitt 2000). In contrast to mast cells that are found in connective tissues throughout the body, basophils circulate through the body in the blood (Delves and Roitt 2000).

Cellular-mediated immunity: Any adaptive immune response in which antigen-specific T cells have a main role.

Complement system: Part of the innate immune system activated during the early stages of infection. It is made up of a large number of different plasma proteins that interact with one another both to opsonize parasites for engulfment by phagocytes and to induce a series of inflammatory responses to help fight infection. The final components of the complement pathway damage certain bacteria by creating pores in the bacterial membrane resulting in lysing. The complement system can be activated by three pathways: the classical pathway is initiated when antibodies bind to the surface of a parasite; the lectin pathway is initiated when mannose-binding lectin or ficolin binds carbohydrate on surfaces of parasites; and the alternative pathway is initiated when component C3 of complement in plasma is spontaneously activated and binds to the surface of a parasite (Murphy et al. 2007).

Cytokine: A large family of proteins with a small molecular weight involved in regulating cellular activity, particularly within the immune system (Delves and Roitt 2000). Interactions between cytokines are complex and results in different endpoints depending on other cytokines present (Zimmerman et al. 2014). Cytokines also act as integrator molecules linking the immune system to other physiological systems and processes including milk production in mammals and stress responses (Watson 2009, Zimmerman et al. 2014).

Cytotoxic T cells (CD8, killer T cells): A T lymphocyte that typically carries the coreceptor CD8 and that kills its target cell through perforin and lysis (Murphy et al. 2007, Muehlenbein 2010). Cytotoxic T cells recognize complexes of peptides and major-histocompatibility-complex class I molecules displayed on the target cell membrane

(Murphy et al. 2007). They are important for eliminating intercellular parasites such as viruses (Muehlenbein 2010, Murphy et al. 2000).

Dendritic cells: White blood cells that are part of the innate immune system and involved in antigen presentation (Murphy et al. 2007). They are found in most tissues, including lymphoid tissues, and are classified into two functional groups (Murphy et al. 2007). Conventional dendritic cells take up antigen in the peripheral tissues, and then travel to the peripheral organs where they stimulate a T-cell responses (Murphy et al. 2007). Plasmacytoid dendritic cells take up and present antigens, but their main function is to produce large amounts of antiviral interferons. There are also follicular dendritic cells that present antigens to B cells in lymphoid follicles (Murphy et al. 2007).

Ectoparasite: see "Parasite"

Eosinophils: White blood cells that are part of the innate immune system; they attack extracellular parasites by the release of various chemical mediators (Muehlenbein 2010). They also help during recovery from an inflammatory response by releasing histaminase to degrade histamine (Venge 1990).

Extracellular parasite: see "parasite"

Heterophils (neutrophils in mammals): Phagocytic white-blood cells that are part of the innate immune system; they target and kill cell that have been tagged with antibodies and complement proteins (Demas et al. 2011b).

Humoral immunity: Immunity due to antibody response. Humoral immunity can be transferred to a naïve recipient by serum antibody, in contrast to cellular immunity that cannot be transferred to by serum antibody (Murphy et al. 2007).

Immunological memory: The ability of the immune system to recall an encounter with a specific antigen and to mount a qualitatively and quantitatively superior secondary immune response on reencountering the antigen. This process involves the generation of memory T and B cells during the primary immune response and is part of adaptive immunity (Delves and Roitt 2000).

Immunoglobulin: A family of proteins that includes antibodies and B-cell receptors (Murphy et al. 2007).

Innate immunity: The early, physiological immune response (Murphy et al. 2007). This branch of the immune system includes a variety of innate resistance mechanisms that recognize and respond to the presence of a parasite. The innate immune system is always present and does not increase with repeated exposure to a given parasite. It does discriminate between groups of similar parasites, for example gram-positive and gram-negative bacteria. Processes in the innate immune response are precursors to adaptive immune responses; without innate immune responses the adaptive immune responses are not activated (Murphy et al. 2007).

Intercellular parasites: see "parasite"

Leukocyte: White blood cell

Lymphocyte: A white-blood cell that is derived from a common lymph progenitor; includes natural killer cells, B cells and T cells (Murphy et al. 2007).

Macroparasite: see "parasite"

Macrophages: Mononuclear white blood cells that are involved in phagocytosis, cytokine secretion, chemotaxis, antigen processing and presentation.

Major histocompatibility complex (MHC): is a highly polymorphic cluster of genes that encodes a set of membrane glycoproteins called the MHC molecules that present antigenic peptides to T cells (Murphy et al. 2007).

Mast cells: White-blood cells that are part of the innate immune system and contain large granules that store a variety of proteins, such as histamine, that are secreted upon activation (Murphy et al. 2008). Mast cells are activated by IgG causing the production of a local or systemic immediate hypersensitivity reaction that is part of the immune response to parasites that are too large to be engulfed by macrophages and phagocytic cells (Wakelin 1996, Murphy et al. 2007). Mast cells also play a critical role in allergic reactions (Murphy et al. 2007). In contrast to basophils that circulate through the body in the blood, mast cells are found in connective tissues throughout the body (Delves and Roitt 2000).

Microparasites: see "parasite"

Natural killer cells: White-blood cells that are part of the innate immune system, and non-specifically attack and lyse infected cells (Demas et al. 2011b).

Neutrophils: see "Heterophils"

Parasite: Within the ecoimmunology literature, parasite is often defined broadly using the ecological definition of parasite (Anderson and May 1979), that is any species that makes a living by uses the resources of another species and causing the host species harm. Under this definition, parasites are often partitioned into two categories: microparasites and macroparasites. **Microparasites** include bacteria, viruses, fungi, protozoans, and other microscopic parasites. **Macroparasites** include helminthes, arthropods, and other macroscopic parasites. In traditional immunology, parasites are often partitioned into intercellular, extracellular, and ectoparasites. **Intercellular parasites** reside within cells; for example *Rickettsia* spp. and viruses. **Extracellular parasites** reside within the body, but are not within a cell; for example helminthes, *Escherichia coli*, *Mycoplasma* spp., *Streptococcus pyrogenes*. **Ectoparasites** reside on the outside of a host's body; for example fleas and mites. Sometimes the word parasite is used as shorthand for macroparasite or extracellular parasite. Because different parts of the immune system target different types of parasites (in the broad sense), it is important to understand what type of parasite is being discussed in a particular study.

Pro-inflammatory cytokines: Cytokines that promote inflammatory responses including interferon-γ (IFNγ), interlukin-1β (IL-1β), interleukin-2 (IL-2), interleukin-12 (IL-12), and tumor necrosis factor alpha (TNF-α) (Muehlenbein 2010, Demas et al. 2011b). IL-2 and IFNγ are secreted by Type 1 helper T cells (Th-1) and promote cell-mediated immunity (i.e., the activation of macrophages and cytotoxic T cells) and are involved in defense against intracellular parasites (Delves and Roitt 2000, Zimmerman et al. 2014). IL-1β increases proliferation, phagocytosis, migration, and antibacterial activity of leukocytes, and induces fever and anorexia (Zimmerman et al. 2014). IL-12 is produced mainly by monocytes, macrophages, and dendritic cells; it is important in the defense against intracellular parasites and is the main driver of Th1 responses (Zimmerman et al. 2014). TNF-α is produced mainly by macrophages in responses to stimuli such as endotoxins, viruses, parasites, and other cytokines; it is a key cytokine involved in the activation of inflammation in responses to injury and infection, and the acute phase response including fever and sickness, in addition to inducing anorexia (Zimmerman et al. 2014). Zimmerman et al. (2014) review the function of proinflammatory cytokines.

Regulatory T cells: T cells that inhibit T-cell responses (Murphy et al. 2007).

Sickness behavior: A behavioral response that is part of the acute phase response and innate immunity. It includes reduced activity, anorexia (reduced food intake), adipsia (reduced water intake), and lethargy (Hart 1988).

Suppressor T cell: See “Regulatory T cell”

T cells: A type of lymphocyte. T cells can be further divided into different subtypes, notably cytotoxic T cells (killer T cells), T helper cells (Th), and suppressor or regulatory T cells (Treg). See definitions of each subtype for further details about each subtype.

Helper T cells (CD4): CD4 T cells that assist B cells in making antibodies in response to antigenic challenge; both Type 1 and Type 2 helper cells can carry out this function (Murphy et al. 2007).

Type 1 helper T cell (Th1): Cells that secrete cytokines interleukin-2 (IL-2) and interferon-γ (IFNγ) which promote cell-mediate immunity (i.e., the activation of macrophages and cytotoxic T cells). Th1 cytokines also inhibit Type 2 helper cells (Delves and Roitt 2000).

Type 2 helper T cell (Th2): Cells that secrete cytokines interleukin-4 (IL-4), interleukin-5 (IL-5), and interleukin-6 IL-6) which promote humoral immunity (i.e., the production of antibodies by B cells). Th2 cytokines also inhibit Type 1 helper cells (Delves and Roitt 2000).

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Shrub regeneration after removal of feral sheep from Santa Cruz Island, California

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I assessed shrub regeneration 29 years after removal of feral sheep (*Ovis aries*) from Santa Cruz Island by measuring shrub density during 1980 and 2013. Collectively, shrubs showed a three- to four-fold increase in density and a near-doubling of species richness. Individually, most species increased, some dramatically so, but a few species showed little change or even decreased. The explanation might be differing strategies for regeneration; most shrubs that did not increase lack a persistent seedbank and germinate best in mesic conditions, under the canopy in a substantial litter layer, and such conditions have been slow to develop. These shrubs should eventually regenerate and could even become dominant, highlighting the importance of a long-term perspective in assessing recovery of insular vegetation from herbivore damage.

Key words: chaparral, exotic herbivore, feral sheep, fire persister, fire recruiter, island recovery, *Ovis aries*, Santa Cruz Island, shrub regeneration, vegetation recovery

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Domesticated sheep (*Ovis aries*) and goats (*Capra hircus*) were introduced to islands around the world, and many populations subsequently became feral (Rudge 1984). Long-term overgrazing by feral sheep and goats has devastated the vegetation of numerous islands, often resulting in the wholesale alteration of community composition and structure, sometimes to the point of desertification (Coblentz 1978, Van Vuren and Coblentz 1987, Chynoweth et al. 2013). Damage to woody vegetation on islands is particularly important because of its role as habitat for endemic animals, many of which have declined to rarity or even extinction because of habitat degradation by exotic herbivores (Van Vuren and Coblentz 1987, North et al. 1994, Chynoweth et al. 2013). Because of these impacts, feral sheep and goats have been eradicated or excluded on many islands (Schuyler 1993, Campbell and Donlan 2005), and subsequent regrowth of native vegetation is often swift and dramatic (Campbell and Donlan 2005, Chynoweth et al. 2013). However, not all species respond quickly to cessation of overgrazing; for some native trees and shrubs, regeneration can be delayed or, perhaps, even precluded by factors such as depletion of seed banks due to prolonged overgrazing (Mueller-Dombois 1979), herbivore-caused alteration of soil conditions necessary for seedling germination (Hamann 1993), or competition with exotic grasses (Thaxton et al. 2010).

Santa Cruz Island, California, once supported a large population of domestic sheep. Sheep were introduced in the 1850s, reached numbers of 50,000 or more by the late 1800s, and became feral by the 1920s (Van Vuren and Bakker 2009). Decades of overgrazing by feral sheep had a major impact on shrubs and trees by preventing regeneration, altering growth form, and reducing large contiguous populations of woody plants to isolated clumps (Brumbaugh 1980, Van Vuren and Coblentz 1987, Junak et al. 1995). All sheep were removed from Santa Cruz Island, first on the western 90% of the island during 1981-1989, then on the eastern 10% of the island during 1997-2001, with a total of 47,000 sheep removed (Schuyler 1993; Faulkner and Kessler 2011). Recovery of woody vegetation over much of the island has been obvious, and analysis of aerial photos has revealed a dramatic increase in the cover of coastal sage scrub, island chaparral, and Bishop pine (*Pinus muricata*) communities, with a concomitant decrease in grasslands (Cohen et al. 2009). However, aside from a study of regeneration in the Bishop pine forest shortly after sheep removal (Wehtje 1994), responses by individual shrub species to the cessation of grazing remain unknown. My objective was to assess the response of individual shrub species by comparing densities before and 29 years after removal of feral sheep.

MATERIALS AND METHODS

Santa Cruz Island (249 km^2) is the largest of the eight Channel Islands located offshore of southern California. A system of interior valleys, including the large Central Valley, is oriented in a generally east-west direction along a geological fault. These valleys are bounded by the Northern Ridge (elevation 750 m) and Southern Ridge (elevation 465 m). Climate is an oceanic, Mediterranean type characterized by hot, dry summers and cool, wet winters. Precipitation averages 50 cm per year, most of which falls as rain from November through April. The island is botanically diverse, with 480 taxa of native plants identified, of which ≥45 are endemic (Junak et al. 1995). Several plant communities have been described (Junak et al. 1995); in 1980, most of the island comprised grassland (46%), island chaparral (31%), oak woodland (7%), and coastal sage scrub (6%) communities in terms of proportion of the island covered (Minnich 1980).

My study was conducted on the south slope of the Northern Ridge, immediately north of the Santa Cruz Island Reserve Field Station of the University of California, in several parallel canyons that drained south into the Central Valley. The 170-ha study area (34° 00' N, 119° 43' W) was characterized by steep, rugged topography, and elevation ranged 75-400 m. Vegetation in 1980 was classified as grassland admixed with woody vegetation (Minnich 1980). Common shrubs were island scrub oak (*Quercus pacifica*), island cherry (*Prunus ilicifolia lyonii*), mountain mahogany (*Cercocarpus betuloides*), island big-pod ceanothus (*Ceanothus megacarpus insularis*), chamise (*Adenostoma fasciculatum*), and lemonade berry (*Rhus integrifolia*). Grassland vegetation was dominated by exotic annual grasses (*Avena* spp., *Bromus* spp., *Festuca* spp., and *Lamarckia aurea*), but scattered individuals of native perennial grasses (*Stipa* spp.) were present.

As part of a study investigating browse preferences by feral sheep (Van Vuren and Coblentz 1987), shrub density was measured in two strip transects, each 5 m wide and 1,000 m long. The exact locations of the transects were determined randomly, but the location of Transect 1 was constrained to a generally east-west direction, and that of Transect 2 to a generally north-south direction, such that the two transects crossed and approximately quadrisected the study area. On 15 April 1980 I walked the center of each transect and counted all shrubs ≥1 m tall that were rooted within 2.5 m of my line of travel; multiple stems that appeared to originate from one base were counted as one shrub. I omitted shrubs rooted outside the transect, whether or not the canopy extended into the transect. Feral sheep were removed from the area during 1984 (P. T. Schuyler, personal communication). On 14 April 2013 I censused shrubs in each transect again, using identical procedures. I calculated density as the number of shrubs per hectare of strip transect, and I classified shrubs that normally grow to ≤2 m tall as short-stature, and those >2 m tall as tall-stature, based on life-history information from Junak et al. (1995).

RESULTS

Results from the two strip transects were generally consistent. During the 29 years after removal of feral sheep, total density of shrubs increased dramatically, from 210-246/ha in 1980 to 666-1148/ha in 2013. Species richness increased as well, from 8 species in each transect in 1980 to 14-15 species in 2013 (Table 1). These data do not include shrub seedlings <1 m tall, which were largely absent in transects in 1980 and too abundant to count in 2013.

TABLE 1.—Density (plants/ha) of short-stature (≤2 m) and tall-stature (>2 m) shrubs along two strip transects during April 1980, when feral sheep were abundant, and during April 2013, 29 years after feral sheep were removed from Santa Cruz Island, California.

	Transect 1		Transect 2	
	1980	2013	1980	2013
Short-stature shrubs				
Island deerweed (*Acmispon dendroideus*)	0	42	0	178
Coastal sagebrush (*Artemisia californica*)	0	0	0	66
Santa Cruz Island buckwheat (*Eriogonum arborescens*)	0	142	0	144
Northern island hazardia (*Hazardia detonsa*)	0	0	0	12
Monkey flower (*Mimulus* spp.)	0	2	0	8
Tall-stature shrubs				
Chamise (*Adenostoma fasciculatum*)	30	14	34	20
Manzanita (*Arctostaphylos* spp.)	0	6	0	0
Coyote brush (*Baccharis pilularis*)	0	0	0	2
Mule fat (*Baccharis salicifolia*)	0	2	0	0
Island ceanothus (*Ceanothus arboreus*)	0	6	0	0
Island big-pod ceanothus (*Ceanothus megacarpus insularis*)	24	86	36	280
Mountain mahogany (*Cercocarpus betuloides*)	72	240	66	270
Toyon (*Heteromeles arbutifolia*)	2	4	12	14
Island cherry (*Prunus ilicifolia lyonii*)	8	8	12	14
Island scrub oak (*Quercus pacifica*)	62	56	80	64
Island redberry (*Rhamnus pirifolia*)	10	40	2	32
Lemonade berry (*Rhus integrifolia*)	2	16	4	44
Willow (*Salix* spp.)	0	2	0	0

All short-stature shrubs increased in density, especially island deerweed (*Acmispon dendroideus*) and Santa Cruz Island buckwheat (*Eriogonum arborescens*); neither species was identified in transects at all in 1980 but both had become abundant by 2013 (Table 1).

Most tall-stature shrubs showed major increases in density as well, especially island big-pod ceanothus, mountain mahogany, island redberry (*Rhamnus pirifolia*), and lemonade berry, but some shrubs did not. Toyon (*Heteromeles arbutifolia*), island cherry, and island scrub oak were common or even dominant in transects in 1980 but showed no evidence of an appreciable increase in density by 2013. One shrub that was common in 1980, chamise, appeared to have decreased in density by 2013 (Table 1).

Discussion

In 1980 the study area was located within a portion of Santa Cruz Island that was considered to be severely impacted by feral sheep (Van Vuren and Coblentz 1987). In severely impacted areas, which totaled over one-third of island area, sheep density averaged about 2/ha, herbaceous vegetation was mostly or completely consumed, denuded soil appeared dominant, and little or no shrub foliage was present below about 1 m in height (Van Vuren and Coblentz 1987). Within the study area, shrub seedlings were scarce or absent and for those shrubs that produced basal sprouts, sprouts were rapidly consumed by feral sheep (Van Vuren and Coblentz 1987). Because of long-term defoliation by feral sheep, the continued existence of shrubs was thought to be a function of longevity instead of reproduction, suggesting the possibility of an impending die-off as shrubs became increasingly senescent (Van Vuren 1981). A similar dynamic was evident on other islands infested with exotic herbivores (Hamann 1993, Bullock et al. 2002, Stratton 2009).

My results indicate that 29 years after sheep removal, shrubs on Santa Cruz Island have shown remarkable regeneration, with a three- to four-fold increase in total density and a near- doubling of species richness. Further, many of the shrubs that increased are insular endemic taxa (Junak et al. 1995), which are of conservation concern. The physical structure of the community has changed as well, with the proliferation of short-stature shrubs; of the five taxa recorded in 2013, only monkey flower (*Mimulus* spp.) was identified in the area in 1980, and the few individuals encountered along transects fell well below the 1-m height criterion. Monkey flower, which is considered of low palatability to sheep (U.S. Department of Agriculture 1937), remained at low densities in 2013. In contrast, Santa Cruz Island buckwheat (*Eriogonum arborescens*) and coastal sagebrush (*Artemisia californica*), two species considered vulnerable to sheep grazing (Coblentz 1978, Brumbaugh 1980, Minnich 1980), increased from absent to abundant on one or both transects. Buckwheat and sagebrush are important components of the coastal sage scrub community, which was severely depleted on Santa Cruz Island by sheep grazing (Brumbaugh 1980). For both of these shrub species, germination does not appear to be constrained by seed limitation, but seedling establishment is reduced by competition with exotic annual grasses (Yelenik and Levine 2009), as has been demonstrated for native shrubs on the island of Hawaii (Thaxton et al. 2010). Disturbance by feral pigs (*Sus scrofa*), which were common on Santa Cruz Island, created gaps in grassland vegetation that likely facilitated seedling establishment for Santa Cruz Island buckwheat and coastal sagebrush (Yelenik and Levine 2009). Feral pigs were eradicated from the island during 2005-2006 (Ramsey et al. 2009), and the result might be reduced recruitment of Santa Cruz Island buckwheat and coastal sagebrush (Yelenik and Levine 2009).

Island deerweed and northern island hazardia (*Hazardia datonsa*) were two other short-stature shrubs that were absent in transects in 1980 but present or even abundant in

2013; similarly, Wehtje (1994) reported that these two shrubs were absent from a Bishop pine forest on Santa Cruz Island when sheep were present but appeared after sheep were removed. The foliage of palatable shrubs that typically grow to less than 2 m tall would be mostly or entirely within reach of browsing sheep, likely resulting in death via defoliation or trampling. Removal of sheep allowed regeneration of short-stature shrubs from residual seeds or from relict plants surviving in sheep-inaccessible locations.

Most tall-stature shrubs increased in density after sheep removal, some dramatically so. Those shrubs that increased dramatically were recorded in transects in 1980; hence, a local seed source would have been readily available. Four shrubs, however, did not increase or even declined. For three of these shrubs, island scrub oak, toyon, and island cherry, the cause might reflect differing regeneration strategies among shrubs. Most of the shrubs identified on transects are common members of island chaparral, a community that is generally similar in composition to California chaparral on the mainland. California chaparral is a fire-adapted community, but shrubs differ in their adaptations to fire. Many chaparral shrubs, such as *Ceanothus* spp. and *Rhus* spp., are considered "fire-recruiters" and produce relatively small, long-lived, refractory seeds that accumulate in a persistent seed bank, resulting in rapid germination after a disturbance such as fire (Keeley 1991). Germination by seeds of these shrubs is often enhanced or even necessitated by exposure to heat or the chemicals in charred wood (Keeley 1991). There has been no fire in the study area since sheep were removed, and, in fact, the frequency of naturally-occurring fires on Santa Cruz Island in the past appears to be less than that on the mainland (Carroll et al. 1993). However, seeds of at least some shrubs on Santa Cruz Island are less dependent on fire to germinate than are their mainland counterparts, suggesting adaptation to a lower fire frequency (Carroll et al. 1993). Hence, the dramatic response of some shrubs to the removal of sheep probably resulted because of the presence of a large seed bank adapted to germinating in conditions of direct sunlight and minimal soil litter, but in the absence of fire, which characterized the study area at the time sheep were removed. Presumably the seeds of these shrubs were germinating before sheep removal, but all seedlings were killed by consumption or trampling.

In contrast, some chaparral shrubs, including mainland scrub oak (*Quercus dumosa*), hollyleaf cherry (*Prunus ilicifolia*), and toyon, are considered "fire-persisters" that can survive fire and produce relatively large, fleshy, short-lived, non-refractory seeds that do not generate a persistent seedbank (Keeley 1991). Further, seeds of these shrubs are specialized for animal dispersal (Keeley 1991). Hence, seeds produced after sheep were removed would have been vulnerable to consumption by feral pigs; feral pigs prefer acorns and cherries, which are sterilized by passage through the pig's digestive tract (Peart et al. 1994). Perhaps most important, seeds of scrub oak, cherry, and toyon germinate best in mesic conditions, such as those present under the shrub canopy and in association with a substantial litter layer (Keeley 1992). In 1980 the shrub canopy was minimal and the soil surface was bare and eroded, probably providing poor conditions for seed germination. Drought is another possible explanation for a lack of regeneration of fire-persisters, whose seeds are particularly vulnerable to low soil moisture (Keeley 1992). However, the years 1987 through 2011 exhibited average annual rainfall (48 cm) that was near the long-term average (50 cm) and included five different years when rainfall was ≥25% above average.

Chamise is a fire-recruiter species that produces refractory seeds that persist in the seed bank and rarely germinate under the shrub canopy (Keeley 1991, 1992), similar to several other fire-recruiter species that increased dramatically in density after sheep removal. Nonetheless, density of chamise declined about 50% between 1980 and 2013, and the cause is unclear. Chamise seeds in California chaparral require fire to germinate (Keeley 1992); perhaps chamise seeds on Santa Cruz Island also require fire to germinate, unlike some other island shrubs (Carroll et al. 1993), with the decline caused by a lack of recruitment coupled with a gradual die-off due to senescence.

Twenty-nine years after removal of feral sheep, shrubs on Santa Cruz Island have shown remarkable regeneration, but response has varied among species. Most species have increased in density, including several insular endemic taxa, and for some the increase has been dramatic. A few species, however, have shown little change or even decreased. A similar pattern of regeneration was observed for woody vegetation on Pinta Island, Galapagos, after removal of feral goats; regeneration was rapid for some species but for one species was hindered by the lack of a moderate vegetation cover important for seed germination (Hamann 1993). The future trajectory of shrub regeneration on Santa Cruz Island might be inferred from successional patterns in California chaparral on the mainland. In the absence of fire, species characterized as fire-persisters such as scrub oak, toyon, and hollyleaf cherry begin germinating with the development of a shrub canopy and adequate soil litter; because they can outcompete fire-recruiter species such as *Ceanothus* by overtopping, fire-persisters can come to dominate the community in a successional process that can take 100 years (Keeley 1992). If island chaparral follows this pattern, then in future years island scrub oak, toyon, and island cherry should show increased regeneration, potentially to the point of becoming dominant. Concurrently, the cessation of grazing should increase fuel loads and hence the frequency of wildfires (Carroll et al. 1993), which could alter this trajectory by periodically enhancing recruitment of fire-recruiters, especially chamise. These results highlight the importance of considering a long time frame in assessing the recovery of insular vegetation after removal of exotic herbivores.

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Nest site characteristics, nesting movements, and lack of long-term nest site fidelity in Agassiz's desert tortoises at a wind energy facility in southern California

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Nest site selection has important consequences for maternal and offspring survival and fitness. Females of some species return to the same nesting areas year after year. We studied nest site characteristics, fidelity, and daily pre-nesting movements in a population of Agassiz's desert tortoises (*Gopherus agassizii*) at a wind energy facility in southern California during two field seasons separated by over a decade. No females returned to the same exact nest site within or between years but several nested in the same general area. However, distances between first and second clutches within a year (2000) were not significantly different from distances between nests among years (2000 and 2011) for a small sample of females, suggesting some degree of fidelity within their normal activity areas. Environmental attributes of nest sites did not differ significantly among females but did among years due largely to changes in perennial plant structure as a result of multiple fires. Daily pre-nesting distances moved by females decreased consistently from the time shelled eggs were first visible in X-radiographs until oviposition, again suggesting some degree of nest site selection. Tortoises appear to select nest sites that are within their long-term activity areas, inside the climate-moderated confines of one of their self-constructed burrows, and specifically, at a depth in the burrow that minimizes exposure of eggs and embryos to lethal incubation temperatures. Nesting in "climate-controlled" burrows and nest guarding by females relaxes some of the constraints that drive nest site selection in other oviparous species.

Key words: Agassiz's desert tortoise, *Gopherus agassizii*, nest site selection, nest fidelity, pre-nesting movements, renewable energy, Sonoran Desert

Nest site selection (NSS) is important because it affects the survival and fitness of offspring, ultimately affecting the fitness of mothers as well. In some species, maternal selection of a nest site is the only form of post-ovipositional "parental care" provided to offspring. The "maternal manipulation hypothesis" posits that females enhance the fitness of their offspring by selecting nest sites with conditions that enhance survival and performance phenotypes in those offspring (Shine 2012). Females select sites for nests when their placement is non-random with respect to a particular area (Wilson 1998) based on differences in microhabitat (Valenzuela and Janzen 2001). Nest site location influences the microhabitat for incubation and can affect incubation duration and thus time of emergence (Ennen et al. 2012a, Lovich et al. 2012), survival from abiotic factors like flooding (Pignati et al. 2013), survival from biotic factors like predators (Spencer and Thompson 2003, Micheli-Campbell et al. 2013), and parasitoids of eggs (Iverson and Perry 1994) and hatchlings. NSS also influences gene flow in metapopulations (McGuire et al. 2013). Experimental results demonstrate increased survival of hatchlings in nest sites selected by females relative to random sites (Wilson 1998, Hughes and Brooks 2006).

Various performance measures of hatchlings show the benefits of nest sites selected by females versus random sites, thus potentially improving fitness of the offspring (Shine 2012), the parent (Schwarzkopf and Andrews 2012), or both. NSS contributes to neonates hatching earlier with fewer developmental or teratological anomalies and greater mobility (Peet-Pare and Blouin-Demers 2012). In addition, nests selected by mothers affect the behavior and activity of neonates in ways that may enhance their survival (Shine and Harlow 1996, Peet-Pare and Blouin-Demers 2012). Shine and Harlow (1996) were quick to point out that putative fitness advantages of a particular physical or behavioral phenotype were not established for their study organism (the Australian lizard, *Bassiana duperreyi*). However, subsequent studies demonstrated that NSS resulted in offspring traits under strong positive selection in a snake species (Brown and Shine 2004). NSS also affects animals with environmental sex determination, like many turtles (Ernst and Lovich 2009), through the influence of the temperature regime experienced by developing embryos. In fact, nest site philopatry (discussed further below) has been used as an explanation for the evolution of environmental sex determination (Reinhold 1998), although not without some controversy (Valenzuela and Janzen 2001). Nest site philopatry has also been invoked as an explanation for female-biased sex ratios in turtles since it is a sex-specific, culturally inherited trait (Freedberg and Wade 2001). Females of some turtle species select nest sites based on egg size, placing clutches of larger eggs in warmer environments more likely to produce females

(Roosenburg 1996). Conversely, clutches of smaller eggs are oviposited in cooler sites more likely to produce males due to growth and maturity benefits accrued differentially by the sexes.

Assuming that NSS is under strong natural selection, then it stands to reason that females might return to the same nest site year after year if it continues to meet the requirements for improving their fitness and that of their offspring (Lindeman 1992). As a group, turtles exhibit varying degrees of nest site fidelity at different spatial and generational scales. For example, females of many marine and freshwater species return to the same nesting beaches or areas repeatedly (see reviews in Ernst and Lovich 2009). In some cases, females even exhibit natal homing or philopatry, returning to their place of birth to nest when they are mature (Meylan et al. 1990, Valenzuela and Janzen 2001, Freedberg et al. 2005, Sheridan et al. 2010, Watanabe et al. 2011). Other species nest in the same general area year after year (Loncke and Obbard 1977, Obbard and Brooks 1980, Lindeman 1992, Tucker 2001, Walde et al. 2007, Micheli-Campbell et al. 2013), but it is unknown if that represents true natal homing. Still other species appear to nest in proximity to their previous nest but with no particular fidelity to a specific location (Nordmoe et al. 2004). In theory, terrestrial species, like Agassiz's desert tortoise (*Gopherus agassizii*) are not limited to narrow fringes of nesting areas surrounding aquatic habitats as are aquatic turtles. However, selective forces are expected to drive NSS in *G. agassizii* for all the theoretical and empirically verified survival and fitness benefits discussed above.

We examined characteristics of nest sites, nest site fidelity, and pre-nesting movements in a population of *G. agassizii* at a wind energy generation facility near Palm Springs, California in two field seasons, separated by more than a decade, a time period that is consistent with the duration of nest site fidelity reported by other turtle species (Mitrus 2006). We did not explicitly test nest site selection with spatial hypotheses (e.g., Hays et al. 1995) or by comparing actual nest sites to available nest sites as done previously at our study site for nesting burrows by Ennen et al. (2012a). Rather, we provide a detailed description and comparison of nest sites of the same cohort of females over time. The landscape at the study site is spatially diverse, presenting females with a wide range of slopes, aspects, elevations, plant communities (Lovich et al. 2011b), and burned or unburned areas (Lovich et al. 2011c) for nesting. A previous analysis suggested that NSS was not observed at the landscape level, but possibly at the level of a tortoise burrow, where most nests are located (Ennen et al. 2012a). We tested the hypothesis that females exhibited nest site fidelity, returning to nest in the same general microsite or locality (*sensu* Leibold et al. 2004) of their known activity area (Lovich et al. 2011c). We hypothesized that the mean distances within and between years would be similar if interdecadal nest fidelity was observed. That is, nests in the same year are expected to be close together due to the small activity area size of female desert tortoises, and if nest site fidelity is exhibited, the distances between years would be expected to be similarly proximate. In addition, based on prior field observations, we hypothesized that once shelled eggs were detected in individual female tortoises, they would move shorter distances each day as the date of oviposition approached, possibly as a result of narrowing down their search for a suitable nest site. Although our sample size of nests from the same females in both 2000 and 2011 is small, no other long-term data on nest fidelity are available for this species in the wild.

MATERIALS AND METHODS

Study site and field techniques.—The study site, known locally as the Mesa wind farm, is located approximately 13 km northwest of the city of Palm Springs, California (33° 57' N, 116° 40' W), at the western edge of the Sonoran Desert (Lovich et al. 2011b). The site has been a focus of long-term research on behavior and habitat use (Lovich and Daniels 2000; Lovich et al. 2011c, Ennen et al. 2012b), reproductive ecology (Lovich et al. 1999; Lovich et al. 2012, Ennen et al. 2012a, Agha et al. 2013), and other aspects of the ecology of *G. agassizii* (Lovich et al. 2011a). A large wind energy generation facility has operated at the site since 1983 and currently includes 460 turbines and an associated infrastructure of roads, transformers, and substations. Habitat utilized by *G. agassizii* in the area ranges from 600 to 900 m elevation and is characterized by a semi-desert chaparral vegetation community, with plants representative of coastal sage scrub, chaparral, Sonoran Desert, and Mojave Desert ecosystems. Both large and small fires have affected the landscape, with little measurable effect on individual activity areas, body condition indices, or annual reproductive output of female *G. agassizii* (Lovich et al. 2011c). Additional details of the study site and tortoise population are given in references cited immediately above.

Although detailed data on reproduction were collected from 1997 to 2000, 2009 to 2011 and during 2013, actual nest locations were determined only in 2000 and 2011. Changing project priorities resulted in reduced nest finding efforts in 2011. The field procedures we used were previously described by Ennen et al. (2012a). For the sake of convenience, we describe the basic techniques here and refer the reader to that publication for more information. Adult female *G. agassizii* were outfitted with small radio transmitters and tracked at approximately 7–10 day intervals during March –August, a period that bracketed the production of shelled eggs and oviposition (Lovich et al. 2012). At each capture females were X-radiographed (Hinton et al. 1997) in the field to determine the presence of shelled eggs, clutch size, and clutch number (up to three clutches are produced by a female in a given year) before being released at the point of capture. If shelled eggs were visible, females were also fitted with thread-trailing devices that allowed discrimination of fine-scale movements. Females were then tracked daily until a substantial weight loss indicated oviposition. We then followed the thread trail to find nest sites, concentrating on tortoise burrows since females at this site normally nest in their burrows (Ennen et al. 2012a). During the year 2000 we identified both 13 first- and 10 second-clutch nests of 13 females. In 2011, only a single nest was located for each female ($n = 8$) that included both first and second clutches. This allowed comparison of nest sites and tests of nest site fidelity for five females with known nest locations in both 2000 (two nests each) and 2011 (one nest each).

At each nest site we collected GPS locations and measured distance (m) to the nearest living perennial plant and burrow orientation in degrees. In 2000 we also measured burrow dimensions (Table 1). Using GIS we quantified slope angle, elevation, and slope aspect of each nesting location.

Statistical analyses.—To measure dispersion of nest sites within and between years we used GIS-based analyses to estimate three-dimensional landscape distance (m) between clutch locations of each female within and between sampling years, similar to the analysis of Lindeman (1992). Of the 22 adult females we monitored during the study, only five met the following criteria: 1) they had known nest locations in both 2000 and 2011, and 2) they produced at least two clutches in 2000. Only one nest was detected for each female in 2011

Table 1.— Summary statistics for environmental attributes of nest sites used by Agassiz's desert tortoises (*Gopherus agassizii*) near Palm Springs, California, 2000 and 2011. Means are followed by range, *SD* and (sample size). Means and *SDs* for slope aspect and burrow orientation are calculated as circular statistics. Burrow dimensions were only available for 2000. Data include all nests in both years including those for the five females discussed in the text with known nest locations in both years and two clutches in 2000.

	Environmental attribute							
Year	Slope angle (degrees)	Elevation (m)	Slope aspect (degrees)	Distance to nearest perennial plant (m)	Burrow orientation (degrees)	Burrow length (cm)	Burrow height (cm)	Burrow width (cm)
2000	13.7	757.5	170.9	0.55	166.0	55.4	13.8	32.4
	2.4–28.3	683.7–841.1	74.5–331.7	0–2.0	12.0–312.0	28.0–105.0	11.0–18.0	27.0–49.0
	8.4 (23)	40.1 (23)	77.9 (23)	0.65 (21)	80.0 (23)	23.4 (22)	1.6 (22)	5.3 (22)
2011	14.8	755.1	188.4	3.14	160.2			
	1.1–32.0	682.7–844.0	120–240	0-6.25	110.0–225.0			
	10.9 (8)	57.2 (8)	40.7 (8)	2.23 (8)	40.5 (8)			

but again, our sample included both first and second clutches. Within-year distances were calculated as the distance between first and second clutches of each individual in 2000 ($n = 5$ distances) only. Between year distances were calculated as the distance from both first and second clutches in 2000 to the same female's single clutch in 2011 ($n = 10$ distances). Mean distances were tested using a paired *t*-Test.

For all relocations after a female was identified to be carrying eggs we calculated the distance moved over the previous day and the number of days since the female was originally identified as carrying eggs. If the female had not been located on the previous day, the interval was not explicitly included in our analysis. In order to test the hypothesis that tortoises move ever shorter distances in the days prior to laying eggs, we fit a Cox (1972) proportional hazards regression model with distance moved on the prior day as the predictor. Cox proportional hazards regressions combines a nonparametric model of the probability of laying eggs (in this application) as a function of the time since the individual was known to be gravid, with a parametric model of how covariates alter this nonparametric model. Based on our hypothesis, we expected the sign of the coefficient associated with distance moved since the prior day to be negative. We tested for statistical significance based on a Wald test.

All data were tested for normality and transformed as necessary prior to analysis. Circular data were analyzed with Oriana® statistical software. Statistical analyses were conducted using SYSTAT version 13.00.05 and R version x64 3.0.2. Statistical tests were considered significant at probabilities ≤ 0.05. All tests were *a posteriori* as the primary focus of the research was not on nest site fidelity. Research was conducted under permits from the U.S. Fish and Wildlife Service, California Department of Fish and Wildlife, and the Bureau of Land Management. We are grateful to the Institutional Animal Care and Use Committee of Northern Arizona University for reviewing and approving our research procedures.

Results

The locations of nests by year and female tortoise are shown in Figure 1. None of the females returned to the exact spot to nest twice but most nested in the same general area within and between years. An exception was female #69 in the western portion of the study

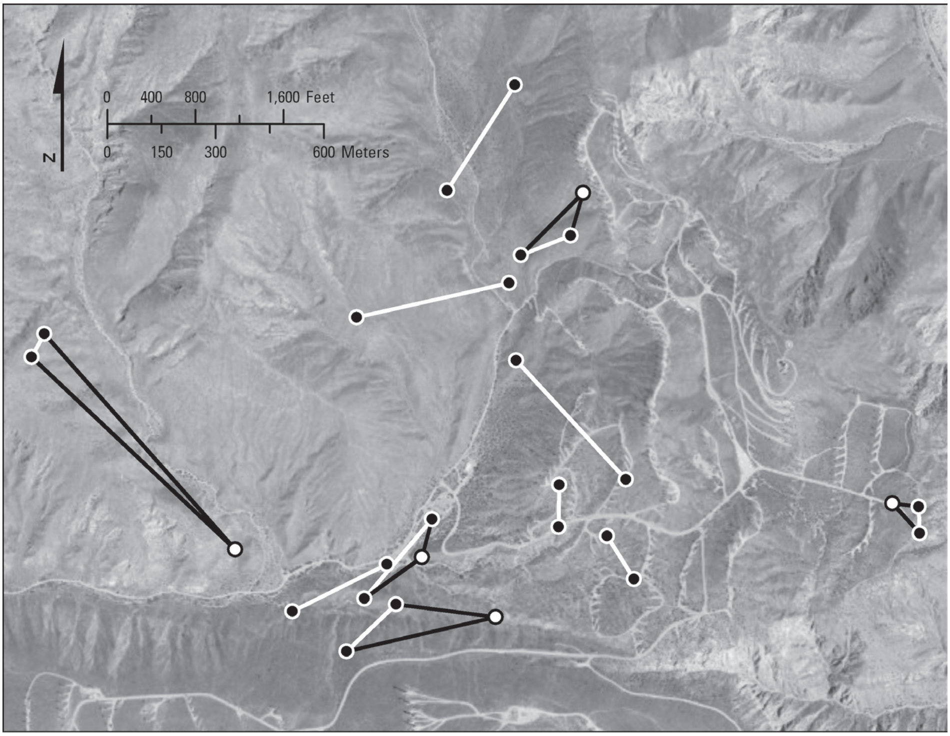

Figure 1.—Aerial photograph of study area showing locations of Agassiz's desert tortoise (*Gopherus agassizii*) nests in the years 2000 (black dots) and 2011 (white dots). White lines connect first and second clutches of each female in 2000. Black lines connect nests from 2000 to a single nest for each of the same females in 2011. For the year 2000, only verified locations for nests of females that produced a first and second clutch are shown. None of the nest locations shown contained a known triple clutch. Triangles detail the nest locations of the five females discussed in the text with known nest locations in both years and two clutches in 2000. The other white lines and black dots show the nests of other females in 2000 without known nest locations in 2011. Wind turbine access roads can be seen as "tic-marks" off the main roads on the right side of the photo. Center of map is approximately 13 km northwest of Palm Springs, Riverside County, California.

area because her nest in 2011 was far from her nests in 2000. First- and second-clutch nests of each female in 2000 ranged from 73.1 to 291.0 m apart ($\bar{x} = 157.3$, $SD = 91.1$). Distances between first and second clutches of a female in 2000 and her single nest in 2011 ranged from 73.8 to 822.0 m ($\bar{x} = 321.4$, $SD = 279.4$). Comparing nest site differences within and between years using $\log_{10}$-transformed distances and a two-sample *t*-Test with pooled variance failed to reject our null hypothesis that the means were the same ($t_{13} = 1.26$, $P = 0.23$).

Summary statistics for the environmental attributes we measured at nests are shown in Table 1. The mean direction of nesting burrow orientation in 2000 was not statistically different from the mean for 2011 using the Watson-Williams *F*-test for circular data ($F_{1,\,29} = 0.05$, $P = 0.83$). Similarly, the slope aspect of nesting burrow locations between the years was not statistically different using the same test ($F_{1,\,29} = 0.42$, $P = 0.52$). Using the three non-circular variables (elevation, slope angle, and $\log_{10}$-transformed distance to nearest perennial plant) in a MANOVA revealed a significant difference in the attributes between years (Wilks' Lambda = 0.28; *F-ratio* = $11.15_{3,13}$, $P = 0.001$). Somewhat paradoxically, individual univariate F-tests on the same variables were insignificant with the exception of $\log_{10}$-transformed distance to nearest perennial plant ($F_{1,15} = 21.98$, $P < 0.001$). MANOVA for the same variables, this time comparing attributes among females, was insignificant as were all univariate tests.

As we hypothesized, the coefficient associated with daily distance a female moved after detection of shelled eggs and prior to nesting was negative (untransformed value of -0.009 with standard error of 0.003) and statistically significant according to a Wald test (7.1 on 1 *df*, $P < 0.01$). Figure 2 illustrates how different values of distance moved and days since an individual was known to be carrying shelled eggs change the expectation of whether a female is likely to continue to carry her eggs or oviposit.

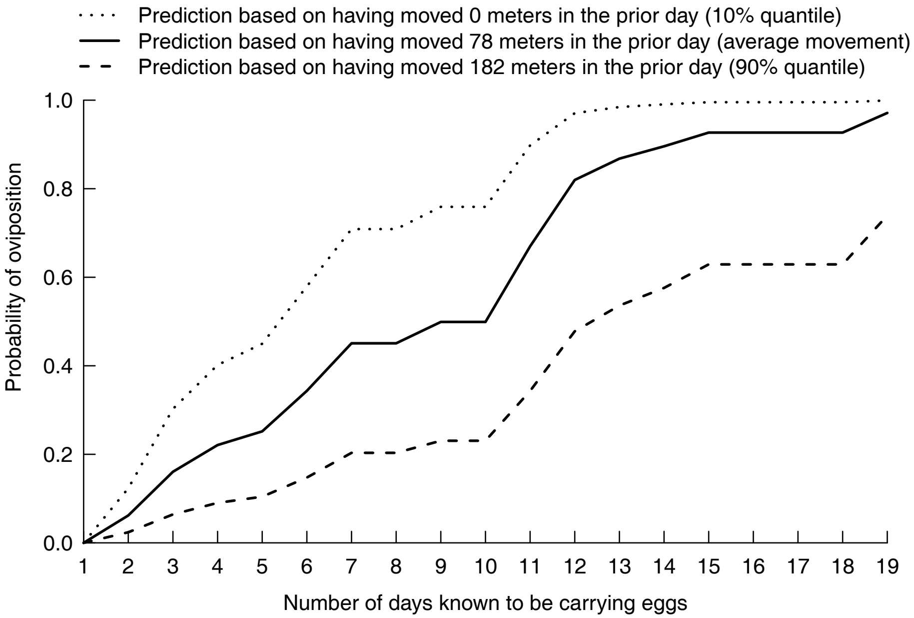

Figure 2.— Daily movements and the number of days that Agassiz's desert tortoises (*Gopherus agassizii*) are known to have been carrying shelled eggs jointly predict the probability of oviposition. For example, tortoises that are known to have been carrying shelled eggs 12 days or more and cease moving are highly likely (>95%) to oviposit. Study site was approximately 13 km northwest of Palm Springs, Riverside County, California.

DISCUSSION

Nest site fidelity has been reported in a diversity of turtle species (e.g., Christens and Bider 1987, Szerlag-Egger and McRobert 2007). For example, female green sea turtles (*Chelonia mydas*) return to their natal beaches at least 70% of the time (FitzSimmons et al. 1997, Mortimer and Portier 1989). Another example of an aquatic species that also displays nest site fidelity is the European pond turtle *Emys orbicularis* (Najbar and Szuszkiewicz 2007). During a three year period, nests of individual females were found within 0.75 – 8.5 m of each other. Another study of the same species found that two individual turtles displayed nest site fidelity to within a distance of less than 20 m over more than 10 years

(Mitrus 2006). However, during that 15 year study, other females had nest locations that measured up to 840 m apart. Painted turtles (*Chrysemys picta*) in Idaho demonstrated nest site fidelity both within and among years during a three-year study (Lindeman 1992). The issue of spatial scale (Levin 1992) needs to be considered, as the nesting beach for sea turtles can be much larger than suitable nesting areas available to a freshwater turtle living in a smaller wetland habitat.

We found little evidence to support the concept of nest site fidelity in Agassiz's desert tortoises at our study site over an 11-year period. Previous researchers noted that "Desert tortoises do not migrate in California, although some females move from habitual areas to other sites to lay eggs" without providing details about fidelity (Turner et al. 1986). At our study site, distances between a given female's nests in one year and her nests 11 years later ranged from 73.1 to 822.0 m. Wide variation in the degree of nest site fidelity has been observed in other turtle populations (Rowe et al. 2005, Mitrus 2006). With the exception of female #69 mentioned above, all nest sites fit largely within the core activity areas (measured as minimum convex polygons of capture locations; Lovich et al. 2011c) of each female from 1997 to 2010. Those activity areas ranged from an estimated 2.85 – 42.63 ha during two time intervals: 1997 to 2000 and 2001 to 2010 (Lovich et al. 2011c). It appears that a female's choice of nest sites is more a reflection of the boundaries of her activity area (Jackson and Walker 1997) than it is to deliberate searching outside that zone of familiarity. In fact, previous research suggested that although tortoises at our study site appear to select burrow locations that differ from random locations (Lovich and Daniels 2000), they do not exhibit nest site selection when comparing environmental attributes of burrows with nests to burrows without nests (Ennen et al. 2012a).

We are not suggesting that nest site selection is unimportant to *G. agassizii*. Our earlier research also demonstrated that the location and depth of nests in tortoise burrows varied predictably. The microhabitat of the burrow is typically cooler and higher in humidity and, therefore, aids in reducing water loss at certain times of day (Bulova 2002, Walde et al. 2009), and may account for why nests located farther into the burrow were shallower than nests located closer to the burrow entrance (Ennen et al. 2012a). Previous researchers suggested that nest site selection inside the burrow increases tortoise embryo survival by protecting them from lethal incubation temperatures (Baxter et al. 2008). It is also likely that this behavior affects sex determination in hatchling *G. agassizii* since warmer nests produce females and cooler nests produce males (Spotila et al. 1994). Thus, females appear to select nest sites more at the microsite scale (Leibold et al. 2004) inside the burrow rather than larger scales like the landscape. However, it is possible that females select nest sites at multiple scales. For example, females may select nest sites that are a tradeoff between predation risk in the overall environment and local vegetation cover (Spencer and Thompson 2003). Similarly, females of some sea turtles demonstrate individual consistency in their nest placement above the highest spring tide line, but very little consistency in nest placement and fidelity on an axis parallel to the shoreline or even the same nesting beach (Kamel and Mrosovsky 2004). Ultimately, the nest site selected is expected to optimize the minimization of risk at multiple scales.

Nest site environmental attributes we measured were consistent among females based on MANOVA and ANOVA, but varied between years due mainly to differences in distance to the nearest perennial plant. We suggest that the difference is due to the effects of multiple fires at our study site during the period of study, resulting in high mortality of widely-spaced, long-lived, dominant plant species like creosote bush (*Larrea tridentata*) and their replacement by closely-spaced, fast-growing, successional species like brittlebush (*Encelia farinosa*) (Lovich et al. 2011c). These changes affect the spatial distribution of perennial plants based on their sensitivity to fire (Brown and Minnich 1986, Abella 2009).

Nest site selection is also important in reducing vulnerability of eggs and embryos to predation as discussed above. Desert tortoise nests are exposed to a wide variety of predators (Ernst and Lovich 2009) and from 12 to 70% of nests are destroyed annually (Ennen et al. 2012a). Vulnerability of tortoise nests to predators may be minimized by two factors. First, desert tortoises at the site typically nest inside their burrows (Ennen et al. 2012a) where nests are better protected. Burrows at our site can be over 3 m in length but most are less. Second, predation risk might be mitigated by female nest guarding. Desert tortoises protect nests at our study site, either passively by sitting over the top of them and blocking the entrance to the burrow by turning sideways, or aggressively by pushing perceived predators away (Agha et al. 2013).

Nesting in the "climate controlled" conditions of tortoise burrows also mitigates against the temperature extremes in the larger scale of a desert landscape and, in conjunction with nest defense, relaxes some of the constraints that drive NSS in other turtle species. Based on analysis of our data it appears that tortoises nest within their activity areas on the broader landscape. This is in contrast to some turtle and tortoise species (e.g., Obbard and Brooks 1980, Stubbs and Swingland 1985), especially sea turtles, that leave foraging areas and migrate for considerable distances to nesting beaches (Hart et al. 2012). Desert tortoises then appear to select specific locations for their burrows (Lovich and Daniels 2000). Our data showing the shortening of daily movements as the date of oviposition approaches suggest that females are narrowing down their search for a suitable burrow. This is in contrast to the conclusion of Ennen et al. (2012a) that there was no evidence of nest site selection among burrows, perhaps due to the fact that the suite of environmental attributes used in the earlier analysis did not adequately reflect those that are important to females. After selection of an appropriate burrow, females then select nest locations within the burrow (Ennen et al. 2012a) that increase survivorship of hatchlings (Baxter et al. 2008). Since tortoises use multiple burrows during a single season (Bulova 1994, Rautenstrauch et al. 2002, Harless et al. 2009), any of which might have suitable microclimates for nest development and protection, returning to the same one to nest repeatedly may be unnecessary. However, finer-resolution data (e.g., annual) might reveal more or less fidelity than our data spanning 11 years between the nests of individual females.

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The historical distribution of bighorn sheep in the Sierra Nevada, California

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Bighorn sheep in the Sierra Nevada disappeared from most of their historic range, surviving in only 3 populations west of the town of Independence in the Owens Valley. As a primary basis for restoration of these sheep, we compiled historical sightings and skull remains for Sierra Nevada bighorn sheep by twelve geographic regions, along with early estimates of population sizes where they existed. Historic sightings suggest that at least 10 populations survived to the twentieth century of which 2 persisted to the middle of that century before disappearing; but the sighting record does not distinguish viable populations from those that may have been declining to extinction. While it is possible for some populations to assign a decade when they disappeared, those populations may have lost viability earlier. Our data base probably represents the historical north-south distribution of these sheep and provides distributional details for some populations. However, it is remarkably sparse for some regions, suggesting that it may not have captured the full historical distribution of this animal, particularly west of the Sierra crest, where the earliest population losses may have occurred. Restoration efforts need to recognize this potential shortcoming.

Key words: bighorn sheep, endangered species, historical distribution, *Ovis canadensis sierrae*, Sierra Nevada

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Information on historical distribution is an important foundation for wildlife restoration programs. Bighorn sheep in the Sierra Nevada (*Ovis canadensis sierrae*; SNBS) disappeared from the majority of their native ranges following the appearance of Europeans and their domestic animals in the mid 19th century. By the 1970s SNBS persisted in only three populations in a region from George Creek to Taboose Creek west of the town of Independence in the Owens Valley, Inyo County, California (Wehausen 1979, 1980). Translocations were used to begin restoring extirpated populations during 1979–88 (Bleich et al. 1990). While those restoration efforts succeeded in re-establishing populations in three regions, subsequent reductions in all populations of SNBS led to the listing of these sheep as endangered under state and federal laws in 1999. Those actions ultimately placed a stronger emphasis on further restoration of extirpated populations as one criterion for removal of these sheep from endangered species status (U.S. Fish and Wildlife Service 2007).

Two fundamental adaptations substantially dictate the nature of suitable habitat for bighorn sheep: keen eyesight and agility on steep rocky slopes. The first is how these sheep detect predators and the second is how they evade them. Preferred habitat is visually open (low vegetation) and on or close to steep, rocky slopes. The extensive alpine habitat along the crest of the Sierra Nevada provides a large expanse of relatively continuous suitable habitat that is steep, rocky, and visually open. The pattern of uplifting of the Sierra Nevada fault block has resulted in a considerably steeper eastern slope compared with the western side of the range (Hill 1975), with the former providing a considerable amount of steep and rocky terrain needed by bighorn sheep.

Additionally, because of the prevailing direction of winter storms and the strong rain shadow effect of this high mountain range, the eastern slope of the Sierra Nevada is much drier than the western side. This climatic pattern also has enhanced bighorn sheep habitat on the eastern side of the range by limiting the height and density of many plant communities, resulting in patches of low stature vegetation below timberline. This is particularly evident along the eastern base of the escarpment where the rain shadow is strongest and the plant community consists of Great Basin desert scrub types below and in conjunction with the lowest trees in the mid-elevation forest belt. In contrast to the extensive forested habitat found at mid elevations on the western side of the Sierra Nevada, forested habitat on the drier eastern slope of this range is more fragmented and often with low tree density on steep rocky slopes, thereby providing habitat used by SNBS. The result is a network of suitable habitat along the eastern side of the range at these mid elevations.

In the southern Sierra Nevada the Kern River drainage is a deep north-south canyon sandwiched between the main crest of the range and the Great Western Divide, a separate high alpine crest parallel to the main crest to the west with its own rain shadow. There is historical evidence that resident populations of SNBS also occupied a portion of the Great Western Divide.

While alpine habitat in the southern and central Sierra Nevada is relatively continuous, this does not imply that the native bighorn sheep were one continuous population. Bighorn sheep in general show a great deal of population substructuring defined by separate female home range patterns, and these female home range patterns are the fundamental building blocks of metapopulations for the species (Bleich et al. 1996). In contrast to the extensive alpine habitat, suitable low elevation winter range habitat on the eastern slope of the Sierra Nevada is quite discontinuous and limited in area, consisting of patches of varying size. The low elevation patches used by SNBS in winter and early spring naturally divide them into separate demographic units typically known as herds, and some existing historical data are specific to such herds. There are also larger natural distribution gaps, such as the Kern River drainage, that separates the two southern alpine crests. Those larger gaps were recognized in the recovery plan for SNBS where they were used to define four larger distributional units termed recovery units (U.S. Fish and Wildlife Service 2007).

In general, male bighorn sheep range considerably further than females. The much larger horns and supporting skull structure of male bighorn sheep allow skull remains to persist much longer than those of females, resulting in a very male-biased historical data base of documented remains. While skull data provide important historical information, there is a need to recognize this bias in interpreting these data relative to the distribution of native herds of reproducing females.

SNBS are a unique and clearly distinguishable subspecies of bighorn sheep (Wehausen and Ramey 2000, Wehausen et al. 2005), and can be viewed as alpine specialists relative to habitat use patterns and life history, which distinguishes them from most desert bighorn sheep. Consequently, the native distribution of SNBS can be defined in part relative to alpine habitat, limiting the southern distribution to Olancha Peak and the Great Western Divide, while historical evidence puts the northern end of the native distribution in the Sonora Pass region. The details of historical distribution within that region are the subject of this paper; specifically, we attempt to synthesize all historical evidence of bighorn sheep within that geographic area. In so doing we address the temporal pattern of herd losses to the extent possible, and provide information on habitat attributes and historic herd sizes where available.

Data Sources

A variety of authors addressed questions about SNBS beginning in the late 19th century (Muir 1894, 1898; Ober 1911, 1914, 1931; Grinnell and Storer 1924; Bailey 1932; Grinnell 1935; Dixon 1936), but the first attempt to catalogue historical information was that of Jones (1949), particularly the appendix, which is lacking in the subsequent publication (Jones 1950a). Wehausen (1979, 1980) added to that compilation, and further evidence in the form of skull remains has emerged since then.

We critically examined potential evidence and mapped only data that clearly documented the presence of bighorn sheep either as location-specific sightings or skull remains in our maps of historical evidence (Figure 1, Figure 2). Clyde (1971) noted that male mule deer (*Odocoileus hemionus*) can utilize high alpine habitats. They leave tracks that cannot be reliably distinguished from bighorn sheep, and the same can be said of visual identification of their feces. In recent years the first author has genetically analyzed numerous fecal samples from alpine habitat outside of the known range of SNBS where the collectors believed the samples were from SNBS. Most have proven to be from mule deer. Consequently, in this data synthesis we excluded all reported sign of bighorn sheep, recognizing that in some cases this meant ignoring what could have been good information. In addition to skulls and sightings, there were also historical, subjective estimates and even counts for some populations. These were not plotted; instead, this information was brought into regional narratives along with other pertinent information.

Some focused data collection on surviving native herds began in the 1960s (Riegelhuth 1965, McCullough and Schneegas 1966, Dunaway 1970). Since our purpose was largely to describe the distribution of extirpated populations, we did not consider that information to be historical and pertinent to this study and did not include it. However, we included earlier sighting data for surviving native herds that were entered into a class called historic sightings, defined as pre-1960 sightings. This allowed comparisons of numbers of recorded sightings between regions, such as surviving versus extirpated herds. For extinct herds that survived into the second half of the 20th century it was also important to acknowledge and utilize more recent data, so we included a second category of recent

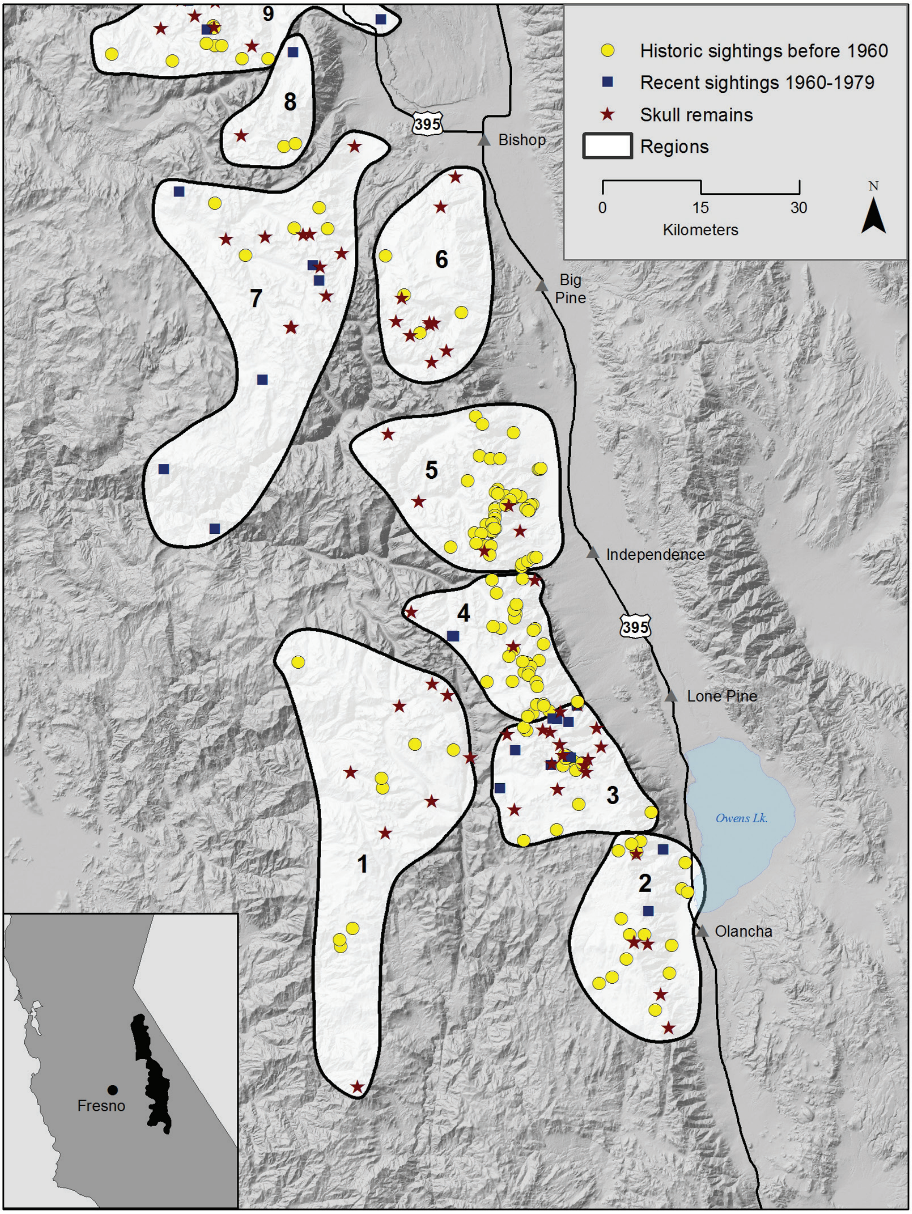

FIGURE 1.—Locations of historic sightings of Sierra Nevada bighorn sheep (before 1960), recent sightings (1960–1979), and skull remains by geographic regions identified by numbers for the southern half of the historic range.

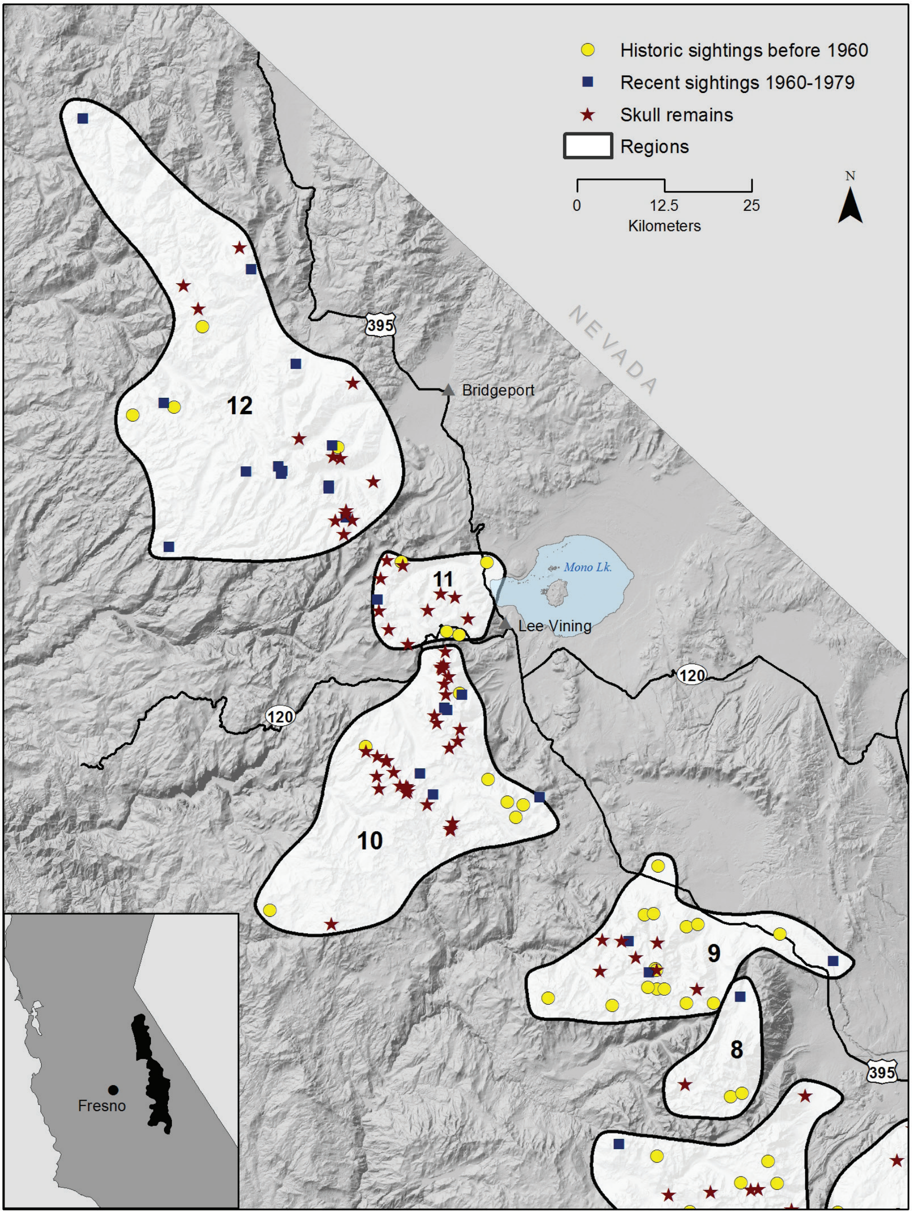

Figure 2.—Locations of historic sightings of Sierra Nevada bighorn sheep (before 1960), recent sightings (1960–1979), and skull remains by geographic regions identified by numbers for the northern half of the historic range.

sighting data for 1960–1979. Skull remains were treated as a third class in our data base and on maps, and all skull data were included for extirpated herds regardless of when found.

We divided the historic range of SNBS into twelve geographic regions numbered 1–12 from south to north. Those regional boundaries were defined in a way that would not place any extant or historic population in multiple regions, but some regions include the ranges of multiple populations, while others represent the range of a single population.

Early field observers lacked the tools needed to identify seasonal migration patterns that are typically used to define separate populations (herds), and they consequently sometimes made false assumptions regarding population definitions that have been corrected in recent decades. We point these out where appropriate.

Our regional boundaries are included on the maps that summarize our data base and below we discuss the historic information by region. We discuss this evidence of historic presence of SNBS beginning with the Great Western Divide.

Great Western Divide (1).—Bighorn sheep occupied a region of the Great Western Divide at least from the Kaweah Peaks to Mineral King and further south to Maggie Mountain (Figure 1). Early cattlemen operating in this region noted that SNBS could be found most commonly at the head of Big Arroyo (an alpine basin west of the Kaweah Peaks), and on Red Spur, a prominent point along the Kern River at the eastern end of the Kaweah Peaks (Jones 1950a). The Mineral King area had an estimated 125 SNBS in the 1870s distributed as 75 in the Farewell Gap area and 50 around Sawtooth Peak according to Guy Hopping, an early superintendent of National Park Service lands in that region (Jones 1950a).

Guy Hopping told the second author of a die-off of bighorn sheep in the Kaweah Peaks in the 1870s which was attributed to scabies, presumably contracted from domestic sheep. This is the only documented die-off of SNBS, but it apparently did not eliminate that population, as sightings of SNBS continued to be made in this region of the Great Western Divide to about 1918 (Table 1).

Table 1. Summary of historic data compiled for Sierra Nevada bighorn sheep. Historic sightings are pre-1960. Recent sightings are for 1960–1979. E = extirpated; N = native.

Region	History	Historic Sightings	Recent Sightings	Earliest Year	Latest Year	Skulls
1. Great Western Divide	E	8	0	1905	1918	8
2. Round Mt. to Muah Mt.	E	16	2	1906	1966	6
3. Cottonwood Cyn. to Lone Pine Cr.	E	17	8	1909	1976	14
4. Mt. Whitney to University Peak	N	33	-	1875	-	4
5. Kearsarge Pass to Taboose Pass	N	53	-	1912	-	4
6. Taboose Pass to Coyote Ridge	E	4	0	1935	1957	11
7. Bishop Creek to Pine Creek Pass	E	5	6	1873	1936	11
8. Pine Creek to Rock Creek	E	2	1	1944	1962	1
9. Mono Pass to Mammoth Pass	E	15	3	1913	1975	7
10. Mammoth Mt. to Mt. Dana	E	7	7	1870	1976	33
11.Tioga Pass to Green Creek	E	4	1	1939	1960	9
12. North of Green Creek	E	4	13	1877	1975	14
TOTALS		168	41			122

In recent decades SNBS living along the main crest of the Sierra Nevada in a variety of locations have demonstrated the ability to live year round at high elevations. Critical to that behavioral pattern are networks of predictably windswept habitat on and just east of the Sierra crest that are substantially free of snow in most winters. The Great Western Divide differs from the main crest of the Sierra Nevada in essentially lacking such high elevation snow-free habitat. The very limited historical information on the bighorn sheep that once occupied the Great Western Divide lacks data on where they wintered. While the east-facing slope of the Kern River Canyon and south-facing habitat near the mouths of Big Arroyo, Rattlesnake Canyon, and Laurel Canyon are likely candidates, there may have been winter range patches used on the western side of the Great Western Divide. This is suggested by multiple historic sightings in the Maggie Mountain area that lies about 14 km southwest of the extensive high alpine summer range near Mineral King. Not far from Maggie Mountain to the north is Sheep Mountain, which may have been named because of regular use by bighorn sheep. The recovery plan for SNBS postulated that two populations inhabited this region historically (U.S. Fish and Wildlife Service 2007), and restoration of SNBS to this region via translocations began in 2014.

Round Mountain to Muah Mountain (2).—This region once supported the Olancha Peak herd. Olancha Peak lies near the southern end of this region and contains the southernmost alpine habitat in the Sierra Nevada; but it is a small somewhat isolated patch of alpine habitat that is connected to the extensive alpine of the main crest of the Sierra Nevada north of the Kern Plateau only via the steep eastern escarpment west of Owens Lake. The historical information on SNBS in this region (Table 1, Figure 1) clearly indicates that SNBS occupied Olancha Peak and the habitat east of the Kern Plateau between Olancha Peak and the Mount Langley region to the north and perhaps some areas of the Kern Plateau. There are multiple patches of good, low-elevation winter range at the base of the escarpment in this region. Because Olancha Peak is otherwise a small isolated patch of habitat, gene flow across the habitat above Owens Lake with the Mount Langley herd would have been critical for the persistence of this population.

The largest sighting in this region was 19 sheep of all sizes in 1916, after which no sighting exceeded 4. Jones (1949, 1950a) treated the Olancha Peak herd as part of the Mount Langley herd, but given the natural population structure of bighorn sheep there is a high likelihood that it contained an independent population of females. When this population disappeared is not clear. Of 15 scattered sightings after 1920, 7 are specified to be males, and many others may have been the same. These may have been primarily rams from the Mount Langley herd. It is possible that the Olancha Peak herd was no longer a viable reproducing population by the early 1920s. SNBS were restored to Olancha Peak via translocations in 2013 and 2014.

Cottonwood Canyon to Mount Hitchcock and South of Lone Pine Creek (3).—The native Mount Langley herd was probably the last population to go extinct, with many reported sightings in this region (Figure 1) in the first half of the twentieth century and continuing into the second half of that century, even to the 1970s (Table 1). Of note is some evidence in the form of skull remains that historically SNBS (at least males) may have used the suitable habitat patch around Boreal Plateau and Rocky Basin Lakes. This may reflect what once was an important stepping stone in a migration route connecting the Mount Langley herd with sheep on the Great Western Divide. A steep rocky canyon connects the Boreal Plateau area to the Kern River in the region of historic SNBS range on the Great Western Divide.

SNBS were successfully restored to Mount Langley beginning in 1980 (Bleich et al. 1990) and have grown to a population slightly larger than 100 (Few et al. 2012). While this population currently utilizes much of the potentially suitable habitat in this region, it is not clear that it yet utilizes habitat as fully as the native herd did. One historic sighting is of 15 bighorn sheep at low elevation in Cottonwood Canyon in 1946, and suggests that this excellent patch of low elevation habitat may once have been a winter range for the Mount Langley herd. In recent years this habitat patch has been utilized only occasionally by small numbers of males.

Mount Whitney to University Peak (4).—This region supports one of the persisting native herds, the Mount Williamson herd. Mount Williamson itself represents the distribution center of this herd, where females reside year round. In the past four decades males have utilized habitat as far north as Pinyon Creek, as far south as Vacation Pass, and west along the Kings-Kern Divide, especially Diamond Mesa, but also further west (Figure 1). Two reported ram skulls in the Milestone Basin at the northern end of the Great Western Divide might have been from this herd, but also could have been from the extirpated population in the Kaweah Peaks. There is also historical evidence from sightings that females utilized habitat at the eastern end of the Kings-Kern Divide from Junction Pass to Forrester Pass.

To the south of Mount Williamson there is historical evidence that females used the high plateau between Mount Barnard and Trojan Peak, and areas south of Mount Barnard probably to Vacation Pass, but evidence of SNBS further south suggests only ram use of Mount Russell and Mount Carillon. Evidence of SNBS in the Mount Whitney area is sparse, but not entirely lacking. Clyde (1971) noted that in about 50 ascents of Mount Whitney from all directions, he had never seen any evidence of bighorn sheep, but there are a few historical data points (Figure 1), including the carcass of a female in 1933 at Whitney Portal that was probably from the Mount Langley herd.

Kearsarge Pass to Taboose Pass (5).—This section of the range continues to support native populations. The persistence of SNBS in this region is evidenced by numerous references through time (Ober 1911, 1914, 1915, 1916, 1931; Clyde 1936; Dixon 1936; Blake 1941, 1949) and many recorded sightings (Table 1, Figure 1). Its persistence allowed Joseph Grinnell to obtain permission to collect 5 sheep for the Museum of Vertebrate Zoology at the University of California, Berkeley in 1911 (Grinnell 1912).

When focused attention began to be given to surviving bighorn sheep in the Sierra Nevada in the 1960s and 1970s the SNBS in this entire region between Kearsarge Pass and Taboose Pass were all referred to as the Mount Baxter herd. Since the early 1980s this region has been divided into the Mount Baxter and Sawmill Canyon herds because of distinct home range patterns of females, with Sawmill Creek the dividing line east of the crest. Home range fidelity over a series of years by naturally marked sheep observed by the first author was one of the bases for recognizing separate populations, which subsequent radio telemetry data have corroborated. Previously, Ober (1911) used Sawmill Canyon as the division between herds, thereby correctly defining a separate herd in the range of what is currently known as the Mount Baxter herd. North of Sawmill Creek, however, he combined the Sawmill Canyon and Taboose Creek herds into a single demographic unit. So did the 1921 and 1923 Inyo National Forest Fish and Game Reports. In discussing winter observations of those sheep, Ober (1911) noted that they could be found along the snow line as far north as Red Mountain Creek; and the 1921 Inyo National Forest Fish and Game Report noted, "A considerable number ranging from Goodale Mountain to Birch Mountain, and wintering along the foothills in the Black Rock region during heavy snow."

For the past 35 years SNBS from the Sawmill Canyon herd have been known to winter as far north as the north side Goodale Creek, including the front slopes as far as the south-facing slope of Shingle Mill Bench, and to utilize higher elevations on Goodale Mountain extensively in all seasons, but not north of Taboose Creek in winter. This early herd definition therefore appears to have combined the north end of the range of the Sawmill Canyon herd with the Taboose Creek herd to its north.

Ober (1914) stated that only three SNBS herds persisted at that time, of which one appears to have coincided with the current Mount Baxter herd. In 1911 he reported reliable summer sightings of a group of 20 and another of upwards of 40 SNBS observed for this herd, and he proposed that its size was at least 40–50 (Ober 1911). Three years later he recorded having counted 65 different sheep at one time and estimated the population at 85–90 (Ober 1914); but the following year he noted having encountered more than 200 in a two-week period in spring, and intimated that the population was much larger than his earlier estimate (Ober 1915). The 1927 Inyo National Forest Fish and Game report included an estimate of 30 sheep for a Thibaut Creek herd, but for 40 years Thibaut Creek has been just the southern end of the primary winter range of the Mount Baxter herd.

Ober's (1911) description of the combined Sawmill-Taboose Creek herd put its size at about 22, and three years later he increased that estimate to about 30, but gave a geographic description that appeared to be only north of Taboose Creek (Ober 1914). The 1921 and 1923 Inyo National Forest Fish and Game reports, respectively, provided estimates of 40 and 70 sheep for a Goodale-Birch Mountain "band", which also would have been a mixture of sheep from the northern end of the Sawmill Canyon herd winter range and the Taboose Creek herd winter range. These estimates and herd designations illustrate the lack of understanding of what constituted a population in that time period; nevertheless, they clearly documented the continued presence of SNBS in the regions discussed.

This region from Kearsarge Pass to Taboose Pass appears to have the best habitat for SNBS in the entire central and southern Sierra Nevada. While it contains extensive summer range at high elevations with a rich mixture of patches of different alpine and subalpine plant communities, what is notably different is low elevation winter range where SNBS can exploit an early forage growing season and greatly increase annual nutrient intake (Wehausen 1992). In the middle of this region the eastern base of the escarpment extends further east and to lower elevations than any other SNBS winter range, allowing SNBS to feed in winter and early spring as low as 1,460m on either side of Sawmill Creek. These lower elevations translate to warmer winter temperatures and more rapid progression of forage growth once it is initiated (Wehausen 1992), providing greater nutrient availability compared with other, higher winter ranges. This difference is coupled with higher plant species diversity than other winter ranges. Additionally, lower elevations also result in much larger areas of visually open habitat lacking taller vegetation. This is particularly evident in the Mount Baxter winter range immediately south of Sawmill Creek that in recent decades has supported the largest population (150 in 1978) of SNBS recorded to date (30% higher than the next largest population). The high habitat quality in this region may have played an important role in the persistence of native SNBS in this region. This region was the source of SNBS translocated in the 1979–1988 restoration efforts (Bleich et al. 1990).

Taboose Pass to Coyote Ridge (6).—As noted above, one of Ober's (1914) three SNBS populations used habitat north of Taboose Creek that is now referred to as the Taboose Creek herd unit. The 1921 and 1923 Inyo National Forest Annual Fish and Game reports also made reference to this population with estimates as high as 70 sheep. These population definitions apparently combined sheep from the northern winter range of the Sawmill Canyon herd with the Taboose Creek herd; however, in noting SNBS wintering north of Taboose Creek, these sources effectively documented the existence of a Taboose Creek herd that was presumably distinct from what is now known as the Sawmill Canyon herd. The Taboose Creek herd apparently used lower elevation winter range from Taboose Creek to Red Mountain Creek.

Compared with other herds of SNBS in the southern Owens Valley, the Taboose Creek herd is conspicuous by the sparsity of specific sightings that would support its existence (Table 1, Figure 1). Despite Ober's earlier discussions of this herd (Ober 1911, 1914), Ober (1931) made no mention of it, suggesting that it may have disappeared during the intervening 15 years. Such an early extirpation could explain the lack of sightings. Specific evidence of the Taboose Creek herd consists only of some weathered ram skulls and occasional sightings of live rams, all of which could have reflected rams wandering north from the Sawmill Canyon herd. The evidence supporting the past existence of a Taboose Creek herd as a potentially reproducing population consequently consists only of the discussions of SNBS wintering in the region from Taboose Creek to Red Mountain Creek in the 1921 and 1923 Inyo National Forest Fish and Game Reports and Ober (1911, 1914). While there is the possibility that only rams used winter ranges north of Taboose Creek, there is extensive summer range in that area that would appear suitable to support a reproducing population, and it has been recognized as an extirpated population (U.S. Fish and Wildlife Service 2007).

In summer one might expect the distribution of this herd to extend further north, but Ober (1914) indicated that these sheep did not go further than the south fork of Big Pine Creek. Yet further north the Sierra crest branches, with the eastern branch terminating at Coyote Ridge. While there are patches of habitat suitable for bighorn sheep on this spur, including some potential winter range along its eastern base, and some scattered historical evidence of SNBS (Figure 1), there is a lack of any historical evidence suggesting that this region once supported a reproducing population. This is the reason why it was not listed as a herd unit requiring occupancy as part of recovery goals for SNBS (U.S. Fish and Wildlife Service 2007).

Bishop Pass to Pine Creek Pass (7).—Ober (1914) identified a Mount Tom herd as the last, and second largest, of the three SNBS herds he knew to exist at that time, and he later reaffirmed its existence (Ober 1931). He estimated its size at 40–50 in 1914 and 35 in 1931 (Ober 1914, 1931). Ober described this herd as wintering and summering on Mount Tom. Additional evidence indicates that this herd ranged further south along the crest and west of the crest in summer. There were sightings west of Piute Pass in 1934 (Jones 1949) and on Mount Emerson in 1936 (1936 Inyo National Forest Fish and Game Report). Fred Ross (pers. comm. 19 January 1979) reported having occasionally seen bighorn sheep west of the Humphreys Basin in the area of Mount Senger, Turret Peak, and Mount Gemini in the 1930s, and that he knew of several skulls having been found in that area, as well as on the Glacier Divide. John Muir described in his journal an encounter with members of this population on 27 September 1873 west of the Sierra crest that occurred one day prior to his reaching the crest from the west (Wolfe 1938). Sightings from this area in the mid 1930s appear to be the last evidence of this herd, which apparently died out during that decade.

Pine Creek to Rock Creek (8).—The 1921 and 1923 Inyo National Forest Annual Fish and Game Reports both mentioned a herd referred to as the Pine Creek - Rock Creek band, which wintered at the base of Wheeler Ridge, and Jones (1949) interviewed locals who knew of the presence of SNBS in this region as early as 1910. The Inyo National Forest Fish and Game Reports from 1921 and 1923 estimated this herd at 25 and 30 sheep, respectively. However, Ober (1911, 1914, 1931) never mentioned this herd, and we have found no reference to it after 1923. Additionally, we found only a single reference to skull material from this area (a ewe horn) and the only other specific sighting data are each lone males that might have wandered in from herds to the north or south: one observed in Pine Creek in 1944 (Sequoia and Kings Canyon National Parks files), and one killed by boys in Pine Creek in 1948 (Jones 1949). The sparsity of historic data for this herd (Table 1, Figure 2) is difficult to explain for habitat that has recently supported a population a little in excess of 100 sheep (Stephenson et al. 2011) resulting from restoration efforts beginning in 1979 (Bleich et al. 1990). This was the first location chosen for the restoration of SNBS because of its extensive winter range and apparent overall habitat potential for supporting a viable bighorn sheep population.

Mono Pass to Mammoth Pass (9).—SNBS in this region have been referred to as the Convict Creek herd since Jones (1949, 1950a) defined it. While Jones (1949) did not have time to investigate this region on the ground, there were numerous reliable reports of SNBS persisting in this region (Table 1, Figure 2). As such, it was one of two populations (along with the Mount Langley herd) that did not disappear until the second half of the twentieth century. The Convict Creek herd apparently disappeared early in the second half of the twentieth century, given that there is only a single recorded sightings of live sheep after Jones (1949) compiled evidence of the existence of this herd in 1948. By the 1960s reports were only of skulls. The 1936 Inyo National Forest Deer Census and Game Survey reported 30 bighorn sheep between Laurel Creek and Convict Creek. In 1955 Joe Smith of Laws stated that just after 1900 there were about 40 bighorn sheep between Rock Creek and Convict Creek (California Department of Fish and Game files). Together these two figures speak to the approximate numbers of SNBS that might have once occupied this herd unit. This herd unit now supports a small population of SNBS as a result of a recent range expansion of the Wheeler Ridge herd.

Mammoth Mountain to Mount Dana (10).—This region apparently lost its populations of SNBS early. Grinnell and Storer (1924) concluded that SNBS in the Yosemite region had essentially disappeared by the early 1880s, which appears to be supported by Muir's (1898:624) statement just prior to the twentieth century that "Few wild sheep, I fear, are left hereabouts". One result of this early extirpation is the limited opportunity for historical evidence in the form of sightings of live sheep, leaving evidence of the former presence of SNBS in this region largely in the form of numerous skull remains.

Muir (1894) reported 3 SNBS in Bloody Canyon in winter prior to 1874 that were so snowbound that mountaineers crossing the range in that season were able to kill them with an axe. This may be the only recorded sighting of live bighorn sheep in the northern part of this region. At the southern end of this area a deer hunter killed a bighorn ram on San Joaquin Mountain in 1954 (Yosemite National Park files). In that same year U. S. Forest Service employees reported several bighorn sheep near Glass Creek on the eastern side of San Joaquin Ridge and another observer reported seeing single and small groups of bighorn sheep on San Joaquin Ridge from the air during 1955–1957. From a metapopulation standpoint

San Joaquin Ridge is geographically a critical habitat corridor for bighorn sheep in this region, which would have allowed migration between populations to its south and north. San Joaquin Ridge itself, however, does not appear to have habitat that would have supported a resident population of bighorn sheep. The reports from the 1950s are consequently difficult to interpret, but they may have in some way reflected the persistence of SNBS in the Convict Creek herd to the immediate south into the second half of the 20th century.

There were multiple recent sightings of bighorn sheep in this region (Table 1, Figure 2) that are unexpected and not easily explained given many prior decades without any evidence of live individuals. Intensive investigations in summers and winters of 1977 and 1978 failed to find any evidence of bighorn sheep in this region (Wehausen 1979), and further evidence has not surfaced.

This region has a large number of documented skull remains (Table 1, Figure 2), including a mummified ram found emerging from under the Mount Lyell glacier in 1933 (Sharsmith 1938, Wasmund 1938). While there is the expected scattering of such data along the crest from Mount Dana and the Dana Plateau southward, there is also a noteworthy concentration further west along a considerable length of the Cathedral Range from Mount Ritter to Parsons Peak (Figure 1). Because those specimens are all male, they may simply reflect a separate summer range utilized only by males, as documented for the native Mount Baxter herd (Wehausen 1980). The divide that Donahue Pass crosses would provide a continuous high-elevation habitat corridor to this region of the Cathedral Range. However, there also may have been a separate population in that region that had its own winter range somewhere west of the Sierra crest. This high concentration of skulls may simply reflect the early creation of Yosemite National Park and the long-standing attention of the National Park Service to recording and preserving historical information.

SNBS were restored to this area unintentionally in 1986 when three of the females translocated to Lee Vining Canyon earlier that year (Bleich et al. 1990) migrated south with two lambs born in Lee Vining Canyon to found a separate herd (Chow et al. 1993).

Tioga Pass to Green Creek (11).—Grinnell and Storer's (1924) suggestion that bighorn sheep in the Yosemite region largely were gone by the early 1880s also applies to this region. The proximity to the large mining community at Bodie may have played a role in early extirpation of SNBS in this northern region. A surviving restaurant menu from Bodie included mountain sheep meat. This population also suffers from a lack of early records of bighorn sheep sightings (Table 1, Figure 2). The few that exist all stem from more than half a century after the early 1880s beginning with eight rams at Burro Lake in 1939. About the same time (1954–1955) that bighorn sheep were recorded on San Joaquin Ridge (see above), there were also three sightings near Lee Vining. The remaining observation for this region was in 1960 near Mount Conness and included both a ewe and a ram. Like the sightings on San Joaquin Ridge and more recent ones south of Tioga Pass, these scattered sightings are difficult to interpret. This region also was part of the investigation in the late 1970s which found no evidence of an extant population (Wehausen 1979).

We found nine records of old skull remains in this region, all scattered south of the ridge that separates the Lundy Canyon and Virginia Lakes drainages (Table 1, Figure 2). Two Native American hunting blinds at high elevations apparently situated for hunting wild sheep provide further evidence that this region once supported a population of SNBS. One of these is at the northeastern corner of Mount Warren next to the Deer Creek drainage. In recent years the bighorn sheep restored to this area created a trail immediately adjacent to that blind. The other hunting blind is on Dunderberg Peak (C. Millar, U.S. Forest Service, pers. comm.). SNBS were restored to this region via translocations in 1986 and 1988 (Keay et al. 1987; Bleich et al. 1990, 1991).

North of Green Creek (12).—This region encompasses the remaining historic range of SNBS and extends northward to the Sonora Pass region. Here SNBS also apparently suffered early extirpation, leaving little opportunity for recorded sightings. The notable exception was about a dozen bighorn sheep observed on the east side of Sonora Pass in three successive summers (1876–1978; Grinnell and Storer 1924). Grinnell and Storer (1924) and Jones (1950b) both cited anecdotal information that suggested that some bighorn sheep may have persisted past 1900 in this northern region.

Similar to the other areas north of Mammoth Lakes, this region includes a number of sightings from long after the apparent extirpation of SNBS. Unlike those other two regions, however, this region has more recent sightings than any other region (Table 1) and they include a set of nine sightings that cluster both geographically (Matterhorn Peak to Grouse Mountain) and temporally (1968–1975), and are detailed enough to specify observations of females in four cases. Some of these sightings were a prime focus of investigations in 1977–1978 that failed to find any evidence of bighorn sheep in that region (Wehausen 1979), and no additional sightings have surfaced since that time. We found references to 14 skull remains in this region (Table 1, Figure 2).

DISCUSSION

In addition to adding information that has emerged since the compilation by Jones (1949), we categorized and discussed data by regions defined geographically relative to known populations, and we mapped the historical information by three categories (Figure 1, Figure 2). The historic distribution of SNBS includes about a 290 km linear distance of the Sierra Nevada between northern and southern extremes. Our historical database included 168 sightings prior to 1960, 41 more recent sightings for 1960–1979, and 122 skull remains (Table 1). Given the large area involved, this is a rather meager data set. A number of factors are probably involved. One is the early decimation, if not loss, of many populations, and the resulting lack of opportunity for sightings. Another is that SNBS occupy habitat that most people do not venture into because it is steep, rocky, and lacks trails, and there were considerably fewer people in California and the Sierra Nevada in the late 19th and early 20th centuries. However, our limited data probably largely reflect the fact that only a small percentage of information of this sort is ever recorded. Even today, most of the public has little understanding of why the reporting of such information might be useful, and in earlier periods this may have been even more the case. Our database includes only five sightings from the 1800s!

The lack of any coordinated interest in these sheep in early years appears well illustrated by the lack of consistency among different sources relative to where populations persisted, and the fact that multiple populations that persisted well into the 20th century were unknown to state or federal employees that filed reports on these sheep. Our research suggests that at least nine SNBS populations in the eastern Sierra persisted to the second and third decades of the twentieth century: Olancha Peak; Mount Langley; Mount Williamson; Mount Baxter; Sawmill Canyon; Taboose Creek; Mount Tom; Wheeler Ridge; and Convict Creek. During his tenure as a game warden in the Owens Valley in that time period, Ober

(1911, 1914, 1915, 1916, 1931) failed to recognize the existence of five of these populations (Olancha Peak, Mount Langley, Mount Williamson, Wheeler Ridge, and Convict Creek), despite his numerous written contributions and an apparent keen interest in bighorn sheep. Our finding that fish and game reports from the local National Forest recognized two populations never mentioned by Ober (Wheeler Ridge and Convict Creek) suggests both a lack of coordination and a lack of communication among personnel representing different agencies, but both of those sources failed to report three surviving populations in the southern Sierra Nevada from Mount Williamson to Olancha Peak. These discrepancies and shortcomings suggest that development of data on these sheep was incidental to other priorities, which is consistent with the overall low amount of historic data on these sheep. The differential knowledge of extant populations by individuals from different governmental agencies may simply reflect the locations where these government personnel were stationed and the travel difficulties of that era. Ed Ober was stationed in Big Pine, while the National Forest headquarters were further north in Wells Meadow at the base of the Wheeler Ridge herd winter range — a population documented by that agency, but not by Ed Ober. The low density of our historical data begs a number of questions, which follow.

Does this data base include some representation from all habitat patches occupied by SNBS in 1850? Probably not! We found remarkably little historical evidence for the Wheeler Ridge herd (Region 8 in Table 1 and Figure 2); yet, it is excellent habitat that now supports about 100 animals resulting from restoration efforts beginning in 1979. That some historic ranges of SNBS may not be represented in our data base is further supported by the apparent natural colonization of habitat on the north side of Bubbs Creek in the second half of the 1990s. That population was discovered through a reported sighting in 2001 and has persisted in habitat entirely west of the Sierra crest since then. There is, however, no historical evidence of bighorn sheep in that region prior to 2001. This situation begs the question of what other locations west of the Sierra crest might once have been occupied by SNBS, but lack any historical evidence because of early extirpation.

Major die-offs from diseases contracted from domestic sheep were most likely the primary cause of population losses of SNBS (Wehausen et al. 2011). Domestic livestock grazing in the Sierra Nevada began in the 1860s during severe droughts that precluded the previous patterns of year-round cattle grazing in the Central Valley (Vankat 1970). Mountain grazing of domestic sheep followed quickly because that species could be herded much further into the mountains than could cattle. Since this began on the western side of the range, SNBS populations that might have existed in suitable west-side habitat patches may have been the first to disappear, and could have done so without any record of their existence.

What our data base appears to provide is adequate documentation of the overall north-south range of SNBS and probably most of the areas along the eastern side of the range that they occupied. While there is some historic evidence of early domestic sheep grazing in the Owens Valley region, more intensive grazing on the eastern side of the Sierra Nevada apparently began later than the western side as a response to implementation of grazing restrictions on the western slope in the 1890s following the creation of Yosemite National Park and Sequoia National Park and the forest reserves that later became national forests (Wehausen 1988). It took some years for enforcement of grazing regulations to be implemented, but one result was an annual grazing circuit that began in winter in the Central Valley, crossed the southern Sierra Nevada to the western Mojave Desert for spring grazing, then moved north through the Owens Valley to summer grazing areas in higher mountains, with a reverse pattern in fall (Austin 1906).

To what extent can our data base be used to track the temporal pattern of herd losses? Are the numbers of sightings for different herds inversely related to how long they persisted? If this inverse relationship is strong, the extant native populations should have the most recorded historical sightings. This expectation is met to the extent that the two regions of native SNBS (4 and 5) clearly have the most sightings in the historic period before 1960 (Table 1). However, when those data are parsed further, this relationship weakens substantially. Region 4 represents just one population (Mount Williamson herd), but region 5 includes two: the Mount Baxter herd south of Sawmill Creek and the Sawmill Canyon herd further north. The Mount Baxter herd accounts for 42 (79%) of the sightings for its region, while there are only 11 for the Sawmill Canyon herd. Thus, there is high variation among the three native herds in the numbers of recorded sightings prior to 1960 (11, 33, and 42), and three extirpated herds exceed the lowest of these values (Table 1), indicating at best a weak relationship between the number of recorded sightings and persistence time. Factors in addition to persistence time have probably greatly influenced the sighting record. One of those factors may be biases in locations to which backcountry users, especially peak climbers, have been attracted.

Relative to the timing of extirpations, the historic information we compiled clearly documented that the Mount Langley and Convict Creek herds survived through the first half of the twentieth century, and that the Mount Tom herd persisted into the fourth decade of that century. Despite the lack of recorded sightings, the Wheeler Ridge herd apparently survived to the early 1920s, while the Taboose Creek and Olancha Peak herds also apparently survived into the beginning of the third decade of the 20th century, but appear to have disappeared in the early 1920s.

Extirpated populations may have declined to where recovery was unlikely (loss of viability) following one or more major disease die-offs, yet produced long temporal tails of sightings as the few remaining sheep declined to extinction. Following the initial major die-off of bighorn sheep of all ages from introduced respiratory disease, the disease organisms can persist in some surviving adults and cause most lambs to die for numerous years, resulting in a steady population decline (Cassirer et al. 2013). Such potential time lags make it difficult to assign meaningful dates of extirpations from a sparse record of sightings. The apparent persistence of SNBS on the Great Western Divide into the twentieth century may be an example of such a lag between loss of viability and the end of sightings.

The historical data we discuss provide considerable information useful for the restoration of SNBS, much of which served as an important basis for the recovery plan for SNBS through input from the first author (U.S. Fish and Wildlife Service 2007). However, it is important that restoration efforts recognize the limitations of these data; they do not necessarily include all habitat patches occupied by SNBS in 1850, and in many regions lack sufficient information to infer seasonal patterns of habitat use. In recent decades a great deal of detailed information on habitat use has been obtained as a result of various types of telemetry collars installed on translocated SNBS as part of restoration efforts during 1979–1988, and more recently on resident and translocated SNBS. This information has steadily expanded the understanding of the variety of habitats SNBS can use successfully. Once regions known to have been occupied historically have been restocked or naturally colonized, restoration efforts might use the growing data base on habitat use to identify additional habitat patches potentially suitable for these sheep, and consider efforts to restock those.

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APPENDIX I: COUNTIES OF GEOGRAPHIC LOCATIONS IN THE SIERRA NEVADA AND REFERENCED IN THIS PAPER

Big Arroyo: Tulare
Birch Mountain: Inyo
Bloody Canyon: Mono
Bodie: Mono
Bubbs Creek: Fresno
Burro Lake: Mono
Cathedral Range: Mono, Madera, Mariposa, Tuolumne
Convict Creek: Mono
Cottonwood Canyon: Inyo
Coyote Ridge: Inyo
Deer Creek: Mono
Diamond Mesa: Tulare
Donahue Pass: Mono, Tuolumne
Dunderberg Peak: Mono
Farewell Gap: Tulare
George Creek: Inyo
Glass Creek: Mono
Goodale Creek and Mountain: Inyo
Great Western Divide: Tulare
Grouse Mountain: Mono
Humphreys Basin: Fresno
Independence: Inyo
Kaweah Peaks: Tulare
Kearsarge Pass: Inyo, Fresno
Kern Plateau: Tulare
Kern River: Tulare
Kings-Kern Divide: Tulare
Laurel Canyon: Tulare
Laurel Creek: Mono
Lee Vining: Mono
Lundy Canyon: Mono
Maggie Mountain: Tulare
Mammoth Pass: Mono, Madera
Matterhorn Peak: Mono, Tuolumne
Milestone Basin: Tulare
Mineral King: Tulare
Mono Pass: Inyo, Fresno
Mount Barnard: Inyo, Tulare
Mount Baxter: Inyo, Fresno
Mount Carillon: Inyo, Tulare
Mount Conness: Mono, Tuolumne
Mount Dana: Mono, Tuolumne
Mount Emerson: Inyo
Mount Gemini: Fresno
Mount Hitchcock: Tulare
Mount Langley: Inyo, Tulare
Mount Lyell: Mono, Madera, Tuolumne
Mount Ritter: Madera
Mount Russell: Inyo, Tulare
Mount Senger: Fresno
Mount Tom: Inyo
Mount Warren: Mono
Mount Whitney: Inyo, Tulare
Mount Williamson: Inyo
Muah Mountain : Inyo
Olancha Peak: Inyo, Tulare
Owens Lake: Inyo
Parsons Peak: Madera, Mariposa, Tuolumne
Pine Creek: Inyo
Pinyon Creek: Inyo
Piute Pass: Inyo, Fresno
Rattlesnake Canyon: Tulare
Red Mountain Creek: Inyo
Red Spur: Tulare
Rock Creek: Mono
Round Mountain: Inyo, Tulare
San Joaquin Ridge/Mountain: Mono, Madera
Sawmill Creek and Canyon: Inyo
Sawtooth Peak: Tulare
Sheep Mountain: Tulare
Shingle Mill Bench: Inyo
Sonora Pass: Mono, Tuolumne
Taboose Creek: Inyo
Taboose Creek: Inyo
Taboose Pass: Inyo, Fresno
Thibaut Creek: Inyo
Tioga Pass: Mono, Tuolumne
Trojan Peak: Inyo, Tulare
Turret Peak: Fresno
University Peak: Inyo, Tulare, Fresno
Vacation Pass: Inyo, Tulare
Virginia Lakes: Mono
Wheeler Ridge: Mono

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Dynamics and social issues of overpopulated deer ranges in the United States: a long term assessment

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Overabundant deer (*Odocoileus* spp.) populations can be detrimental to forests, agriculture, transportation, and human safety, and can alter abundance of flora and fauna causing shifts in ecosystem dynamics and sustainability. Deer populations were classified as irruptive, chronic, or troubled in 1947 and 1986 to document changes over 4 decades. We again conducted a survey of deer biologists in 2013 throughout the U.S. to determine how deer population status has changed since 1986. All states surveyed in 1947 and 1986 were included in the survey, and we also included other states to obtain information on status of their deer herds. We contacted the primary deer biologist in each state and asked a series of questions about status of deer. In 1947, biologists in 30 states reported that they had irruptive, chronic, or troubled deer ranges. In 1986 only Colorado, Massachusetts, New York, Oklahoma, and Texas reported overpopulated deer ranges. In contrast, in 2013, 18 of 47 states surveyed reported issues with overpopulated deer herds in urban areas. In many states the deer population is at or below biological carrying capacity (K) but exceeds social carrying capacity. Many current issues with white-tailed deer are related to an increasingly urban human population that is less tolerant of deer, and not necessarily with increases in deer populations. Mule deer populations have declined from drought, but humans have also encroached upon winter ranges, thereby causing a deterioration of their habitat.

Key words: mule deer, *Odocoileus* spp., overabundance, status, United States, white-tailed deer, urbanization

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Deer (*Odocoileus* spp.) have always been an important aspect of wildlife management due to their popularity by the public for recreation, meat, and aesthetics. When populations exceed carrying capacity (K), however, they can become problematic and result in conflicts with human safety and well being, damage to property, agriculture, and forests, and can alter flora and fauna so that ecosystem dynamics are changed (Rooney 2001, Cote et al. 2004, Allombert et al. 2005). In the U.S. deer overabundance will be a major ecological challenge in the 21st century (Warren 1997). Deer will continue to create biological and ecological challenges, but more importantly they are likely to exceed social K (i.e., deer population density that best satisfies human expectations [Ellingwood and Spignesi 1985]; also referred to as optimum K; McCullough 1992) as human attitudes towards deer change (Warren 1997). Indeed, in a recent issue of *Time*, the cover story was about deer and other abundant species in the U.S. (Von Drehle et al. 2013; Figure 1). The authors presented material that is supported by the scientific literature but in a manner suitable to public understanding. The article exemplified what Leopold et al. (1947) first described and what Warren (1997) meant when citing overpopulation as a social issue that will be a challenge to resolve. Von Drehle et al. (2013) made a good case to the public for managed hunting to avoid problems of overabundance.

FIGURE 1.—Cover of Time magazine (2013) exemplifying issues of overabundant wildlife and the role management and hunting play in solving the problem.

Leopold et al. (1947) conducted the first survey of overpopulated deer ranges in the U.S. and the survey was repeated in 1986 (Krausman et al. 1992). Overpopulated ranges were classified as "irruptive" (i.e., exceeded biological K and the habitat was damaged), "chronic" (i.e., problem area of long standing usually in the post-irruptive stage), or "troubled" areas (i.e., when deer have recently exceeded K but to a lesser degree than when irruptive; Leopold et al. 1947). Since 1992 there have been two proceedings (McAninch 1995, McShea et al. 1997) and a special issue on deer overabundance in the *Wildlife Society Bulletin* (Warren 1997). All of these references and others (Porter and Underwood 1999, Krausman et al. 2011, Polfus and Krausman 2012) have been instrumental in documenting problems with the successful management of deer and advancing deer management in the U.S., especially in urban areas. In this study reference to "urban areas" includes 3 human-dominated landscapes: (1) Urban or areas with a human density of >386 people/km^2 (U.S. Census Bureau 2002); (2) Suburban or the patchwork of residential, commercial, municipal, and industrial land uses and related transportation and utility corridors often adjacent to urban centers (Knuth et al. 2001); and (3) Exurban areas with approximately 6–25 homes/km^2 that includes urban fringe development on the edge of cities and rural residential developments that have natural amenities (Hansen et al. 2005).

In a literature review, Polfus and Krausman (2012) reported that of 80 studies directly related to effects of human development on ungulates in the Rocky Mountain West, only 25 specifically examined residential development and its influence on focal species. Very few studies linked responses to population-level consequences or tested the cumulative impact that multiple developments and types had on ungulate behavior. Most research has been short term and of small scale.

The studies of Leopold et al. (1947) and Krausman et al. (1992) were, in part, designed to be helpful in wildlife classes, and to emphasize problems associated with abundant deer populations. Thus, our objective was to determine how status of deer populations in the U.S. has changed in the past 27 years, the reasons why, the social implications of, and management efforts used to minimize overabundance.

Materials and Methods

We obtained our data from phone interviews with deer biologists (i.e., deer program biologists, big game program managers, survey specialists) from state wildlife agencies using open-ended questions (Dillman 2007:4-42). We contacted each biologist and sent him or her copies of the previous papers by Leopold et al. (1947) and Krausman et al. (1992), a copy of the questionnaire (see results), and arranged times to discuss the survey. Interviews were conducted from August 2013 to January 2014 and took 20–40 minutes each. If we were not able to make phone contact with biologists, we left messages asking each to return the completed questionnaire.

Results

We attempted to contact deer biologists in all states except Hawaii. We received responses from biologists in 48 of 49 states (99% response rate; West Virginia did not respond). Biologists in all states did not respond to all questions on the survey because the question was not applicable to their jurisdiction; thus, some percentages presented are based on <48 responses. Number of responses is provided when <48.

In 1947, 99 deer ranges were classified as irruptive, chronic, or trouble areas (deer on Nantucket Island, Massachusetts were "exterminated"; Leopold et al. 1947), but in 1986 only Mount Desert Island, Maine was still similar to the 1947 survey (i.e., high densities; Krausman et al. 1992). Eight areas in six states in 1986 had populations above K or above long-term goals for that state (Appendix I; Krausman et al. 1992). Records were not kept by most states on the specific overabundant ranges described by Leopold et al. (1947), so we summarized data on a state-wide basis (Appendix I). Results of the responses follow the nine open-ended questions from the survey (in italics).

1.—What is the recent statewide status of your deer populations (mule deer [Odocoileus hemionus], white-tailed deer [O. virginianus], or Columbian black-tailed deer [O. h. ssp.] compared to that reported by Krausman et al. (1992)? Deer populations across the U.S. have been dynamic since 1986 (Appendix I). Four state biologists reported that status (i.e., population level relative to management goals) of white-tailed deer populations have not changed and two biologists from those states reported the same for mule deer. Twelve state biologists reported stable white-tailed deer populations and three reported stable mule deer populations. Twenty-two states reported an increase in white-tailed deer but no increases in mule deer populations. Most increases (86%) of white-tailed deer occurred in the midwestern and eastern U. S. (Appendix I). Urbanization, habitat improvement, reduced antlerless hunts, limited access for hunting, low hunter effort, and mild winters were the most cited reasons for increases in white-tailed deer populations (Appendix I).

Biologists in Texas and Idaho reported white-tailed deer encroaching into mule deer habitat and increasing at the expense of mule deer (Appendix I). Mule deer declined in 10 states and white-tailed deer declined in nine states. Numerous reasons were provided for declining deer populations; they declined more from drought, an increase in carnivores, and habitat deterioration than from other factors. White-tailed deer declined due to limited antlerless harvests and carnivores more than from other factors (Appendix I).

Biologists in Alaska were not included in the first two surveys, but we did include them in the 2013 survey. Populations of Sitka black-tailed deer (*O. h. sitkensis*) were regulated by severe winters and they do not have overabundant herds. Most of the concerns of deer biologists in Alaska are with low deer numbers due to reduced habitat quality from logging, or increased predation.

2.—Where in your state do you have irruptive areas, trouble areas, or chronic areas (if any)? Twenty-four states with >80 problem deer herds were surveyed by Krausman et al. (1992) that had been identified by Leopold et al. (1947) with irruptive, chronic, or troubled areas. Although Idaho, Pennsylvania, South Dakota, and Wyoming were included in the 1992 survey, their responses were not clear enough to be included in this paper. Only six states reported continued problem areas in 2013. In Colorado, deer in Dinosaur National Monument continued to be at densities less than the long-term objective, but in Rocky Mountain National Park, deer were at Colorado's long-term population objective. The other two areas in Colorado (Kanna Creek and Gunnison Basin) maintained populations lower than the long term average.

Biologists in Illinois reported that deer in the Rockford population were still at K, but they reported additional trouble areas in Fulton and Skyler counties. Biologists in Maine continued to report trouble areas on islands, and in Texas biologists reported continued populations above K in the Edwards Plateau. Vermont is experiencing trouble areas in the southeast and southwest, and all farmland in Wisconsin were classified as a trouble area. In addition to the states addressed by Krausman et al. (1992), biologists from 9 more states reported chronic or trouble areas (Table 1). Biologists in 18 states reported that most of their problems with deer were in urban areas, primarily with white-tailed deer, but mule deer were problematic in Montana and Nebraska in some urban areas.

Table 1.—Irruptive (I),Chronic (C), or trouble (T) areas caused by deer in states (in bold) not addressed by Leopold et al. (1947) or Krausman et al (1992) and states with continued problems.

State	Problem areas
Connecticut	Islands and peninsular areas especially Chimon Island, and Sheffield Island, (C), and Fairfield County (T).
Delaware	WM Zone 1A, Zones 7, 11, 12, 14, and coastal communities(T)
Indiana	Switzerland, NW, and east of Lake Michigan (T).
Kansas	Shawnee Mission Park (I); Kirwin, Quivira, Marcias des Cygnes National Wildlife Refuge, Cedar Bluff, Kaw, Norton, Kanapolis, Webster reservoirs; Grord Osage wildlife area (C)
Kentucky	Mammoth Cave National Park, Fort Knox (T); 17 counties >management goals
Maine	Islands, and southwest (T)
Maryland	Statewide (C)
Minnesota	North-central and northeast (C)
Pennsylvania	Northwest (C)
Texas	Edwards Plateau (C)
Virginia	Northern mountains (C); northern Virginia, including metropolitan Washington, D.C. (T)
Wyoming	Black Hills (I)

3.—One conclusion from Krausman et al. (1992) was that the terminology of irruptive, trouble, and chronic were not satisfying terms to biologists. Can you recommend better terms to characterize deer overabundance? The term “irruption” was “unsatisfactory as applied to deer” (Leopold et al. 1947:163), and biologists in 1992 did not like the terms, irruptive, chronic, or trouble in relation to overpopulation. Biologists in 38 of 47 states (81%), however, did not suggest alternative terms. Biologists in nine states (19%) made suggestions for more meaningful terms. Biologists in Colorado and Maine suggested terms should be tied to the management objectives of the state (e.g., for Maine terms would be tied to forest health, deer health, or social tolerance). Biologists in Louisiana preferred using high, medium, or low as measures of abundance, whereas biologists in Arkansas and Tennessee preferred increasing, decreasing, or stable as descriptors. Biologists in Nebraska, North Carolina, Washington, and Wyoming suggested terms should be tied to biological and social K.

4.—What has been your most successful management option for decreasing overabundant deer populations? Rank the top 3 among increased antlerless harvest, public bow hunting, public gun hunting, increased use of crossbows, special or controlled hunts (i.e., any hunt with additional restrictions to state regulation or traditional deer-hunting season, and taking place in a localized area), lethal targeted removal such as sharpshooting or trap-and-euthanize programs (i.e., culling deer in a localized area using bait, spotlights at night, suppressed firearms, and operated by a contracted agent or by government or law enforcement staff), habitat alteration, agricultural depredation permits aside from traditional deer-hunting season or bag limits, non-lethal methods (trap-and-transfer or contraceptive programs), predator introduction or recolonization, and other. Most biologists (96%) listed increased antlerless harvests as the most successful to decrease abundant deer herds. Most tools used by biologists to decrease populations involved some form of harvest (Table 2).

Table 2.—Successful management options (top 3[a]) used to decrease deer populations in 37 states of the United States.

Response	%
1. Antlerless harvest	96
Weather	4
2. Special or controlled hunts	27
Public gun hunting	20
Public bow hunting	18
Agriculture depredation hunts	16
Habitat alteration	7
Lethal removal	4
Other: land acquisition	2
Water distribution	2
Unlimited permits	2
3. Special or controlled hunts	36
Agricultural depredation hunts	15
Lethal removal	13
Public bow hunting	10
Public gun hunting	8
Antlerless hunts	3
Carnivore introduction	3
Other: public participation	
In deer management	3
Vehicle collisions	3
Education	3

[a] 47, 45, and 39 biologists in states responded with choices in the first, second, and third categories, respectively.

5.—Please rank the top 3 reasons for deer population overabundance: hunting weapon discharge restrictions (gun or bow, including discharge setbacks from roads and dwellings), private land access restrictions, low hunter effort (for any deer), low hunter effort (for antlerless harvest specifically), increased supplemental food resources (including landscaped or garden variety plants, baiting or feeding programs, or access to concentrated food plots), reduced predator populations, optimal natural habitat, low weather related mortality, regulatory or statutory restrictions to using alternative deer management approaches, and others. Private land access restrictions and hunting weapon discharge restrictions were the top reasons for deer increases; there were, however, numerous reasons noted for deer overabundance (Table 3).

Table 3.—Top 3[a] reasons for deer overabundance in the United States since 1986.

Ranking	Reason	%
1	Private land access restrictions	41
	Hunting weapon discharge restrictions	20
	Low hunter effort for does	7
	Low hunter effort for any deer	4
	Optimal natural habitat	4
	Increased supplemental food	2
	Reduced carnivore populations	2
	Regulatory or statutory restrictions	2
2	Private land access restrictions	32
	Low hunter effort for any deer	25
	Hunting weapon discharge restrictions	11
	Increased supplemental food	14
	Regulatory or statutory restrictions	7
	Low weather related mortality	5
	Low hunter effort	2
	Reduced carnivore populations	2
	Optimal natural habitat	2
	Other: hunting for trophies	2
	Historic management	2
3	Hunting weapon discharge restrictions	32
	Optimum natural habitat	21
	Low hunter effort for any deer	13
	Low hunter effort for antlerless deer	13
	Reduced carnivore populations	11
	Increased supplemental food	8
	Private land access restrictions	3
	Regulatory or statutory restrictions	3
	Social issues	3
	Less interest in game meat	3

[a] Biologists from 46, 44, and 38 states responded to rankings 1, 2, and 3, respectively.

6.—Have you identified a threshold or range (either through deer density estimates or a target number of human-wildlife incidents/unit area) for social carrying capacity when managing deer toward a population objective or goal? Response = yes or no. If yes, please list and describe by category (e.g., human health, human safety, and property damage incidents, or any other type of identified threshold). Most biologists (34 of 48; 71%) responded that they have not established a threshold; the remainder had. Many of the thresholds were based on social K and landowner attitudes (e.g., Maryland, Massachusetts, North Dakota, Ohio, Pennsylvania, Vermont). In Delaware, Mississippi, and Washington, tolerance was based on agricultural and property damage, whereas in Maine, Rhode Island, and Wisconsin social K towards deer was based on human health and public safety. Utah also used social K with range trend data, and Illinois incorporated deer vehicle collisions into their 10-year deer plans. Human tolerance of deer is a dominating factor in contemporary deer management.

7.—What do you measure to determine an "overabundant" deer population? Choose all that apply: derived population density estimates or trend counts from harvest data, minimum count data (or other non-harvest survey, including aerial survey), native habitat condition, vital rates within a deer population, negative human-wildlife conflicts (deer vehicle collisions, Lyme's disease reports, agricultural depredation), observations by deer hunters during hunting season, observation rates by non-deer hunters during other hunting seasons (e.g., moose or bear), and other. Biologists from 47 states (98%) responded to this question. Most biologists measured overabundance from derived population measures from harvest data (74%), followed by the number of negative human-wildlife conflicts (65%), native habitat condition (43%), vital rates (41%), observations by deer hunters during the hunting season (33%), minimum count data (26%), observations by non-deer hunters (7%), forestry models (4%), and fawn: doe ratios (2%).

8.—Has deer overabundance measurably reduced native biodiversity in any of these ranges? If yes, briefly describe and include any pertinent publications. Most biologists (33 of 48; 69%) reported that they did not monitor biodiversity related to deer abundance. Fifteen (31%), however, did so at varying spatial scales (Delaware, Illinois, Indiana, Maine, Maryland, Minnesota, Mississippi, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, Virginia, and Wisconsin). Of the fifteen, 66% reported monitoring efforts were fine scale studies of vegetative communities or forest regeneration, and resulted in technical reports or qualitative summaries only. Massachusetts, New Jersey, Pennsylvania, Virginia, and Wisconsin provided 6 specific peer-reviewed manuscripts that were published as a result of these efforts (Tilghman 1989, DeCalesta 1994, Healy 1997, McShea and Rappole 2000, Rooney and Waller 2003, Eschtruth and Battles 2009). Pennsylvania was the only state that incorporated annual measures of forest health at a deer management unit scale, although New York and Virginia reported plans to incorporate similar measures in the future.

9.—Have resources for management and research of deer been reduced and diverted to other wildlife species programs since 1986? If yes, briefly describe which species have been allocated funding. Most states (32 of 46; 70%) have not had funds for deer research reallocated to other species or projects. Fourteen states (30%), however, diverted funds to other species of big game, other game, non-game, feral hogs, carnivores, upland game birds, and wildlife research (Table 4).

Table 4.—States that have reallocated resources from deer to other activities in the United States between 1986 and 2013.

State	Resources reallocated from deer to:
Arkansas	Feral hogs and public relations
California	Other big game
Idaho	Carnivores
Indiana	Purchasing land
Maine	Other game
Massachusetts	Non-game
Minnesota	Non-game and fisheries
Mississippi	Non-game
Missouri	Rare and endangered species
Montana	Wildlife research
Nevada	Carnivores and law enforcement
New York	Non-game
Oklahoma	Upland game birds
Tennessee	Feral hogs, elk, and chronic wasting disease

Discussion

When the special issue on deer overabundance was published (Warren 1997), the editor distinguished between urbanization and urbanism. While urbanization is the increase in human populations and structures,"…Urbanism is a way of looking at life. It is an outlook. It is a much broader concept than urbanization… [T]he single, biggest obstacle, to good deer management that urbanization brings is urbanism. Urbanism results from the plastic environment—and the profound ignorance of the natural world by the people living in it. Today's urbanites differ from their city-dwelling predecessors in this regard. Three or 4 generations from a rural life seems to end all direct functional ties to—and spiritual bonding with—the Natural World… Most importantly, now we have a public that seems to be developing a very unnatural relationship with nature" (Marchinton 1997:21-22). The importance and impact of this "detachment from natural things" was discussed by Louv (2008), citing profound impacts on child development. Indeed, expansion of the human population and associated expansions in urbanism will challenge wildlife management with unprecedented impacts on natural systems (Liu et al. 2003, Von Drehle et al. 2013). The social significance of wildlife management was identified by Leopold (1933) when he wrote that human "progress" in the U.S. has skyrocketed over the past 20 centuries. However, that "progress" has not been accompanied with "…the capacity to live in high density without befouling and denuding his environment, nor a conviction that such capacity, rather than such density, is the true test of whether he is civilized. The practice of game management may be one of the means of developing a culture which will meet this test (Leopold 1933:423)".

That is a test we appear to be failing. Even understanding how urbanization is influencing deer is in its infancy, despite historic (Leopold et al. 1947) and current warnings (Von Drehle 2013). In a review of impacts of residential development on ungulates in the

Rocky Mountain West, only 20 studies reported on the actual influence of development on mule deer and white-tailed deer (Polfus and Krausman 2012). However, urbanization and human population growth were clearly important reasons for explaining trends in deer populations throughout the U.S. in 2013 (Appendix I, Table 3).

Due to increased urbanization in the midwestern and eastern U.S., it is not surprising that white-tailed deer have increased in these areas as evidenced by recent investigations (Hygnstrom et al. 2011, Polfus and Krausman 2012). Deer biologists claimed that the main reasons for white-tailed deer abundance was from restrictions on access to land resulting in low hunter effort, and restrictions on weapons discharge (Table 3). Thus, managers are limited in what they can do to manage deer in urban areas. It is a lot easier for deer to habituate to human activity when they are not hunted or harassed (Thompson and Henderson 1998). White-tailed deer commonly habituate to humans in urban settings (Swihart et al. 1995, Kilpatrick and Spohr 2000), where they have high survival rates due to decreased movements, decreased mortality from hunting, limited predation, and increased forage from ornamental plants, shrubs, fertilized lawns, and supplemental feeding areas (Swihart et al. 1995, Etter et al. 2002, Grund et al. 2002, Porter et al. 2004).

Mule deer have also become habituated to urban areas as reported herein by biologists in Texas and Wyoming. Habituation of mule deer was also reported by Kloppers et al. (2005). Biologists in mule deer range more commonly reported decreases in mule deer and overall, biologists did not report increased mule deer populations. The decreases were related to weather and drought and a reduction of habitat. In their review of deer and residential developments, Polfus and Krausman (2012) reported that much of the habitat that was lost to mule deer was the result of land development on winter ranges.

The issue of effects of urbanization again arose when we asked biologists about irruptive, chronic, and trouble areas in their states. Irruptive areas have decreased since the earlier surveys (Leopold et al. 1947, Krausman et al. 1992). Biologists did, however, report chronic or trouble areas in 12 states not included in earlier surveys (Table 1), most of which were white-tailed deer; chronic and troubled areas arose from urbanization in the eastern U.S.. Mule deer in the Black Hills in Wyoming have been described as irruptive since the 1947 study (Leopold et al. 1947). As urbanization increases in the West, it is likely that mule deer will increasingly create similar overpopulation issues in urban areas.

The terms related to overabundance were generally considered passe, likely because management has been able to maintain populations that can be controlled and there are very few irruptive areas. Biologists did prefer that terms related to overabundance be changed to reflect the management objectives of the state. At, above, or below management objectives is straightforward, easily understood by the public, and management objectives typically consider social K; thus, the terminology is changing with the issues deer present to managers. If terms are tied to management objectives, managers may be able to avoid the problems of doing too little too late, as described by Leopold et al. (1947) and may be able to avoid the nebulous concept of carrying capacity.

We were not surprised that hunting was the primary tool to control deer abundance. Harvest has been recognized as important by biologists for decades and is a central theme of the North American Model of Wildlife Conservation (Organ et al. 2012), which emphasizes the role of hunting in conservation and management. Recent articles in major news outlets (e.g., *Time* [Von Drehle et al. 2013] , *The Economist* [Anonymous 2013], and *The New Yorker* [Rosen 2014]) related the positive aspects of hunting to the public and indicate how important hunting is to wildlife management and successful co-existence between humans and wildlife.

Biologists in most states did not have specific thresholds to determine when deer were too abundant, and those that did generally relied on social K related to human health and safety, and the level of negative human-wildlife interactions. These negative interactions must be addressed because they can undermine public support for management agencies and conservation initiatives (Kretser et al. 2009), in addition to the problems they create. Overall, biologists used a variety of biological measures (74%) to assess when a population was too high, but negative human-wildlife interactions (65%) were also a widely used metric.

Biologists in 32% of the states indicated that abundant deer populations measurably reduced biodiversity. The remainder did not have measures in place to measure biodiversity. Overabundant deer in deciduous or mixed forest communities reduced regeneration of native tree species, altered vegetative community composition, reduced migratory songbird abundance, reduced abundance of endangered plant species, and reduced forest nesting songbird diversity (Tilghman 1989, DeCalesta 1994, Jones et al. 1997, Healy 1997, McShea and Rappole 2000, Rooney and Waller 2003, Eschtruth and Battles 2009). In states that reported reduced biodiversity but had less rigorous measurements or lacked well-documented findings, biologists reported a general reduction in native vegetation and reduced regeneration of some native trees. Minnesota indicated active communication with forestry professionals for additional measures of forest health on public lands in relation to deer herbivory. It was clear that most states do not systematically collect information on impacts of deer populations on native species diversity, but most biologists commented on anecdotal signs of intensive deer herbivory in areas of deer overabundance.

Finally, our survey suggested that funds for continued deer research and management were shifting in nearly a third of the states to other species and issues (Table 4). Many of these states are in the midwestern and eastern U.S., where there are serious issues related to white-tailed deer and more funds, not less, are needed. For example, biologists in Mississippi reported that their white-tailed deer population has “exploded” in the past 27 years and more management and research are needed to address issues related to this increase.

This survey has revealed that deer management in the U.S. continues to be an important aspect of wildlife management, and that managers still struggle with populations that are too low or too high. However, there has been a shift in how society thinks about overabundant deer populations. We have moved from a biological concern for overabundant populations, when exceeding biological K was the norm, to considering deer populations overabundant when they exceed social K. This illustrates the importance of human dimensions in wildlife management and ensuring that the public is involved in deer management issues and initiatives from the beginning.

The survey also pointed to areas of research and management that need more attention. There is room for more information about deer populations and their management on islands with dense human habitation, and with restrictions on land access and weapons discharge. Understanding how deer alter biodiversity is also an important concept to explore through long-term monitoring of plant composition and change. That 32% of the states did measure, and reported, changes in biodiversity suggests that if the other 68% of states did the same, we would learn more about alterations to habitat caused by deer, learn more about community ecology, and be able to better manage deer populations and their habitats. It is important to note, however, that habitat management is often the responsibility of land management agencies and not wildlife agencies, which we surveyed.

Research is also needed to determine acceptable methods to remove deer from urban areas while educating residents to accept and allow efficient and safe harvest methods to be used to reduce herd size. This will coincidentally require an outreach program that educates urbanites of the issues pertaining to overabundant deer and the need to reduce their populations to ensure human safety, minimize property damage, and maintain the ecological integrity of adjoining ecosystems. Lastly, our survey demonstrates clearly that deer population issues, particularly regarding white-tailed deer, are national in scope and quite consistent in management goals and harvest methodologies. With this in mind, there must be a multi-state effort to monitor deer populations (such as the National Feral Swine Mapping System coordinated by the Southeastern Cooperative Wildlife Disease Study). Disease issues are becoming critically important and a national database on deer herd distribution and herd dynamics could be useful for assessing disease spread and impacts, and other applications to ensure sound and sustainable deer management programs throughout the United States.

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Appendix I: Status (social K [SK], irruptive [I], long term average [LTA], decreasing [D], stable [S]) of mule deer (MD) and white-tailed deer (WT) in relation to carrying capacity (K) in the United States from 1986 to 2013.

State	Overall change	Stable to stable to increased (SI)	Increased, >social K (>SK), >long term average (>LTA)	Decreased, <K, <LTA, decreased to stable (DS)	Reason for change[a]
Alabama		WT			1, 2, 13
Arizona				MD, WT	1, 4, 8, 12, 19
Arkansas		WT			1, 3, 18
California	WT/MD[b]				9, 21
Colorado		WT (SI)		MD	5, 10, 20
Connecticut			WT (at K)		30
Delaware			WT (increased 3X)		3, 9, 29
Florida		WT (SI)			2
Georgia			WT (>SK)		2, 6
Idaho		WT[c]		MD	4, 5, 10, 14
Illinois	WT				1, 29
Indiana			WT (<K)		2
Iowa				WT	1
Kansas			WT		3
Kentucky			WT		2, 3, 7
Louisiana				WT (DS)	1, 22, 23
Maine			WT		2, 4, 11,29
Maryland			WT (>SK)		2, 6, 7, 11
Massachusetts		WT			6, 7
Michigan			WT (lower pennisula)	WT (upper pennisula)	1, 8
Minnesota			WT		1, 11
Mississippi			WT[d]		6, 7, 25
Missouri				WT (<K)	1, 6
Montana			WT(>LTA)	MD (<LTA)	1
Nebraska				WT, MD	5,8,11,16, 25
Nevada				MD (DS)	4, 5, 24
New Hampshire			WT		4, 25
New Jersey				WT	3, 6, 11
New Mexico				WT, MD	4, 8, 15, 29
New York			WT		2, 6, 25
North Carolina		WT			1, 9
North Dakota	WT,MD				4, 17, 28
Ohio			WT		1, 7
Oklahoma		WT			1
Oregon		WT		MD (<K)	4, 5, 8, 15
Pennsylvania		WT (W and SE)		WT (central)	1
Rhode Island			WT		2
South Carolina	WT				8, 14, 18
South Dakota		WT,MD			6, 7
Tennessee			WT (>SK)		3, 26
Texas			WT[c]	MD	2, 4, 5
Utah		MD			2, 3, 5, 8, 14
Vermont			WT (<K)		1, 2, 6
Virginia			WT (>K)		2, 4
Washington		WT, MD (SI)			4, 8, 9, 16
Wisconsin			WT		11, 25
Wyoming			WT (Irruptive)	MD (<LTA)	2, 5, 17

[a] 1 = antlerless harvest, 2 = urbanization, 3 = habitat improvement, 4 = habitat deterioration, 5 = drought, 6 = limited access for hunting, 7 = low hunter effort, 8 = predators, 9 = increased human population, 10 = severe winters, 11 = mild winters, 12 = special hunts, 13 = more accessible land for hunting, 14 = increased highway traffic, 15 = livestock over-browsing, 16 = disease, 17 = energy production, 18 = forestry practices, 19 = water distribution, 20 = competition with elk and cheat grass, 21 = anti-hunting groups, 22 =longer hunting seasons, 23 = liberal weapon use, 24 = fire, 25 = reduced doe harvest, 26 = greater law enforcement, 27 = lack of predators, 28 = vehicle collisions, 29 = liberal hunting, 30 = unknown.

[b] Generally the same but appears to be a slow overall decline.

[c] WT are moving into MD habitat.

[d] Population exploded in the past 20 years.

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History of the conservation of critical deer ranges in California: concepts and terminology

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Mule deer (*Odocoileus hemionus*) are a highly visible, well-known large mammal of great recreational, conservation, and scientific interest. They are among the best-studied ungulates in North America, with a long history of conservation and management in California. Mule deer also are important because they frequently serve as a surrogate for the requirements of less well-studied species, particularly those dependent on early successional habitats. Numerous terms or phrases have been coined over the past century to categorize or describe those areas used by mule deer for all or part of their life history cycles. In this paper, we describe some of the regulatory and legislative efforts to codify the importance and protection of mule deer habitat in California and review the historical context of the origin and evolution of terms used to describe those areas, and present a standardized list of terms used to address habitats used by mule deer that, hopefully, will become commonplace and simplify conservation planning or other efforts to protect wildlife habitat.

Key words: California, *California Fish and Game*, critical range, deer range, fawning habitat, habitat, holding area, migration, mule deer, *Odocoileus hemionus*, summer range, wildlife corridor, winter range

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> "*Despite the evidence to the contrary, despite the dreams of the dreamers and the schemes of the schemers, the area of wild land which may be devoted primarily to deer will decrease as the century progresses.*"
>
> W. P. Dasmann, 1952

Mule and black-tailed deer (*Odocoileus hemionus* ssp.) inhabit much of the wild land in California (approximately 20 million ha [≈50 million acres]) and occupy a wide variety of habitats. The ranges used by deer populations were traditionally identified as winter range or summer range. As knowledge increased over many decades, use of more refined terms—such as critical winter range, key winter range, critical summer range, holding area, fawning area, and migration corridor—have been added to the jargon used to describe the landscape for deer.

The relationship between deer ranges and conservation of many wildlife species is reflected in this statement, "*While decline in deer numbers may be alarming in itself, it becomes more alarming when considered as a symptom of a common malady affecting wildlife in general... What affects one most certainly has an impact on the rest of the community*" (California Department of Fish and Game [CDFG] 1976). Because deer management in California has been a priority for many years, CDFG (beginning in 2014, the California Department of Fish and Wildlife; CDFW) has, over the decades, collected and sponsored work to identify and map seasonal ranges throughout the state. Results exist in digital format at varying scales and specificity, and are available for planning and management purposes using Geographic Information System (GIS) analyses. Information about deer ranges is frequently used in project review and conservation planning to help identify important habitats for wildlife in general.

Inconsistent interpretation of terms has resulted in some confusion, particularly in the context of land use planning efforts. Confusion in terminology is not unique to wildlife scientists, and Hall et al. (1997) recommended standardizing terms used in wildlife science. Substantial dialogue involved the labeling of ranges as "critical winter range" or, merely as "winter range." In 1947, CDFG (then Division of Fish and Game) considered much of the west slope of the Sierra Nevada, as well as portions of the east slope, as critical range for deer. Statewide ballot initiatives in 1988 (Proposition 70) and 1990 (Proposition 117) and policy adopted by the California Fish and Game Commission (CFGC; 1984) explicitly indicated the "critical" status of deer ranges.

In this paper, the intent behind development of various terms is discussed using historical references to California deer management, policies, and state law. Conservation recommendations posited by wildlife biologists—pursuant to California Environmental Quality Act (CEQA) review of proposed developments—have long relied on deer range maps and migration routes or corridors as a basis for evaluating wildlife habitat in the absence of data for other wildlife species. Indeed, biologists have, for years, provided deer range information for local and county plans undergoing CEQA review in an effort to achieve consideration of wildlife values: about 21% of the land area acquired by the state on behalf of wildlife conservation was acquired for its value as deer range, but indirectly benefits associated species of wildlife, fish, and native plants for which the agency has trustee responsibility (CDFW 2014a).

Mule and black-tailed deer in California occupy a variety of habitats and ranges throughout their life histories (Hall 1927, McLean 1940, Longhurst et al. 1952, Zeiner et al. 1990, Cronin and Bleich 1995) (Figure 1). Seasonal ranges inhabited by deer in California have been described by various terms and meanings among wildlife professionals and, more recently, conservation planners. As managers continue to study deer distribution, abundance, movement patterns, and habitat use, we gain specific information and use such terms to infer the importance of geographic areas for deer management. For example, density estimates

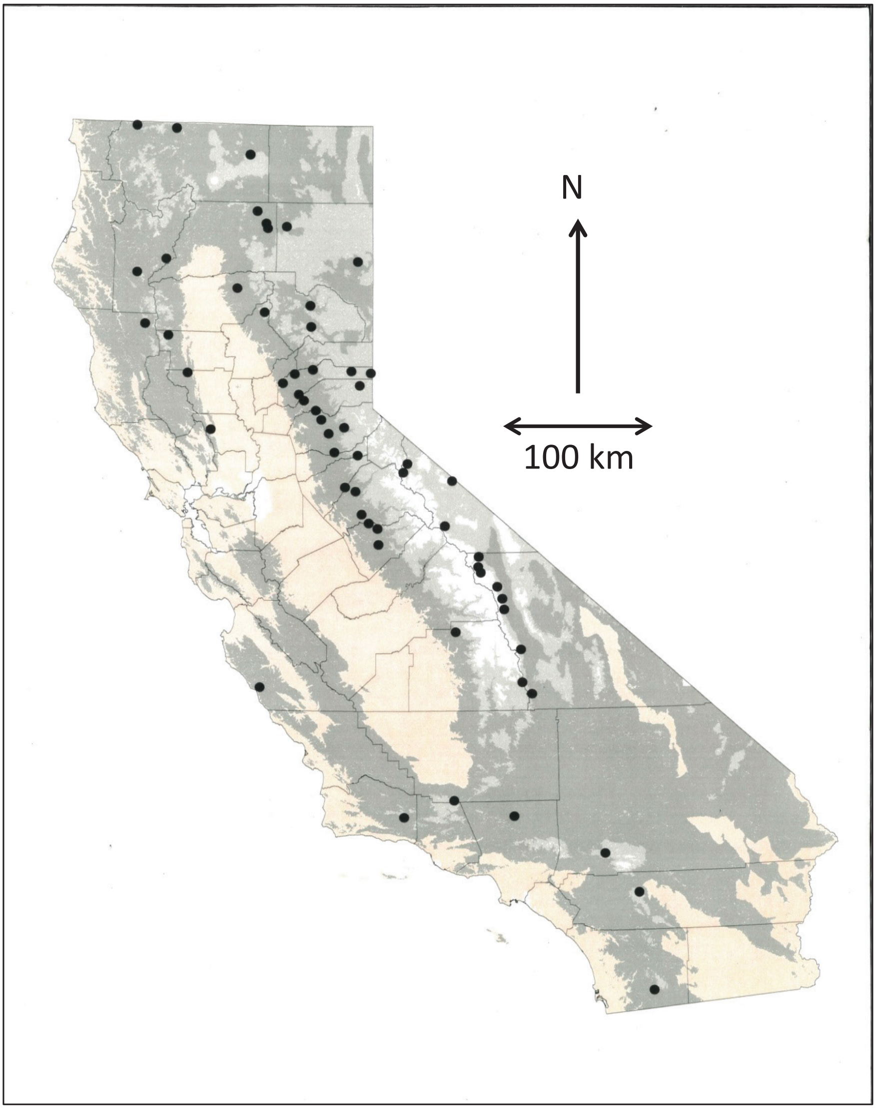

Figure 1.—Approximate locations (●) of areas in California considered for the status of critical deer ranges by the California Department of Fish and Game in 1947. County lines (—) and approximate elevation zones (≤300 m; >300–1525 m; >1525m–2600m; >2600 m) also are shown. Adapted from CDFG (1947).

(i.e., deer per unit area; Longhurst et al. 1952) have been used to assess whether a range is "key" or "critical" as opposed to merely "winter" or "summer" range, and spring and fall holding areas or migration routes have been defined by monitoring groups of radio-collared deer. Some terms have been used interchangeably in studies, while other terms describing deer range have been incorporated in CFGC policy and regulations, or state law in the California Fish and Game Code.

Questions about whether a given deer range was key, critical, or neither often have arisen during planning efforts initiated by the United States Forest Service (USFS), Bureau of Land Management, California Department of Parks and Recreation, or local governments. Similarly, the inconsistent use of terms when a GIS project to map migratory deer ranges throughout California was initiated has been discussed for decades. Terms used to describe ranges are often self-explanatory and unambiguous; however, range information converted to GIS coverages—now a standard technique in natural resource management—sometimes is supported with inconsistent metadata such as labels of "key," "critical," or some other descriptor, absent any interpretation of intent. We submit it is desirable to revisit definitions of deer ranges to encourage use of a consistent system. We would also like to stimulate thoughts about the degree to which deer can represent wildlife habitat for use in California. Consequently, our purposes here are to (1) review California's history regarding the use and intent of deer range terms; (2) discuss some of the broader implications of terms used to describe deer range in relation to habitat conservation; and (3) suggest use of standardized terms related to deer ranges for conservation planners. An additional, more subtle, purpose is to emphasize the historical relevance of papers published in *California Fish and Game* to the management of deer in California in this centennial anniversary volume.

Methods

We reviewed literature, either formally published in scientific journals or as other sources (sometimes described as "gray literature") to establish the initial use, or evolution of terms applicable to deer management or the conservation of deer habitat in California. We also reviewed a variety of lesser-known documents, including the minutes of relevant meetings or unpublished reports to various committees, because of their historical relevance to the derivation of various terms and the resulting importance of those documents to conservation. Additionally, we reviewed regulations or legislation addressing mule deer management or conservation, and describe their implications for the persistence of mule deer and their habitat in California. Based on these sources, we derived a list of standardized terms that will be useful in simplifying land use planning efforts as well as conserving mule deer and their habitat in the future.

Historical Perspectives on Terminology

Deer management in California benefits from a long history of ecological investigations. At least 117 notes, papers, or bulletins relating to California deer ecology and management published beginning in 1913 by CDFG personnel, and since 1914 in *California Fish and Game* alone, were tallied by the authors. Many of these papers—some are considered historically relevant, and even classics, in the field of wildlife conservation—were reviewed to provide the basis for describing deer ranges in California. A few additional papers on California deer published through other professional outlets such as *The Journal of Wildlife Management* or *Journal of Mammalogy* were also reviewed and incorporated herein.

Seasonal movements and ranges.—Observations of deer movements, trails, areas of concentration during winter, and movement patterns during hunting season prior to the mid-1900s provided the foundation for our current understanding of deer movements and seasonal ranges. Later, marking deer with dyes, flagging, ear tags, or bells was used by wildlife managers to evaluate deer movements (Cronemiller and Bartholomew 1950, Leopold et al. 1951, Clover 1954, Jordan 1958, Taber and Dasmann 1958, Ashcraft 1961, Bauer et al. 1968). These early efforts provided little quantitative information on deer movements, but did help develop a general knowledge of seasonal ranges. From the 1970s to the present, development of radio telemetry monitoring techniques has greatly enhanced our ability to determine seasonal deer ranges and migration routes (Schneegas and Franklin 1972, Bertram and Rempel 1977, Loft et al. 1987, Kucera 1992, Monteith et al. 2011). Monitoring of deer using GPS-based telemetry collars is now underway in California, and will further enhance our knowledge of deer life history and movement patterns.

In one of the first references to deer migration, Clarke (1913) mentioned movement to higher altitudes in summer and lower altitudes in autumn. Fither (1922) described winter range along the Trinity River from, "*...Junction City to Taylor's Flat...*" as an area where the snow, "*...drives these deer into a section of country about five or six miles wide and about thirty miles in length*." Hall (1927) indicated, "*In most parts of California the mule deer have separate summer and winter ranges. In spring, as the snow melts, the deer work up into the mountains... with the first heavy snowfall they migrate down to their winter range...*". Russell (1932), a widely read early reference on deer migration, reported that mule deer do not yard in winter as do white-tailed deer (*Odocoileus virginianus*) but, instead, choose open hillsides where the snow is not too deep to prevent moving freely about. This was the beginning of officially distinguishing some wintering areas from others.

Deer populations inhabiting ranges subject to abundant winter snow are not the only ones to exhibit seasonal movements. McLean (1930) and Longhurst and Chattin (1941) mentioned that the burro deer in the Colorado River area of California is found nearer the river during the dry seasons than during the rainy seasons when they may be in mountain ranges as far as 100 km (≈60 mi) away. Taber and Dasmann (1958), in a comprehensive report on the black-tailed deer of California's north coast chaparral, described seasonal movements of approximately 0.6 km by deer to take advantage of warm, south-facing aspects during winter and cooler, north-facing aspects during summer.

As part of implementing deer herd management plans, biologists have conducted radio telemetry studies of varying intensity and duration on many migratory deer ranges in the state. These have resulted in largely unpublished internal reports that describe winter, transitional, and summer ranges, as well as general migration routes. However, a comprehensive statewide analysis has not been completed.

Relative importance of seasonal ranges.—As knowledge about deer movements increased, it became evident to investigators that not all seasonal ranges were of the same value to deer (e.g., Russell 1932). Dixon (1934), in a classic publication on California deer, implied that not all winter ranges were the same: "*I found that buck brush (Ceanothus cuneatus) is utilized heavily by mule deer in winter when heavy snows crowd them down into the lower winter range...*" and, "*...during January...deer...were abundant on the warm south side of the ridge.*" Dixon (1934) refers to Pilot Ridge, Mariposa County, as one of the "*...most important wintering grounds of deer in the State...*", thereby suggesting a relative ranking of winter ranges existed at least in the minds of biologists. Similarly, McLean (1940) referred to "*...four principal winter concentration areas...*" in Modoc County. Fischer et al. (1944) was one of the first in California to describe the elimination of browse needed for "critical winter periods" as a consequence of overuse on the Modoc National Forest.

The 1940s became an active period for deer management in California (Dasmann et al. 1958): there were too many of them. Deer became a "problem" of great magnitude, as 37 of 71 deer ranges surveyed during 1946–47 indicated that populations were out of balance with their habitats resulting in, "*...depletion of range and waste of deer...*" (CDFG 1947). Indeed, Storer (1932) described the problem in the early 1930s as represented by increasing damage by deer to agricultural crops as the deer population was apparently increasing. The increase in crop damage was attributed, in part, to more regulated harvest of deer with the initiation of game laws, aggressive control of predators, and the decreasing occurrence of fires on forested lands.

During the next 25 years and into the mid-1960s, deer populations in California would reach their peak and then begin a decline that CDFG attempted to moderate both through active harvest management and habitat manipulation (Longhurst et al. 1952, Dasmann et al. 1958). It was during this period that extensive habitat evaluations and deer investigations were initiated, and use of the terms "critical" and "key" became standard terminology in describing deer ranges. California's initiation of antlerless hunting (i.e., the "1956 doe hunt" that still looms large over California deer population management), an attempt to manage the deer population rather than merely the buck harvest, was implemented to address the impact of deer on their ranges (Dasmann et al. 1958, CDFG 1963). This period of deer management brought strong public criticism of CDFG and resulted in substantial legislative change with the adoption of the "Busch Bill" in 1957, legislation that effectively turned the approval of "doe hunting" in much of California over to 37 affected counties.

Designating deer ranges as critical.—Perhaps the first reference to "critical" deer ranges in California was in 1947 (CDFG 1947). A "survey of the critical summer and winter deer ranges of California" was conducted to determine deer range conditions, particularly where reports of "starvation, crop and range damage, and the increase of the reported deer kill" occurred (CDFG 1947). Input was sought from throughout the state and among agencies, resulting in a list of 71 areas to be considered for critical deer range status in California (Figure 1). At the time, CDFG recommended 37 of the areas be retained as critical deer range (Table 1), and that 34 (Table 2) not remain on the list. There was no explicit definition provided by CDFG (1947) for the designation of ranges as critical; however, two areas of intent or criteria can reasonably be inferred: crop damage and habitat condition.

Crop damage and critical deer range.—Areas where substantial crop damage (depredation) by deer occurred appear to have been unquestionably considered critical deer range (CDFG 1947). In such areas, CDFG rarely provided deer range condition information, and none of the areas removed from the list were crop damage areas, confirming that these areas were considered critical from at least a socio-political aspect. Eleven of the 37 areas identified as "critical" were a consequence of crop damage. It is certain the designation of critical was partly used to identify specific deer ranges where conflicts with agriculture were substantial and needed to be addressed. Deer versus agriculture was an important issue that received substantial attention from CDFG and the University of California during the 1950s and 1960 (e.g., Longhurst et al. 1962), and persists in some areas today. Depredation permits issued by CDFG were one barometer of measuring conflict with agriculture, and a record 2,484 permits to kill deer were issued in 1961 (Thomson 1963). By comparison, 80 and 174 depredation permits were issued for deer in California during 2012 and 2013, respectively.

Table 1.—Deer range areas in California considered to be "critical" by CDFG (1947) and warranting retention on the list for further investigation.

ID Number	Geographic Area	County	Area (km^2)	Range Condition	Influencing Factors[1]
1	Williams' Creek, near Covelo	Mendocino	324	Poor	G
2	Hayfork area	Trinity	Unspecified	Good	C
3	French Gulch area	Shasta	Unspecified	Fair	D, G
6	Hat Creek Rim	Shasta	129	Poor–Fair	G, W
8	Burney-Rising River	Shasta	Unspecified	Poor–Fair	Unkown
10	Secret Valley	Lassen	Unspecified	Poor	G
11	Antelope Creek	Tehama	890	Poor	G
13	Genesee Valley	Plumas	Unspecified	Unknown	C
16	Sugar Loaf Hill-Bridgeport	Nevada	18	Poor	G, D
21	Long Canyon	Placer, Eldorado	169	Fair	Unknown
23	Pacific Ranger Station area	Eldorado	154	Poor	T
26	Salt Springs Reservoir	Amador	67	Poor	T
39	Taboose Creek	Inyo	11	Undetermined	G
40	Tinemaha Creek	Inyo	22	Fair	Unknown
41	Area west of Big Pine	Inyo	32	Fair	G
43s	Tahquitz Valley	Riverside	4	Poor–Fair	Deer overpopulation
46s	Black Butte area	Glenn	246	Poor	Unknown
47	Stonyford	Colusa	392	Undetermined	C, G
48	Capay Valley	Yolo	Unspecified	Undetermined	C
49s	Monache Meadows	Tulare	640	Poor	G
50s	Buckhorn Creek	Siskiyou	322	Fair–Good	Unknown
51	Red Ledge Mine	Sierra	23	Undetermined	G
52	Round Valley	Inyo	8	Poor	Recent fire
53	Oak Creek (N. Fork)	Inyo	47	Good	Unknown
54	Sage Flat-Summit Creek	Inyo	6	Fair	Unknown
55	Haiwee grazing allotment	Inyo	14	Fair	Unknown
59	Northeast slope Mt. Tamalpais	Marin	Unspecified	Undetermined	C
60	Clear Lake-Crowder Flat-Lost Valley	Modoc	1505	Poor–Fair	G, T, other reasons
61	Ojai Valley	Ventura	Unspecified	Undetermined	C
62	Santa Clara Valley	Ventura	Unspecified	Undetermined	C
63	Leonas Valley-Ritter Bros. Ranch	Los Angeles	49	Poor	G
64	Doyle area	Lassen	531	Fair	G, mostly private
65	St. Helena area	Napa	Unspecified	Undetermined	C
66	Pebble Beach area	Monterey	Unspecified	Undetermined	C
68	Little Shasta Valley (Lema Ranch)	Siskiyou	Unspecified	Undetermined	C, G, private land
69	Placerville area	Eldorado	Unspecified	Undetermined	C
70	Kennedy Meadows	Tulare	Unspecified	Fair	G

[1] G = Livestock grazing overuse; C = Crop damage by deer; D = Deer range is considered decadent; W = Water development needed; H = Highway or train mortality high; P = Area in proximity to other critical area, hence recommended for later reconsideration if needed; or area should receive additional consideration for placing on list; T = Succession to timber types has reduced habitat quality.

Table 2.—Deer range areas in California originally nominated as "critical" by CDFG (1947), but not retained on that list following further review.

ID Number	Geographic Area	County	Area (km^2)	Range Condition	Influencing Factors[1]
4	Cedar Creek	Siskiyou	Unspecified	Unspecified	G
5	Cedar Mt.	Siskiyou	206	Good	G
7	Rock Creek	Shasta	178	Good	Unknown
9	Clark's Valley-Horse Creek	Lassen	Unspecified	Good	Private land
12	Sloat area	Plumas	129	Good	H
14sp	Carpenter Valley	Nevada	47	Excellent	Unknown
15	French Point-Missouri Bar	Nevada	12	Good	Unknown
17	Goat Rock (w of Colfax)	Nevada	59	Excellent	Private land
18	Floriston-Verdi	Nevada	36	Excellent	H
19s	Tinker Knob- Sereno Creek	Placer	27	Excellent	Unknown
20	Shirttail Creek	Placer	Unspecified	Good	Private land
21	Mosquito Ridge	Placer	16	Good	P
22	Slate Mountain	Eldorado	60	Poor	Unknown
24	Happy Valley	Eldorado	140	Poor–Good	P
25	Leonis Station	Eldorado	105	Poor	T
27	Calaveras Ranger Station area	Calaveras	99	Poor–Good	G
28	American Camp-Grant Ridge	Tuolumne	161	Poor–Good	G
29	Mt. Provo-Sugar Loaf Mt.- Jawbone Ridge	Tuolumne	148	Poor–Good	G, P
30	Kassabaum Meadow-Ferretti Ranch	Tuolumne	41	Fair–Good	C, G
31	Trumbull Peak-El Portal	Mariposa	65	Poor	Unknown
32	Buck Mdws-Moore Ck.- Bower Cave area	Mariposa	27	Poor	T
33	North Fork of the Kaweah River	Tulare	Unspecified	G-E	Park land
34s	Bodie area	Mono	Unspecified	Good	Private land
35s	Leavitt Creek	Mono	69	Excellent	Unknown
36	W. Fork Walker River	Mono	311	Poor–Good	Unknown
37sp	Rush Creek	Mono	227	Fair–Excellent	Unknown
38s	Buttermilk area	Mono	45	Excellent	Unknown
42s	Head of Santa Ana Canyon	San Bernardino	Unspecified	Good	Recent fire
44s	Laguna Mountain	San Diego	147	Poor–Good	G, recent fire
45	Big Pine Mountain	Santa Barbara	Unspecified	Good	Unknown
56s	Philbrook Reservoir area	Plumas	24	Poor–Good	G, recent fire
57s	Frazier Mountain	Ventura	61	Good	C
58	Limekiln Creek-San Antonio River	Monterey	Unspecified	Good–Excellent	Military base
67	Anderson Flat	Mariposa	155	Excellent	Unknown

[1] G = Livestock grazing overuse; C = Crop damage by deer; D = Deer range is considered decadent; W = Water development needed; H = Highway or train mortality high; P = Area in proximity to other critical area, hence recommended for later reconsideration if needed; or area should receive additional consideration for placing on list; T = Succession to timber types has reduced habitat quality.

Napa, Sonoma, and Santa Barbara counties were areas of highest depredation rates. Biehn (1951) attributed the crop damage in California to (1) the more than doubling of the deer population between 1900 and 1950; (2) reduction of natural feed and watering areas as a result of settlement and agricultural development; and (3) the planting of crops on historical deer ranges.

Habitat condition and critical winter deer range.—The majority of deer ranges identified as critical based on their habitat condition (CDFG 1947) were winter ranges. Excessive grazing and browsing by livestock and deer, and a shift from grass-forb-shrub habitats to tree-dominated habitats were the primary reasons given for the resultant poor to fair condition of those ranges and a critical designation (Table 1, Table 2). Hence, deer ranges were considered critical, or not, based in part on their range condition. For example, the report for one area indicated, "*...allotment heavily stocked, but has beautiful stand of bitterbrush. Area should be deleted from critical list*." Today, biologists generally consider areas with bitterbrush (*Purshia* spp.) in any condition to be critical deer ranges. It was also implied, however, that these deer ranges had a high importance to management and conservation and this was accepted as fact by CDFG as well as by the USFS, which participated in the survey. Indeed, CDFG (1947) noted that, "*A tentative agreement with the U.S. Forest Service has been reached to reclassify critical winter deer ranges so that these areas can be set aside for wildlife use only, if the survey indicates such action as advisable*" (whether the tentative agreement was adopted by the agency is unknown to the authors); and for one area specifically, "*Because it is an important winter range of black-tailed deer, land in this critical area* [regarding Antelope Creek in Tehama County] *is being acquired by the state... By having control of grazing, it is hoped to restore this range to former productivity*." This area subsequently became part of the Tehama Wildlife Area (18,964 ha) for the conservation of California's longest distance (≈160 km annually) migratory deer herd (Longhurst et al. 1952).

CDFG (1947) did not limit the scope of designating critical ranges to specific areas, but rather took a landscape approach to wildlife and habitat management that has become popular with land management agencies and conservation advocates. For example, "*...some of the areas fall into geographical units. In suggesting certain areas for detailed investigation, it becomes necessary to study the entire units rather than the individual areas. The most extensive unit is the winter range on the west slope of the Sierra Nevada Mountains. This unit of critical areas extends for about 150 miles and is primarily restricted to the yellow pine belt...*" (CDFG 1947). Based on the list of areas evaluated (Table 1, Table 2), the "unit" considered critical was deer winter range from Tehama County south to at least Amador County. To the west, another unit occurred in Mendocino County, centering around Black Butte. There, three areas were considered linked by a widespread deer population, but serious range depletion by all herbivores was considered a cause of heavy mortality during severe winters.

Leopold et al. (1947) evaluated overpopulations of deer in the United States, including 12 areas identified for California, wherein overpopulations were reflected by damage or degradation of their range leading to malnutrition of the population. These areas were among the areas identified by CDFG (1947). Krausman et al. (1992) revisited the Leopold evaluation, and concluded that most of California's deer herds were still exceeding the capacity of their ranges because females are not harvested and because of a long-term decline in habitat quality.

Following the 1946–1947 survey was the initiation of "California Deer Studies" on 1 July 1947 when the CFGC, "*...transferred to the University of California responsibility for conducting studies of deer populations in the state which studies would form the basis for future deer management policy. Federal Pittman-Robertson funds to the Department were made available to the University, under terms of a three year contract, to carry on these investigations*" (Leopold 1948). This research project (known as Project 28-R) was administered by the university's Museum of Vertebrate Zoology, and resulted in two of the foundational works (Leopold et al. 1951, Longhurst et al. 1952) on California deer that served as the basis for much of current management. These studies discussed the importance of seasonal deer ranges, and used the term critical as well as "key" in their descriptions.

Designating winter range as key.—In addition to describing ranges as "critical", use of the term "key" has been in place for several decades and is used to describe geographic areas as well as important forage species. Dasmann (1948), using terminology likely developed for range management purposes (e.g., Stoddard et al. 1975), described "key areas" as, "*...those mid-winter concentration areas that are subject to more intense cropping than those occurring elsewhere on the range.*" Key areas were regarded as areas where use was heaviest; for example, "*...where stocking does not exceed carrying capacity on key areas, the range will not suffer elsewhere either*" (Dasmann 1948).

"Key species" for deer (Dasmann 1948) were used to help define key areas by identification of preferred deer browse. Confounding the terms however, these browse species were considered to be, "*critical foods on deer ranges*" and were the basis for defining what were regarded as critical deer ranges. For example, Leopold et al. (1951) identified buck brush as the most important deer food in the Jawbone area (identified as a critical range in 1946–47; Table 1) of the central Sierra Nevada, and areas where buck brush was concentrated was the "*key range area.*"

In northern California, the Interstate Deer Herd Committee (IDHC) was an organized effort by state and federal agencies formed in 1945 to investigate the declining deer population and habitats on the Modoc National Forest. The IDHC followed the concept of key browse or forage species such as bitterbrush to identify key areas as those places on the winter range that furnish the bulk of the winter forage. For example, IDHC (1949) noted that, "*If proper balance of use against forage production is maintained within the key areas, the remainder of the range should be automatically safeguarded.*" We now know that this proper balance was not maintained, and that much of the area in question has seen significant increases in western juniper (*Juniperus occidentalis*) at the expense of key browse species (Schaefer et al. 2003).

Relationship between critical and key winter range designations.—In the early 1950s, any distinction between the terms *critical* and *key* became blurred. Soon to be Director of CDFG, Seth Gordon (1950) recommended that the purchase of range land for big game by the recently created Wildlife Conservation Board should be, "*...limited to very important key areas only*" such as concentration areas for wintering deer. He further reported that, "*... public land administrators are receptive to working out many adjustments in their program of land use to benefit deer. Examples of such cooperation are the reservations of winter deer ranges on the Plumas... Modoc, Lassen, Tahoe, Inyo, El Dorado, Sequoia, Klamath, Trinity, and Mendocino national forests.*" Dasmann (1952) described critical deer forage as vital to the best survival of the animals on a specific range, and key areas were described as, "*Too critically important to sacrifice...*". Schneegas and Franklin (1972) located and mapped the key winter range in the Mineral King area of Tulare County as a result of development proposed by the Walt Disney Corporation and USFS for recreation purposes. Browning et al. (1973) mentioned critical habitat and key habitat of deer on the west slope of the Sierra Nevada for the Railroad Flat area in Calaveras County.

A sometimes-heard perspective from deer biologists on the meaning of critical or key ranges has been that they are areas, "…where deer go to die…", meaning that such ranges were areas of last resort for food, cover, or both during harsh winters. It implied that range condition was poor and unable to sustain deer (otherwise they wouldn't die), resulting in die-offs, usually in the late winter period. Use of the terms key or critical in the context above supports the original concept that critical ranges are in poor shape. Leach (1956), in summarizing his investigation of deer food habits for the Great Basin deer herds in California reported, "*In severe winters, deer are forced to rely on browse species which normally are eaten less extensively... it is apparent deer will utilize whatever food is available and preference becomes secondary to survival in periods of adverse conditions.*" Leach (personal communication to E. Loft in the 1990s) indicated that deer on the Lassen-Washoe range had essentially died of starvation with full stomachs of dry annual grasses of low nutritional quality. Dasmann and Hjersman (1958) also studied deer from 1951 to 1956 in that area and reported, "*...deep snows forced deer into marginal wintering areas at lower elevations, where browse was either scarce or made up of species of sub-standard food value... unusually heavy snows pushed deer below the bitterbrush zone on some ranges.*"

Another large unit of winter range is the eastern slope of the Sierra Nevada adjacent to the Owens Valley, in Mono and Inyo counties. This unit presents a problem distinct from most of the rest of the state. In general, the deer have a comparatively unlimited summer range near and over the crest of the Sierra Nevada, but are forced onto a narrow belt of winter range at the base of the steep escarpment that characterizes much of the eastern slope. A rain shadow limits moisture on the east side (Bleich et al. 2006), and rural development and agriculture in the valley further constrain deer onto a very limited range.

To characterize terminology describing winter range, it is evident the terms critical and key were often used interchangeably. Evaluating these descriptions of deer ranges suggests that key areas and key plant species occurred within deer ranges that were, overall, considered critical. Intuitively then, a reasonable conclusion is that key areas were a subset of a broader critical deer range.

Summer range.—Historically, summer ranges have received less attention than winter ranges as a concern for deer in the state because of abundant long-term forest disturbances that favored deer and other species associated with early successional habitats. By default, designation of summer ranges for deer in California included the areas of deer range not considered winter range. Longhurst et al. (1952) estimated there were 217,900 km^2 of summer range and 138,700 km^2 of winter range in California. Leopold et al. (1951) estimated summer range comprised seven times the area (692 vs 96 km^2) of winter range in the Jawbone deer herd range. Most summer range remains wildland managed by federal government agencies (primarily USFS and National Park Service). Such summer ranges generally are not at risk of being lost as wildlife habitat, although the quality of the habitat does change over time with plant community succession, forestry practices, fire suppression, and livestock grazing (Bleich et al. 2012). Changes in conservation goals and increased fire suppression have led to reduced levels of disturbance to California's forests. Consequently, the quality of deer habitats, both summer and winter, has declined.

Dixon (1934) observed that, "*...on our forest lands serious complications result if the range is overstocked early in the summer with domestic sheep or cattle; so that little or no green grass remains by the time the fawns should be weaned.*" Similar concerns about summer range conditions have been echoed over time (Longhurst et al. 1952, Salwasser et al. 1978, Bowyer and Bleich 1984, Loft et al. 1993, CDFG et al. 1998). Bleich et al. (2006) estimated that fawn survival to six months of age in the Sierra Nevada was approximately 28 percent, and not dissimilar from previous studies (e.g., Salwasser et al. 1978) , illustrating that some combination of factors between summer and winter result in high mortality and an early reduction in potential recruitment into the population.

There were a few areas of summer range initially considered critical in the 1947 assessment, and among them was Monache Meadows and vicinity in Tulare County. This area of deer summer range reportedly had been overgrazed since at least the 1947 report, and remains an area of great concern for mule deer today, but also for the native California golden trout (*Oncorhynchus mykiss aguabonita*) (Stephens et al. 2004).

The concern for habitat conditions on summer ranges has increased over time. Forested areas of checkerboard ownership, such as north of Lake Tahoe or among the northern counties in California, have substantial private forestland that is subject to more intensive harvest strategies than neighboring public forest lands. Additionally, some of these private lands have the potential to be developed to the point they are no longer viable as habitat.

Bowyer and Bleich (1984) evaluated spring-summer ranges of deer in the mountains of San Diego County, and suggested that livestock grazing negatively influenced deer use of mountain meadows. Similarly, the negative aspects of excessive livestock grazing on key riparian habitats and its implications to deer home range size, availability of cover, and negative interspecific interactions have been reported (Loft et al. 1993, CDFG et al. 1998).

Critical summer range.—Critical summer range was a term that has been used in the northern Sierra Nevada by one of the Department's administrative regions (Region 2; now called the North Central Region). The term was used in the original report (CDFG 1947) with a few areas identified (Table 1, Table 2), and was further developed in a northern Sierra Nevada planning effort during the 1980s when CDFG was developing maps and overlays to assist county planning efforts. Specific areas of deer summer range had been identified—through study, investigation, and best professional judgment—as being critical for a deer herd, much like winter ranges had traditionally been identified. These areas were primarily known fawning areas and corridors or routes for migration. The intent of such designations was to identify certain areas as being more important for deer populations than the greater area of summer range. In the southern Sierra Nevada, Schneegas and Franklin (1972) previously had evaluated the Mineral King deer herd because of a proposed recreational development. In that study, they identified both key winter and key summer areas.

A difficulty with interpretation of a critical summer range designation statewide is that only one administrative region has used the term, and no statewide inventory of "critical summer ranges" exists. Hence, a look at a statewide map with these designations would misrepresent the summer range areas CDFG believed were most important for deer. No similar level of detailed consideration has occurred elsewhere in the state, although similarly important areas could likely be identified with additional studies.

Fawning area.—Development of wildlife telemetry in the 1970s aided immensely in the identification of specific components of deer range such as fawning areas, holding areas, and migration routes. Fawning areas are typically considered to be complexes of high quality foraging habitat, with abundant cover interspersed, where adult females give birth and nourish fawns. Meadow, riparian, and shrub types with deciduous tree (e.g., quaking aspen, [*Populus tremuloides*] or white alder [*Alnus rhombifolia*]) or conifer overstory in proximity create a complex of vegetation structures and canopies that appear to be important for hiding fawns from predators (Welker 1984, Loft et al. 1993). Schneegas and Franklin (1972) mentioned key fawning areas needing protection at critical times. Bowyer and Bleich (1984) and Loft et al. (1987) similarly described the importance of hiding cover and succulent forage on summer range fawning areas, and the implications of livestock grazing.

The terms “propagation unit” and “population center” are other terms related to fawn production, but are infrequently used. The long-term study of the North Kings Deer Herd in the Central Sierra Nevada (Ashcraft 1975, Bertram 1984) first used these terms that were adapted from Grange (1949). Propagation units are defined as places where single does find adequate food, water, cover and other necessities to rear their fawns. Population centers are defined as an aggregation of propagation units. Fawning area has become the more widely used and general term to describe such areas.

Holding area.—Holding areas were identified by Bertram and Rempel (1977) as those areas along migration corridors that deer used as temporary stopping points during spring and fall migrations. Spring migration is typically a gradual upward move in elevation as deer follow the receding snowlines. Deer may delay in these holding areas for a few days to several weeks, depending on the weather. Loft et al. (1987) reported radio-collared female deer giving birth on holding areas in 1983, a year when their Stanislaus National Forest summer range they had used in 1982 was covered in snow until July, and then moving up to their traditional summer ranges. Fall holding areas differ from Spring holding areas in that they appear to be situated in areas where a rapid descent in elevation is possible with the onset of a storm (Bertram and Rempel 1977). Fall holding areas on the west slope of the Sierra Nevada include areas of abundant oak (*Quercus* spp.) mast, an important food source for deer prior to winter (Loft et al. 1987). Kucera (1992) reported extensive use of Spring holding areas by mule deer on the east slope of the Sierra Nevada as they waited to ascend the steep mountains and cross the Sierra Crest to summer range. Monteith et al. (2011) evaluated the timing and factors potentially influencing deer migration to and from the winter ranges of Round Valley, Inyo and Mono counties, and elsewhere near Bishop, and concluded that a combination of weather and plant phenology influenced migration timing. Monteith et al. (2011) emphasized that during Spring deer also use holding areas on their way to summer ranges. These areas include shrub-dominated basins and flats of big sagebrush (*Artemisia tridentata*) and bitterbrush. Kucera (1992) however, did not detect or report such a holding pattern in his study area during fall where there was an abrupt elevation change between summer and winter ranges.

Migration routes and corridors.—Fawning areas, holding areas, and migration corridors are best delineated with the use of telemetry because they are focused, linked areas within a route between seasonal ranges. Most areas in California have been identified by site-specific investigation and telemetry studies. As a result, comprehensive information is lacking for those areas that, like critical winter ranges, likely constitute an essential part of annual life history requirements.

Of increasing concern among biologists is whether the winter ranges of California’s migratory deer herds are becoming so modified by anthropogenic processes that there have been changes in the proportion of a deer herd that are migratory versus year-round resident, such as has occurred among deer wintering in Round Valley (Monteith et al. 2014). As anthropogenic changes increase in the foothill and winter range elevations, where much of the land is privately owned, there is believed to be a consequent increase in food availability to deer through pastures, gardens, agriculture, and general landscaping. Nevertheless, increases in human populations have the potential to yield increases in the number of predators, particularly black bears (*Ursus americanus*), that are the primary cause of death among fawns born to deer from Round Valley that summer on the west side of the Sierra Crest (Monteith et al. 2014). These changes could result in higher than previously possible densities of deer at lower elevations, while at the same time altering the proportion of migratory and non-migratory animals comprising the population on winter range. Simultaneously, long-term declines in habitat disturbance on summer ranges used by migratory deer could be reducing the amount and quality of summer range habitat, resulting in a decrease in carrying capacity for migratory deer.

Overall, the designation of holding areas, migration routes or corridors, and fawning areas on transitional range and on summer range is incomplete in California, and has largely been based on site-specific investigations. Where those areas have been identified, they provide additional information to assist in conservation and land use planning. Similarly, the designation of critical summer range has been inconsistently applied in California and is also site-specific. In terms of using the term to place a value on summer range habitat for deer, it might serve the same purpose to simply identify the types of habitats that deer rely on and prefer during summer, as they are the same riparian, wetland, and aspen habitats preferred by most terrestrial wildlife species.

DEER RANGE TERMINOLOGY IN POLICY AND LAW

In addition to the deer life history work, investigations and resulting biological and ecological findings, there are operational documents, policies, and laws that relate to deer ranges in the state. These policies and laws appear to interchangeably use the terms “critical” and “key” in discussing deer ranges. As a start, the CFGC adopted a Deer Management Policy in 1950 that remains in effect today. Dasmann (1953) provided an analysis of the policy, concluding in part, “*The lands on which deer occur in California may be zoned in accordance with the areas and values which predominate: Zone A- Public lands with deer priority, such as critical winter areas, where intensive habitat improvement may be justified. Zone B- Public lands where deer must fit in with other uses.*” The zone A or B designation described by Dasmann (1953), however, does not appear to have been adopted by any government entity. Additional policy in California’s deer management handbook (CDFG 1957) provided instructions for deer range surveys in that, “*...surveys will ordinarily be confined to the more important range areas, such as key winter areas, summer concentration areas, or other portions that may serve as indicators of general range use and deer population levels.*”

The landmark California Fish and Wildlife Plan (CDFG 1966) was written to identify, “*...actions which must be taken to maintain or improve California’s wildlife resources...*”. The plan discussed deer habitat improvement and stated that, “*Deer habitat improvement is usually aimed at providing more available nutritious browse during the critical time of the year... [in the] South Coast... [the] critical period is usually during the summer... [the] critical period on most migratory ranges is in the winter, although shortage of summer range forage is becoming more common on migratory ranges.*” The plan did not specifically distinguish deer ranges in terms of quality or importance.

The California Legislature, in setting the direction for the management of deer placed in law that individual deer herd plans shall “*...develop programs to maintain and increase the quality of deer habitat statewide... Emphasis shall be directed towards identifying critical deer habitat areas and the maintenance and management of such areas...*” (Fish and Game Code section 450-460). The legislation, however, was silent on whether these areas were already in critically poor condition. The Plan for California Deer (CDFG 1976) described some of the “*...human impact on deer...*” such as “*...key winter range areas were* *inundated by the new lake...*", indicating that evaluations of deer range had been accomplished to some level.

In the early 1980s, the CFGC and CDFG followed up the 1976 plan with a policy to identify deer herd management units and develop management plans for each of the herds. This was the initiation of >80 deer herd plans around the state. The CFGC policy for this effort stated, "*The goals of such plans shall be the restoration and maintenance of critical deer habitats to perpetuate healthy deer herds in the wild state as set forth in the appropriate deer herd management plans.*" This policy reaffirmed earlier reporting (CDFG 1947) that critical winter ranges included areas in poor (i.e., critical) condition as deer habitat. These were considered areas where intensive improvement efforts could be justified. Other lands, "*...with deer priority...*" could be included as well.

In 1988, Proposition 70—The Wildlife and Natural Areas Conservation Act—appropriated $6,000,000 for "critical habitat areas" including "winter deer ranges", thereby confirming that winter deer ranges are considered critical habitats. Two years later, California voters passed the California Wildlife Protection Act of 1990 (this was the controversial Proposition 117 that designated mountain lions [*Puma concolor*] as California's only "specially protected mammal"; Bleich and Pierce 2005). As a result of passage of that act, California Fish and Game Code section 2780 states, "*Much of the state's most important deer winter ranges have been destroyed in the last 20 years... Critical winter ranges of migratory deer in the Sierra Nevada and Cascade mountain ranges are increasingly subject to incompatible land uses. In some counties, over 80 percent of the critical winter ranges fall on these lands. The potential for incompatible land uses on these lands is a major threat to the survival of many migratory deer herds... This chapter shall be implemented in the most expeditious manner. All state officials shall implement this chapter to the fullest extent of their authority in order to preserve, maintain, and enhance California's diverse wildlife heritage and the habitats upon which it depends.*"

These declarations by the people of California (statewide ballot propositions 70 and 117) indicated deer winter ranges are considered critical up and down the Sierra Nevada and elsewhere, and interestingly, they directed all state officials, not just CDFG officials, to preserve, maintain, and enhance those winter ranges. More recently, Proposition 84—The Safe Drinking Water, Water Quality and Supply, Flood Control, River and Coastal Protection Bond Act of 2006—while not specifically mentioning deer conservation as an objective, did identify the maintenance of habitat linkages as a criterion for evaluating restoration or acquisition projects. The recent focus of wildlife conservation in California includes assessment and analyses for the identification and maintenance of wildlife connectivity in California, and specifically in the Sierra Nevada, (CDFW 2014b) that would be important to migratory deer populations.

Conclusions

The requirements of mule deer for habitat continuity at a large scale—having winter range, summer range, and linkages connecting them—has required land managers to consider landscape-level management strategies. As early as 1913, Frank Clarke, of CDFG wrote, "*Their are many large tracts in California...that are excellent regions for game reservations. An ideal system would be to create such reservations all over the state, in close proximity that game could pass from one reservation to another. Such a commingling of individuals is apt to be of greatest necessity in the future, to prevent the natural outcome* *of inbreeding, which might result among isolated groups of animals or even birds...*". It can be reasonably argued that if deer ranges were considered critically important in the 1940s, they are more critical now—both in terms of their physical condition and their importance to the maintenance of deer populations, as well as populations of hundreds of other wildlife species that co-occur with mule deer.

Deer are among the most studied wildlife species in California, a result of decades of interest in them as a principal game animal. For some herds, data exist as far back as the early 1900s. Because deer are so widely distributed in California, they are considered a reasonable indicator of California's changing wildland environment. Population trends of deer have been monitored over decades and reflect general habitat trends as influenced by factors such as plant succession, fire, grazing, and direct loss of habitat through human encroachment. Because of the existence of long-term data on deer populations and seasonal ranges, and when combined with their well established popularity and economic value, deer have been an important species in the environmental review process (i.e., the review of proposed projects that are subject to the California Environmental Quality Act [CEQA]). Additionally, their requirements for habitat continuity at a large scale—having winter range, summer range, and linkages connecting them—has required land managers to consider landscape-level management strategies.

Based on the papers reviewed herein, we propose a series of standardized definitions and meanings for use by deer biologists as well as conservation planners (Appendix I). Until more refined data become available, we also recommend conservation planners continue to use available mapped deer movement and seasonal data on migratory ranges of California as at least one layer in GIS analyses, and as a surrogate for other species to ensure viable deer populations and intact wildland ecosystems in California. We strongly encourage, however, the development of more robust data with respect to habitat selection, migratory movements, habitat quality, and delineation of seasonal ranges. Although the methodology is not perfect (Frair et al. 2004, Villepique et al. 2008), the advent of telemetry collars incorporating modern GPS technology (Tobler 2009) combined with archival logging and remote downloads (Millspaugh et al. 2012) now yield opportunities to develop information that can be used to better define seasonal ranges, migration corridors, or other specific geographic areas important to mule deer.

Movement information, when combined with habitat data obtained via remote sensing, can be used to build robust habitat selection models (e.g., Congalton et al. 1993, Marshal et al. 2006, Bleich et al. 2008) or to evaluate ecological hypotheses (e.g., Bleich et al. 2010, Villepique et al. 2014) that previously were impractical because acquistion of information adequate to produce meaningful results was costly and time-consuming. Thus, landsat imagery and lidar applications have the potential for great utility in wildlife and habitat investigations, conservation, and management, and "*...their value outweighs their costs when information is incorporated into products that help managers make wise decisions about natural resources*" (O'Neil et al. 2012).

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APPENDIX I. COMMON TERMS AND RECOMMENDED INTERPRETATIONS USED TO DESCRIBE DEER, SEASONAL HABITATS, AND DEER RANGES IN CALIFORNIA, 2014

TERMS TO CHARACTERIZE INDIVIDUAL DEER OR THE DEER POPULATION

Migratory—Deer that migrate to distinct summer (in Spring) and winter ranges (in Fall). Separate summer and winter home ranges (seasonal home ranges) and migration routes can be distinguished.

Non-migratory—Deer inhabit a localized area and home range year-round. No migration routes exist although there may be corridors habitually used to move about the home range. Where migratory deer occur, they may share the same areas in winter, hence resident deer range may also serve as winter range for migratory deer.

Resident—Same as non-migratory.

Seasonal range shifts—Generally short movements by non-migratory (resident) deer to other parts of their home range as environmental conditions change (e.g., from south-facing slopes to north-facing slopes); within season movements to alternate winter or summer range by migratory deer as a response to changing environmental conditions.

TERMS TO DESCRIBE SEASONAL RANGES FOR A GEOGRAPHIC AREA

Critical Habitat—This is an Endangered Species Act of 1973 designation. It is used to define critical habitat for threatened and endangered species, and is not recommended for any other purpose.

Key summer range—Uncommonly used. For migratory as well as non-migratory deer herds, this represents areas (or more appropriately habitats or geographic areas) that are considered of greatest importance to deer because of the proximate juxtaposition of necessary elements (food, water, cover). It is not recommended for use unless comprehensive data are available to define such areas.

Critical winter range—(1) That portion of a winter range considered most important for sustaining a deer herd. (2) That portion of the winter range in poor condition as a consequence of long-term overuse by herbivores. Portions of critical winter range may have key areas within it.

Fawning area—That area of summer range considered important to adult females for rearing fawns. Proximity to water, abundant cover, and high quality herbaceous and shrub forages during this nutritionally demanding and risky period of deer life history is necessary.

Holding area—An area (or areas) along Spring or Fall migration routes where deer delay, or hold, for at least several days. In Spring, such areas may be used for weeks if environmental conditions at summer range elevations are not “ready” in terms of snow depth or plant phenology. Holding areas can be located within an area of summer range.

Key winter range—An area within the winter range identified as having the most desirable forage species for deer. Additionally, it may be a localized area that is most useful and representative in indicating the level of grazing or browsing use over the winter range as a whole. These ranges typically occur on south-facing exposures of ridges or canyons, usually areas where where snow depth is not normally limiting and there is abundant high-quality browse such as *Purshia tridentata* or *Ceanothus* spp.

Migration corridor—An area of suitable habitats containing migration routes between winter and summer ranges that sustain deer as they migrate. The term corridor provides an areal component beyond a linear migration route and ensures connectivity between seasonal ranges.

Migration route—Travel routes between distinct winter and summer ranges; typically portrayed as a line, but with no width or area associated with the route.

Population center—An aggregation of propagation units. This term is not widely used.

Propagation unit—An area of summer range and mix of habitats used for fawning; an area where adult females find adequate food, cover, and water to rear fawns. This term is not widely used.

Summer range—An area that migratory deer may inhabit from late Spring to early Fall. Areas at higher elevations, but typically not above timberline, in the Sierra Nevada, Cascade, and Coast Ranges are considered summer ranges.

Winter range—An area that migratory deer may inhabit from the Fall to Spring. For example, the elevation belt of approximately 500–1,500 m through much of the west slope of the Sierra Nevada is generally considered deer winter range.

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Bringing science to waterfowl management in the California Department of Fish and Wildlife

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In this invited paper we summarize some of the scientific work produced to inform waterfowl management in California and the Pacific Flyway, with an emphasis on those contributions by Department of Fish and Wildlife (Department) waterfowl biologists assigned to Federal Aid in Wildlife Restoration Project W30R and chronicled in *California Fish and Game.* Investigations carried out by other Pittman-Robertson projects also contributed substantially to the Department's science-based programs for waterfowl, particularly regarding waterfowl disease and food habits investigations. Important information needs, addressed by the best scientific methods of the day, included population abundance and trend, breeding and wintering distributions, critical habitat needs, vital rates (survival, recruitment), the establishment of appropriate hunting regulations, and how problems identified could best be addressed to maintain the abundance and distribution of waterfowl for future generations.

Key words: California, Federal Aid in Wildlife Restoration, management, Pittman-Robertson Act, science, waterfowl

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Waterfowl management and wetland conservation in California and North America have benefitted from the efforts of thousands of dedicated, passionate professionals and private individuals. In addition to this human element, the dedication of billions of dollars from public and private funds for waterfowl conservation is a fundamental cause for success.

This combined effort has allowed most waterfowl populations to flourish in the face of ever-expanding anthropogenic changes on the landscape.

METHODS

We reviewed literature, either formally published in scientific journals, or available from other sources (primarily progress reports or final reports supported by Federal Aid in Wildlife Restoration Project W30R), including some unpublished material. Through this effort, we summarize some of the scientific work produced to inform waterfowl management in California and the Pacific Flyway. We have especially recognized those contributions by California Department of Fish and Wildlife (Department) waterfowl biologists chronicled in *California Fish and Game.* We acknowledge the many individuals, agencies and organizations in California and across North America that have made, and continue to make, meaningful contributions to the scientific management of the continent's waterfowl. We also identify some of the important management events, and the resulting conservation strategies supported by scientific inquiry, that benefitted waterfowl in California over the past 100 years. In this review we emphasize information on abundance and distribution surveys, wintering habitat evaluations, breeding habitat, nesting studies, and key events in waterfowl management affecting California and the Pacific Flyway.

RESULTS AND DISCUSSION

The passage of the Migratory Bird Treaty Act in 1918 in response to dramatic declines in the abundance of migratory birds provided a coordinated nation-wide approach under the purview of the U.S. Fish and Wildlife Service (Service). Prior to World War II, the Department's principal role in waterfowl management was protection through enforcement of the regulations governing use of waterfowl (Leach 1997). A few waterfowl management areas were operated to provide food sources for birds and for recreational use, primarily hunting, by humans. The Department began a more robust scientific process to understand and manage waterfowl resources after World War II, bolstered by the passage of the Pittman-Robertson Wildlife Restoration Act and the availability of those funds to establish the Waterfowl Investigations Project (Project). By 1952 the Department had eight full-time biologists assigned to the Project; currently, the Project is staffed by two full-time scientists.

Investigations by other Pittman-Robertson projects made important contributions to the Department's science-based programs for waterfowl conservation. Of particular importance were waterfowl disease and food habits investigations. Food preference was determined by analysis of gizzard contents of thousands of waterfowl and used as a basis for plant selection in moist soil management on public and private wetlands. (George 1963, Clary and George1983). Laboratory and field investigations of diseases affecting waterfowl have been an important function of the Department's Wildlife Investigations Laboratory since the early 1950s. Emphasis was placed on detection, cause and treatment of avian cholera (Hunter and Rosen 1967, Titche 1979) and botulism (Hunter 1969, Hunter 1970, Hunter et al. 1970) and the effects of pesticides (Littrell 1986, Littrell 1988).

At about the same time as the passage of the Pittman-Robertson Wildlife Restoration Act, the Service adopted the concept of waterfowl management by four flyways (Chattin 1964). Flyway boundaries approximated north-south waterfowl migration patterns in the

United States and Mexico, but did not extend into Canada. As a result, the Service began establishing hunting regulations on a flyway basis, rather than on a nationwide basis. After much deliberation, councils of state membership were in place in each of the four flyways by 1952 through a resolution of the International Association of Fish and Wildlife Agencies (Bartonek 1984). The flyway system afforded the states the opportunity for coordination in understanding the status of waterfowl, and through memoranda of understanding between the four flyways and the Service, a unique partnership to develop waterfowl hunting regulations. The Service then established a flyway representative position in each flyway to coordinate and facilitate state participation in flyway studies and management functions (Bartonek 1984).

By the mid-20th century waterfowl again were abundant, visible and valuable to California's economy, although probably still much reduced from the late 1800s. Management actions up to that time were based on limited scientific information. Several key questions arose and many of these continue to be a focus of research and management efforts. These information needs, addressed by the best scientific methods of the day included population abundance and trends, breeding and wintering distributions, critical habitat needs, vital rates (survival, recruitment), the establishment of appropriate hunting regulations, and determining how any problems identified could be addressed to maintain the abundance and distribution of waterfowl into the future.

Abundance and distribution: surveys.—To address abundance and trend, both the Service and the Department (USDI 1988) designed standard protocols and implemented several aerial surveys. The Breeding Ground Survey (BGS) was implemented in 1948 (CDFG 1948) and consisted of complete aerial coverage of the waterfowl habitats in northeastern California (thought to be the primary waterfowl production area), and transects in the Central Valley (Chattin et al. 1949). In 1989 the BGS was redesigned to include randomized transects in areas of California with large blocks of contiguous habitat that supported breeding ducks, and double-sampling was employed to estimate visibility bias (Deuel and Yparraguirre 1989, Zezulak et al. 1991, CDFG 1992). A review of this methodology (Smith 1985) and its continued use (USFWS 2014a) demonstrate the acceptance of these survey protocols. This statistical design provides an estimate of waterfowl in the survey areas and a measure of precision, and this more robust design led to the explicit use of the California survey results in the annual regulation setting process by the Service (USFWS 2008).

The Midwinter Waterfowl Survey (MWS*)* is the oldest of the continental surveys, having been conducted in one fashion or another throughout the conterminous United States since 1936, and in California since 1955. The MWS is a cooperative effort between the Service and the various states. Conducted annually, generally during the first week in January, observers estimate the numbers of all species of waterfowl in major concentration areas. Once the primary means of monitoring population status for setting hunting regulations (Blohm 1989), the MWS now provides indices of relative winter abundance and distribution, and is not used explicitly for management decisions except for black brant (*Branta bernicla)* and tundra swans (*Cygnus columbianus*) (Pacific Flyway Council [PFC] 2001, 2002).

The MWS is not a total census; it is merely an index of waterfowl populations. Yet, variations in survey coverage, weather, observers, and distributional patterns of waterfowl markedly influence these annual indices (Eggeman and Johnson 1989). In 2011, the Pacific Flyway Council, through its Study Committee (PFSC) participated in a nationwide review of the MWS to determine its necessity and usefulness, risks associated with aerial coverage of survey areas, and ways to improve the design, logistics, and safety of the survey. The

PFSC is currently revising this long-running survey to improve statistical design, standardize methods, improve observer training, and create greater availability of qualified observers and appropriate aircraft.

In California particularly, conditions under which the MWS is conducted have changed. Prior to 1992, the survey was routinely completed in 1 to 2 days by surveying important sanctuary areas; after 1992, the practice of flooding rice for straw decomposition led to hundreds of thousands of acres of lightly disturbed habitat (Blank et al. 1993, Bird et al. 2000). This meant the survey took more days, and winter weather conditions not conducive for flying resulted in a longer period to complete the survey. Waterfowl movements among survey areas during this longer period are potentially adding variation in the value of these indices.

The most common uses for MWS results include documenting winter waterfowl distribution, providing information to the public, and developing information for winter waterfowl habitat conservation. An important use of this survey was to establish habitat protection and enhancement objectives for the Central Valley Joint Venture (CVJV), established in 1988 as an implementing function of the North American Waterfowl Management Plan (USFWS 1986). Using known energy (i.e., food) needs for ducks and geese, and an index to the wintering population and its distribution, specific habitat objectives were established for nine basins in the Central Valley (CVJV 2006).

The Mid-September Inventory (MSI) was conducted from 1953 to 2002 to better describe the abundance of ducks in the Central Valley where habitat conversions to agriculture led to waterfowl depredation, especially on the maturing rice crop (CDFG 1953). To alleviate crop depredation on private lands, waterfowl hunting seasons were sometimes delayed on public hunt areas to provide food for the newly arriving waterfowl on publicly-owned wetlands. Debates about the number and distribution of ducks led to this survey.

The survey was flown in mid-September on the major waterfowl concentration areas. By mid-September, duck migration into California is well underway and occurs simultaneously with rice crop maturation. Before population surveys were conducted it was common to hear reports of millions of ducks consuming rice crops. In order to meet administrative deadlines the decision of whether to delay the opening of waterfowl season on public hunt areas was needed in advance of the MSI and this survey was terminated.

Bi-weekly Surveys (BWS) were conducted from 1958 to 1979 during the fall and early winter to describe the timing and distribution of waterfowl throughout the Central Valley and Klamath Basin (CDFG 1958, F. M. Kozlik and J. R. LeDonne, California Department of Fish and Game, unpublished data). Aerial estimates in a manner similar to the MWS were made for the major waterfowl concentration areas during six bi-weekly surveys. The BWS also provided information to the public. These surveys were halted because higher priority surveys were needed to estimate declining goose populations from the Yukon-Kuskokwim Delta (YKD) (Pamplin 1986, Fischer and Stehn 2013, USFWS 2014b).

Fall Goose Surveys (FGS) were initiated in 1979 (Smith 1980). Declines in abundance of several YKD nesting goose populations (particularly white-fronted geese, *Anser albifrons* and cackling Canada geese, *Branta canadensis minima*) (Pamplin 1986) led to this survey in California—the primary wintering area for these geese at the time—to better describe fall populations. Indices from these surveys monitor progress towards population objectives developed in the various species plans, as well as fulfilling commitments made under the Yukon-Kuskokwim Delta Goose Management Plan (see section below).

A special December survey was also added for white geese (collectively lesser snow geese [*Chen caerulescens*] and Ross's geese [*C. rossii*]). This survey is supplemented by a trinnial ground survey following a specific protocol (McLandress 1979) to estimate the proportions of white geese that are snow geese and Ross's geese (Kelly et al. 2001, Weaver 2011) because those species cannot be reliably separated during an aerial survey.

Distribution.—Banding has been a long standing method to determine waterfowl migration routes (Crissey 1955). Waterfowl banded in breeding areas and recovered primarily by hunters described associations between breeding and migration and wintering areas. Each year since 1922 waterfowl have been captured and marked by state, Service, and private waterfowl conservation organization biologists with individually numbered leg bands to determine where and when birds are taken by hunters (USDI 1988). The Project has banded more than 350,000 waterfowl in California since 1947 (Table 1, Figure 1). To address the practical aspects of dealing with large numbers of bandings, Project staff developed certain aids to keep bands in numerical sequence and speed banding operations (Miller and Henry 1952) that are still in use today. Despite relatively large samples, it usually took decades for sufficient recoveries to occur to provide information adequate for analysis. Several studies of geese have been conducted in California using auxiliary markers that allow multiple "re-captures" of individual birds. In addition to describing the distribution of waterfowl, analyses of band returns (recoveries) have been the primary method used to assess the impact of hunting mortality on waterfowl populations (Rogers et al. 1979) by estimating vital rates such as harvest rates and survival rates.

TABLE 1.—Summary of waterfowl banded by California Department of Fish and Game personnel, 1947–2013.

Species	Number banded
Northern Pintail	161,879
Mallard	80,399
Canada geese	46,657
American Wigeon	20,645
All others	56,389
Total	365,969

FIGURE 1.—Nearly 50,000 Canada geese have been banded in California since 1947.

An early effort to describe lesser snow goose wintering distribution in California, and in their northward spring migration, was conducted from 1954 to1955 (Kozlik et al. 1959). Three chemicals were used to temporarily dye a sample of geese (Figure 2) in an effort to determine how some individual geese used various habitats of the Central Valley, and what areas were visited in spring migration. These birds were sighted in spring and summer in eastern Oregon and Montana; Alberta and Yukon Territory, Canada; and in western Alaska. Rienecker (1965) expanded on the fall and spring distribution of lesser snow geese by analyzing recoveries of standard leg bands and documented two distinct migration routes between the breeding grounds and California.

Figure 2.—Lesser snow geese color-marked with various dyes in an effort to determine local movements and migration routes (Kozlik et al. 1959).

The wintering distribution of Canada geese (*B. c. moffitti*) that nest and molt in northeastern California was also described by marking samples with uniquely numbered neck collars that were observed throughout the wintering period (Rienecker 1985a). With this technique, more information was used to describe wintering distribution than would be available through normal recoveries through bands encountered and reported by hunters. Additional studies using auxiliary markers deployed by Project personnel to describe distribution and other aspects of population ecology of geese included studies of cackling geese (Raveling and Zezulak 1992) and Aleutian Canada geese (*B. c. leucopariea)* (Woolington et al. 1979, Sanders and Trost 2013). Other neck collar marking projects with tule greater white-fronted geese (tule geese; *Anser albifrons elgasi*) by Project staff were used to describe population ecology on breeding areas in Alaska (Ely et al. 2006, Ely et al. 2007). Marking of tule geese with neck collars incorporating VHF radio transmitters and surgically implanted satellite transmitters (Figure 3) provided new insights to migration routes and stop-over areas across North America (Figure 4). Information from the VHF radio transmitters, combined with cooperative ground surveys, is currently used to estimate the population size (Yparraguirre and Weaver 2008) of the smallest population of any subspecies of geese in the world (Baldassarre 2014).

Analyses of standard leg band recoveries that described distribution included studies of redhead (*Aythya americana*) (Rienecker 1968); American wigeon (*Anas americana*) (Rienecker 1976); canvasback (*Aythya valisineria*) (Rienecker 1985b); northern pintail (*Anas acuta*) (Rienecker 1987a, Raquel 1988); Canada geese (*B. c. moffitti*) (Rienecker 1987b) and mallards (*Anas platyrhynchos*) (Rienecker 1990).

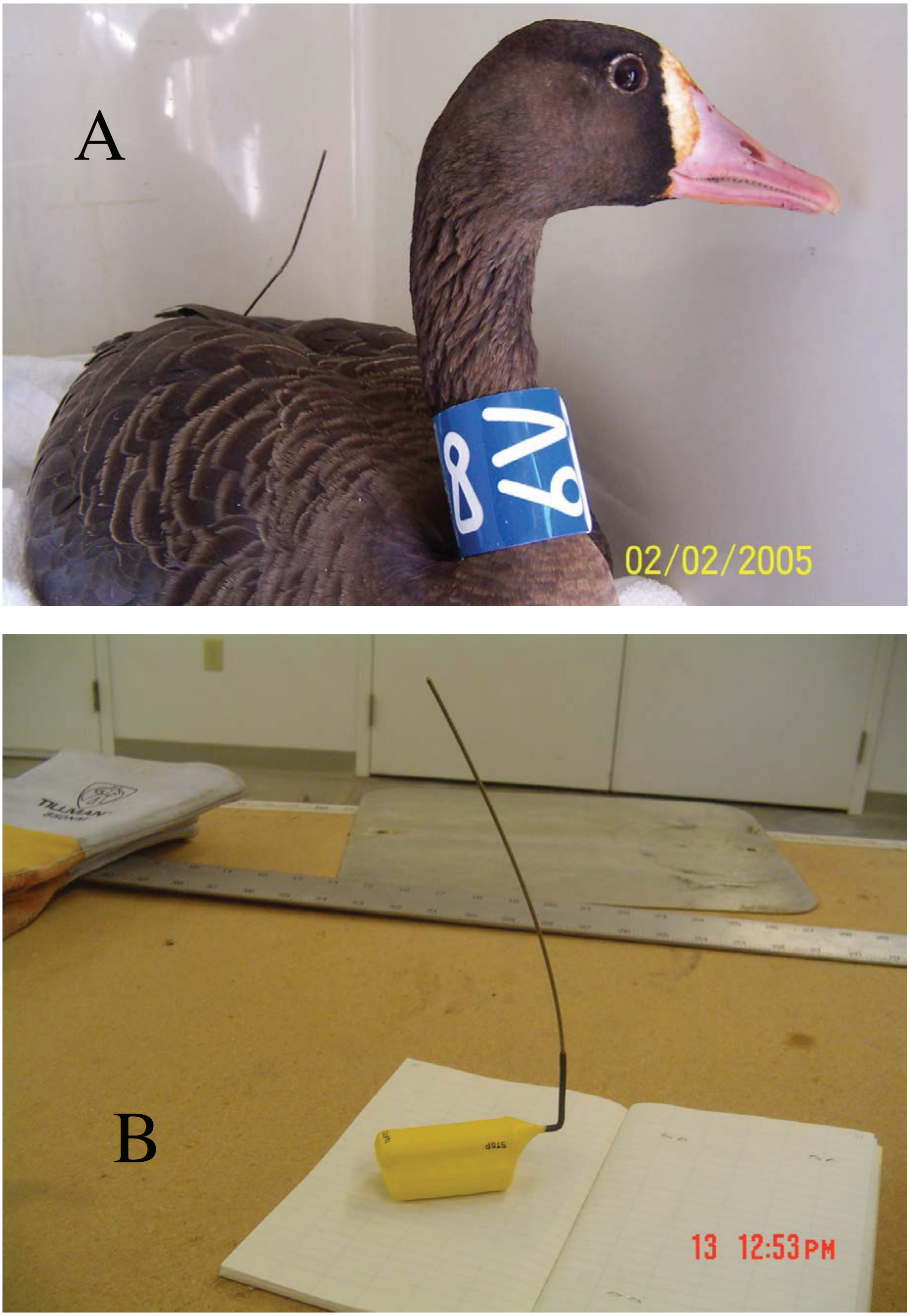

Figure 3.—(A) An adult tule white-fronted goose recovering from anesthesia following surgical implantation of an internal satellite transmitter. (B) These transmitters were placed in geese captured near Maxwell, California, during 2005 and 2006, and have been indispensable in determining migratory patterns of this subspecies.

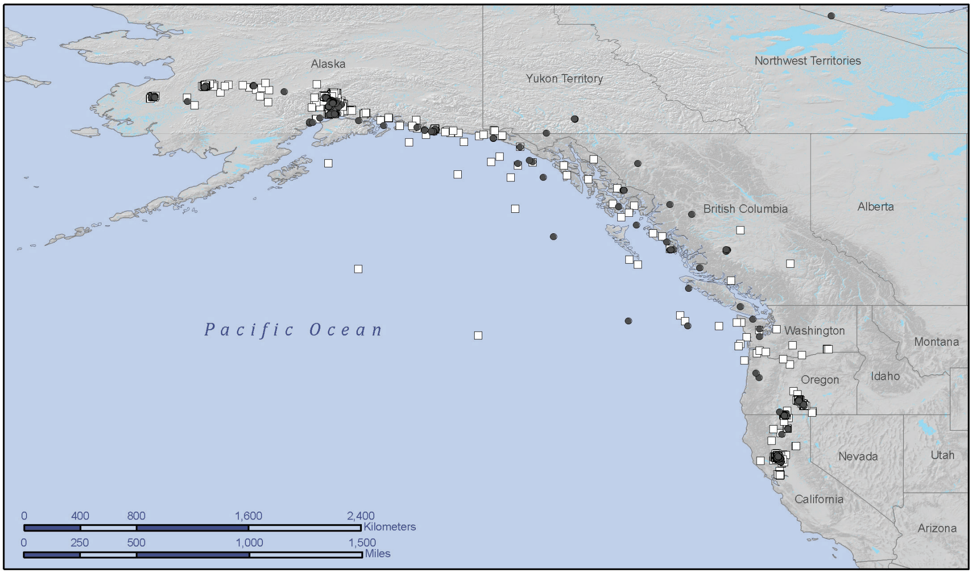

Figure 4.—Locations of satellite-based telemetry detections of tule white-fronted geese during 2005 (white squares) and 2006 (dark circles). Locations depicted are only the highest location quality for all birds marked. All (*n*=23) but one of the geese were adults when marked. Geese were captured and marked near Maxwell in the Sacramento Valley, California in a cooperative project with the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service.

Wintering habitat evaluations.—While the Central Valley of California was well known as a critically important wintering area for waterfowl in North America (Day 1949), Project personnel and others applied scientific methods to improving the habitat conditions for wintering waterfowl (Clary and George 1983). Three habitat management guides (Miller and Arend 1960, George 1963, Ermacoff 1968) were produced by Project personnel to aid in the management of wetland habitats.

The progression in habitat management was often guided by food habits studies for the particular species involved. Early studies utilized the gizzards from hunter-harvested birds (Anderson 1959). As a result, much of the early management work focused on providing grains and hard seeds which were prevalent in the food analyses (CDFG 1965a, CDFG 1965b, CDFG 1965c, CDFG 1966). Subsequent analyses identified a bias in food habits analysis from gizzard contents (Dillon 1958, Swanson and Bartonek 1970). When the contents of the esophagus and proventriculus were included, the results indicated an important intake of invertebrates (Connelly and Chesemore 1980, Miller 1987). The digestive process early in the digestive system was making the detection and identification of invertebrates virtually impossible once that food item reached the stomach. This revelation led to a much more robust management for vegetation and water that favored invertebrate food sources, in addition to that reflected by Miller and Arend (1960), George (1963), and Ermacoff (1968).

The majority of the seasonal wetland habitat in California is privately owned and is managed for waterfowl habitat and hunting (CVJV 2006). To determine the extent, management regime and trends of this habitat, surveys of duck clubs were conducted by

Project and other Department staff (CDFG 1975). As technology improved in the early 2000s, the use of satellite imagery and Geographic Information Systems (GIS) (Kempka et al. 1992) replaced the field surveys, interviews with land owners, and aerial photography (CDFG 1975) used previously to identify and monitor trends in wetland habitat managed as duck clubs.

Breeding habitat and nesting studies.—Although the large wintering waterfowl populations and their needs were a priority for research, the Project at the outset recognized that it would be critical to include studies to describe the nesting habits, habitats, and basic population parameters of common nesting waterfowl. Miller and Collins (1953) conducted a nesting study of Canada geese (*B. c. moffitti*) on the Tule Lake and Lower Klamath national wildlife refuges and determined that nest success was high and predation was not a factor in the successful production of these geese. Subsequent studies of Canada geese on the Honey Lake Wildlife Area and surrounding lands (primarily the Susan River) by Naylor (1953) and by Naylor and Hunt (1954) documented similar nest success but also documented high desertion rates (Naylor and Hunt 1954). Artificial nest structures for wood ducks (*Aix sponsa*) (Naylor 1960) and Canada geese (Rienecker 1971) were designed and tested as a way to further increase the recruitment of these species by providing “habitat” that reduced predation.

Studies of other nesting waterfowl occurred at the same time that documented high nest success for ducks (Miller and Collins 1954, Hunt and Naylor 1955, Rienecker and Anderson 1960, Hunt and Anderson 1966). These nest-success estimates were generally higher than those from more well-known duck nesting areas in Prairie Canada and the north-central United States (Klett et al. 1988, Beauchamp et al. 1996). Similar studies were expanded to other parts of California (Anderson 1956, 1957, 1960). Naylor (1960) added to the work of early ornithologists (Grinnell 1915, Dixon 1924) documenting the abundance and distribution of nesting wood ducks in California. Later, research by McLandress et al. (1996) indicated production of mallards in California was an important contribution to wintering mallard populations. The results of these studies confirmed that California was providing important nesting and production habitats for certain species of waterfowl (Kozlik 1975).

Public use and its management.—An early contribution of the Project documented the expansion of hunting opportunities for “un-attached” hunters (Kozlik 1955). As with habitat management, producing information for the public about waterfowl in California was a high priority (Kozlik et al. 1985).

The hunting program for waterfowl on state-managed lands has been closely monitored since its inception (Kozlik 1955), and substantial changes in the size and species composition of the harvest on public hunting areas has occurred over the ensuing decades (Gilmer et al. 1989, Fleskes et al. 1994). At a state and flyway-wide level, the ability to differentiate species from wing and tail feathers submitted by hunters (Carney 1992) was an important contribution. However, as changes in the environment occur over time, some methods were shown to need adjustment (Oldenburger et al. 2011).

Perhaps the greatest scientific contributions arise from the synergistic effect of the population monitoring (i.e. surveys and banding) accomplished in California by the Project and, more importantly, throughout North America by Service and other biologists, to inform harvest management (Geis et al. 1969) and investigate the role of harvest in population dynamics (Oldenburger et al. 2008, Sedinger and Herzog 2012). Advances in analytical processes led to a more advanced understanding of the role of harvest in duck population dynamics (Martin and Carney 1977) and, further, to the development of an adaptive management approach to setting duck harvest regulations (Williams and Johnson 1995, Nichols et al. 2007). Some questioned whether this more robust approach resulted in real improvements to the understanding of the fundamental processes (Humburg et al. 2000) but, by 2008, population surveys in California (along with Alaska and Oregon) were formally adopted by the Service when duck hunting regulations for the Pacific Flyway are developed (USFWS 2008).

A continuing issue of importance in California has been the establishment of hunting regulations for northern pintail. The effect of harvest on pintail has been disputed (Raveling and Heitmeyer 1989), and this work was informed by work conducted by Project biologists (Rienecker 1987c). The Project maintains an active banding program for northern pintail.

Key events.—Funding for wildlife conservation has never met the needs. In 1971, Governor Ronald Reagan signed legislation creating the first state duck stamp in the nation, modeled after the Federal Migratory Bird Hunting and Conservation Stamp introduced by the Service in 1934. These stamps are required of adult hunters for hunting waterfowl.

Since its creation, sales of the California stamp have been primarily to hunters and have provided more than $24 million for the conservation and management of habitats for waterfowl in California. In addition to providing a financial commitment for improving waterfowl and wetland conditions in the state, the enabling legislation specified a portion of the funds derived from the sale of the stamp go to Canada. This unusual specification is an indication of how strong sentiments were for improving waterfowl nesting conditions on prairies in Canada. Another example of support for prairie projects is the number of projects named in honor of their California sponsors. Indeed, three projects in Alberta, the Will Reid Project, the Lake San Francisco Project with funds from the San Pablo Rod and Gun Club; and the Walt Disney Project indicate that support (F.A. Reid, Ducks Unlimited, personal communication). This importance of the prairies of Canada as nesting sites for several species of ducks (particularly pintails), which are a principal component of the wintering ducks in California, was firmly established by the banding program (Hestbeck 1993a, 1993b) conducted by the Project personnel and other contributors.

The development and implementation of the YKD Goose Management Plan in 1984 is an example of an unprecedented emergency action to alleviate a serious problem affecting two goose species (Bartonek 1986). The numbers of cackling geese and white-fronted geese that nested in the YKD of Alaska and wintered primarily in California experienced a precipitous decline in cackling geese during the 1970s and early 1980s (Pamplin 1986). The underlying reason for the decline appeared to be overharvest (Raveling et al. 1992), but whether the harvest was on the nesting or wintering grounds, or both, was a matter of dispute. Remedial action through normal Service-Native channels could not be effected in a timely manner. Thus, the Department, its sister agency in Alaska, the Service, and a committee representing the Native villages in the YKD reached an agreement that special hunting of these species on the YKD in summer should be eliminated and hunting in California in winter severely reduced. As a result, Natives shifted their spring subsistence take to other species on the YKD. The California Fish and Game Commission, through emergency action, immediately closed the season on cackling geese and subsequently reduced the season and bag limit on white-fronted geese. Both species responded to the actions taken, and populations returned to normal and above normal within several years. The result is an example of cooperative discussions and action taken in good faith by all parties, yielding a successful conclusion. The use of previously developed science-based findings about harvest was instrumental in reaching mutual accord in this matter.

The North American Waterfowl Management Plan (NAWMP) and its related Act, the North American Wetlands Conservation Act (NAWCA) of 1986 and 1989, respectively, provided an unprecedented venue for restoring and conserving waterfowl habitat throughout North America. NAWMP was implemented in 1986 in the United States and Canada (USFWS 1986) and expanded to include Mexico in 1994. NAWMP has been updated four times since 1986 (USFWS 2014c). The first NAWMP set objectives to achieve waterfowl populations numbers prevalent in the 1970s. Improvements to and expansion of wetland habitats are the core elements employed in this plan. Program-oriented joint ventures are the main venues for implementing those habitat projects, which are funded through grants awarded through NAWCA. Non-federal matching funds are required in grant proposals. Usually, these partnerships are formed at the local level to cooperatively implement projects that achieve specific joint venture goals. The program has been operational for more than 25 years and through the partnerships is expected to continue well into the future. From 1990 to the present, approximately 5,000 partners in 2,421 projects have raised nearly $1.3 billion in NAWCA grants. They have contributed another $2.7 billion in matching funds to affect >11 million ha of habitat (USFWS 2014d).

Five joint ventures are operational in California: two are completely within the state and three include territory outside the state as well. In California through 2013, NAWCA-sponsored projects have improved about 310,000 ha at a cost of $460 million (USFWS 2014e). The Department, primarily through a role representing the Pacific Flyway Council, has served more than twenty years on various functions of NAWMP and NAWCA. During this time, the Department has encouraged the use of science in both programs, wherever feasible. Currently, the Action Plan for the 2012 update of NAWMP encourages the use of science wherever appropriate, including the process of adaptive management.

ACKNOWLEDGMENTS

The great diversity and abundance of waterfowl is a valuable and treasured part of California's natural heritage. Using scientific methods to provide for the conservation and wise use of waterfowl has been the focus of many individuals in California and elsewhere, which are too numerous to list here. For this invited review, we have focused on the contributions, primarily from the Pittman-Robertson Waterfowl Investigations Project published in *California Fish and Game* and elsewhere, but this approach does not provide sufficient credit to those individuals that have been a part of the Waterfowl Project since its establishment in 1947. In addition to the authors, W. Anderson, P. H. Arend, J. Chattin, B. D. Collins, B. E. Deuel, H. A. George, D. Hinz, F. M. Kozlik, J. R. LeDonne, H. McKinnie, A. W. Miller, A. E. Naylor, S. L. Oldenburger, W. C. Rienecker, D. A. Skalos, and J. D. Waithman have all been assigned to Project W30R.

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Evolution of ungulate capture techniques in California

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When a great need, the right people, and the right tools come together, history is sometimes made. From the late 1970s through the late 1980s that happened in California. At that time there was a need to capture elk, then deer and pronghorn, then bighorn sheep—the "big game species"—in previously unprecedented numbers. The need focused primarily on translocation to re-establish populations in areas of historic range and to consolidate gains in lands available for wildlife conservation. These efforts also advanced wild ungulate research and management. The tools were helicopters, dart guns and new drugs, various ways to physically capture wildlife including net guns, and other advances in capture technology. The right people were a small group of California Department Fish and Game employees, contract pilots, graduate students, and a host of other agency personnel, friends and volunteers. The history they made lives on in the mountains, savannahs, deserts, and grasslands of California as a wildlife legacy of more elk, deer, pronghorn and bighorn that, with continued conservation, will pass from generation to generation of future Californians.

Key words: *Antilocapra americana*, bighorn sheep, capture methods, *Cervus elaphus*, chemical immobilization, drive-net, drugs, elk, helicopter, history, mule deer, net gun, *Odocoileus hemionus*, *Ovis canadensis*, pronghorn, trapping, ungulate

Market hunting of California's wildlife from the mid-19th through the early-20th centuries in part explains why big game species, with the exception of mule deer (*Odocoileus hemionus*), were present in only small numbers in California as recently as the mid-1970s. Add habitat loss and the pervasive impacts of disease to unregulated take (market hunting or poaching), and populations of most ungulates (a term for species that walk on their hooved toes) had declined substantially from their historical levels. Prior to 1849, when gold was discovered in central California, development was limited primarily to small agricultural endeavors, the Spanish mission system, and a few coastal, towns. Although elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), and mule deer were used as sources of meat at that time, their numbers and the extent of their ranges were little diminished. During the 30–40 years following the discovery of gold at Sutter's Mill, however, hundreds of thousands of Americans flooded into the Golden State in search of fortune, and all those mouths needed to be fed. With only small herds of cattle on the range, game was the major source of red meat for many years, and the once abundant wild ungulates of California were slaughtered indiscriminately.

Historical Distribution and Early Declines of Ungulates

At the time of the gold rush, tule elk (*C. elaphus nannodes*), which were endemic to California, roamed in large numbers in riparian areas of the San Joaquin and Sacramento valleys and the oak-grassland savannas of the western foothills of the Sierra Nevada (McCullough 1969). Roosevelt elk (*C. e. roosevelti*) were present in the Siskiyou Mountains and in the northern coastal areas of the state (Harper et al. 1967). Rocky Mountain elk (*C. e. nelsoni*) occupied northeastern California (Doney et al. 1916, McAllister 1919). Various subspecies of mule deer (including the black-tailed deer, *O. h. columbianus*) occupied the Cascade Range, the coast ranges and peninsular ranges, the western foothills of the Sierra Nevada, and the high deserts east of the Sierra Nevada crest (Wallmo 1981; but, see Longhurst et al. 1976). Large herds of pronghorn roamed the alkali grasslands of the interior valleys of California, the Great Basin Desert of the eastern and northeastern parts of California, and the Mojave and Sonoran deserts (Nelson 1925). Bighorn sheep were abundant at higher elevations in the Siskiyou and Cascade mountains, including Mount Shasta (Doney et al. 1916). Bighorn sheep were also present in extreme northeastern California near the borders with Oregon and Nevada (Buechner 1960), the Sierra Nevada (Jones 1950), in the transverse and peninsular ranges of southern California (Weaver 1968, Weaver and Mensch 1970, Weaver et al. 1972, Freel 1984), and in essentially all of the island-like mountain ranges of the Mojave, Sonoran, and Great Basin deserts (Cowan 1940, Wehausen et al. 1987, Berger 1990, Wehausen 1999).

By the late 1880s tule elk were nearly extinct, despite the fact the California Legislature had passed a law in 1852 that provided for a closed season of six months in 12 counties, and that was extended to the entire state in 1854 (California Department of Fish and Game 1928, as cited by McCullough 1969). In 1872 protection was extended to 8 months of the year, and in 1878 the Legislature established a moratorium on the take of any female elk for four additional years. Rancher Henry Miller, who owned the vast Miller-Lux ranches of the southern San Joaquin Valley, was a strong advocate for protecting tule elk and cooperated with elk preservation programs (Pavey 2014). In 1932, one ranch near the town of McKittrick, Kern County, became the Tupman State Tule Elk Reserve (Burtch 1934). Eventually, tule elk that inhabited the Miller-Lux ranches were the source of the successful introduction to the Owens Valley (Dow 1934, Moffitt 1934), and those last few animals became the progenitors of all tule elk inhabiting California today (McCullough 1969, McCullough et al. 1996).

Similarly, pronghorn were slaughtered and completely exterminated from the interior of California and all of southern California. By the early 1940s, remnant herds remained only in Modoc and Lassen counties in the far northeastern part of the state (McLean 1944, CDFG 2004). The same 1872 law that protected elk also prohibited the take of pronghorn for eight months each year, and the subsequent 1878 legislation established a four-year moratorium on the take of pronghorn (Bleich 2006).

Mule deer and black-tailed deer are more dispersed, more secretive, and sometimes solitary or occur in small groups. This made them more difficult to slaughter in large numbers and they better survived the first 50 years of post-gold rush development in California than did elk or pronghorn. The same laws that protected pronghorn and elk for eight months of the year also extended to female deer. When compared to earlier periods, mule deer actually increased in numbers during the 1920s–1950s (Longhurst et al. 1976), when their predators (wolf [*Canis lupus*] and grizzly bear [*Ursus arctos*]) had been exterminated, or severely suppressed by bounty hunting (mountain lion [*Puma concolor*]).

Bighorn sheep were an important source of camp meat for desert prospectors in the 1800s and provided trophies for big game hunters in California, including Theodore Roosevelt. Even more importantly, herds of domestic sheep that were grazed in the Sierra Nevada, the Cascade and Siskiyou mountains, and in parts of the Mojave and Sonoran deserts, brought diseases that were devastating to bighorn sheep. To this day these diseases limit the potential for bighorn population recovery (Wild Sheep Working Group 2012, Brewer et al. 2014). In response to the near extinction of bighorn sheep, legislative actions in 1872 and 1878 that protected elk, pronghorn, and female mule deer also extended protection to bighorn sheep. In 1883, a moratorium on the harvest of bighorn sheep was extended indefinitely, and in 1933 that species became California's first fully protected mammal (Bleich 2005a, 2005b). Bighorn sheep inhabiting the peninsular ranges (*O. c. nelsoni*) subsequently were listed as threatened by the California Fish and Game Commission (FGC), and as an endangered distinct population segment by the U.S. Fish and Wildlife Service (Torres and Bleich 1999). Similarly, bighorn sheep occupying the Sierra Nevada (*O. c. sierrae*) initially were listed as threatened (eventually upgraded to endangered) by the FGC (Bleich and Torres 1999), and as an endangered taxon by the U.S. Fish and Wildlife Service in 2000 (Bleich 2006). Federal recovery plans were completed for bighorn sheep inhabiting the peninsular ranges and the Sierra Nevada in 2000 and 2007, respectively.

Initial Restoration Efforts

Several early efforts were made to move tule elk to other locations in the first half of the 20th Century. In 1904 a small number of elk was moved to Sequoia National Park (Merriam 1921; Figure 1), and in 1921 others were released in Yosemite National Park (McCullough et al. 1996). Both locations were beautiful, but not ecologically suitable, and those elk failed to thrive. Several additional translocations occurred from 1904 to about 1933 (McCullough et al. 1996) but, so far as is known, only those translocated in 1922 to Cache Creek in Yolo and Colusa counties have contributed to the current population (McCullough et al. 1996). A small group of tule elk was moved to the Owens Valley after the "water wars" deprived the Owens Valley of most of its irrigation water and drove farmers out of the bottom lands by allocating most of the flow in the Owens River to the city of Los Angeles. Previously tule elk had not occurred east of the Sierra Nevada (McCullough 1969).

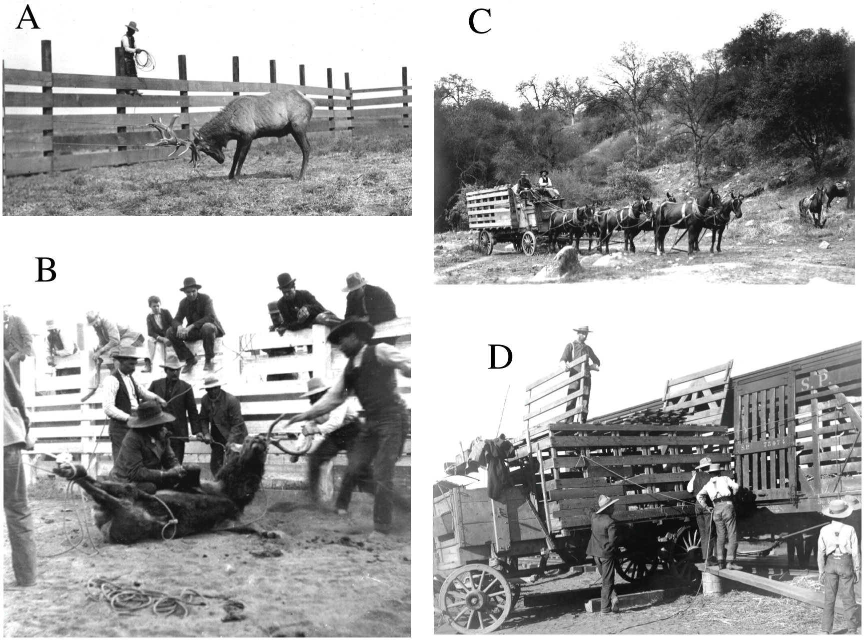

Figure 1.—An early effort to conserve large mammals involved the capture and translocation to Sequoia National Park on the western slope of the Sierra Nevada, California. In 1904, tule elk were driven into a winged corral trap on the Miller and Lux ranch near Buttonwillow, Kern County, California by approximately 35 horsemen (Merriam 1921, Pavey 2014). This effort involved several complex steps, all of which remain in place today, although the methodology has evolved substantially. (A) Bull elk were physically restrained inside the corral with ropes. (B) Antlers were then removed with a saw, a standard practice that is still used. (C) Elk were transported from Buttonwillow to a railroad siding in horse-drawn wagons. (D) The animals were then loaded into railcars and moved to the park. Photographs are by John Rowley and C. Hart Merriam, courtesy of the Museum of Vertebrate Zoology at the University of California, Berkeley, and the California Academy of Sciences.

This translocation was successful, and several hundred elk occupied the Owens Valley by the 1970s (Blankenship et al. 1986, CDFW 2014a). The population was kept in check by hunting, poaching, and accidents for many years.

Remnant herds of pronghorn in the far northeastern counties had recovered sufficiently by 1942 to allow limited drawing hunts, in large part to keep numbers from increasing to the point that their grazing created problems with ranchers. These hunts were held sporadically until 1964, and annually thereafter (CDFG 2004). Beginning in 1986, Roosevelt elk were hunted in very small numbers in northwestern California (CDFW 2014b). Limited opportunity hunts for Rocky Mountain elk were held from 1969 to 1972, closed from 1973 to 1986, and then resumed in 1987 (CDFW 2014b). Since hunts for both subspecies were all in northern California, their management was carried out largely by personnel in Region 1, the northern California administrative region of the California Department of Fish and Game (CDFG).

By the mid 1970s, only mule deer were an important "big game" animal in most of California, and the Wildlife Management Division (WMD; currently the Wildlife Branch) of CDFG offered few other big game hunting opportunities. Despite a period of intense research on big game species from the 1940s to the early 1960s, during the 1970s CDFG devoted little additional research or management effort to them. That situation changed with legislation in 1976 that mandated individual management plans for each deer herd in California; the law also established a deer plan coordinator in WMD. Following the field investigations described by Weaver (1972), another staff position in WMD was split among bighorn sheep, black bear, and mountain lion. Management authority for bighorn sheep had been with the Legislature since the late 19th Century and bighorn sheep remained a low priority for biologists in Region 5, the southern California administrative region of CDFG, where small herds remained in many of the desert mountain ranges.

In the late 1970s tule elk occurred in only two free-ranging populations (Owens Valley and Cache Creek), and two captive populations (Tupman and the San Luis Wildlife Refuge—a population started from Tupman and zoo animals in 1974). Poaching and predation seemed to keep the Cache Creek herd from growing too quickly, and there was a lot of land into which they could expand. The Owens Valley was never historic elk habitat, but early pioneers had painstakingly developed much of that area into farm and orchard land through irrigation. As the numbers of introduced tule elk increased to >400 animals (Figure 2) in six distinct herds from north of Bishop to south of Lone Pine in Inyo County, conflicts with the remaining agricultural operators and elk-vehicle collisions on U.S. Highway 395 resulted in pressure to cull animals or to allow hunting. The Friends of the Tule Elk, allied with other preservationist groups, favored translocation over culling or hunting as a management tool. They argued that approximately 500,000 tule elk once occupied the Sacramento and San Joaquin valleys, adjacent oak grasslands, and coast ranges, and that there were a number of potential locations where additional tule elk herds could be established.

For several years the opposing politics—groups wanting to increase hunting to limit the numbers of elk in the Owens Valley, and anti-hunting groups who opposed that—played out in local meetings, as well as in the California Legislature and the Governor's office. Efforts by CDFG to accommodate both sides ultimately opened the door for the large-scale capture and translocation efforts that would facilitate restocking of tule elk and other species of large mammals in suitable habitat throughout California (Clark 1978).

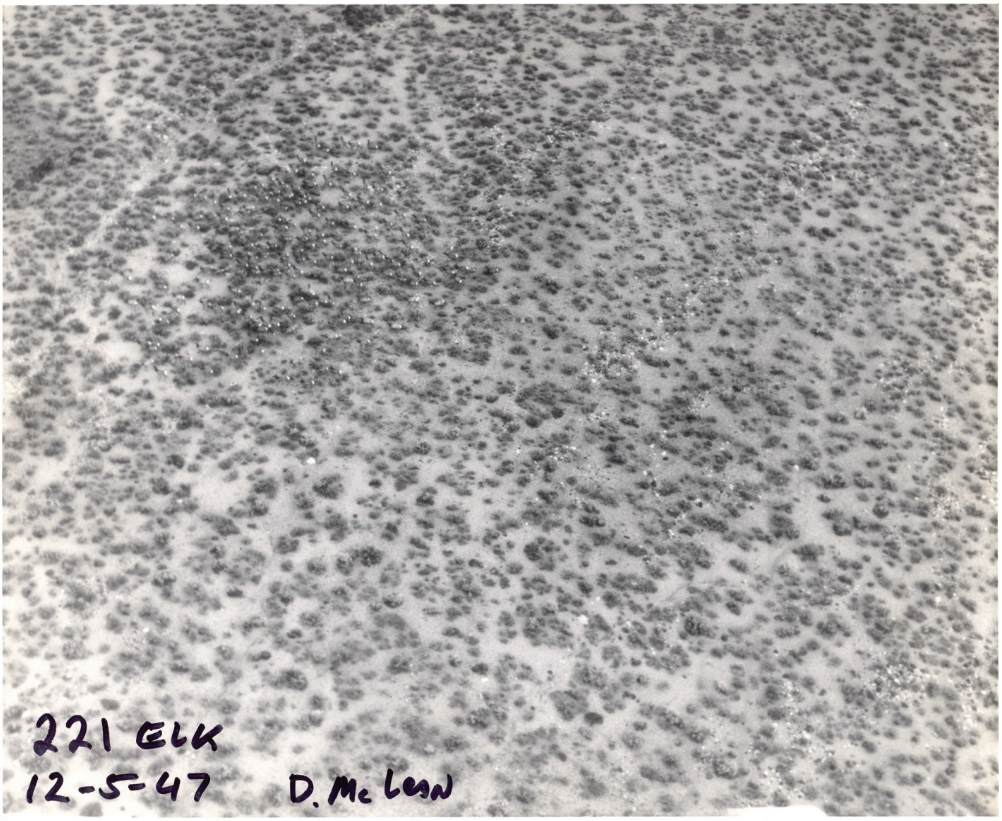

Figure 2.—During the 1940s, tule elk increased substantially in the Owens Valley, Inyo County, California. Using data from annual aerial counts, the population was managed by carefully controlled recreational hunting (photo by Donald McLean, 5 December 1947).

Compromise legislation mandated that hunting of tule elk in California could resume, but only when there were more than 2,000 animals statewide, or it was determined that no further habitat, either on public or private land (Clark 1978, Bleich and Koch 1992), was available to support them. That legislation also mandated a maximum of 490 elk in the Owens Valley (Blankenship et al. 1986). Elk had to be captured and moved in fairly large numbers to comply with these laws; it was clear that ground darting and the use of the currently available types of drugs would not be an option, and also that CDFG personnel would play a central role in the capture, relocation and restoration of California's tule elk herds.

Technological Advances

Early attempts to capture mule deer and bighorn sheep were inefficient, and generally resulted in the capture of individuals rather than groups of animals. Among these methods were leg-hold traps (Frakes 1910, Hornaday 1922), foot snares (Ashcraft 1957, DeForge 1980), and a drop-gate corral trap (Turner 1971). The successful restoration of large mammal herds in California would require efficient, large-scale capture efforts and necessitate large investments of personnel and funds (Clark 1978, Bleich 1990), and would be possible through close interagency cooperation (Keay et al. 1987, Bleich et al. 1991). Efforts to capture and translocate large mammals to historical ranges were highly successful, though, because of several technological advances, including improvements to rotary-winged aircraft, net guns, drug delivery systems, and pharmacological agents.

Helicopters.—The first commercial helicopter license was granted for the Bell model 47B in 1946, and the performance of the Bell H-13 (the military version of the Bell 47D) in the Korean war as a medical evacuation vehicle greatly advanced the technology. Limited use was made of the various Bell model 47 "whirlybirds" for herding game animals in Africa and the USA in the 1960s.

The initial use of helicopters for wildlife-related activities in California occurred in the 1950s (Dick 1979), but routine use of those aircraft by CDFG did not really begin until the late 1960s (Bleich 1983). The gasoline-fueled piston engines of the Bell 47B and similar Hiller models (12E and 12E-4) limited the ability to hover for long periods, work at higher elevations and in hot weather, or to maneuver quickly at the low levels above ground necessary for precise herding or approaches. The Vietnam War era U.S. Army light observation helicopter (LOH) competition from 1962 to 1965 resulted in the design of two totally new turbine-powered aircraft that became the Hughes 500 and the Bell Jet Ranger series. Hughes won the competition, but Bell put its design into commercial production, thereby beating Hughes into the marketplace by several years. The performance characteristics of the turbine-powered LOHs available at the onset of aerial wildlife captures in North America have been detailed elsewhere (Jessup 1982).

The increased power, maneuverability, and stability of turbine-powered helicopters greatly enhanced the use of chemical immobilization to capture the larger ungulates (moose [*Alces alces*], caribou [*Rangifer tarandus*], elk, bighorn sheep) in North America, but darting agile deer in dense brush or forests or swift pronghorn was problematic. But helicopters proved very effective at herding pronghorn into wing traps (O'Gara et al. 2004) and later for herding deer into standing drive nets (Thomas and Novak 1991). As capture operations grew more complex and sophisticated, animals caught in remote locations were flown to central processing sites for examination, treatment, marking, loading, and transport. Later, in some CDFG capture operations, multiple helicopters were used, with one serving as the capture ship and another as a "hook ship" to transport captured animals to a central processing area. In some instances, the second helicopter was also used to transport animals to remote holding areas prior to release. In one operation during 1983, a capture ship, a "hook ship", and two U.S. Navy UH-1 aircraft—into which multiple specially constructed animal transport boxes could be placed—worked simultaneously to capture, transport, and release bighorn sheep in the Eagle Crags, an area on the China Lake Naval Weapons Center, San Bernardino County, from which they had been extirpated. Helicopters also aided in delivering medical treatment. During 1987–1988, desert bighorn sheep were remotely vaccinated by shooting them in the rump with a small, dissolvable "biobullet" containing a vaccine, just as bighorn had been previously treated for scabies with biobullets containing a parasiticide in New Mexico (Jessup et al. 1991a, Jessup 1993; Figure 3).

Figure 3.—A Hughes 500 flown by Mel Cain was used in 1987 and 1988 to remotely inject bighorn sheep with a vaccine against parainfluenza-III virus. Small bioabsorbable bullets, manufactured by BallistiVet delivered the vaccine "on-the-run" in the Santa Rosa Mountains and Anza Borrego Desert State Park, California (photo courtesy of Dave Jessup).

At about the same time that commercial LOHs became common in the 1970s, the need to capture large wild animals in greater numbers increased, and the drugs and other methods required to do so were being developed (Clark 1982a). In California, these advances were spurred by increases in conservation and wildlife management needs and expectations, along with commensurate funding. All that was then needed was to combine improved methods of delivery and capture drugs, the right group of people to employ them, and a helicopter and a pilot with "the right stuff."

Chemical capture and handling techniques.—It is difficult and dangerous (some might argue crazy) to handle large, wild animals without some form of anesthesia. Efforts by CDFG personnel to capture elk in the early 1970s with the paralytic drug succinylcholine chloride resulted in several well publicized mortalities and undermined public confidence and political support for CDFG. Then Director G. Ray Arnett decreed that darting equipment and drugs belonging to CDFG would be centralized in the Wildlife Investigations Laboratory (WIL), a unit of WMD in Sacramento, to be used under supervision and training provided by WIL. Although cheap, readily available, and effective and quick when dosed correctly, succinylcholine left animals paralyzed but completely aware of their surroundings and sensitive to pain and stress. It also had a very low safety margin (10% too little was ineffective, 10% too much and the animal could suffocate from paralysis of respiratory muscles). Additionally, it was chemically unstable—breaking down with time so that dosage effects were inconsistent—and came to be regarded as inappropriate and inhumane.

From the 1950s to the 1970s, anesthesia of humans and animals was based largely on injectable (primarily intravenous) barbiturates or inhaled volatile gas anesthetics, both usually supplemented with tranquilizers. The use of narcotic drugs was generally limited to pain relief and sedation because they had serious side effects, like respiratory depression, and were generally long-acting and not reversible. These drugs, and their various combinations, had very limited application to free-ranging wild animals. For example, to achieve optimum effect, barbiturates have to be administered intravenously (not very feasible with a wild struggling animal), gases need to be precisely delivered via a controlled airway, and tranquilizers alone are not powerful enough to immobilize free-ranging elk, mule deer, pronghorn, or bighorn sheep.

The goal was also to transport free-ranging ungulates to a new location involving >12 hours of travel, so drugs could help reduce the stress and fear of confinement and risk of injury. By the 1970s, the utility of drugs to aid in the capture of truly wild animals was in its infancy and their efficacy was mostly an illusion fostered by the television program *Wild Kingdom*. The methods available for capturing free-ranging wild ungulates, including darting with drugs, were primitive and mortality rates associated with capture often exceeded 10%.

Several new classes of drugs were developed in the 1960s and early 1970s that would eventually prove useful in wildlife anesthesia. These included psychotomimetic drugs (phencyclidine and ketamine) that separated the conscious brain from the portions of the brain that govern vital functions like heart beat and respiration; powerful (but reversible) narcotics like etorphine and fentanyl; and alpha adrenergic sedative-tranquilizers like xylazine. Charged with developing safe and reliable drug combinations for use on elk and other species, CDFG personnel had successfully darted elk on refuges and in zoos from the ground with a combination of the narcotic etorphine and the tranquilizer acetylpromazine. The dilute form of those drugs required the use of large darts (5–7 cc), but the combination was fairly effective and was reversible (Clark 1978). A narcotic antagonist, diprenorphine, could subsequently be given and the elk would start breathing deeply and were able to stand and walk within minutes. Etorphine is 600–1,000× more potent than morphine—it could (and had) killed people that were accidentally injected and, as a Schedule II narcotic drug, had legally restricted availability. Additionally, it remained to be determined if the combination would work on wild elk that were highly excited after being chased from the air, and in the rough volcanic terrain of the Owens Valley. It also had to be determined whether it could be delivered accurately and safely by dart gun from a helicopter. During a few fateful days in the fall of 1977, author Bill Clark and Don Landells—the first helicopter pilot in California with "the right stuff" (and who had >20,000 hours of helicopter flight time)—would meet to decide if all the pieces were in place to capture and relocate tule elk (but more on that later).

The net gun.—Although it is not the primary subject of this review, many improvements and refinements were made in net gunning, both during the 1980s and subsequently. Net gunning as a method for wild ungulate capture had its origin with New Zealand's red deer capture industry. Tim Wallis, one of the premier New Zealand pilots and net gun capture practitioners, visited Sacramento in 1982 and met with Dave Jessup and Bill Clark. Mel Cain, another New Zealander, loaned Don Landells—a pioneer in the helicopter industry (deJesus 2012) and the owner of Landells Aviation—a helicopter-skid-mounted net gun built on a .303 Enfield receiver (Figure 4). Corey Gray developed the Coda net gun, which became the primary model licensed for sale and use in North America. Dave Jessup and Jim DeForge of Bighorn Institute were the first to capture bighorn with a net gun in California using the first Coda model, which had a triangular net.

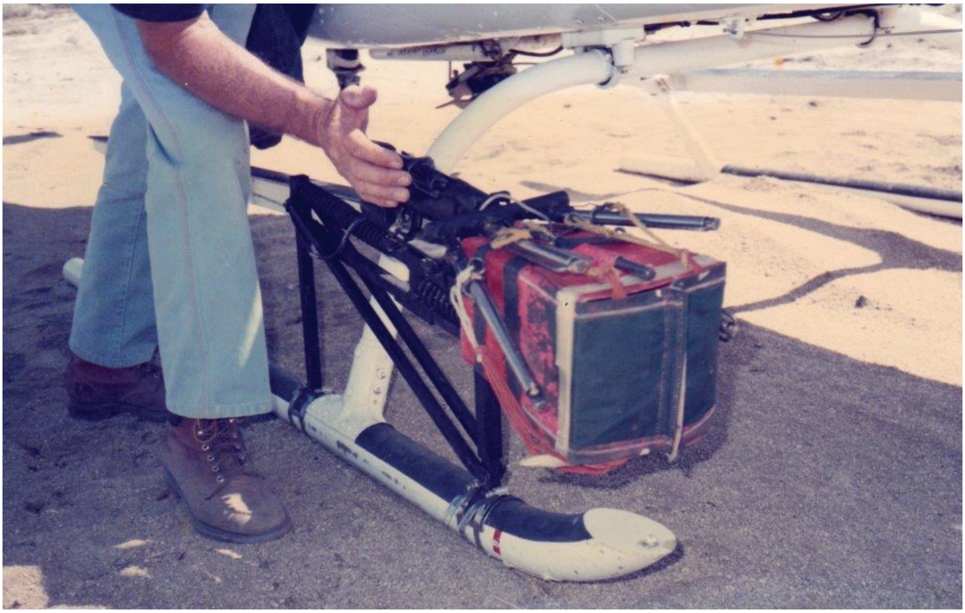

Figure 4.—The skid-mounted net gun loaned by Mel Cain to Don Landells and used to capture bighorn sheep. It was a hand-held model, but Don Landells constructed the external mount to secure it to the right skid of the Jet Ranger helicopter so that the pilot could "aim" the net gun at the target animal and then fire it. Note the recoil-absorbing spring located immediately behind the canister and below the Enfield receiver (photo by Charlie Jenner).

Author Dave Jessup and Rick Clark, a contract veterinarian, working under the supervision of Dick Weaver, made the early transition to net gunning for bighorn sheep capture operations (Jessup 1988, Jessup et al. 1988b). During a number of efforts from 1985 to 1987, up to 20 bighorn were captured by net gunning in three-day, or "long weekend" operations with a pilot, fuel truck driver, and a support crew of 3 or 4 individuals. During an operation in 1986, Don Landells and Bureau of Land Management wildlife biologist Jim Bicket died in a helicopter crash (Bleich 1987a, 1987b); Dick Weaver was very seriously injured in that same accident. After Don's death, and for the subsequent decade-and-a-half, author Steve deJesus and Brian Novak, both highly skilled pilots with Landells Aviation, took over the flying. Steve became the primary pilot for most capture efforts involving bighorn sheep, deer, and elk, most of it net-gunning. Brian also participated in net-gun captures, and became especially skilled at hazing mule deer into drive nets.

Improvements in technology, pilot skills, gunner skills, and the experience gained while working with net gunning bighorn sheep were quickly applied to deer and pronghorn and the net gun became a favored capture method (Figure 5). Eventually net gunning was used for elk, and even feral donkeys in the Sonoran Desert (Marshal et al. 2008, 2012), although bigger and heavier nets were needed. Bob Teagle, a technician at WIL, became the lead person for net-gunning in the 1990s. Baiting deer and elk into traps and bighorn sheep under drop nets, as well as ground darting and other methods were, nevertheless, still used.

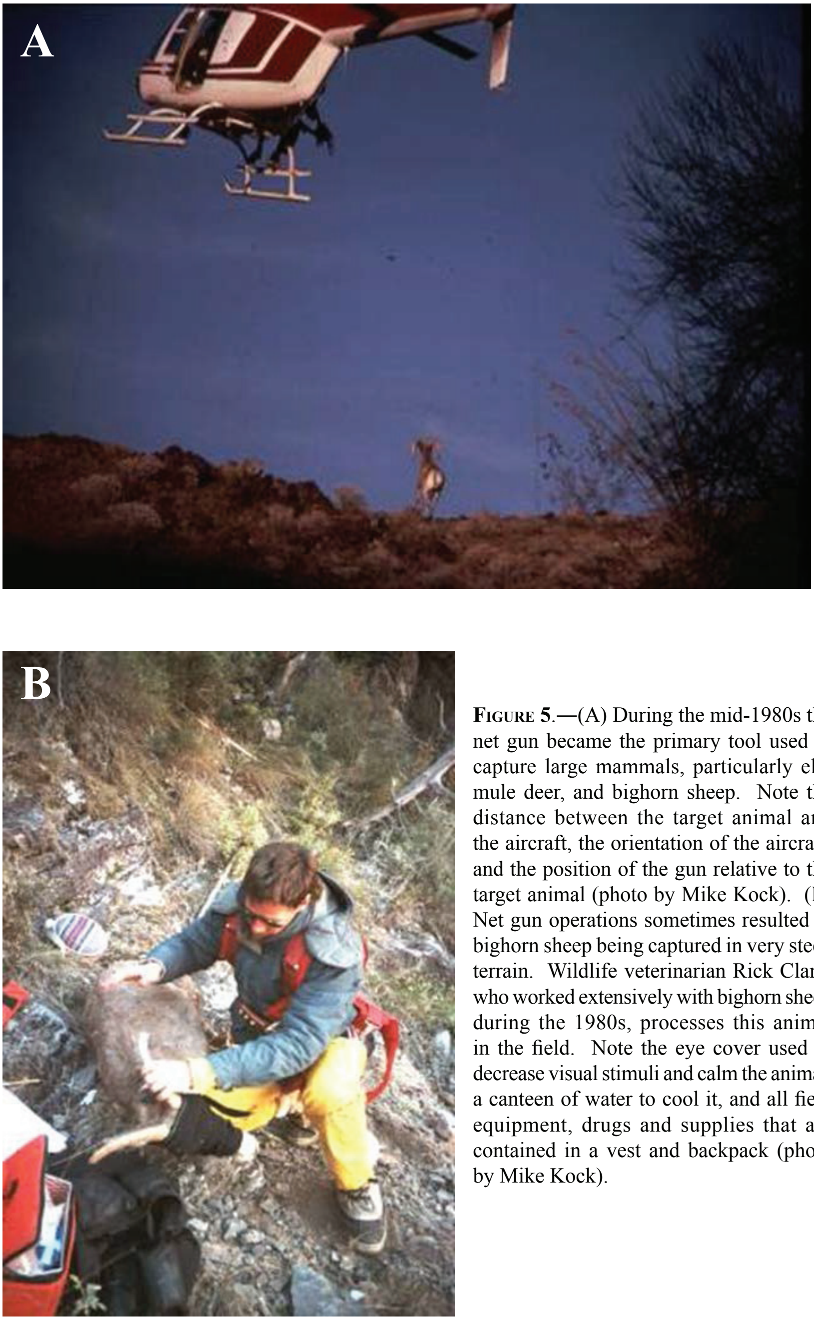

Figure 5.—(A) During the mid-1980s the net gun became the primary tool used to capture large mammals, particularly elk, mule deer, and bighorn sheep. Note the distance between the target animal and the aircraft, the orientation of the aircraft, and the position of the gun relative to the target animal (photo by Mike Kock). (B) Net gun operations sometimes resulted in bighorn sheep being captured in very steep terrain. Wildlife veterinarian Rick Clark, who worked extensively with bighorn sheep during the 1980s, processes this animal in the field. Note the eye cover used to decrease visual stimuli and calm the animal, a canteen of water to cool it, and all field equipment, drugs and supplies that are contained in a vest and backpack (photo by Mike Kock).

A Period of Intensive Capture and Restoration

Starting with elk, 1977–1978.—The job of determining whether elk in the Owens Valley could be successfully darted from a helicopter and relocated to start new herds was assigned to Bill Clark. In September 1977, Bill and Don Landells spent a day making aerial approaches on elk with a dart gun in various Owens Valley locations. They worked with Banky Curtis and Tom Blankenship, Region 5 Unit Managers in Inyo County, who had spent several years studying tule elk and were the CDFG experts on the ground. They decided that it was indeed possible to dart elk, immobilize them, pick them up and move them by truck or helicopter cargo sling, place them in a shipping crate, and then load them into horse trailers, after the immobilizing drug was reversed (Clark 1978). Bill reported this to Red Hunt, the Chief of WMD. Although it may seem like "the rest is history", it still had to be done, not just considered possible.

As the supervisor of WIL, Brian Hunter was involved in early elk darting efforts and in the first 1977 elk capture, but he soon moved on to different positions in WMD. Patti Perkins, a technician at the time, did the "lions share" of the planning, packing and managing equipment, and also handling the vital record keeping that made it possible to learn from each change in procedures. Later, Karen Jones would assume those responsibilities and become the key to organization of the biomedical teams. Other critically important staff in the early years included Ken Moore, whose capability as a field biologist and ability to fix aging state vehicles and to rewire old and borrowed (and highly modified) horse trailers made him indispensable, and Bill Grenfell, who was a steadying influence and would take on virtually any task to help ensure success. Dave Jessup was the principal veterinarian for elk capture efforts for many years, and worked to improve drug combinations, monitoring of vital signs, treatments of injuries and stress, tranquilization during transport, and prevention of disease after release. Numerous veterinarians and veterinary students came along for the experience, fun and excitement. Many other individuals played important roles in those early years, and personnel were recruited from various administrative regions within CDFG to help and to learn.

In the fall of 1977—and again in 1978—three field operations of about one week each were mounted to capture tule elk in the Owens Valley and move them to historic habitats (Clark 1978; Figure 6). All animals captured on any one day generally had to be put on the road to arrive at their destination the next morning because wild elk couldn't be kept from killing themselves or each other in closely confined trailers much longer than that. Three small horse trailers were modified to prevent easy escape; internal swinging dividers were added to facilitate loading and separation of animals, as were darkened openings that channeled in air and vented heat. Because CDFG was not yet fully committed to the elk capture and translocation program, no investment was made in professional-quality trailers or vehicles. This subsequently resulted in injuries and stress to both the elk and their captors.

Capture days began at "zero dark thirty" and each brought many new lessons. Gas-pressure dart guns were not reliable because ambient temperatures were highly variable and CO_2 cartridges were quickly exhausted. When .22 caliber blank cartridge-powered dart guns were used, the darts struck too hard; darts had to be pushed halfway down the barrel so the increased volume of the gas expansion chamber would slow the dart and keep it from embedding in the elk. On really cold mornings, drugs could freeze in the dart, so they were kept in cigar tubes (to contain the potentially lethal drugs) in a pouch inside the shooter's

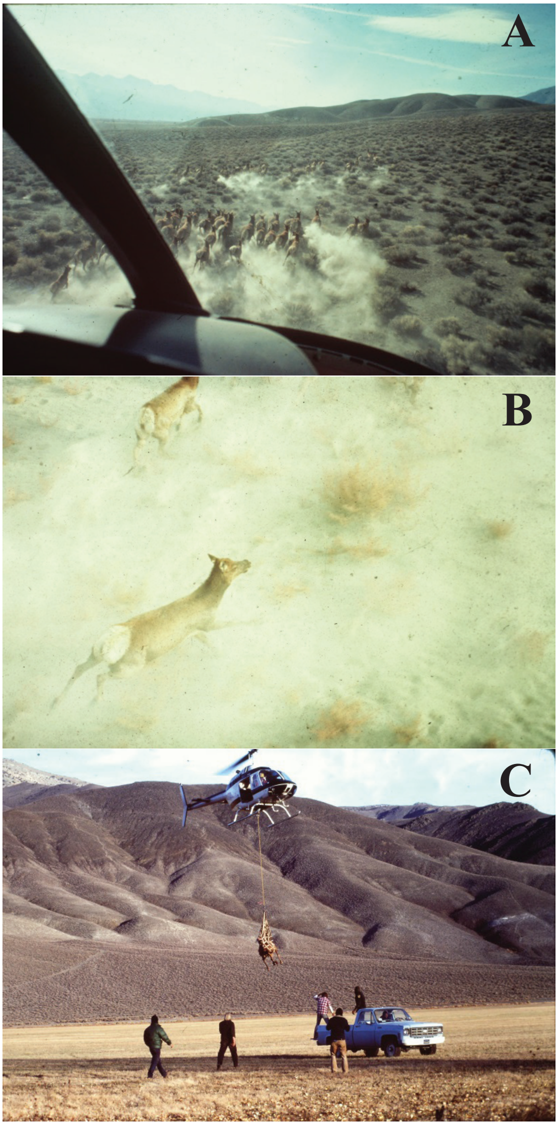

Figure 6.—(A) Beginning in 1978, free-ranging elk in the Owens Valley were captured with the use of a low-flying helicopter. (B) Individuals were darted with a narcotic-tranquilizer combination, and hobbled and blind-folded once immobile. (C) Each animal was then transported to a base camp where they were medically assessed, treated, marked, sampled, and loaded into trailers after the narcotic was reversed. These actions helped reduce the Owens Valley population and start new populations in areas of historic tule elk habitat in western and central California (photos by Dave Dick).

jacket. As the gunner leaned further and further out the back seat of the helicopter, and eventually stood on the skids, to improve accuracy, it became clear seat belts did not provide adequate restraint, even with the addition of duct tape to ensure that buckles would not pop open. A safety harness was quickly made from belts and leather hobbles until more professional safety harnesses were developed.

Dilute drugs meant large darts, and darts larger than 5 cc were too heavy and aerodynamically unstable. Sometimes after being darted, elk did not go completely down, likely a result of the combination of excitement, low dosage rates, dilute drugs, slow absorption, or poor dart placement. Some elk would stand stupefied but, if a person approached them slowly—bent over and walking elk-like, holding a brown and white eye cover that looked like an animal's rump patch—it was possible to walk up to a drugged—but still standing—animal, place the cover over its eyes, and gently get it to lie down so it could be hobbled and further restrained (Figure 7). Initially, war surplus Army chest bandages were used as eye covers and secured with gauze. Reducing or eliminating visual stimuli and keeping voices and foreign sounds to a minimum helped animals relax. As operations evolved cut-off pant legs were used as a quicker form of eye cover, and then custom made spandex eye covers with Velcro straps. These simple improvements in eye covers proved to be even more useful when handling deer, pronghorn and bighorn sheep. We

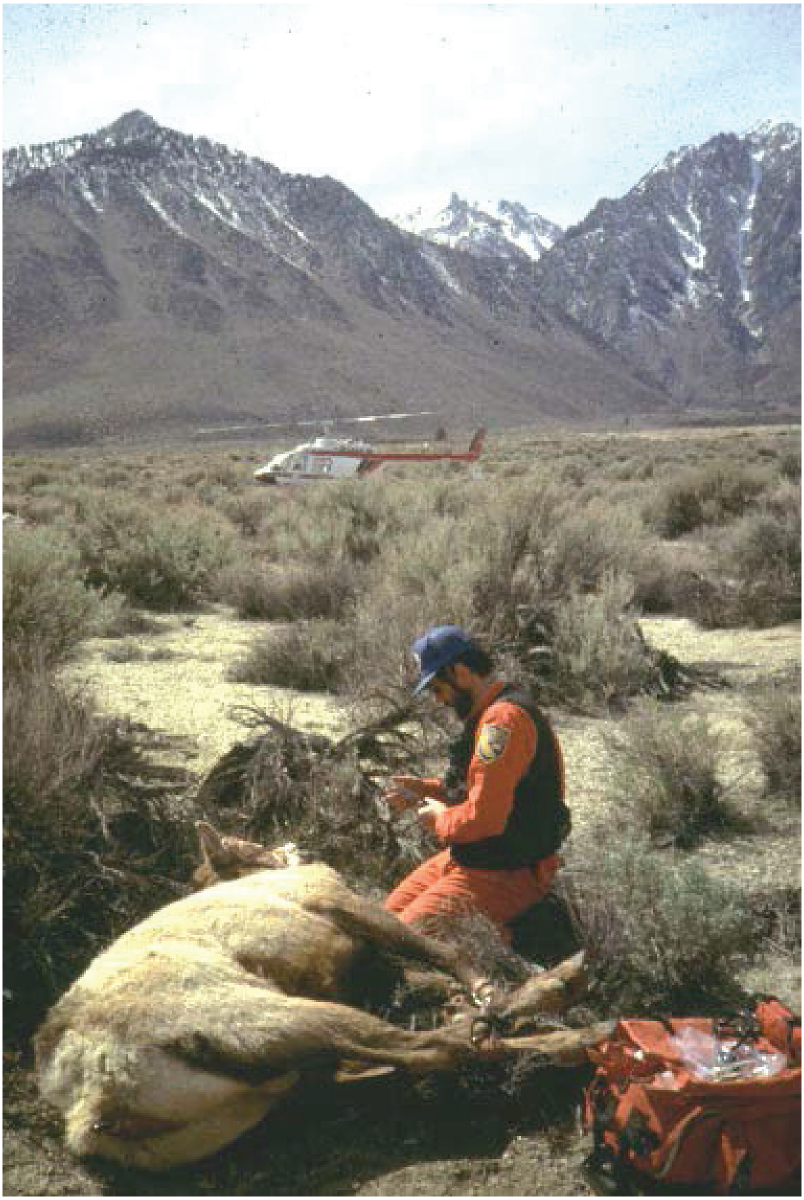

Figure 7.—Don Koch, the CDFG Elk Coordinator at the time—and who later would be appointed Director of the California Department of Fish and Game—processes a female tule elk that had been immobilized with carfentanil and xylazine, and fits her with a radio collar. The carfentanil and xylazine were reversed with naltrexone and yohimbine (respectively) and the elk released on site to supply information on habitat utilization in the Owens Valley, Inyo County, California (photo courtesy Dave Jessup).

learned that when releasing bighorn in the wild their eyes needed to adjust to sunlight for a few seconds or they would stumble and fall on steep terrain. Use of eye covers, along with leather hobbles to bind the feet together in case they startled, made handling lightly anesthetized wild ungulates safer and more effective. Anything that could be done to reduce sensory stimulation and fear helped the process.

After a couple of elk choked and died when being transported out of a remote area in a cargo net, litters were built from the heavy, steel frames of a fish hatchery raceway screen from which the screen had been removed and replaced with netting; Don Landells then designed and fabricated several light-weight litters that could be transported between the skids of the helicopter, and then by long-line below the aircraft after they were loaded with animals (Figure 8). Litters allowed elk and other species to be transported from a capture site to a central processing area without any possibility of pressure on the throat, and also made it much easier to carry the heavy animals from place to place while they were

Figure 8.—(A) Authors Bill Clark (R) and Vern Bleich discuss the transport of bighorn sheep strapped to litters used to move animals following capture in Cattle Canyon in the San Gabriel Mountains, Los Angeles County, California, in 1985. These animals were captured with a drop-net and sedated with xylazine, which was reversed upon their delivery minutes later to a central processing area. Note the heavy steel transport litter in the foreground, and the lightweight, aluminum transport litter in the background, which was designed and fabricated by Don Landells to transport individual tule elk from capture sites to a central processing area, and later proved invaluable for transporting multiple bighorn sheep. (B) A secondary benefit of the "Landells Litter" was the ability to stow it between the skids helicopter and to move multiple crates containing bighorn sheep into remote, mountainous areas prior to release. In this 1985 photograph, helicopter pilot Brian Novak delivers three crates containing bighorn sheep to San Rafael Peak, Ventura County, California, to restore them to an area from which they had been extirpated (photos © B. Moose Peterson).

unconscious. The litters fabricated by Don Landells were of great value in other ways: they could be carried between the skids immediately below the helicopter fuselage, and during translocations up to three crates containing bighorn sheep could be moved into remote areas for release. Ultimately, mesh bags were developed that were more portable than litters and provided better positioning and support and no risk of choking during aerial transport.

It was quickly discovered that elk chased for more than 5 minutes would get too hot and could die if darted. Monitoring body temperature (at that time with a glass, large-animal rectal thermometer) and other vital signs was a critically important task. Despite efforts to cool animals that included dousing them with cold water and alcohol baths at base camp, and even dunking them in canals or icy streams, some animals died of hyperthermia. Besides limiting chase time, we learned that pulling the helicopter back immediately from a darted elk allowed it to rejoin the herd and relax while the drugs took effect, generally providing better all-around results. By wetting hot animals in the field, we learned that they cooled down considerably while they were flown to a base camp.

By organizing everything so elk could be processed very quickly we could reverse them sooner, which restored normal respiration and optimized cooling and recovery. While age, sex and other information and observations were recorded, vital signs (temperature, respiration and heart rate) were taken, ear tags and some radio collars for follow-up studies were attached, prophylactic (antibiotics, vaccinations, and stress relieving) medications were administered, and blood samples were drawn. The latter eventually provided an extensive health history for most of California's elk herds, and allowed California elk to be recognized as free of brucellosis and not subject to quarantine and testing. Routine blood sample collection and testing became standard protocols for other species, as each capture event was seen as a unique opportunity to look at the health of individuals and populations. Every day, and every trip, brought new lessons and knowledge, and adjustments were made "on-the-spot" as the need was realized. Following each capture season personnel spent weeks going over data and laboratory results. These sessions would help us understand what worked and what didn't, and how we could improve.

The high body temperatures and slow response to drugs experienced in 1977 led to modification of the drug combination. The sedative xylazine was substituted for the less potent tranquilizer, acepromazine. Doing so allowed more narcotic to be used, and resulted in more rapid "down times." The xylazine also helped keep elk drowsy in the transport trailers. Diazepam (Valium) was often given to elk in trailers as it both calmed and relaxed muscles, but didn't result in animals laying down and getting trampled as could happen with acepromazine. In the 1980s a new, extremely potent narcotic (carfentanil) was tested. It allowed much smaller darts (1 or 2 cc) to be used and also afforded much more rapid immobilization (Jessup et al. 1985a).

In 1977, and again in 1978, trailers full of elk arrived at Grizzly Island Wildlife Management Area, Concord Naval Weapons station, Point Reyes National Seashore, the Hewlett-Packard Ranch in Santa Clara County, and several places in Potter Valley, Mendocino County. But, even though elk could be successfully and selectively captured from the various elk herds of the Owens Valley, the costs were high and the numbers removed barely kept the total below the maximum allowed. Another method had to be found to remove more elk more quickly and less expensively.

Game changer.—In the spring of 1979 Bill Clark and Dave Jessup stood on a hill just east of Highway 395, about 50 km south of Bishop and just north of the Tinnemaha

Reservoir, and looked at what seemed to be a perfect place to build a large corral trap. There were many elk trails from the alfalfa fields to the north leading into the wooded riparian area along the reservoir, and it was at the edge of a hill separating it from Highway 395. A year later, after several weeks spent building long fences—also referred to as wings—to funnel animals into a central corral, and covering the wings with brush and disguising the corral with burlap, the great experiment in mass elk capture was ready. Don Landells used his helicopter to haze 66 elk into the trap and they were captured, processed, loaded, and shipped in a single day (Figure 9). A new page had been turned and although chemical immobilization was still in use—all bulls had to be darted to remove their antlers—CDFG was moving more and more toward larger capture operations and physical capture techniques.

The ability to herd elk into corral traps and remove them in larger numbers changed everything. It made the capture and removal of substantial numbers of elk from the Owens Valley feasible, and allowed control of the overall size of the population in a more cost-effective manner. Repeated several times in the Owens Valley, corral trapping was also used to capture and remove elk on occasion from Grizzly Island—where the first translocated herds had quickly outstripped the available forage and begun to consume toxic plants (Jessup et al. 1986a). Baiting elk into corral traps and loading them through chutes also worked to

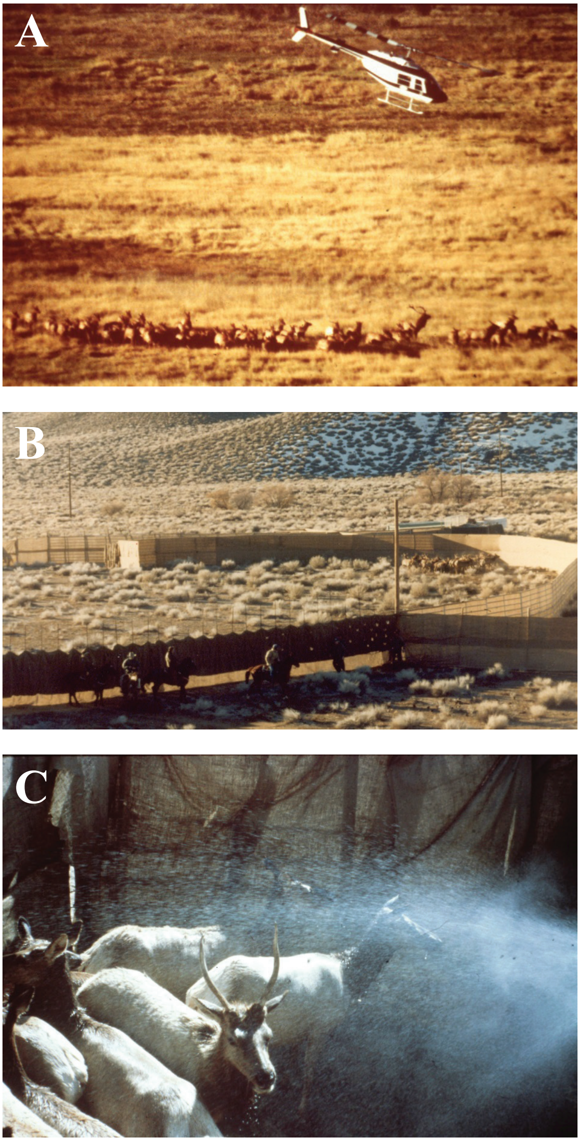

Figure 9.—(A) Don Landells herds tule elk toward a corral trap equipped with long "wings" just north of Tinnemaha Reservoir, Inyo County, California, in 1979. This was the first mass capture of tule elk in the Owens Valley and 66 elk were captured, processed, loaded, and shipped in one day. Photo by Dave Dick. (B) Tule elk in a corral trap, Owens Valley, Inyo County, California, 1981. Horsemen helped herd these animals into the trap and then a sliding curtain was closed to prevent their escape. The western "wing" of the trap extends northward from the powerpole immediately to the right of the horsemen (photo by Jeanne Clark). (C) Elk captured in corral traps frequently were hyperthermic. Trucks with thousands of gallons of water provided by personnel from the Mount Whitney Fish Hatchery were used to help cool the elk following long drives (photo by Dave Jessup).

reduce the herd at Tupman Tule Elk Reserve State Park and at Concord Naval Weapons Station. Roosevelt elk were baited into corral traps at Gold Bluffs Beach and at Prairie Creek State Park in Humboldt County. All of those elk served as founders of new herds on public lands, as well as on private ranches where limited elk hunts could now be planned (Bleich and Koch 1992).

Between 1977 and 1988 a total of 813 tule elk, including 422 from the Owens Valley, were captured and translocated to 18 sites in California to start new herds (Jessup 1988, Jessup et al. 1988a). After the legislative mandates were reached, hunting was reinstated in 1989 as a tool to manage tule elk populations in the Owens Valley and elsewhere. Over the same 12 years, 130 elk were captured and translocated from Tupman Tule Elk Reserve State Park, which by then had essentially turned into an elk feedlot. Eighty-four others were removed from San Luis National Wildlife Refuge and used to restock other suitable, but vacant, areas of California. One hundred and twenty four were removed from Grizzly Island Wildlife Management Area, a herd that was founded in 1977 as a result of the early translocation efforts. Tule elk, a distinct subspecies endemic to California, were successfully restored to some of their historic range, and Californians had another big game species that could be sustainably harvested (McCullough et al. 1996). Today, revenues from elk hunting pay for much of the costs of elk management. Elk hunting and viewing provide excellent outdoor recreational opportunities that previously were extremely limited or non-existent before intensive capture and translocation operations were implemented and new herds were started.

Advances in deer capture.—Prior to 1977 there were only a few ways deer were captured in California: foot snares (Ashcraft 1957), by attracting them to bait in panel traps (Figure 10) or Clover traps (Clover 1954, 1956; McCullough 1975) and physically restraining them (Figure 11), or by darting them with drugs—usually from a vehicle. Each of these methods was very time consuming, physical handling was dangerous and resulted in many injuries to workers and animals, and these methods yielded, at most, only one or two animals per day; nevertheless, those methods continue to be useful in some situations (Pierce et al. 2000).

New drug combinations were developed that were more effective and allowed darts to be reduced in size, increasing accuracy and reducing injuries to targeted animals. CDFG personnel were on the forefront of developments in wildlife pharmacology for a decade and a half, and pioneered use of carfentanil and its reversal, first naloxone and then naltrexone (Jessup et al. 1984, 1985a). Several non-narcotic drug combinations also were developed. By freeze-drying ketamine and reconstituting it with xylazine, a safe and non-narcotic combination was developed. This combination was partially reversible with the drug yohimbine, and could be used to dart deer (Jessup et al. 1983). This combination was eventually replaced with another partially reversible combination of Telazol and xylazine. In a different ratio of ketamine to xylazine the combination would prove useful on a very wide variety of carnivores and omnivores. Xylazine could also be used to sedate deer in Clover traps, thereby reducing the likelihood of physical trauma or injury to both deer and handler, then reversed with yohimbine (Jessup et al. 1985b). In the 1980s and 1990s, medetomadine would largely replace xylazine and atipamezole would replace yohimbine.

The knowledge gained as a result of all of this work was presented in CDFG-sponsored courses for biologists and veterinarians that were developed and taught by WIL personnel, and published in leading biology and veterinary journals. Additionally, CDFG

Figure 10.—This panel trap baited with alfalfa hay was used to capture mule deer from the Devil's Garden area, Modoc County, California, in 1948. Forty mule deer from that area were translocated to the Providence Mountains in the eastern Mojave Desert, San Bernardino County, California (Longhurst et al. 1952, Cronin and Bleich 1995; photo courtesy of Vern Bleich).

Figure 11.—A substantial improvement over panel traps occurred with the development of the Clover trap in the 1950s, particularly those designed to be collapsed on the animal—usually a mule deer— inside the trap. Deer so captured could be more easily handled and even sedated with xylazine and, after marking and processing, reversed with yohimbine, as demonstrated by Martha Schauss, Henry Coletto, and Walt Smith (photo by Mike Oliver).

biologists or wardens working in field settings were required to be certified in animal restraint techniques every five years. These standards were adopted by adjacent states (Oregon, Washington and Nevada) and eventually became widely accepted across the USA and Canada.

In 1982 CDFG began using drive nets, a method that had been pioneered earlier in New Mexico (Beasom et al. 1980). The first nets used by CDFG were borrowed from the New Mexico Game and Fish Department, and when they proved effective for mass capture of deer and bighorn sheep, CDFG procured nets custom made by commercial fishing supply companies in San Pedro, California. Deer, usually from winter range concentrations, were gently herded by helicopter into sections of large-mesh gill nets ≈35-m long and ≈3-m in height and set up in various configurations using terrain features to obscure them (Thomas and Novak 1991). Although deer sometimes avoided the nets or managed to escape, it was common to catch 3 or 4 on any one drive, and 20 or more per day (Figure 12).

Figure 12.—Deer and bighorn sheep were frequently captured in standing drive nets during the 1980s and 1990s. These nets are being set to capture migratory mule deer on a winter range immediately west of Manzanar, Inyo County, California, in 1983 (photo by Dave Jessup).

In the late 1980s, helicopter pilot Brian Novak successfully herded >120 deer into drive nets over 2.5 days along the California-Nevada border, where a veterinarian and a large crew of biologists from CDFG and Nevada Division of Wildlife were waiting to restrain them. Most of those animals were tagged or radio-collared and released on site, and >80 were sampled for a variety of diseases and other health factors. Although these operations were labor intensive for a few days at a time, the era of catching one or two deer per day was over.

The purpose of most deer captures at that time was for marking and the study of migration and habitat utilization, not for translocation. An exception was an effort to remove deer from Angel Island in San Francisco Bay, where they had increased from 25 to over 200 and had devastated the forage resources. Every technique available (drop net, drive net, darting, clover traps) was used to capture deer from the island, and 201 deer were removed in an effort to reduce the population and lessen the effects of disease and malnutrition (Clark 1982b, McCullough 1983; Figure 13). The translocation of deer from the island was demanded by animal rights advocates and supported by decision-makers outside CDFG concerned about the animals' welfare; unfortunately, the deer had no experience with predators, were in generally poor nutritional condition, and were dependent upon supplemental feed; as a result, survival among the translocated animals was very poor (O'Bryan and McCullough 1985, Jessup et al. 1988a).

Baiting deer and bighorn sheep under drop nets was also used successfully (Figure 14). When deer are captured with this method, however, they panic and fiercely fight capture, creating a dangerous and stressful situation; thus, drop nets have not commonly been used to capture them. Eventually net gunning from a helicopter proved an efficient and highly selective method for capturing deer for research (Pierce et al. 2000, 2004; Bleich et al. 2005; Monteith et al. 2011, 2013). For example, skilled pilots and capture personnel have been able

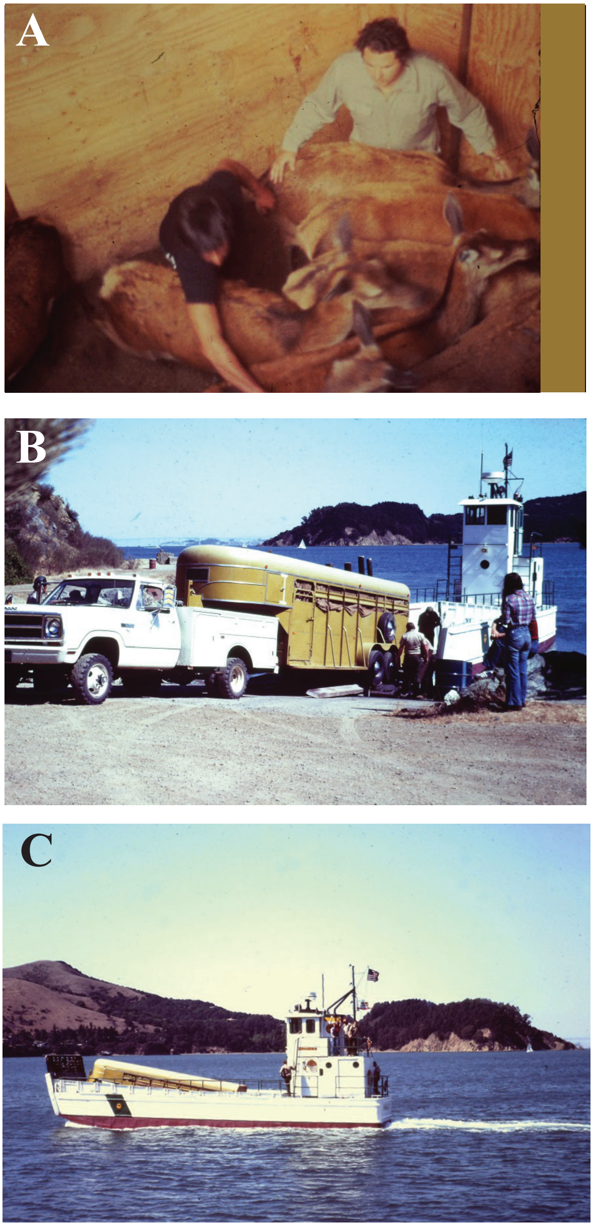

FIGURE 13.—Many methods were used to capture starving deer on Angel Island in 1982. (A) Deer sedated with xylazine and diazepam were gently sorted inside a darkened custom-built pen where they were held until transportation off the island could be scheduled. (B) Captive deer were then placed in specially modified trailers for transport to a boat dock. (C) The trailers were loaded on a LST for transport to the mainland in Marin County where they were off-loaded and then towed to Cow Mountain in Mendocino County, where the deer were released. More than 200 mule deer were removed from the island, which has an area of about 5 km^2 (photos by Dave Jessup)

Figure 14.—Drop nets were used very successfully to capture bighorn sheep and mule deer under the appropriate circumstances. In 1983, 1985, and 1987 volunteer Bill McIntyre (seen here in his trademark red jacket), a member of the Society for the Conservation of Bighorn Sheep, camped alone in remote areas of the San Gabriel Mountains for >2 months to facilitate three successful capture efforts. Bill's dedication ensured the successful translocation of 65 bighorn sheep to historically occupied areas in the Prairie Fork of the San Gabriel River (*n*=22) and San Rafael Peak (*n*=43), Ventura County, from the South Fork of Lytle Creek and from Cattle Canyon, respectively (photo © B. Moose Peterson).

to capture numerous marked or radio-collared individuals multiple times over periods of many years to better understand the reproductive histories and nutritional status of individual animals in Round Valley, California (Monteith et al. 2011, 2013).

Advances in pronghorn management.—By the 1970s pronghorn occurred in 6 or 7 herds in Lassen, Modoc and Shasta counties, where their numbers were controlled by carefully regulated harvests. A small number of pronghorn also existed in Mono County, the result of several translocations from 1947 to 1950 (CDFG 2004), but that interstate population was not hunted in California. In some locations in northeastern California, harvest rates did not provide sufficient control to keep pronghorn out of alfalfa fields and the choice was to remove them using lethal means or use them for restocking historically occupied geographic areas. When in a herd and being pursued, pronghorn behave much like a school of fish, grouping tightly and moving together. Other states previously had success herding them with a helicopter into very large funnel-shaped traps with long wings that led to a central corral with an opaque, flexible curtain that could be closed quickly to prevent animals from escaping after they entered the trap (O'Gara et al. 2004). California began using this method because earlier efforts to herd pronghorn with vehicles or people with bells and noisemakers were not successful.

Led by Bud Pyshora, Doug Thayer, Dave Smith, and Tim Burton, 650 pronghorn were captured for translocation from 1977 to 1988 by herding them with a helicopter into specially constructed wing traps (Jessup et al. 1988a, CDFG 2004; Figure 15). The wings

Figure 15.—Pronghorn have excellent vision, are highly excitable, and have evolved to outrun coursing predators. They can be driven with a helicopter into winged corral traps constructed with see-through netting but later covered with burlap after the pronghorn are captured so that the sides of the corral appear to be solid. Pronghorn captured in this manner generally are in large groups comprised of males, females, and young that are exhausted and physiologically stressed, as demonstrated by these animals captured in Modoc County, California, in 1979 (photo by Tim Burton).

and corral were made of a large, fairly open mesh that did not appear solid to the pronghorn. Once in the corral burlap was quickly pulled up to make the walls appear solid. It proved relatively easy to capture groups of 30-60 at a time, but very difficult to separate them into smaller groups and load them for transport. Most pronghorn captured were translocated to establish additional populations in Lassen, Los Angeles, Mono, San Luis Obispo, San Benito, and Tehama counties, or to augment an existing population near Bodie, Mono County.

Net gunning proved to be useful for capturing individual pronghorn for marking, but their speed requires that the shooter "lead" the animal more than would be the case with deer, elk, or bighorn sheep. The net gun was not, however, efficient for mass capture. The only meaningful pharmacologic contributions to the capture of pronghorn were in the area of tranquilizers that reduced stress and injury during transport. Again, conservation activities and translocations were beneficial to the residents of California through the re-establishment of pronghorn on native ranges, with a secondary benefit of enhanced public hunting opportunities.

Advances in bighorn sheep conservation.—Until 1986, when the California Legislature gave CDFG authority to again manage bighorn sheep, there was relatively little effort put into research and management of this species, and there was no hunting (Bleich 2006). Nevertheless, the first translocation of bighorn sheep in California occurred in 1971, when 8 females and 2 males were captured on a game farm in British Columbia, and released at Lava Beds National Monument, Siskiyou County (Blaisdell 1972, Weaver 1972). That population grew to over 60 animals. In February 1980, an effort to herd these bighorn into a very large, solid corral at Lava Beds turned tragic when six of ten animals died of capture myopathy (Figure 16), and only four were translocated to the Warner Mountains, Modoc County (Sleznick 1980). But, this event indirectly resulted in the advancement of bighorn

Figure 16.—(A) Author Dave Jessup carries a live bighorn yearling captured at the Lava Beds National Monument enclosure located in Siskiyou County, California, in 1980. Of 10 animals captured, only four survived this tragic episode in California Department of Fish and Game's otherwise stellar history of translocating large mammals (photo by Diane Plechner). (B) Deep discussions among those leading the capture effort ensued immediately, as author Dave Jessup, project leader Dick Weaver, and author Bill Clark consider the outcome. This event led to private funding to study capture methodologies, physiology, and medical treatment, which resulted in many improvements that benefited bighorn sheep and other wild ungulates (photo by Diane Plechner).

sheep management and translocation techniques when the Shikar Safari Foundation—a private organization of dedicated hunter-conservationists—donated $64,000 (a large amount that the time) to fund a study of capture stress and muscle damage (myopathy) caused by various capture techniques used on bighorn sheep, the morbidity and mortality they caused, and subsequent survival.

This study of bighorn capture methods prompted by the Lava Beds sheep deaths resulted in a 4-year Western States regional investigation (wildlife agencies in Oregon, Nevada and Arizona cooperated by allowing California researchers to participate, and to collect data and samples) and the publication of a series of papers (Kock et al. 1987a, 1987b, 1987c; Jessup et al. 1988b) comparing capture methods that, even 25 years later, remain definitive contributions. Those investigators demonstrated convincingly that, under most prevailing conditions in California, net-gunning was the safest, least stressful, and most cost-efficient method for capturing free-ranging bighorn sheep in locations where they could not be attracted to bait.

Drop-netting proved to be useful in some locations where bighorn could be habituated to bait (usually fermented apple pulp, alfalfa, or salt). Drive-netting was more widely applicable, but the terrain favored by bighorn made it very difficult to set up nets, and bighorn seldom were captured in the numbers necessary to justify the effort. Darting with etorphine, and then carfentanil combinations, was tried but rejected early on, although tranquilizing sheep with low doses of xylazine or diazepam to reduce stress and facilitate transport was done quite regularly. Net-gunning became the favored method, and early captures involved the use of both skid-mounted and hand-held versions. With bighorn, as with elk and deer, various capture methods were tried, improved upon, and adjusted as needed. Each capture operation brought new knowledge and refinement of methods.

At first, the capture of bighorn sheep was primarily for translocation to historic ranges from which they had been extirpated by disease, habitat degradation, or market hunting. In 1979, ten "California" bighorn sheep (now recognized as Sierra Nevada bighorn sheep, *O. c. sierrae*), were captured using a drop-net in the central Sierra Nevada, Inyo County, and translocated to establish a new population at Wheeler Ridge in that same mountain range (Bleich 1990a). From 1979 to 1982, an additional 50 bighorn were captured in the same area and moved to three locations in the Sierra Nevada that historically had supported populations, and to the Warner Mountains, Modoc County (Bleich et al. 1990a, 1996a). Drop nets and drive nets were used, and the same helicopter pilot (Don Landells) and many of the same capture personnel that participated in elk capture work were involved. These early bighorn translocations were led by Dick Weaver of WMD, and included Tom Blankinship, author Vern Bleich, John Wehausen, the WIL crew, and many others. In 1986 and 1988 another 43 of these bighorn were captured to supplement the three recently established Sierra Nevada populations (Bleich et al. 1990a, 1996a). Unfortunately, the bighorn sheep at Lava Beds National Monument, as well as those in the Warner Mountains that largely came from the Sierra Nevada, died as a result of respiratory disease that developed following their contact with domestic sheep (Foreyt and Jessup 1982, Weaver 1983, Weaver and Clark 1988).

In 1983 CDFG was charged by the California Legislature with surveying all bighorn sheep habitat in California and, to the extent possible, capturing, marking, and sampling bighorn in every occupied mountain range (Bleich 2006). The goal was to establish a baseline of biological, ecological, genetic, and health information to optimize population management. Capture for translocation and starting new herds was also authorized. The two most productive desert bighorn populations, those at Old Dad Peak and the Marble Mountains, were used as stock for translocating bighorn to historically occupied desert ranges. Most capture was by net-gunning, although drive nets were also employed. The San Gabriel bighorn population in Los Angeles County was also productive enough in some years to allow the translocation of animals to vacant ranges in Los Angeles and Ventura counties (Bleich et al. 1990a). In the San Gabriel Mountains, the use of the drop net baited with alfalfa hay and salt blocks was very effective.

From 1983 to 1988, primarily under the direction of author Vern Bleich, approximately 330 bighorn sheep were captured for translocation to sites in 11 mountain ranges where they had historically occurred, or at the time occurred in low numbers. Bighorn sheep were restored to ranges in Riverside, San Bernardino, Inyo, Mono, Los Angeles, and Ventura counties (Clark et al. 1988, Bleich et al. 1990a). When it was possible to transport bighorn sheep to a release site by truck and trailer, that method was used; however, when the release site was in a remote mountainous area—as were those in the Bullion Mountains and the Eagle Crags (San Bernardino Co.), the Chuckwalla Mountains (Riverside Co.), Mt. Baden-Powell (Los Angeles Co.), and San Rafael Peak (Ventura Co.)—animals were transported via helicopter into the range (Figure 8) and held in an enclosure prior to release for several hours after the last individuals had arrived. We had learned from our initial experiences at the Eagle Crags and in the Prairie Fork, where bighorn sheep were released as they arrived via helicopter, that repeated flights and releases stimulated the sheep to scatter further and further from the release site. So we developed and used the holding pen at release sites accessible only by helicopter, so that all animals could be released simultaneously (Figure 17). We also learned that there was no difference in the grouping behavior of bighorn sheep released from such an enclosure and those released simultaneously from a vehicle (Thompson et al. 2001).

Figure 17.—U.S. Forest Service Biologist the late Steve Holl (right) and author Vern Bleich release bighorn sheep from an enclosure at a remote location near San Rafael Peak, Ventura County, California in 1985. These animals had been held for several hours after the last individuals had been transported to the enclosure via helicopter. To allow the animals to disperse cohesively following the release, several weeks passed before the pen was dismantled and flown out (photo © B. Moose Peterson).

In addition to animals that were translocated, >600 other bighorn were captured for marking and sampling in remote mountain ranges, and released on site. The legislative mandate to sample and investigate disease, genetics, and ecology of bighorn resulted in a large number of scientific publications. The importance and effects of various diseases and parasites were clarified (Dunbar et al. 1985; Clark et al. 1985; Boyce et al. 1991a, 1991b; Mazet et al. 1992; Goff et al. 1993; Thomford et al. 1993; Jessup et al. 1993a). A clearer and more accurate picture of genetic relationships between bighorn populations began to emerge, and this information helped pave the way for the taxonomic reclassification of a number of populations.

By marking bighorn in many populations with radio collars, information was gleaned regarding movement patterns, critically important habitat, and previously undocumented movements among populations. Investigators posited that bighorn sheep in California existed as a metapopulation (Schwartz et al. 1986, Bleich et al. 1990b, 1996b). Subpopulations comprising the metapopulations were subsequently defined and became primary units for conservation (Torres et al. 1993, 1994). Estimates of size of the subpopulations were also refined (Torres and Bleich 1999). Combined with more accurate and meaningful demographic data, this information resulted in greater confidence in proposed management strategies, and helped justify the implementation of limited hunting of older adult males beginning in 1987 (Bleich 2006). This, in turn, began to provide much of the funding to support ongoing management of all bighorn sheep in California, including the small number of populations that were hunted as well as the numerous other non-hunted populations. Funds generated from the bighorn sheep hunting program now pay for most of the research and management efforts undertaken to conserve bighorn sheep in the Golden State.

SUMMARY

Tremendous advances, both in the physical and chemical capture of deer, elk, pronghorn, and bighorn sheep in California took place during the 1970s and 1980s. These advances were made available internationally in a series of courses, manuals (Jessup and Clark 1980, 1982; Jessup et al. 1986b), and books (Jessup et al. 1991b), as well as numerous professional publications. Courses on wildlife capture taught by CDFG personnel throughout the western United States resulted the availability of instructional manuals with new information to hundreds of wildlife biologists throughout the Western U.S. and around the world. Under a series of sole-source contracts, Landells Aviation was employed by CDFG for more than two decades. During the 1980s, pilots Steve deJesus and Brian Novak joined the capture crews, and assumed the roles of capture pilots in 1986, following the tragic accident that killed Don Landells and BLM wildlife biologist Jim Bicket.

The many advances in capture technology that led to the restocking of big game species in California was the work of many dedicated people. Don Landells would be the first to credit all the other folks who worked so hard to conserve and care for the animals, but he gave at least as much to that effort as did any other individual. The legacies of the convergence of people, capture methods, and the conservation needs of big game species are several and substantial. Tule elk (and to a lesser extent Roosevelt elk), bighorn sheep, and pronghorn are much more widely distributed across suitable and historically occupied habitats in California than they were 35 years ago, and certainly are more numerous than they were 100 years ago, when the first issue of *California Fish and Game* was published. Tule elk can regularly be seen along Highway 152 around the San Luis Reservoir, Point Reyes National Seashore, and other locations throughout the state. Elk at Mount Hamilton and and in the Coast Ranges move from one herd to another, and northward into eastern Alameda county. In a number of places the presence of these restored game species has changed land management policies. On the Carrizo Plain in eastern San Benito, eastern San Luis Obispo, and western Kern counties, the restoration of tule elk and pronghorn after an absence of nearly 100 years has been described as restocking an "American Serengeti." The presence of Roosevelt elk in the Marble Mountains of northern California has changed some Forest Service policies. Forest Service and other federal agency policies and priorities have been modified to accommodate the needs of bighorn sheep in many locations in the state.

Californians can anticipate that these magnificent animals will continue to thrive for many generations, provide ecosystem services, serve as umbrella species for wildlife conservation programs on publically owned lands, be seen and photographed, and in some locations can even be hunted. California Department of Fish and Wildlife and the management of these species now benefit from greater public support, and from hunting revenue that is dedicated to species management efforts. Much more is known about the animals themselves because all of the capture and relocation efforts were well documented, were usually used as an opportunity to assess the health of the species, and were often coupled with telemetry-based investigations of habitat use and basic biology. Because most of the scientific information derived was published, other scientists and wildlife management efforts elsewhere have benefitted, and many personnel gained a fuller understanding of the biological and health implications associated with wildlife capture efforts (Jessup et al. 1993b).

The efforts to improve "big game" distributions and to enhance management did not end in the 1990s, and they continue today. But after 1988 the emphasis began shifting to hunting as a tool for managing surplus populations of elk and pronghorn, rather than translocation. Further, many of the areas historically occupied by elk, pronghorn, and bighorn sheep that California's history had left empty, were getting filled. And, conflicts—as much political as biological—between agricultural interests and conservation interests began to be felt in Sacramento and elsewhere, and reduced support for restocking public lands with wildlife (Koch 1987).

Perhaps the best way to summarize this history is that for about a decade in the last quarter of the 20th Century, there was an opportunity to reestablish depleted native ungulate populations in California, and the right people and the right tools came together at the right time to accomplish that important conservation work. Because that work was undertaken with an eye toward learning from each effort, improving the constantly evolving methods (what we now call adaptive management), and the acquisition of solid scientific data and subsequent analyses, those contributions included not only the acquisition of new knowledge but pragmatic application of that knowledge, resulting in many more animals "on the mountain" in California and elsewhere.

It wasn't always easy or fun, often it was dirty, exhausting and frustrating, even heartbreaking. All of us were driven by various inner angels and demons. Nevertheless, it was real, it was important, we all worked together selflessly for the critters, and we were all as alive as we would ever feel.

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William E. (Bill) Clark passed away unexpectedly prior to completion of the manuscript; thus, any errors or omissions in this historical account are solely the responsibility of the other authors. Bill's dedication to and support of the evolution of capture methodologies were vital to many of the successes described here. Don Landells, with a sly grin, would often refer to Bill as "The Wagonmaster" after the Ward Bond character in the 1950s and 1960s TV series of the same name. Like that character, in his element Bill could command, inspire, convince, or cajole just about anyone to do what he thought needed to be done.

Don Landells lent his skills and expertise to those efforts involving the use of helicopters, and provided many years of service to the development and evaluation of capture methods and to the restoration of large mammals to historical ranges. Following Don's untimely death, Brian Novak shared capture duties with co-author Steve deJesus, and became very skilled at implementing drive-net captures.

We thank the many dedicated employees of the California Department of Fish and Game and other agencies that participated in early efforts to translocate elk, pronghorn, bighorn sheep, and mule deer; many of them volunteered their time to do so, and we suspect that they will recall participation in such events as being among the highlights of their professional careers. Among those that played important roles in the evolution of capture methods but not previously mentioned are CDFG employees Randy Imai, John Parrish, Les Coombes, Ron Thomas, Rocky Thompson. Don Pine, Jim Lidberg, Andy Pauli, and Vern Koontz, and veterinarians Bud Adams and Pat Gullett. Dozens of others, far too numerous to acknowledge individually, contributed in many meaningful ways. We thank S. Osborn and J. Clark for many helpful suggestions that resulted in a markedly improved manuscript, and J. Hobbs and J. Fischer for providing important reference material and background information. This is Professional Paper 107 from the Eastern Sierra Center for Applied Population Ecology.

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Enumerating mountain lions: a comparison of two indices

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Assessing mountain lion (*Puma concolor*) populations is difficult due to their inherently low densities, secretive nature, and a near absence of demographically closed populations. We developed and compared two methods of indexing the number of mountain lions within a subset (referred to in this paper as the core area) of a total study area. The study area was defined as the outer boundary of combined home range polygons for all collared mountain lions. Therefore, the study area was regularly occupied by uncollared individuals whose home ranges overlapped the study area boundary. We determined through intensive capture efforts and monitoring that the much smaller core area was used only by adult mountain lions that we had identified and collared and was not used in any significant manner by uncollared adults. We derived two indices to the number of lions using the core area. One index is based on location data from VHF aerial telemetry ("fixed wing index"); the second index is based on a combination of fixed wing locations and GPS collar data combined ("location data index"). The fixed wing index yields the mean number (and variance) of adult individuals located in the core region of the study area each of 15 winters during weekly telemetry flights. The location data index is based on the sum of the proportions of locations for each individual that are within the core area each winter. The two indices were highly correlated, and the trends generally were in the same direction and changes in each were of a similar magnitude. These methods are preferable to attempting total counts because the periphery of any study area will occasionally be occupied by unmarked animals. Our methods account for those individuals, but they are not afforded the same weight as mountain lions that use the area frequently or exclusively. Managers with GPS radio collar data are encouraged to delineate a core area, where all lions known to use the area are collared, and use the sum of the proportion of locations from each individual in that area to index density, population size, number of animals present, or use.

Key words: abundance, density, index, mountain lion, puma, *Puma concolor*

There are a number of methods for assessing mountain lion (*Puma concolor*) population size and population trends; however, none of these has proven to be consistent and reliable (Jenks 2011). Further, the use of differing methods by managers among jurisdictions makes comparisons across regions difficult and questionable. Population estimators are inherently biased because the methods used to collect the data are biased. Nevertheless, many researchers believe that the most reliable estimates of density (individuals/unit area) are derived from long-term radio-telemetry studies that attempt to mark and keep track of all animals in a given geographic area (Jenks 2011). This method, however, is best considered a minimum count for which no variance can be calculated. Despite this potential shortcoming, that method is used widely by researchers and is considered the "gold standard" for determining mountain lion numbers, against which indices to mountain lion abundance should be compared (Seidensticker et al. 1973, Hemker et al. 1984, Logan and Sweanor 2001). Other methods, including non-invasive camera traps (e.g., Hughson et al. 2010), scent stations (e.g., Long et al. 2003)—or a combination of the two (Munoz-Pedreros et al. 1995)—and genetic techniques using material obtained from hair snares or feces (e.g., Ernest et al. 2000) also are problematic (see Rinehart et al. 2014 for a comprehensive review).

An index is a number that is monotonically related to population size. The best indices are linearly related to the true size of the population (Cougar Management Guidelines Working Group 2005). However, unless detection probabilities are known or estimated from the data, index values can reveal little about other parameters of interest, such as adult survival or fecundity (Anderson 2001, 2003), as re-emphasized by B. L. Pierce et al. (2012). Many indices to the abundance of mountain lions have been developed and, despite the admonition of Anderson (2003), the application of an index does not automatically imply an inappropriate procedure (Engeman 2003), as they can be useful in detecting large changes in a population or determining directional trends. Most indices, however, are never calibrated with a population of known size (B. L. Pierce et al. 2012).

Track surveys, which have been widely used for many decades are not reliable (Grigione et al. 1999) because they can be biased by habitat type, substrate, skill of the tracker, weather conditions, the likelihood of missing a transient animal, traffic volume, or the ability to distinguish among individuals. McBride et al. (2008) developed an index based on the minimum number of lions known to be alive, but it is most useful for small closed populations studied for a long period of time, such as those isolated by urbanization. However, it should not be relied upon for inferences about population trends (Cougar Management Guidelines Working Group 2005). Additionally, hunter returns can be affected by hunting effort, harvest bias for sex or age class, and variance in the ability of individual mountain lions to elude hunters.

Choate et al. (2006) reviewed the most commonly used population indices for mountain lions while testing their accuracy with radio collared populations. They found that track surveys, catch per unit effort, and other methods—such as harvest models and scent stations—performed poorly. Those authors noted, however, that multiple indices used after an initial population estimate could be used conservatively to support short-term management decisions. As a result, Choate et al. (2006) maintained that an intensive effort to radio collar individual lions is the most reliable method to enumerate population size, estimate density, and determine trends in population growth. Similarly, Rinehart et al. (2014) described biases associated with various methods of calculating population densities of secretive carnivores and concluded, "... radio-telemetry remains the most viable option for certain carnivore species, pumas among them."

Choate et al. (2006) calculated density by dividing the total number of individuals estimated to be present by the size of the study area, expressing density as the number of animals/unit area. Density estimates for species with overlapping home ranges, however, can be subject either to extrapolation bias or residency bias (Rinehart et al. 2014). Extrapolation bias results when scaling a density to a spatial extent that differs from that of the study area upon which the estimate was based; residency bias occurs when the reference area for the density estimate is inappropriate (Rinehart et al. 2014). Using a series of modeling exercises, Rinehart et al. (2014) concluded that density estimates are biased upward for open populations; estimates projected "backwards" from large to smaller areas resulted in negative bias, and the extrapolation "forwards" from a small area to a larger one resulted in positive bias.

Some genetic substructuring has been reported among mountain lion populations (Walker et al. 2001, Ernest et al. 2003), but populations in the western United States and throughout their range are rarely isolated from each other (Sinclair et al. 2001, Stoner et al. 2006, Andreasen et al. 2012). Indeed, mountain lions are capable of seasonal, long-distance migratory movements (Pierce et al. 1999), and are known to travel hundreds of kilometers when dispersing from natal areas (Thompson and Jenks 2010). Moreover, both home range size and the distribution of mountain lions can be affected by sex, or availability of resources such as prey (Seidensticker et al. 1973, Pierce et al. 2000b; see Pierce and Bleich 2003 for a comprehensive review). Therefore, the designation of a study area, based on the extent of the movements of collared mountain lions is problematic and the estimation of population size and population trends for mountain lions based on study area boundaries can be misleading.

As a result of these demographic and life history characteristics, use of a study area by known individuals whose home ranges overlap the pre-established boundaries are overestimated because some individuals might be present in the study area only infrequently. Additionally, transient animals could be counted as unique individuals, even if only present on the study area temporarily. Mountain lion populations that are radio collared after intensive efforts to catch a majority of individuals present remain the best method for calculating population estimates and trends (Rinehart et al. 2014). We tested the idea that collaring every lion within or near a particular geographic area is the most meaningful method to determine population density and trend if the proportional amount of radio telemetry data for each individual within that geographic area is considered. Further, we compared the results of two indices derived from that method.

Materials and Methods

Study area.—Round Valley (118° 28' W, 37° 28' N), located east of the Sierra Nevada in eastern California, is the winter range for a migratory population of mule deer, and the mountain lions that prey upon them (Kucera 1988, Pierce et al. 2004, Monteith et al. 2011, B. M. Pierce et al. 2012, Monteith et al. 2014). Mean monthly temperatures range from 8° C to 16.8° C. The predominant vegetation type in Round Valley is sagebrush steppe (Pierce et al. 2004), characteristic of the western Great Basin.

Methods.—During 1991–2007 we used hounds or snares to capture mountain lions that used the Round Valley winter range and, beginning in 2000, individuals throughout the eastern Sierra Nevada including Round Valley, for the purpose of protecting Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), an endangered taxon (USFWS 2007). We considered any mountain lion that was no longer dependent on its mother to be an adult. We conducted regular and intensive searches for mountain lions throughout the study area during 1991–2007. These intensive searches provided strong evidence that all mountain lions that used the winter range in Round Valley were fitted with radio collars by 1993, a situation that remained constant throughout our investigation. Detailed descriptions of searches for mountain lions and mule deer killed by predators were provided previously by Pierce et al. (1998, 2000a, 2000b; B. M. Pierce et al. 2012).

We focused our efforts for this study during winter because we were interested in the impacts of mountain lion predation on mule deer and bighorn sheep on winter ranges. Both species use concentrated areas in Round Valley during winter; additionally, we discovered that during summer, some mountain lions made long distance movements, following the migrating mule deer to the west side of the Sierra Nevada, or moved east to other mountain ranges (Pierce et al. 1999) . Those long distance movements made collecting location data more difficult, and expanded the study area causing it to overlap a much larger number of unmarked mountain lions. Therefore, the core area was representative of the collared mountain lions using winter ranges but not summer ranges.

We developed the fixed wing index prior to the availability of GPS radio collars for mountain lions. Following the deployment of GPS collars on mountain lions in 1998 (Bleich et al. 2000), we continued with the fixed wing flights and were able to compare that index to one using the proportion of locations from VHF data alone (fixed wing index) and combined VHF and GPS data (location data index). We determined the mean number of collared mountain lions on the study area during telemetry flights at weekly intervals from November to April each year, and used that value to index the number of adult mountain lions on the winter range annually. We excluded winter 1991–1992, because we captured the first mountain lion during December 1991 and continued to capture new, unmarked lions in Round Valley until November 1992, by which time we had captured 12 adults. From then on, our intensive effort to detect and capture new, unmarked lions was constant from year to year (Pierce et al. 2000a, 2000b). All research methods were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks, and complied with guidelines published by the American Society of Mammalogists for research on wild mammals (Committee on Acceptable Field Methods 1987).

We delineated a 450 km^2 core area within the intensively hunted Round Valley study area (Figure 1). Fixed-wing telemetry flights for mountain lions emphasized locating all animals known to use the core area in Round Valley. We used the same pilots and aircraft as those used by Nicholson et al. (1997) and Oehler et al. (2004), and location error (±170 m) was small (12.5 ha) compared to the size of the core area (450 km^2).We plotted locations using ArcView 9.3, and the number of adult mountain lions located within the core area during each weekly flight was averaged for each winter. The average number of mountain lions located within the core area during telemetry flights constituted the fixed wing index for each year. Concurrently, location data from combined aerial telemetry and GPS collar locations for adult mountain lions known to use the core area were plotted. The proportion of locations that landed within the core area during winter was calculated for

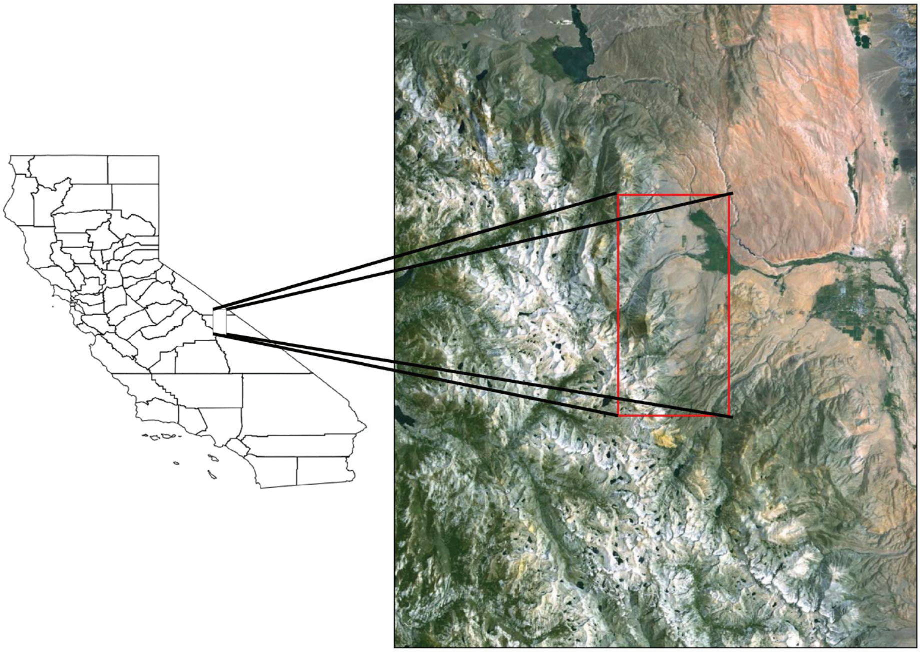

FIGURE 1.—The study area and pre-defined core area encompassing Round Valley (118° 28' W, 37° 28' N), Inyo and Mono counties, California, that was established to develop indices to the number of mountain lions (*Puma concolor*) present in the core area each winter from 1993 to 2007, as described in this paper.

each individual, and those proportions were summed to produce the location data index. For example if there was a total of two mountain lions known to use the core area during a particular winter, a mountain lion with 50% of its total locations within the core area and a mountain lion with all of its locations in the core area, the first lion would receive a score of 0.5, while the second would receive a score of 1.0. Those values would then be summed, yielding a location data index of 1.5 mountain lions for the winter.

We tested for association between the indices over 15 years (1993–2007) with the Spearman Rank Correlation Coefficient (ρ; Siegel 1956). We used a 2-tailed Wilcoxon Matched-Pairs Signed-Ranks Test (*W*; Siegel 1956) to compare changes in index values in the estimated numbers of mountain lions present in the defined area based on aerial telemetry methods (e.g., $\mathrm{FWI}_{1994} - \mathrm{FWI}_{1993}$) and estimates based on proportion of use each year (e.g., $\mathrm{LDI}_{1994} - \mathrm{LDI}_{1993}$) over 14 winters from 1994 to 2007 (Table 1). We set $\alpha=0.05$, and performed statistical tests using VassarStats (Lowery 2014). We present the test statistic and associated probability derived from each test, as well as the equivalent t-value or z-value and associated probability, as calculated by Lowery (2014).

Table 1.—Number of collared mountain lions each winter known to have used a core area at least once, mean number of lions present and standard error (*SE*) derived from aerial telemetry during winter, and the cumulative proportion of mountain lions present each winter in the predefined area of 450 km^2 encompassing Round Valley, Inyo and Mono counties, California, 1993–2007.

Year	Available lions (N)[a]	Fixed-wing Index(SE)[b]	Location Data Index[c]
1993	10	6.09 (0.744)	7.56
1994	9	5.83 (0.599)	4.56
1995	8	5.38 (0.195)	5.15
1996	5	4.27 (0.258)	3.23
1997	4	2.80 (0.159)	2.31
1998	4	2.29 (0.187)	2.51
1999	2	1.17 (0.150)	0.56
2000	3	1.77 (0.210)	2.83
2001	3	1.62 (0.260)	1.63
2002	4	1.70 (0.272)	2.05
2003	3	1.30 (0.200)	1.56
2004	3	1.00 (0.150)	1.27
2005	6	2.27 (0.260)	3.41
2006	6	1.82 (0.280)	1.97
2007	3	1.57 (0.190)	2.26

[a] Number of collared lions collared in the study area each winter that were known to have used the core area at least once

[b] Aerial index of lions and standard error using the core area each winter

[c] Location data index of lions using the core area each winter

Results

We captured and collared 29 adult mountain lions (16 females, 13 males) that used Round Valley during this investigation and fitted each with a very high frequency (VHF) radio collar or various models of GPS collars. Values for the average number of adults located within the study area during aerial telemetry flights in winter varied from 1.0 to 6.1 (Table 1). Values for the summed proportion of locations for each adult mountain lion within the core area varied from 0.6 to 7.6 (Table 1). We evaluated the relationship between these two indices over a period of 15 years, and the results were strongly correlated (ρ=0.907*,* P<0.001 [t=7.770, P<0.001]; Figure 2). Successive interannual changes in the fixed wing index compared to those determined from the location data index did not differ (W=1, P>0.05 [z=-0.020, P=0.984]). The two indices trended in the same direction for 12 of 15 years, and the sizes of both indices were remarkably similar.

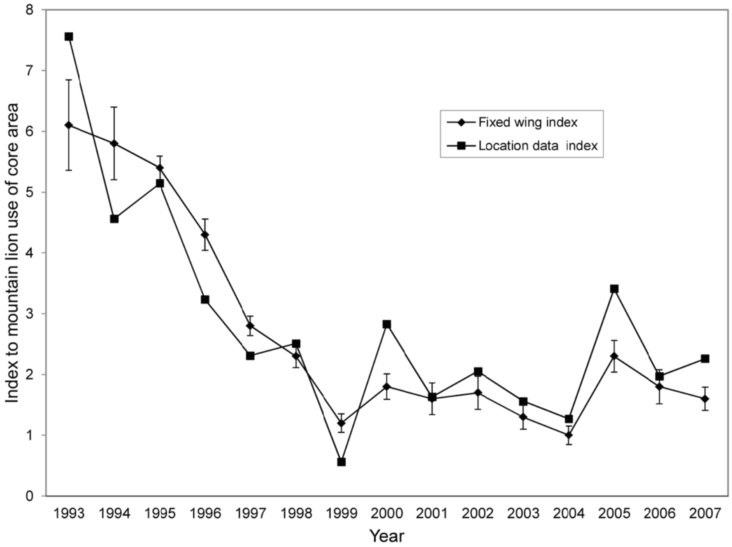

Figure 2.—Fixed-wing index (±*SE*) to the number of mountain lions determined from aerial telemetry locations, and the location data index, which was determined by summing the proportional use of all locations for mountain lions present on the pre-defined core area within the study area encompassing Round Valley (118° 28' W, 37° 28' N), Inyo and Mono counties, California each winter from 1993 to 2007.

Discussion

We used two different indices to assess the number of mountain lions using a specified area of deer winter range. We recognized that other methods did not account for proportional use of an area by individual animals, and they do not provide an opportunity to create a variance around mean estimated density. Methods such as minimum counts based on tracks or location data substantially inflate the actual use of a specified area, as well as the number of individuals present if more than one area is being evaluated. For example, a mountain lion that spent one day on a specified area and then moved to another for the rest of the time would be counted as one lion in each of those areas, essentially doubling the count and greatly inflating the estimate of the number of lions using an area where that individual rarely occurred. For states where mountain lions are hunted, population counts and estimates are often calculated for relatively small management units compared to the extensive movements made by mountain lions, further exacerbating the problem.

Our methods are based on the proportional use of an area by each individual. Further, the probability of detecting a mountain lion present in the defined area through the use of aerial telemetry was essentially 100%, particularly if the individual could be accounted for outside the defined area, and obviated one of the shortcomings voiced by Anderson (2003). Moreover, despite the fact that GPS locality data are not always indisputable (Villepique et al. 2008) and that not every attempted location by a GPS collar is successful (Cain et al. 2005), it reasonable to assume that the probability of detecting a telemetered individual within the defined area approaches 100%. Therefore, the density of mountain lions during any given period can be estimated while accounting for individuals that are present only occasionally.

Both indices described here yielded very similar results (Figure 2). Further, our methods allowed us to visualize actual use of the core area for any given period. We recognized that there were a number of individuals that used the study area only occasionally, and that it would be unlikely that the total number of individuals identified as using it, or any other area, would all be present on any given day.

Despite the close agreement between the indices, our results potentially remain subject to the effects of extrapolation bias and area bias, as described by Rinehart et al. (2014). The scale at which densities are defined will remain problematic, regardless of the accuracy or precision associated with density estimates (e.g., Blackburn and Gaston 1996, Smallwood and Schonewald 1998, Maffei and Noss 2008), and care must be utilized when extrapolating densities from one area to another (Latham et al. 2014). Nevertheless, for predetermined areas, our method accounts for actual use in proportion to other areas that are used by animals that never leave the predetermined area. Our method also decreases the likelihood that a telemetered mountain lion will be included in density estimates for >1 area without accounting for the proportional use of those areas. Finally, depending on the frequency of aerial telemetry or GPS fixes, a variance can be calculated for mean lion density on a longitudinal scale, whether it is weeks, months, seasons, or years.

Our methods require telemetered animals and, therefore, are not available to all managers tasked with determining mountain lion numbers or assessing population dynamics. We suggest, however, that investigators that do have access to such technology use proportional location data to evaluate use of subset areas for species that exist in a continuous population beyond the defined boundaries of their study areas. Additionally, we encourage incorporating a temporal component when seasons cause significant variation in study area size or location data accuracy. Finally, we suggest that the selection of a smaller area that is representative of larger areas can be used to estimate population trends in a meaningful way using these methods. Managers should recognize that censuses determining only the total number of individuals that have been identified in an area often inflate the total number of individuals likely to be present in that area at the same time, potentially leading to erroneous conclusions and, in jurisdictions where offtake is high (road kills, depredation, harvest), overestimates could mask actual population declines.

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Use of water developments by female elk at Theodore Roosevelt National Park, North Dakota

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Development of water sources for wildlife is a widespread management practice with a long history; however, needs of wildlife and availability of water depend on myriad interacting factors that vary among species and localities. Benefits are therefore situational, establishing a need for evaluation of water use in varied settings. We used global-positioning-system (GPS) collars and time-lapse videography to estimate the distribution of elk (*Cervus elaphus*) activity and frequency of water-development use at Theodore Roosevelt National Park, North Dakota, during June–September, 2003–2006. Elk were located further than expected from the Little Missouri River and did not preferentially use areas near developments. Of 26,081 relocations obtained at 7-h intervals, 88% were >800 m and 74% were >1600 m from permanent surface water. Elk were videotaped at water developments on 90 occasions during 19,402 h of monitoring but used water in only 52% of cases (*SE* = 5.3%). The probability of detecting elk at developments during visits was 0.51 (*SE* = 0.08). Nevertheless, elk tracked with GPS collars at 15-min intervals approached to within 100 m of developments on only 2.7% (*SE* = 0.6%) of 766 days, and approached randomly selected locations nearly as frequently ($\bar{x}$ = 2.2%, *SE* = 0.13%). Our results do not rule out use of drinking water by elk at THRO; however, elk were not dependent on water from developments or the Little Missouri River. Prevailing perceptions of water use by elk derive primarily from general associations of elk activity with locations of water sources. Technological advances that permit nearly continuous, precise monitoring present an opportunity to improve understanding of water use by elk, incidental to other investigations.

Key words: elk, *Cervus elaphus*, distribution, North Dakota, Theodore Roosevelt National Park, videography, water developments, water use

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Development of water sources for wildlife is a widespread—but costly and controversial—management practice. From 1940 to 1999, government agencies and private conservation groups constructed approximately 6,000 developments in arid regions of 10 western states (Rosenstock et al. 1999). Developments also have been constructed by federal agencies and private conservation groups, and in less arid areas, including the northern Great Plains. By 1988, the annual cost of maintenance by the Arizona Game and Fish Department reached $1034/site (deVos and Clarkson 1990, Broyles 1995). In Arizona, the construction cost for a typical water development ranged from $25,000 to $50,000 by 1992 (Mouton and Lee 1992).

For decades, needs of ungulates for free water, hence benefits of developments, seemed logical and self-evident (Brown 1998, Rosenstock et al. 1999). Indeed, developments were used frequently by wildlife (Brown 1998, Rosenstock et al. 2004). Observation and radio-tracking often revealed associations between activity or distribution and locations of water sources (Mackie 1970, McCorquodale et al. 1986, Hervert and Krausman 1986). Abundance or distribution of some species reportedly increased concurrently as water sources were developed (deVos and Clarkson 1990, Rosenstock et al. 1999). Since the 1990s, however, high costs and competing interests in management of natural areas have motivated greater scrutiny of evidence and interpretations (Broyles 1995, Bleich 2005, Krausman et al. 2006).

In fact, water needs of North American ungulates are not well understood (Smith and Krausman 1988, Cain III et al. 2006). Lacking access to free water, ungulates employ physiological and behavioral adaptations to reduce water needs while maintaining normal body temperatures (Sargeant et al. 1994, Cain III et al. 2006). Developments may also be used preferentially when natural sources of water, including succulent forage, could suffice. Use of developments is therefore insufficient evidence of a population-level benefit. Evidence for effects on vital rates or abundance is still largely anecdotal (Brown 1998, Krausman et al. 2006). If concentrating ungulates at water sources leads to adverse effects on vegetation, increased predation, or disease, development of water sources for wildlife could even be counterproductive (Broyles 1995).

Controversy surrounding development of water sources for wildlife first emerged, and continues most prominently, in the desert southwest. Polarized views of water management testify to difficulties that are inherent in documentation of water needs and potential effects of water availability on populations. The behavioral and physiological adaptability of ungulates, environmental variability, availability of replicate sites and populations, and costs of experimental control have been difficult to overcome (Cain III et al. 2008). For small populations of large mammals, process variation is likely to obscure any effect on vital rates. Rare events that are unlikely to be observed during a given study may have serious population consequences if they occur (e.g., Swift et al. 2000).

Despite uncertain effects on animal populations, observed use of developments by wildlife in the southwest has encouraged development of water sources in more temperate regions as well. Need remains for knowledge of use in temperate environments because developments clearly do not improve survival, enhance fecundity, or modify distribution if they are not used by the species they are intended to benefit. An understanding of use under conditions that span the range of circumstances encountered in practice can therefore help direct conservation dollars toward projects with greatest potential for benefit.

Development and maintenance of water sources for elk (*Cervus elaphus*) in the northern Great Plains exemplifies extension of a costly management practice to a species and environment where even the potential for benefit is uncertain. We thus used global-positioning-system [GPS] collars and videography to (1) describe relations between the distribution of activity and locations of permanent water sources and (2) estimate rates of use for water developments by female elk at Theodore Roosevelt National Park (THRO), North Dakota.

MATERIALS AND METHODS

Study area.—Theodore Roosevelt National Park encompassed 18,756 ha of unglaciated badlands topography (Laird 1950) near Medora, North Dakota (46° 57' 17" N, 103° 28' 19" W). Most of the area was mixed-grass prairie dominated by needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), threadleaf sedge (*Carex filifolia*) and various forbs; however, stands of juniper (*Juniperus scopulorum*) occurred on some north-facing slopes and stringers of green ash (*Fraxinus pennsylvanicus*) were associated with draws. Stands of cottonwood (*Populus deltoides*) occurred along the Little Missouri River (Hanson et al. 1984). During our study, known sources of permanent surface water included the Little Missouri River, 6–7 functioning water developments, and 3 permanent springs that were not developed (Figure 1; water was not available at SEC

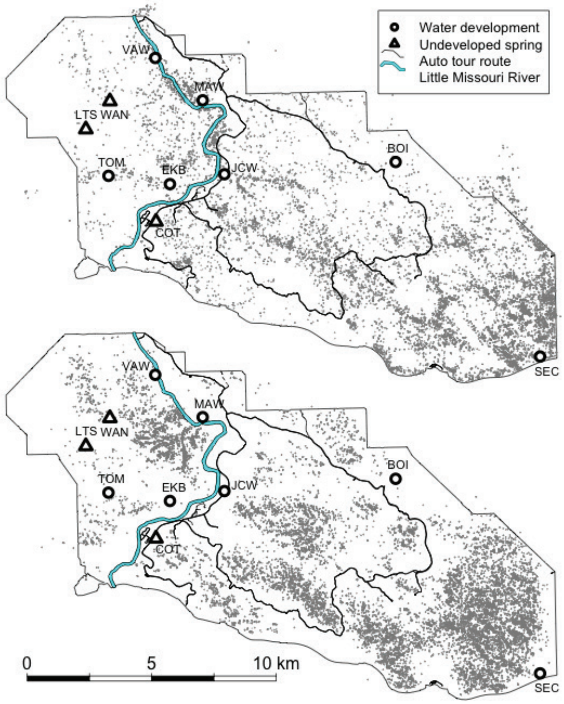

FIGURE 1.—Nighttime (top, n=10,737) and daytime (bottom, random subsample of 10,737 from n = 15,344) distributions of locations for 91 elk marked with global positioning system collars at Theodore Roosevelt National Park, North Dakota, during June through September, from 2003 to 2006. To enhance contrast, shading of each point is proportional to nearest neighbor distance; i.e., points are darkest in regions of greatest point density.

during 2003). Developments consisted of modified springs and seeps or shallow artesian wells that fed 1,200–2,000 liter fiberglass or concrete tanks. Tanks were installed during the 1960s as part of the wildlife management program (Berkley et al. 1998), but also served to prevent degradation of springs and seeps by livestock (NPS files).

Elk numbers in January ranged from approximately 500 in 2003 to 850 by 2006 (Sargeant and Oehler 2007). Other large herbivores included bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorn (*Antilocapra americana*), and feral horses (*Equus caballus*). Bison and horses were confined to the park by a 1.8–2.4-m woven-wire boundary fence. Other species could traverse the boundary through several man-made wildlife crossings.

The climate at THRO was semi-arid. Warm days and cool nights were typical during the summer. Daytime highs averaged 22°C during June and September and 29°C during July and August, with average nighttime lows of 9°C and 14°C for the same periods. Relative humidity ranged from 43% (average daytime low) to 84% (average nighttime high) during June, and from 32% to 77% during July–September. Annual precipitation was approximately normal (41 cm [National Oceanic and Atmospheric Administration 2010]) in 2003 (38 cm) and 2005 (40 cm), and less-than-normal in 2004 (26 cm) and 2006 (20 cm). Precipitation was less than normal (21 cm) during June–September of 2004 (15 cm), 2005 (19 cm), and 2006 and greater than normal in 2003 (26 cm) (National Park Service 2014).

Methods.—We used GPS radio-telemetry collars (Advanced Telemetry Systems, Isanti, Minnesota, USA) to relocate female elk at nominal 15-min or 7-h intervals during June–September. Marked elk were captured in February with a helicopter and net gun by Leading Edge Aviation of Clarkston, Washington, USA. Captures were distributed throughout THRO, approximately proportional to elk numbers in the western, central, and eastern reaches of the park. We monitored each marked elk for approximately 10 months, then used remotely triggered release mechanisms to recover collars and download data stored in collar memory. Research protocols were approved by the Research Advisory Committee and Animal Care and Use Committee at the U.S. Geological Survey Northern Prairie Wildlife Research Center.

Some elk that wintered within THRO occupied summer ranges up to 70 km from the park and did not have access to water sources we studied (G. A. Sargeant, unpublished data). We therefore restricted our analysis to non-migratory residents. We used locations obtained at 7-h intervals to estimate proportions of time spent in the park and to relate the distribution of elk activity to the distribution of permanent sources of surface water. To document approaches to developments and undeveloped springs, we computed minimum distances to water from line segments connecting 24-h sequences of locations obtained at 15-min intervals (trajectories). For comparison, we also computed the minimum distance from each trajectory to 1000 points selected at random from within the area used by the same elk during the same year. To minimize potential for failing to detect visits to developments, we excluded trajectories spanning <23 h. We used characteristic hulls with minimum edge lengths of 0 (Duckham et al. 2008) and locations obtained at 7-h and 15-min intervals to delineate areas used by individual elk. We used characteristic hulls because they do not require equal sampling intervals and do not fragment or extend beyond data when sample sizes are large, yet follow contours of irregularly shaped ranges.

Elk marked with GPS collars could potentially visit water developments during 15-min intervals between relocations, and approaches were not necessarily motivated by interest in water. Hence, rates of detection near developments could have either underestimated or overestimated use. We used time-lapse video cameras to document behavior of elk at water developments from 0300 to 2100 Mountain Standard Time during June–September, 2003–2004. When elk approached to within approximately 50 m of developments, we recorded the site, date, time of arrival and departure, minimum group size, group composition (males, females, young; uncertain), and whether or not the observation involved water use. To minimize effects on elk, we concealed video systems behind topographic features or vegetation 75–200 m from developments and visited weekly, during midday, for routine maintenance and to exchange videotapes. We used video records to estimate durations of visits and proportions of visits that involved use of developments. We used a parametric bootstrap procedure to estimate bias resulting from visits that occurred during intervals between locations (Appendix I).

We assigned GPS telemetry locations to 6 intervals defined with respect to civil twilight. Civil twilight begins in the morning and ends in the evening when the sun is 6° below the horizon, and refers to the period when objects generally can be distinguished without artificial light (U. S. Naval Observatory 2011). “Night” began in the evening at civil twilight and ended at “dawn.” Dawn described an interval centered about sunrise, beginning with civil twilight and lasting 60 (September 30) to 80 min (ca. 21 June). Similarly, “dusk” began 30 min to 40 min before sunset and ended 60 to 80 minutes later, with civil twilight. “Morning,” “midday,” and “evening” partitioned the period between dawn and dusk into three intervals of equal length (collectively, “daytime”).

RESULTS

Our analysis included 91 resident female elk (n = 19–28 annually) that were located within THRO on 91 to 100% (median [$\tilde{x}$] = 99.7%) of occasions. Areas used seasonally by individuals ranged in size from 11 to 57 km^2 ($\tilde{x}$ = 31 km^2, interquartile range [*IR*] = [27 km^2, 37 km^2], n=91). Elk foraged during the night in gentle terrain of valley bottoms, prairie dog towns, or in uplands along the eastern boundary of the park (Figure 1, top), then moved into adjoining, more rugged terrain for the day (Figure 1, bottom). Park-wide, daytime elk activity was concentrated in areas that were distant from roads or concealed by topography and not near permanent sources of surface water. Distances from locations to the Little Missouri River ($\tilde{x}$ = 9097 m, *IR* = [2924 m, 12,232 m]) were much greater than expected ($\tilde{x}$ = 4180 m, *IR* = [1624 m, 8174 m]), and 57% of elk (52) used areas that did not intersect the river. Observed distances from locations to developments and springs ($\tilde{x}$ = 2919 m, *IR* = [1706 m, 4269 m]) were similarly greater than expected distances ($\tilde{x}$ = 2417 m, *IR* = [1295 m, 3767 m]). Elk were located >800 m from permanent sources of surface water in 88% of cases, and >1600 m in 74% of cases.

We obtained 19,402 h of video at 7 developments (6 in 2003 and 7 in 2004) and observed elk on 90 occasions. Elk were observed drinking from developments on 47 occasions (52%, *SE* = 5.3%). Elk that used water typically visited developments singly or in pairs (53% of visits, *SE* = 5.3%); however, minimum group sizes ranged from 1 to 50, and 21% of observations accounted for 65% of visits by individuals. Female elk that used water developments remained within view of cameras (typically within 50 m) for >15 min in 25% of cases and for >8 min in 50% of cases. Approximately 51% (*SE* = 8%) of visits by collared elk should, therefore, have encompassed >1 GPS relocation, and locations typically were accurate to within 35 m (95% of reference locations).

We analyzed 766 trajectories (140 in 2003, 209 in 2004, 164 in 2005, and 253 in 2006) that provided nearly complete records of movement. Each of these spanned ≥23 h, and elapsed time between locations was 15 min for 97% of 67,783 intervals. Elk typically traveled 4.8 to 7.7 km (*IR*) daily. The median travel distance from the center of nighttime activity to the center of midday activity the following day was 1.1 km (*IR* = [0.7 km, 1.8 km]). Distances between centers of activity exceeded 1600 m on 30% and 2400 m on 13% of dates.

Despite the extent of daily movements, elk typically did not approach permanent water sources (Figure 2). Trajectories approached to within 100 m of developments on just 21 occasions (2.7% of trajectories, *SE* = 0.6%) and were located nearly as often (2.2% of traces, *SE* = 0.13%) within 100 m of points selected at random. Approaches occurred during dawn (3), dusk (3), or at night (14), but were distributed among years and developments (i.e., 3–6 approaches per year; 1–4 approaches per development). Trajectories did not approach undeveloped springs.

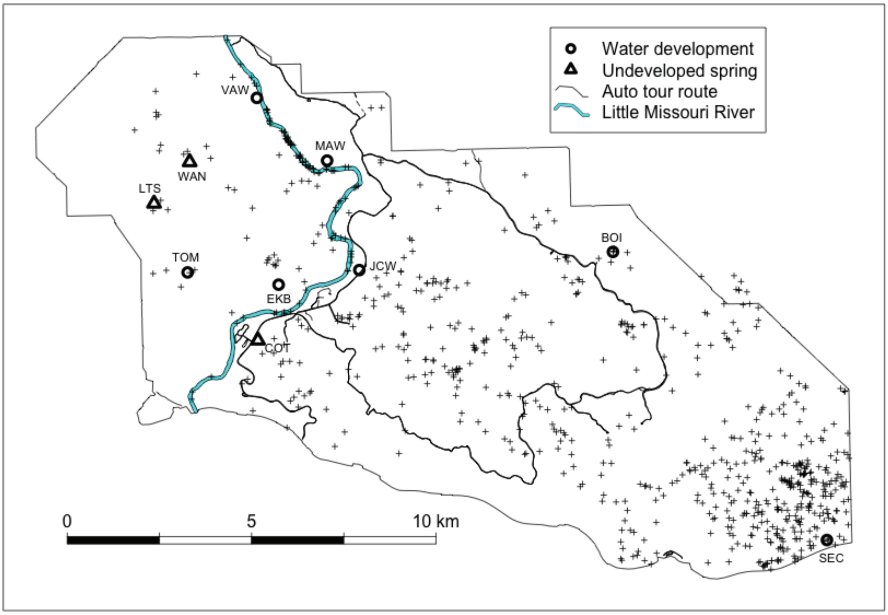

Figure 2.—Nearest location to a water development (BOI, EKB, JCW, MAW, SEC, TOM, VAW), permanent spring (COT, LTS, WAN), or the Little Missouri River for each of 766 24-h sequences of locations obtained at 15-min intervals for 91 female elk at Theodore Roosevelt National Park, North Dakota, during 2003–2006.

Discussion

Expansion of elk populations into arid shrubsteppe, woodland, and forest habitats of the western U.S. has been credited, in substantial part, to development of water sources for wildlife (Rosenstock et al. 1999). More generally, lactating female elk are thought to be seasonally dependent on surface water (Delgiudice and Rodiek 1984, Skovlin et al. 2002). However, water needs have been inferred almost entirely from observed associations between elk activity and locations of natural or developed water sources (e.g., Mackie

1970, Delgiudice and Rodiek 1984, McCorquodale et al. 1986). Contrasting results from THRO suggest a need to further evaluate use of water developments in varied settings and invite scrutiny of evidence for perceived water needs.

Use by target species is an implicit presumption in much discussion of water developments. However, fundamental questions usually remain unanswered (e.g., effects on survival, reproduction, movements, distribution, and habitat use) because use is not an assurance of benefit. With limited understanding of water needs and availability of water from other sources, and without *a priori* knowledge of movements and distribution, preference and association cannot be distinguished from need or causation (Larsen et al. 2012). Interpretation is clearer when developments rarely are used. At THRO, elk approached developments too infrequently to suspect a substantial effect on vital rates or distribution.

Elsewhere, use of developments has been related to site characteristics and discouraged by the presence of feral horses (Ostermann-Kelm et al. 2008, Shields et al. 2012). Similarly, accessibility of the river and avoidance of roads could have discouraged use of some developments we studied. However, elk used areas adjacent to roads at night, when most observed approaches occurred, and we did not observe substantial variation in use that might indicate preference for secluded sites, greater need for sites far from the river, or avoidance of horses (which used predominantly BOI [70% of videotaped visits; G. A. Sargeant, unpublished data]). Regardless, greater use of developments could not have produced substantial gains in survival or reproduction, which approached maxima for elk (Sargeant and Oehler 2007).

Neither our results for THRO nor previous studies of habitat selection support general conclusions about benefits of developments or water needs of elk. On one hand, lack of association with permanent sources may not rule out periodic access to undocumented sources of drinking water. At THRO, for example, heavily eroded clay soils and ever-changing topography are distinctive features of the badlands habitat. These features contribute to formation of ephemeral, locally fed seeps or rainwater pools in gully bottoms (Berkley et al. 1998). On the other hand, use of areas near natural water sources is insufficient evidence of water use because proximity to water often is associated with other features that may attract elk (e.g., low elevation, moist soils, cool microclimates, and green or growing vegetation). In Arizona, for example, Delgiudice and Rodiek (1984) concluded that availability of succulent, digestible forage probably influenced elk preference for areas near water. Similarly, water developments are likely to be situated in areas with characteristics that encourage use by wildlife and facilitate water collection.

Although habitat use may not be indicative of habitat requirements or reveal purposes of habitat selection (Peek et al. 1982, Cook et al. 1998), associations between elk activity and locations of water suggest broader purposes than access to drinking water. Despite the wide distribution and interspersion of areas used during day and night, elk at THRO often traveled >1.6 km from nighttime to daytime centers of activity. Elk in southeastern Idaho traveled considerably further to feed at night in cropland ($\bar{x} = 4.4$ km; Strohmeyer and Peek [1996]). Despite association of activity with locations of natural springs, the average distance between locations on consecutive days was >2 km for elk inhabiting the Arid Lands Ecology reserve in southcentral Washington (McCorquodale et al. 1989). Given such mobility, water needs alone do not necessitate strong selection for areas very near water (i.e., 0.2–0.8 km; examples in Skovlin et al. 2002).

Correlation, rather than causation, is further suggested by preference for areas near water even in moderate environments. In northern Idaho, for example, more than 95% of locations during fall were within 400 m of water, coinciding with a decrease in use of higher elevations (Irwin and Peek 1983). Changes in distribution associated with changes in rainfall (Schoen 1977) may reflect effects on soil moisture and forage (Marcum and Scott 1985), rather than increased use of water sources during dry periods.

Finally, it seems that perceived water needs for lactation, which emerged as an explanation for observed habitat use, may not reflect elk physiology. For captive elk with ad libitum access to water and feed, milk volume began to decline about three weeks post-partum; by August, water volume of milk was 1.5 to 2.1 liters daily, or 0.6 to 0.9% of maternal body mass (calculations based on results of Robbins et al. [1981] and a birth date of 1 June [Hudson et al. 2002]). We could not find estimates for free-ranging elk; however, the marginal cost of lactation for black-tailed deer (*Odocoileus hemionus sitkensis*) was approximately 9% of total water transfer (Parker et al. 1993). As a percentage, the marginal cost of lactation is likely to be greater for species that are adapted for water conservation.

From our results and review, we conclude principally that water needs and water use by free-ranging elk and benefits of water developments are not well understood. Costs of constructing and maintaining developments establish a need to evaluate use, not only in arid environments, but also under diverse circumstances encountered in practice. The information need for elk management is not merely *whether* elk require drinking water or benefit from development of water sources (which we take as a given for sufficiently harsh environments), but when and where.

Noting the anecdotal and correlative nature of evidence for benefits of water developments, numerous authors have suggested a need for experimental evaluations (Ballard et al. 1998, Brown 1998, deVos, Jr. et al. 1998, Simpson et al. 2011). However, such experiments present formidable challenges under the best of circumstances (Krausman et al. 2006, Cain III et al. 2008). As our results show, observational study of animal movements can reveal a great deal about *potentials* for benefit when use of developments is not presumptive. We hope our work will encourage other investigators to explore relations between daily movements of elk and locations of water sources, leading to improved understanding of circumstances that encourage or discourage development of water sources for wildlife.

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APPENDIX I: BOOTSTRAP ESTIMATION OF ELK VISITATION RATES FROM GPS RELOCATIONS

1) Transform durations of videotaped visits, t_i for i in 1:I, to achieve an approximately normal distribution, i.e., $x_i = f(t_i)$, such that $x_i \sim N(\mu, \sigma)$.
2) Substitute estimates, $\hat{\mu}$ and $\hat{\sigma}$, for parameters μ and σ in sampling distributions for the mean and variance of x, i.e., $\bar{x} \sim N(\hat{\mu}, \frac{\hat{\sigma}}{\sqrt{n}})$ and $\frac{(n-1)s^2}{\hat{\sigma}^2} \sim \chi^2_{n-1}$ (Freund 1992). Use resulting distributions to generate J =1000 sets of simulated parameters, $\{\tilde{\mu}_j, \tilde{\sigma}_j\}$.
3) Generate I observations for each of the J sets of parameters by back-transforming random draws from a normal distribution, i.e., draw $\tilde{x}_{(j)i} \sim N(\tilde{\mu}_j, \tilde{\sigma}_j)$ and compute $\tilde{t}_{(j)i} = f^{-1}(\tilde{x}_{(j)i})$.
4) Compare each observation to a random number drawn from a uniform distribution, $\tilde{u}_{(j)i} \sim Unif(0,15)$, representing the time elapsed from arrival at a development until the next scheduled GPS location. Each trial represents a “visit,” which was “detected” if $\tilde{t}_{(j)i} \geq \tilde{u}_{(j)i}$.
5) Compute the mean detection rate for each set of I simulated observations. Use the standard deviation of means to estimate the standard error of the grand mean.

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Density dependence in ungulates: a review of causes, and concepts with some clarifications

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Understanding population dynamics of ungulates is not conceptually simple, in part, because there are many counterintuitive processes. We attempt to disentangle important concepts, including density dependence, density independence, limitation, regulation, compensatory and additive mortality, and top-down versus bottom-up forcing by examining how those ideas are related to the carrying capacity (*K*) of the environment. We contend that the *K*-selected, life-history characteristics of ungulates account for major components of their population dynamics. Those density-dependent attributes of ungulates require different management strategies than for species with attributes that are influenced primarily by density-independent processes. We offer a conceptual framework to help explain how density-dependent processes can be confused with those that are density-independent. We also discuss why regulation is the correct term for describing demographics of ungulates when limiting factors have density-dependent feedbacks. We emphasize that density *per se* is not valuable for understanding density dependence—rather, the population size relative to *K* is the critical factor. Comparisons among populations or within a population through time based on density alone are flawed, because *K* is not necessarily constant and can result in misleading results and conclusions. Whether mortality is compensatory or additive is a function of where the population is in relation to *K*, which is critically important when determining if and when predator control is biologically justified. We provide a model based on life-history characteristics to help parameterize where the population is in relation to *K*, and discuss a new nutritional model (nutritional carry capacity; NCC) for determining the relative degree of compensatory or additive mortality and the proximity of a population to its food supply.

Key words: additive mortality, compensatory mortality, demographics, density dependence, density independence, forcing, life-history characteristics, limitation, predation, regulation, ungulates

Density dependence is an essential component for understanding the population ecology of large mammals—as well as a thoroughly established principle (Caughley 1977; McCullough 1979, 1999; Fowler 1981; Kie and White 1985; Skogland 1985; Clutton-Brock et al. 1987; Boyce 1989, and many others). Nevertheless, debate and confusion continue over exactly what density dependence entails and how it operates, or fails to do so, in populations of large mammals (Fowler 1981, McCullough 1979, Mackie et al. 1990). Misunderstandings abound and stem, in part, from failing to recognize that density dependence is both a life-history characteristic of a species (Stearns 1977), and a measureable parameter of populations (Caughley 1977). Our purpose is to clarify many of the misconceptions concerning the role of density dependence in ungulate population dynamics, relying heavily on our previous experiences and publications.

Ungulates (hooved mammals) exhibit a complex, yet predictable, suite of life-history characteristics. Although variation exists among species (Feldhamer et al. 2007), especially within pigs (Suidae) and peccaries (Tayasuidae), many of those large mammals display an array of traits that result in them being categorized as *K*-selected (i.e., density dependent and slow paced in their life histories) (Williams 1966; McCullough 1979, 1999). Compared with many small mammals, which often are termed *r*-selected (i.e., density independent and fast paced in their life histories), large mammals—in addition to large body size—are characterized by long lives, low adult mortality, delayed reproduction, small litter size, high maternal investment in young, iteroparity (multiple reproductive efforts over a life time), and high, but variable, survival rates of young. Individuals of species that exhibit strong density dependence also may trade reproduction to enhance adult survival (Martin et al. 2010, Monteith et al. 2014), or tradeoff current against future reproduction (Morano et al. 2013). Those life-history traits lead to low intrinsic rates of increase (*r*) for populations compared with their smaller-bodied counterparts (Stubbs 1977, Pianka 1983). As a result of those life-history characteristics, ungulates exhibit striking competitive abilities, and their population dynamics can be affected strongly by intraspecific competition, which changes in relation to the ecological carrying capacity (*K*) of the environment—a topic we will return to later. A characteristic growth curve of numbers over time for these large mammals in a constant environment would be S-shaped, reaching an asymptote at *K*.

Small animals are more likely to be affected by density-independent factors, with populations only occasionally reaching *K* except in unusual environmental situations or under controlled conditions in an experimental setting. Mammals with strong density-independent characteristics tend to be small, have short life-spans, high reproductive rates, and may reproduce but a single time (semelparity; Pianka 1983). Those organisms usually are not limited by intraspecific competition, or the resources available in the environment—for these species *K* is seldom attained because their populations are reduced (and may crash) because of density-independent factors, such as severe weather. Species with strong density independent characteristics are more likely to sacrifice survival for reproduction, because short lifespans generally preclude tradeoffs between current and future reproduction (Ghalambor and Martin 2001). Accordingly, density-independent organisms tend to exhibit a series of J-shaped growth curves over time, with populations that seldom, if ever, approach *K*. The irruptive phase of those J-shaped curves results from high population productivity and is associated with a high *r*. Of course, this stark dichotomy does not hold for all organisms. A continuum of species, with their accompanying life-history characteristics occurs from species exhibiting strong density dependence to those displaying clear density independence (McCullough 1979). Even among ungulate species and the landscapes they occupy, the strength of influence of density dependence and the ability to detect it is not ubiquitous (McCullough 1999, DeYoung 2011).

Disentangling effects of density-dependent and density-independent factors on ungulate populations is not straightforward. Density-independent effects can be masked in populations of most ungulates at low density, because females are in good nutritional condition (Pierce et al. 2012). Hence, variance in most measures of productivity would be low because individuals are well-buffered against climatic extremes, with correlations between weather and productivity of the population most apt to be weak (Milner et al. 1999, Kie et al. 2003). Conversely, populations at high density and near *K* would have a large proportion of animals in poor nutritional condition, and those individuals would be poorly cushioned against effects of severe winter weather or drought (Monteith et al. 2014). Populations at high density in relation to *K* also may be physiologically compromised, and therefore more susceptible to diseases (Sams et al. 1996). Variance in measures of population performance in such populations would be high, as would correlations between weather and productivity of the population. This outcome occurs because those animals in poor condition would be more likely to be helped or hindered by a variable climate than would individuals in good condition (Kie et al. 2003), or because a pulse of high-quality food associated with optimal weather conditions in arid climates promotes productivity (Shea et al. 1992, DeYoung 2011). At sufficiently high density in relation to *K*, however, density dependence may override even beneficial density-independent events (Stewart et al. 2005). Likewise, low population density relative to *K* may mitigate detrimental effects of climate, including drought (McCullough 2001). One circumstance in which the expected relationship between low density with respect to *K* and high productivity of ungulates may not occur is where disease has lowered the nutritional condition of individuals. Even low-density populations of bighorn sheep (*Ovis canadensis*) may exhibit poor nutritional condition after being infected with bacteria causing respiratory disease from contact with domestic sheep (Shannon et al. 2014). Our point, however, is that correlations may not always reflect cause and effect, and strong relationships between the productivity of ungulate populations and weather-related variables can be driven largely by density-dependent feedbacks, via changes in available resources and amount of intraspecific competition for those resources (Stewart et al. 2005, Monteith et al. 2014).

Consider a population that is at low density relative to *K*, and in which forage availability is high and intraspecific competition is low. Individuals would attain a high nutritional plane with resultant excellent nutritional condition, including high fat reserves that, in turn, would promote a high reproductive rate and survivorship. Winters of mild to moderate severity would have little influence on the overwinter survival of those animals, because they are well-buffered against those climatic events by extensive body reserves (Bowyer et al. 2000). An extremely severe winter, however, could still cause high rates of mortality, even among animals in good nutritional condition (Figure 1a).

Now consider a population near or at *K*. Intraspecific competition would be intense, per capita forage availability low, and nutritional condition poor. Under such circumstances, even a winter of moderate severity would be capable of causing high overwinter mortality (Figure 1b). Although mortality caused by winter severity is commonly interpreted as a density-independent factor (Severinghaus 1947, Verme 1968, Bartmann and Bowden 1984), those situations seldom are entirely density independent, because individuals can be buffered against such weather anomalies depending upon the level of density dependence experienced (Figure 1c). In this example, density-dependent processes produce a near-linear relationship between mortality and winter severity, which might be misinterpreted as a strong density-independent effect.

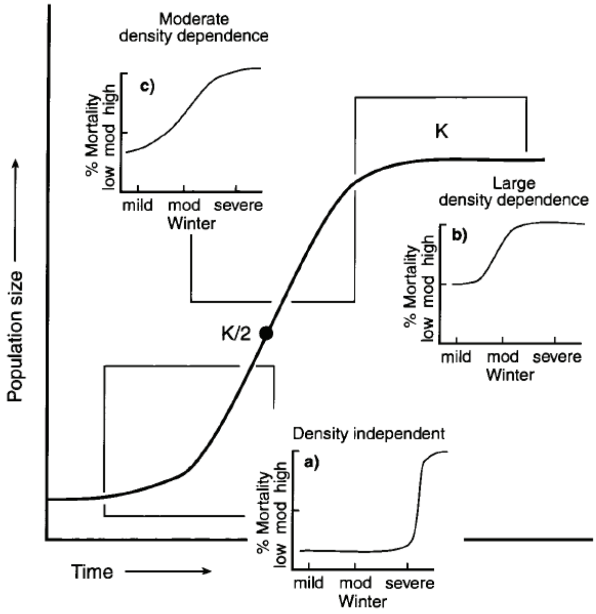

Figure 1.—A conceptual model illustrating relationships among ungulate population density, winter severity, and rate of overwinter mortality. Representative curves are provided for (a) density independent, (b) large density dependence, and (c) moderate density-dependent effects interacting with winter weather. The lines around the inset graphs indicate the area of the growth curve (population size over time) to which each inset corresponds. The shape of the population-growth curve need not be symmetrical for the postulated relationship to hold (from Bowyer et al. 2000).

Winter conditions may interact with density-dependent processes, sometimes with unanticipated outcomes. Mitchell et al. (2015) sampled density of Dall's sheep (*Ovis dalli*) before and during gray wolf (*Canis lupus*) and coyote (*C. latrans*) harvests for 3 years on adjacent treatment (predator harvest) and reference (no predator harvest) areas. Density of sheep on the reference area was similar over 3 years, while density of sheep where canids were harvested increased markedly. A winter of above-normal snowfall combined with crusted snow occurred during the final year of the study. Sheep on the reference area (where predators were not harvested) did not experience a change in density, whereas the population of sheep on the treatment area crashed precipitously. Sheep on the treatment area initially benefited from the harvest of predators, but their population crashed, ostensibly the result of a combination of increased population density brought about by removal of predators, and a subsequent severe winter (Mitchell et al. 2015).

Winter has long been a focus for management and research on ungulate populations, especially in temperate and arctic environments (Mautz 1978, Bergman et al. 2015); however, mounting evidence indicates that nutritional quality of summer range also plays a critically important role in their population dynamics (Cook et al. 2004, Stewart et al. 2005, Couturier et al. 2009, Monteith et al. 2013, Shallow et al. 2015, among others). In separate manipulative experiments, while holding effects of winter constant, Stewart et al. (2005) documented effects of summer nutrition on pregnancy rates and nutritional condition of North American elk (*Cervus elpahus*) by manipulating population density, and Tollefson et al. (2010, 2011) demonstrated effects of summer nutrition on reproduction of adult mule deer (*Odocoileus hemionus*) and growth and survival of young mule deer by manipulating summer diets. Nevertheless, nutritional contributions from seasonal ranges are not independent because carryover effects, including provisioning of young, influence the nutritional state of an individual entering the next season (Bardsen and Tveraa 2012; Monteith et al. 2013, 2014). Consequently, the question of which seasonal range is more important is probably moot, because strength in one may help compensate for the weaknesses in another—thus, they are both important (Kie et al. 2003, Monteith et al. 2013).

The preceding generalizations and examples concerning the life-history strategies and population dynamics of ungulates are at the center of misunderstandings concerning the demographics, conservation, and management of large mammals. Variable environments will seldom have the capacity to support the same number of animals on an annual basis, thereby confounding interpretations and resultant management alternatives (Mackie et al. 1990, DeYoung 2011, Pierce et al. 2012, Monteith et al. 2014). Consequently, the number of animals in relation to *K* determines the potential productivity of the population; identical densities of large herbivores inhabiting a variable environment can exhibit either similar or differing measures of productivity depending upon environmental conditions (Monteith et al. 2014). As a result, density of animals *per se* cannot be used to compare the dynamics of different populations directly. Rather, the relative amount of food on a per capita basis effects nutritional condition of individuals. Thus, the number of animals in relation to *K* determines the potential productivity of a population (Caughley and Gunn 1993, Bishop et al. 2009, Pierce et al. 2012, Monteith et al. 2014). Indeed, searching for direct relationships among metrics of productivity with density can yield spurious results in variable environments, even when strong density-dependent processes are at play (Pierce et al. 2012; Starns et al. 2014, 2015). Unless environmental conditions remain constant, which they rarely do, studies seeking to compare productivity of ungulate populations based on density alone are logically flawed, and likely provide misleading or unreliable results. Density, likewise, can be a misleading indicator of habitat quality (Van Horne 1983).

Density dependence in ungulates manifests itself in changes in vital rates, which is a function of where the population is with respect to *K*. Indeed, such changes in vital rates in relation to *K* often occur in a predictable pattern with increasing population size as a consequence of a conservative life-history strategy: decreased survival of young; increased age at first reproduction; reduced fetal rate; reduced pregnancy rate; and reduced survival of adults (Gaillard et al. 2000, Eberhardt 2002, Bonenfant et al. 2009, Monteith et al. 2014), all of which can affect *r*. In particular, recruitment rate (the number of young recruited per adult) changes as an inverse linear, or relatively linear, function of population size (McCullough 1979, 1999), with recruitment rate being highest at low population size relative to *K*, and lowest at high population size relative to *K* (Figure 2). Moreover, recruitment rate varies with changes to *K* within a population, such that modifications to improve habitat will have a pronounced effect near *K*, but substantially less influence for populations at low density relative to *K*, where predation or other factors may occur and, consequently, competition for forage is low and nutritional condition is high (Figure 2). Thus, inferring that density dependence is not operating at low density relative to *K* simply because that variable is difficult to detect is inappropriate, because there may be other reasons that density-dependent responses are not readily evident. For instance, observations might have been made over too short a period to identify a trend in reproductive rates (McCullough 1990), time lags associated with recovery of resources or intergenerational effects may have delayed a density-dependent response (Fryxell et al. 1992, Monteith et al. 2009), or density may not have changed sufficiently to note differences in that variable over time, especially given the difficulties in reliably measuring that variable (McCullough 1990).

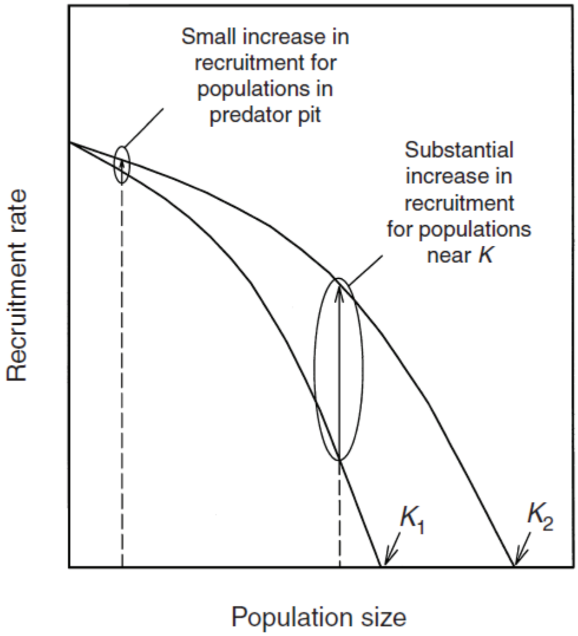

Figure 2.—Variation in recruitment rate (young/adult) with increasing population size relative to *K*. Note that for small population size (such as when ungulate populations are held at low density by predation) there is little increase in recruitment rate from improving *K* (i.e., moving from K_1 to K_2). There is a sizeable increase in recruitment rate, however, for populations initially near K_1 (from Kie et al. 2003).

Life-history characteristics related to density dependence among ungulate populations result in a continuum of reproductive rates that change with population size relative to *K*. Detecting density-dependent changes in demographic parameters for a particular population, however, may be difficult at low density, where productivity is high. In such situations, those demographic changes are less variable across changing densities. Demographic adjustments, however, are relatively easy to detect at high densities relative to *K*, when productivity is low and changes markedly with density (Figure 3). We suggest that most ungulates will exhibit a density-dependent response because of their unique life-history characteristics, but acknowledge, that under particular conditions this outcome may be difficult to detect.

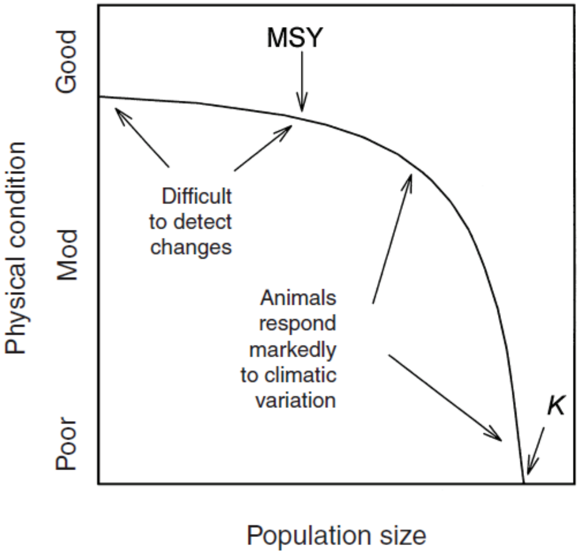

FIGURE 3.—Relationship between physical condition of ungulates and changing population size. Changes in condition and subsequent effects of reproduction and survival may be difficult to detect below maximum sustained yield (MSY), but changes in condition between MSY and carrying capacity (*K*) can be marked (from Kie et al. 2003).

In arid environments characterized by low productivity, but with abundant low-quality forage that meets requirements of maintenance, populations may respond negligibly to changes in density. Large amounts of maintenance forage sustain adults in poor nutritional condition and potentially across a wide range of densities, but yields insufficient resources to enhance recruitment of young (Shea et al. 1992, Owen-Smith 2002, DeYoung 2011). Nonetheless, density-dependent effects can occur at very low density relative to *K* when small amounts of high-quality food are available seasonally, or when density increases following multiple years of optimal forage production (McCullough 1999, DeYoung 2011). In normal years of typically unproductive forage production, populations may fluctuate up and down with no apparent signs of density dependence because of the large forage base that supports maintenance, but not reproduction (DeYoung 2011).

In contrast with the near-linear change in recruitment rate with increasing density, the total number of young recruited has a parabolic relationship with population size for ungulates, which results from the product of population size and recruitment rate at various sizes of the population (Figure 2, Figure 4). Very high and very low recruitment rates (Figure 2) result in a low number of recruits, but intermediate levels of recruitment rate and population size yield the greatest number (Figure 4). The point at the apex of the parabola is termed Maximum Sustained Yield (MSY), and is the maximum annual harvest that a particular population can withstand without moving the population toward extirpation (McCullough 1979; Figure 4).

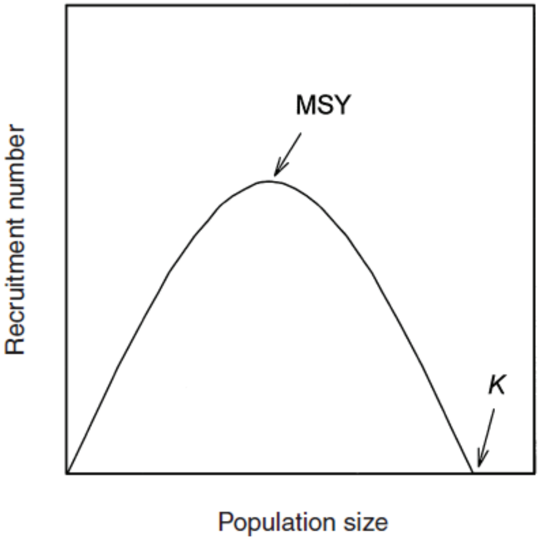

Figure 4.—The parabolic relationship between recruitment number (i.e., the number of young successfully added to the population) and size for an ungulate population. MSY is maximum sustained yield, which is the maximum harvest (or other mortality) that can be sustained by the population. The relationship need not be symmetrical to infer density dependence (from Kie et al. 2003).

Several critical points emerge from these simple theoretical models. First, species with strong density-independent and density-dependent characteristics require different management strategies (McCullough 2001). The J-shaped curves of abundance indicative of density independence denote that there is a surplus of animals that will perish even in the absence of a harvest; moreover, the population rebounds each year following a crash. Those animals that will perish, then, become the "harvestable surplus" described by Leopold (1933) that has been used to set hunting regulations (i.e., the surplus determines the harvest). We caution, however, that the concept of a harvestable surplus has been criticized by McCullough 1979) and Connelly et al. (2012). For density-dependent species, the harvest determines the surplus (McCullough 2001). For example, if the population depicted in Figure 4 is near *K*, and is moved toward MSY by harvesting animals, the surplus initially increases until MSY is achieved, but declines thereafter. As a result, large ungulates in particular cannot be managed effectively by trying to set harvests according to observed surpluses—at best this management results in a very conservative harvest. If the population was near *K* and exhibited low recruitment (Figure 4), then setting a low harvest would result in poor recruitment again the following year (all else being equal), and harvest would remain well below what the population is capable of sustaining over time (McCullough 2001). If a population is already at or near MSY, however, a danger exists in assuming that increased recruitment will result from an increased harvest (Figure 4)—such management may result in declining recruitment numbers, which is the general pattern for an overharvest. This situation does not mean that density-dependent processes were not operating; rather, density-dependent response in recruitment simply was not sufficient to compensate for a sustained overharvest. Furthermore, in the aforementioned example depicting an arid environment with abundant, poor-quality food for maintenance, increasing harvest in a similar fashion would not increase productivity if the density reduction does not concomitantly reduce competition for forage and, thus, yield increased production (DeYoung 2011). This outcome, of course, will vary with the types of habitats and ungulate species involved; the wide distribution and diverse environments inhabited by white-tailed deer (*Odocoileus virginianus*) offer a good example of this variability (McCullough et al. 1999, DeYoung 2011). Such complexity enforces the notion of having a firm understanding of population dynamics to aid in implementing harvest strategies.

Another mechanism that has the ability to reduce the *K* of a habitat for a particular species is interspecific competition. Life-history characteristics of ungulates should make them among the most competitive of all organisms (Stewart et al. 2002). Most studies of ungulates, however, infer competition from the amount of resource partitioning (Putnam 1996). Manipulative experiments are necessary to unequivocally demonstrate competition, yet those are exceptionally difficult to conduct on large, vagile, animals in a natural setting (Stewart et al. 2002, 2011a). Competition may be exploitive, when one competitor uses resources, thereby making them unavailable to another competitor, or involve interference competition wherein a competitor is prevented from using a resource even if it is not reduced in abundance by the competing species—both mechanisms likely operate in ungulates, and could lower *K* for one or both competitors (Stewart et al. 2002, 2011a). Apparent competition also may occur where 2 ungulates share a common predator. If one ungulate is abundant and the other rare, the greater number of predators supported by the more common species can adversely influence the population of the rarer ungulate where their distributions overlap (Johnson et al. 2013). The mechanisms underpinning the population dynamics of competing species of ungulates, however, remain the same. The relationship of population size to *K* helps determine the dynamics of both populations.

Density-dependent species also can exhibit irruptive growth, such as when a population at low density rebounds rapidly towards *K* (Leopold 1943, Klein 1968, Forsyth and Caley 2006, Ricca et al. 2014). This phenomenon occurs when a population has been held well below MSY (e.g., by harvesting animals), which allows for food resources to accumulate (McCullough 1979). In the absence of harvest or a marked reduction in harvest, populations will respond with rapid growth toward and a potential overshoot of *K*. In such an example, the magnitude of the overshoot of *K* will be related to the magnitude of the accumulation of resources; and, the degree of depletion of resources and subsequent population crash will exceed the magnitude of the overshoot of *K* (McCullough 1979, Person et al. 2001).

Irruptive growth in ungulate populations also can occur following newly abundant resources resulting from the creation of large areas of new habitat (McCullough 1979), introduction of ungulates to new areas, or release onto islands without predators (Klein 1968, Ricca et al. 2014). Under the previously listed examples, an overshoot of *K* can cause a concomitant decrease in *K* from overgrazing and resultant loss in habitat quality, thereafter leading to reductions in productivity (McCullough 1979; Starns et al. 2014, 2015). Ungulates possess the capability to have either detrimental or beneficial effects on the ecosystems that they inhabit, which largely are related to their population density relative to *K* (Hobbs 1996; Cote et al. 2004; Stewart et al. 2006, 2009; Speed et al. 2010).

Another term that is sometimes misused is anti-density dependence (also called inverse density dependence). This term has been applied correctly to carnivores preying on declining ungulate populations (Boutin 1992). For ungulate populations themselves, however, this process is thought to occur when the growth of a population is facilitated by increasing population density. For a population increasing from low density toward MSY (Figure 4), the population indeed will grow larger with increasing density. This is a normal part of the density-dependent process; there is nothing "anti" about it. The population would need to increase from the point of MSY toward *K* (Figure 4) as density increased for this to be anti-density dependent (a situation that at best is uncommon among ungulates). The Allee Effect (Allee 1938), wherein a population at a sufficiently low density facilitates a decline in growth rate (perhaps because of a lack of social facilitation necessary for mating or other causes—Berec et al. 2007, McLellan et al. 2010), is an example for which the term may be appropriate. Hoffmann et al. (2010) noted that some evidence for an Allee Effect existed for pronghorn (*Antilocapra americana*), and was thought to be produced by variation in rangeland condition over time. Such changes in condition of rangelands, however, also would likely involve changes in *K*, and hence density dependence. We contend the concept of anti-density dependence often is misused primarily because of the failure to conceptualize the parabolic nature of the curve for recruitment number (Figure 4), and its relationship to the more linear curve for recruitment rate (Figure 2)—nothing represented by those curves can be construed as anti-density dependent. Stephens and Southerland (1999) review circumstances where inverse density dependence is thought to occur without invoking rates of predation.

An additional misunderstanding regarding population dynamics relates to a life-history characteristic of ungulates (Bleich et al. 1997, Barboza and Bowyer 2000, 2001; Bowyer 2004; Stewart et al. 2011b, 2015)—sexual segregation. The sexes of dimorphic ungulates spatially separate from one another for much of the year, but aggregate for mating. This means that females, rather than males, compete most intensively for resources with other females and young for much of the year, thereby affecting nutritional condition of females. Accordingly, the female component is most closely related to the overall dynamics of a population (McCullough 1979). Among polygynous species exhibiting sexual segregation, harvesting males will do little to move a population away from *K* and, consequently, reductions in harvest of males will do little to bolster population growth (Freeman et al. 2014) because abundance of males has little effect on recruitment of young (McCullough 1979, 2001). Nonetheless, males may influence the dynamics of ungulate populations under some circumstances (Mysterud 2002), but those effects are not autonomous from density-dependent processes and sometimes may be overridden by them. Differences in space use, habitat selection, and diets between the sexes have led investigators to suggest that the sexes should be managed as if they were different species (Kie and Bowyer 1999, Stewart et al. 2003, Schroeder et al. 2010, Whiting et al. 2010), and have important implications for conservation (Bleich et al. 1997, Rubin and Bleich 2005). Indeed, examples exist wherein a management action undertaken to benefit the species differentially helps one sex to the detriment of the other (Bowyer et al. 2001, Stewart et al. 2003).

An additional problematic area in the understanding of ungulate population dynamics is the difference between compensatory and additive mortality (McCullough 1979, Bartmann et al. 1992). The concept of compensatory mortality was introduced by Errington (1934), Errington and Hammerstrom (1935) and Errington (1946) based on situations in which prey populations were observed losing what was termed a surplus of animals each year. Under compensatory mortality, one source of mortality compensates for another; with additive mortality, the effects of the sources of mortality are summed. Female ungulates generally attempt to produce more offspring than the habitat can support: attempted recruits exceed actual recruits (McCullough 1979; Figure 5). The difference between the number of attempted recruits and actual recruits that the habitat can support is the component of mortality that is compensatory (Monteith et al. 2014). That is, regardless of the proximate cause of mortality (e.g., predation, malnutrition), resources were insufficient to support those animals that did not survive (Figure 5). Therefore, the consequences of mortality and the degree to which mortality is compensatory or additive result from density dependence and resource limitation, whereby an increase in per capita resources reduces natural mortality rates and enhances potential for survival and reproduction (Boyce et al. 1999).

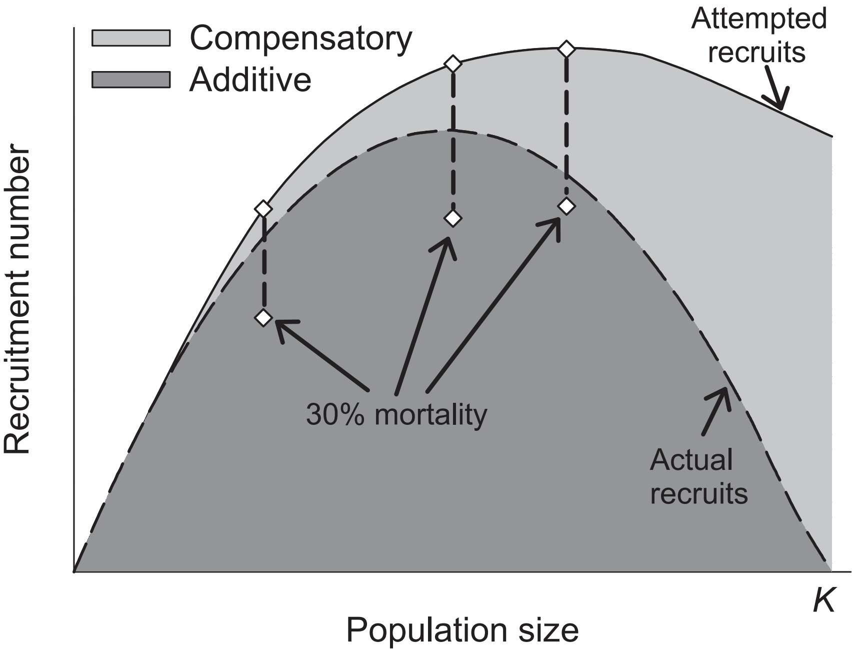

FIGURE 5.—Changes in recruitment number and attempts to recruit with increasing population size of adult female ungulates. Females attempt to add more young to the population than can be sustained by the environment at densities ranging from maximum sustained yield (MSY) to *K* where mortality becomes increasingly more compensatory (one source of mortality substitutes for another). Attempts to recruit young below MSY, however, are more successful because females are in excellent nutritional condition. Consequently, mortality is additive (one source of mortality is added to another) (from Kie et al. 2003, Monteith et al. 2014).

In populations at low density relative to *K*, females are in an enhanced state of nutritional condition, and the resources exist to support most of the attempted recruits (in the absence of predation or other sources of mortality), compared with populations near *K* when females are in poor nutritional condition and most attempted recruits will be lost because resources do not exist to support them. Between those two endpoints is a gradient of an increasing proportion of mortality that is compensatory as resource limitation increases concomitant with rising density relative to *K* (Figure 5). Consequently, unless a population exists at one of those two endpoints, conclusions that all mortality was either compensatory or additive are suspect. Depending upon proximity to *K*, mortality up to a certain point is compensatory, with higher levels of mortality becoming increasingly additive (Monteith et al. 2014). Indeed, compensatory and additive mortality both can operate, to varying degrees, in the same population (Pierce et al. 2012, Monteith et al. 2014).

Another topic of concern is the application of the terms compensatory and additive to characterize contributions of mortality among different predators preying on the same ungulate population. For instance, attempting to differentiate if mortality caused by particular predators was compensatory or additive is meaningless to the dynamics of ungulate prey; only the relationship of population size to *K* and, hence, level of resource limitation affects the degree to which mortality is additive or compensatory (Figure 5). Although a specific predator may have greater potential to have an additive effect than other predators—for example bears killing young within a few days of birth when those neonates are most vulnerable (Bowyer et al. 1998, Zager and Beecham 2006, Monteith et al. 2014)—it is the nutritional potential of the prey population to recruit young, and not the predators, that determines the consequences of mortality (Bartmann et al. 1992, Tveraa et al. 2003, Monteith et al. 2014).

Outcomes from compensatory versus additive mortality, indeed, have huge implications for interpreting effects of predation on ungulate populations (Ballard et al. 2001). For example, if a sample of radio-marked ungulates for a population experiencing strong resource regulation near *K* indicates that mortality of young was largely a result of predation, the need for predator control to benefit the ungulate population would be nil—most young would not have been recruited into the population and removing predators would have little effect on the ungulate population (i.e., most of the mortality was compensatory; Figure 5). Conversely, an identical mortality rate attributed to predation for an ungulate population at low density (or size) in relation to *K*, would lead to a far different conclusion—such mortality would be largely additive because the resources existed to support most of the young lost to predation. Consequently, predator control could be biologically justified (i.e., at least some mortality was additive), if the management objective was to increase the population of ungulates.

The terms "limitation" and "regulation" have engendered considerable debate (Van Ballenberghe and Ballard 1994, Berryman 2004, White 2007). For regulation to occur, there must be a density-dependent feedback (in prey for instance, as a result of predation, or changes in population size as an outcome from harvest) (Holling 1959). Limitation simply requires the death of individuals. Therefore, when limiting factors operate in a density-dependent manner they are, thus, regulating and have the potential to maintain populations at densities lower than what their habitat would allow. Therein, regulation can imply some level of equilibrium (between predator and prey, or harvest and populations size)—albeit uncommon and difficult to attain—among some populations of ungulates (McCullough 1999). For example, a predator pit can result in a prey population maintained at low density by density-dependent predation (Gasaway et al. 1992, Person et al. 2001, Bowyer et al. 2005, Wittmer et al. 2005). The pervasive influence of density-dependent limitation of resources on ungulate populations assures that resource limitation is a regulating factor.

As our previous discussion demonstrates, determining where an ungulate population is in relation to *K* is critically important for understanding its dynamics, and may affect decisions concerning conservation and management. Regression (McCullough 1979) and forage-based models (Hobbs and Swift 1985), as well several other methods (such as time series; Boyce 1989, Beck et al. 2006, Forsyth and Caley 2006) exist to parameterize *K*, but those approaches are data hungry and often cost prohibitive; many years may be needed to parameterize the necessary information (Bowyer et al. 2005, 2013; Monteith et al. 2014). Issues related to the conservation and management of ungulates likely would have been resolved for either good or ill long before many of the aforementioned models could be adequately parameterized (Bowyer et al. 2013). Meanwhile, habitat or environmental changes may well have occurred, potentially nullifying conclusions from the models.

Instead, we recommend using a model based on life-history characteristics of ungulates to determine the relative position of a population in relation to *K* (Table 1). Variation in those population characteristics, with regard to whether the population is near or backed away from *K*, results from changes in nutritional condition of females as a function of resource availability relative to density (Stewart et al. 2005). That suite of variables (Table 1), when considered as a whole, can provide valuable information on where the population is in relation to *K*. Likewise, this same approach can be used to evaluate whether population regulation or limitation is top-down (i.e., from predation) or bottom-up (i.e., via resource availability) (Pierce et al. 2012). Indeed, we contend that this approach is more meaningful and less difficult than collecting data on predator-prey ratios or kill rates, both of which can be misleading (Bowyer et al. 2013).

TABLE 1.—Life-history characteristics of ungulates that reflect the relative differences in a population regulated by top-down versus bottom-up processes (from Bowyer et al. 2005, 2013).

Life-history characteristic	Top-down regulated	Bottom-up regulated
Physical condition of adult females	Better	Poorer
Pregnancy rate of adult females	Higher	Lower
Pause in annual reproduction by adult females	Less likely	More likely
Yearlings pregnant[a]	Usually	Seldom
Corpora lutea counts of adult females[a]	Higher	Lower
Litter size[a]	Higher	Lower
Age at first reproduction for females	Younger	Older
Weight of neonates	Heavier	Lighter
Mortality of young	Additive	Compensatory
Age at extensive tooth wear	Older	Younger
Diet quality	Higher	Lower

[a] Some species of ungulates may show limited variability in particular characteristics.

Whether regulation is top down or bottom up ultimately can dictate important management decisions. We prefer the term "forcing" rather than regulation, because it allows for either top-down or bottom-up effects to change in a particular direction with population size, but without requiring equilibrium—use of the term forcing also avoids the regulation-limitation debate. Making judgments about top-down or bottom-up forcing, however, cannot be based solely on population trajectories. Information on the life-history characteristics of the ungulate population (Table 1) is required to identify such differences (Pierce et al. 2012). Moreover, both top-down and bottom-up forcing can operate in the same population and change in magnitude over time (Pierce et al. 2012, Monteith et al. 2014). This approach for assessing life-history traits also can be used to infer the degree to which predators are regulating prey (Bowyer et al. 2013). In some systems, predators may hold prey at low density in a predator pit in which reduced intraspecific competition results in good nutritional condition of prey with concomitant changes in life-history characteristics (Gasaway et al. 1992, Person et al. 2001, Bowyer et al. 2005). In other ecosystems, however, predators may be less successful in suppressing prey populations (Hurley et al. 2011). Consequently, the relationships presented in Table 1 may offer an alternative to other measures of predation in assessing whether regulation of ungulates is either top down or bottom up (Pierce et al 2012, Bowyer 2013).

The concept of carrying capacity (*K*) is at the heart of most models we have discussed. Contrary to some opinions, we do not find *K* to be a slippery notion (Macnab 1985) but, rather, to be one that is essential for understanding population dynamics of ungulates. We do, nevertheless, recognize that *K* can be easily misconstrued, especially in variable environments, and estimating *K* can be difficult (Monteith et al. 2014). Ecological carrying capacity (i.e., *K*) traditionally has been defined by the number of animals that a particular area can support at equilibrium (Caughley 1979, McCullough 1979). Directional changes (increases or decreases) in *K* can be brought about by perturbations of habitats (Holl and Bleich 2010, Holl et al. 2012), such as intentional manipulation, fire, drought, overgrazing, or overshoots of *K*. Results of such alterations to habitat can include differing equilibria between ungulates and the areas they occupy, which might be accompanied by fluctuations, or time lags of ungulate numbers and in density-dependent influences (McCullough 1999, Monteith et al. 2009, Pierce et al. 2012). Where directional changes in *K* do not occur over time, however, fluctuations in populations could still ensue. Such an outcome results from weather influencing the food supply (or in the instance of deep snow, also the energy budget) for these large herbivores. Managing ungulate populations based only on those fluctuations will, however, result in a very conservative harvest (McCullough 2001).

Productivity may vary from year-to-year depending on patterns of weather; thus, the net number of animals that available habitat can support fluctuates on an annual basis. Nevertheless, those short-term changes in productivity of habitat, and consequently the degree of density dependence each year, create difficulties in understanding the relative role of habitat and number of animals that can be sustained over the long term. To overcome difficulties of parameterizing *K* in a variable environment, Monteith et al. (2014) proposed the use of a new model termed "animal-indicated nutritional carrying capacity" (NCC). NCC is parameterized based on the nutritional condition of a population when $r = 0$ (i.e., no population change), because nutritional condition of a population signifies the position of a population relative to its current food supply (Monteith et al. 2014). Poor nutritional condition of animals relative to that threshold implies a population near or above NCC, and for which the resources for sustained growth of the population are not available, compared with a population in comparatively good nutritional condition, which is typical of a population below NCC and for which resources exist to support population growth. Indeed, the nutritional status of a population at a particular point in time integrates nutritional history relative to forage quality and abundance as a function of density and potential nutritional carryover to the following season (Monteith et al. 2013). Not only does this approach provide a tractable tool for assessing NCC, it also yields the mechanism for examining the consequences of mortality on population dynamics (Figure 6) that is essential for managing populations of ungulates. This innovative approach allows for more comprehensive management of ungulates, because density-dependent processes and potential fluctuations in food supply are inherently integrated in the nutritional status of the population of interest. We note, however, that the conservation and management of ungulates may require more than just an improved understanding of their population dynamics (Krausman and Bleich 2013).

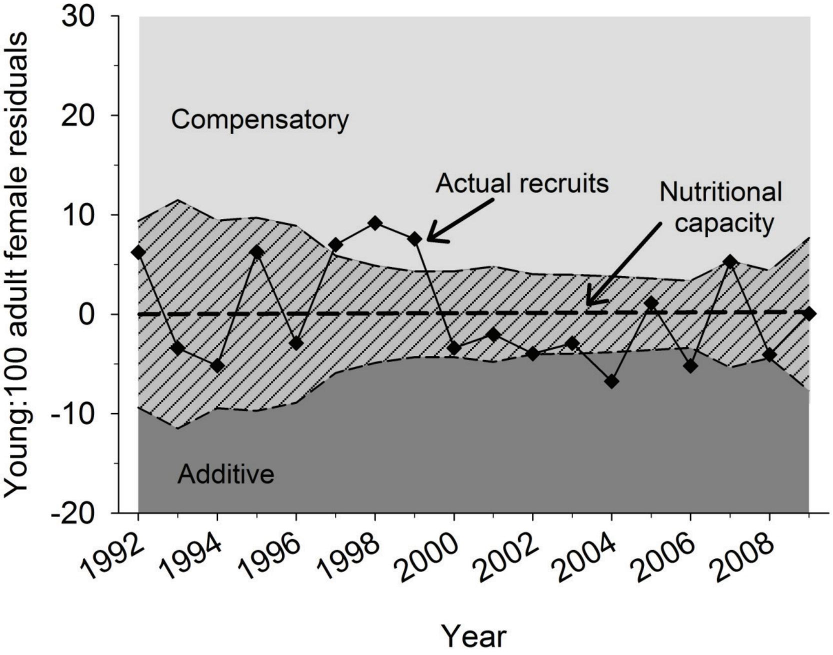

FIGURE 6. —Residuals from a mixed-effects model used to predict the nutritional capacity of female mule deer (*Odocoileus hemionus*) to recruit young relative to attempted recruits (based on fetal rates) and observed recruits (based on the ratio of young to adult females) over time. Residuals in ratios of young to adult female above those predicted (dashed line) indicate mortality was compensatory (light gray); ratios below that expected indicate the amount of mortality that was additive (dark gray). The model included the variables mean March ingesta-free body fat (IFBFat) of the current year, mean March IFBFat of the previous year, mean March body mass, mean litter size, per capita snowpack, summer precipitation, and summer temperature. The hashed areas around the predicted line represent 95% confidence intervals (from Monteith et al. 2014).

Management Implications

We highlight the importance of determining where an ungulate population is in relation to carrying capacity (*K*) to understand the dynamics and, thereby, the management and conservation of that population. Density-dependent processes underpin the nutritional condition and life-history characteristics of ungulates. We offer a method that incorporates such information to parameterize where a population is relative to *K* (Table 1). This cost-effective approach also can be used to help establish and adjust harvest goals in an adaptive manner, and determine whether the population might be regulated by predation. We caution that what appears to be density-independent regulation of a population also may have a strong density-dependent component, especially when there are correlations between population productivity and weather variables (Figure 1). Comparisons among populations based only on density can be misleading, because *K* may vary among populations independent of their density. Winter range has long been thought to be the primary factor influencing productivity of ungulate populations in temperate and arctic regions. Nonetheless, the importance of summer range recently has been documented—both seasonal ranges may be critical in determining the productivity of populations, and carryover effects in nutritional condition may occur across seasons.

Different management strategies are required for species displaying density-independent compared with density-dependent components to their life-history characteristics. Harvesting just the surplus of populations that are strongly density-dependent when near *K* (which will be low) results in low recruitment in the following year (Figure 4), and very conservative management, if the goal is to increase harvest. For density-dependent ungulates, the harvest determines the surplus, and increasing harvest until MSY is reached will continuously increase recruitment; harvesting beyond MSY, however, can move the population toward extirpation (Figure 4). Harvesting only males will do little to affect the dynamics of ungulate populations. When released from harvest or introduced into new environments, ungulate populations may irrupt, with an overshoot of *K* resulting in disproportional damage to habitat relative to the size of the overshoot—a circumstance that should be avoided if possible. Creating new habitat when the population is at low density will do little to promote increased reproduction, yet can be a successful strategy when the population is near *K* (Figure 2). The sexes of ungulates typically spatially separate outside the mating season. Males and females select habitats differently, and effective management may require treating the sexes as if they were separate species—examples exist where habitat manipulations benefited one sex to the detriment of the other.

Understanding differences between compensatory mortality (one source of mortality compensates for another) and additive mortality (one source of mortality is added to another) and how this changes with increasing population size in relation to *K* is critical for the sound management of ungulate populations (Figure 5). Mortality near *K* is mostly compensatory, and reducing harvest or predation will have little influence on changing the size of the ungulate population. Conversely, if a population is at low density in relation to *K* (and, hence, most mortality is additive), the same harvest or losses to the population from predators could have dire consequences by further reducing population size. Under such circumstances predator control may be biologically justified. The relationship of the ungulate population to *K* is the critical element in determining whether mortality will be additive or compensatory—that one predator causes more additive mortality than another is meaningless to the dynamics of ungulate populations—the number of ungulates killed and the relationship of the population to *K* is what is critical. Finally, we offer a new method for understanding year-to-year variation in the nutritional carrying capacity (NCC) of an area, and a technique to determine whether mortality is additive or compensatory (Figure 6). This method should be useful in the long-term management of ungulate populations, especially in variable environments.

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Mallard feeding on kokanee salmon eggs, Taylor Creek, California

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Mallards (*Anas platyrhynchos*) are an abundant breeding duck throughout California (Kozlik 1974) and feed widely on both animal and plant materials (Martin et al. 1961, Swanson et al. 1985, Bellrose 1980, Cederholm et al. 1989). Munro (1923) appears to be the first published record of mallards consuming salmon eggs. In Alaska, Gleason (2007) reported mallards eating salmon carcasses, as well as a personal communication that the use of salmon eggs is a common foraging strategy of mallards. Gleason (2007) also included additional second-hand reports that anecdotally suggest that salmon form an important food source for mallards. Other reports (Munroe 1943, Willson and Halupka 1995), combined with observations from Canada (J. S. Gleason, U.S. Fish and Wildlife Service, personal communication June 2014) and California (E. G. Hunt, CDFW retired, personal communication June 2014) suggest that this foraging strategy is more common than is indicated in the literature. In this note we call attention to the personal observations or personal communications included in previously published papers (Munroe 1923, Gleason 2007). Further, we describe an additional observation of a male mallard consuming eggs of kokanee salmon (*Oncorhynchus nerka*) in a tributary to Lake Tahoe, California. Kokanee were introduced to Lake Tahoe in 1944 when fry were accidentally released (Cordone et al. 1971). Kokanee were planted annually thereafter in most of the major tributaries to the lake, and Taylor Creek, El Dorado Co., California became the major spawning area (Cordone et al. 1971).

At 1208 on 6 October 2013 authors Dieter and Atkinson observed a male mallard at Taylor Creek (38° 56’ 6” N, 120° 3’ 25” W) fly into the creek and actively begin stirring up kokanee redds with his feet and consuming the eggs as they floated to the surface (Figure 1). This behavior continued for approximately 20 minutes while dozens of fish were spawning, and within 3 m of many other people observing the annual kokanee run.

Figure 1.—Male mallard (*Anas platyrhynchos*) stirring kokanee (*Oncorhynchus nerka*) redds with his feet. The mallard repeatedly stirred the bottom and fed on the kokanee eggs as they floated up from the substrate. Taylor Creek, El Dorado County, California, 6 October 2013. Photograph by L. D. Dieter.

The kokanee seemed habituated to this activity, staying within the area disturbed by the mallard; one male kokanee was observed proximate to (i.e., <20 cm) the duck's feet without apparent alarm. On each dabble, the mallard ingested several kokanee eggs. The stirring and dabbling behavior continued as the duck moved upstream through the spawning kokanee. The duck, although habituated to people, appeared to be a normal wild mallard (Figure 2).

Figure 2.—The mallard observed stirring kokanee redds with his feet appeared to be a normal wild bird, albeit tolerant of human presence. Note the slim body conformation and wild plumage, both of which are atypical of domesticated birds. Taylor Creek, El Dorado County, California, 6 October 2013. Photograph by L. D. Dieter.

Mallards are well known to exploit seasonally abundant food resources (Heitmeyer 2006, Lafferty et al. 2013) in order to meet nutrient reserves necessary for reproduction and migration (Krapu 1981, Ankney et al. 1991). The ability to use various habitats and food sources likely explains the widespread abundance of mallards; information included herein further confirms this plasticity in their food habits, and provides an additional description of a foraging behavior that previously has been documented poorly in the formal literature.

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William E. (Bill) Clark: Tough Texan to the "Glass Half-full Guy"

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William (Bill) Clark (1941–2013)

December 9, 2013 was a sad day for the family, friends, and colleagues of Bill Clark. His sudden passing was a loss felt heavily by the wildlife conservation community throughout California. Bill's professional career was cut short by a life threatening stroke in 1995, and we lost him to a similar event in December last year

Bill was a man of contrasts: rough around the edges at times, yet always sensitive to the needs of other people. He was a prime example of a wildlife professional who—through his personality, hard work, and dedication to conserving wildlife—set the California Department of Fish and Game (CDFG) apart from being, "just another State Agency." Underneath a tough exterior, Bill was a people person. As an example, for many years, Bill and his wife Jeanne hosted an annual Fish and Game Picnic at "Rancho Clark"—their home in Newcastle—for 100–150 of their friends. He was a generous and gracious host who loved to share Fish and Game stories with anyone who'd listen.

I met Bill Clark in 1972. He impressed me as a colorful "Tough Texan" on the team at CDFG's Wildlife Investigations Lab (WIL). As an eager, but somewhat naive, graduate student, I was in need of technical support for my Master's project, which focused on physical condition indicators in black-tailed deer as a reflection of habitat quality. The WIL was widely recognized for its technical expertise in wildlife food habits, parasites, and diseases. I showed up looking for handouts in the form of food habits analyses and technical advice, and I talked Bruce Browning into helping me with the food habits work. During my first visit to the Lab and after meeting with Bruce, I recall a brief conversation with Bill. He showed interest in my project, even if it was only to offer encouragement and advice to be thorough in my work and ask questions of experienced people as a means of learning along the way. His advice made a positive first impression.

After completing my graduate degree in 1974, I was fortunate to land a job as a field biologist with CDFG in Monterey County. It didn't take long for me to push my boss to allow me to attend the Department's Wildlife Restraint class taught by the WIL staff, including Bill. Although the WIL team taught hundreds of students in California and other western states, Bill took the time to try and get to know each student, make every session special, and insisted on a post-class review and evaluation to help improve future classes. He used the same approach with respect to wildlife capture projects, where human and animal safety were critically important issues. Bill was a very effective teacher and project leader, and also was a coach and mentor for hundreds of CDFG employees, other agency staff, and university students. Despite his tough exterior, he was always considerate of others and willing to help solve problems by sharing his knowledge and experience.

In late November 1995, life changed drastically for Bill and his wife Jeanne, as well as for those of us who worked closely with him. Bill suffered a major stroke and we nearly lost him. I vividly remember visits to see him in the hospital ICU, holding his hand, and assuring him he'd be OK. It was a difficult time, yet I needed to let him know I was there. It was tough seeing Bill in that condition, yet I felt better doing what I could just to let him know I cared. He repaid the favor many times over in the following years.

Soon after he regained consciousness, Bill demonstrated his toughness during long months of intensive, tedious, and often painful medical treatments that were followed by years of physical, memory, and speech therapy. Despite a few setbacks along the way and the loss of his short-term memory, it didn't take Bill long to show signs of the guy we all knew, including an amazing sense of humor in the face of a life threatening situation. He even joked with one of his doctors about contracting a new disease, which he termed "CRS". When the doctor questioned Bill, he merely smiled and said, "Can't Remember Sh_ _."

Once he gained enough strength to assess his condition, Bill wasted no time getting focused on the positive aspects of surviving his ordeal and making the best of the cards he'd been dealt. One of his favorite sayings became, "Look at the glass as half-full." Since his short-term memory was limited by the stroke, we heard that phrase often, along with a few other original sayings like, "no brain, no pain." Humor served Bill well, and it helped the rest of us deal with his limitations during recovery and adjustment to his new life. It wasn't long before we were out hunting pheasants with our dogs and taking a few trail rides with our horses. Although things were different following Bill's stroke, it was great to just go out and have fun with him doing the activities we both enjoyed. Yes, I was there when he killed his first post-stroke pheasant!

During his career, Bill was widely recognized as an innovator and problem solver. Those traits came to the surface often as he helped develop leading edge techniques for capturing, restraining, and sampling a wide range of wildlife in support of scientific studies and population management and restoration programs. He played a major role in a number of high profile projects, including the restoration of tule elk, pronghorn, and bighorn sheep to many of their native ranges, resulting in numerous populations that now support public use and enjoyment, including regulated hunting.

This tribute would not be complete without describing the close and mutually respectful friendship we shared for many years. In retrospect, I now realize that relationship was unique in that it covered a period in which our roles at CDFG evolved in terms of job duties and reporting relationships. We used to joke about the challenges at various levels in the "food chain" and how it sometimes got a bit lonely as one moved up in the organization. Nevertheless, we maintained a close personal friendship, regardless of our respective roles, including me serving as Bill's supervisor.

Our friendship began when I was as a newly minted biologist and Bill a seasoned WIL staffer. He loved his work, and made the decision to remain there rather than pursue promotional opportunities elsewhere. As fate would have it, things changed over time, with Bill being promoted to WIL Coordinator and me running the gauntlet through the ranks including Big Game Supervisor, Assistant Wildlife Division Chief, Wildlife Chief, and Deputy Director. For >15 years, I was Bill's boss—in title anyway. It's rare that two people stay friends while balancing those roles. Yet, throughout that entire period and beyond, we remained close in a trusting friendship. I didn't fully realize how special that relationship was until I left CDFG in 2002. It became clear to me then, and I think to Bill after he retired, how relationships with people around us can change, especially under challenging circumstances beyond our control.

Bill Clark was a good man and left his mark on the world around him. His legacy is reflected by the many people whom he helped during their careers, and the diverse wildlife resources he worked so hard to enhance for Californians to enjoy. I, and dozens of others that he worked with, hold many great memories of Bill. Our long and mutually respectful friendship sits on top of the stack, as I'm sure it does with many others. Collectively we, and I personally, could not have asked for a better friend and mentor during the more than 30 years that I, and many others, had the privilege to know and work with him. Bill will be greatly missed by the many people whose lives he touched.

Editor's note—On 15 November 2014, Bill's family and friends gathered in the Mojave Desert at Clark Mountain (below), and distributed Bill's ashes and some mementos among the peaks and canyons that he so loved. Dick Weaver–a retired CDFG Wildlife Biologist and who was present that day—who survived the helicopter crash at that location on 6 October 1986 that resulted in the deaths of two of the best friends that bighorn sheep ever had—proclaimed the massive peak would, in the future, be known as Clark's Mountain.

Photo by George Kerr


CDFW Photo by Debra Hamilton


Photo by Becky Pierce


CDFW Photo by Debra Hamilton


CDFW Photo


Photo: Society for the Conservation of Bighorn Sheep


CDFW Photo by Joe Ferreira


CDFW Photo by Joe Ferreira

These photos are presented to commemorate some of the wildlife conservation work completed in California over the past quarter century.


CDFW Photo by Debra Hamilton


CDFW Photo by Debra Hamilton


CDFW Photo by Debra Hamilton


CDFW Photo


CDFW Photo

CDFW Photo by Debra Hamilton

Photo by Chip Hollister

CDFW Photo

CDFW Photo by Debra Hamilton

Photo by Chip Hollister

BOOKS RECEIVED AND AVAILABLE FOR REVIEW

Copies of the following books have been received, and are available for review by interested parties. Individuals interested in preparing a formal review that will be published in *California Fish and Game* should contact the editor (Vern.Bleich@wildlife.ca.gov) with their request to do so.

GOTSHALL, D. W. 2012. Pacific Coast inshore fishes. Fifth edition. Sea Challengers, Monterey, California, USA. 363 pages. $9.99 (E-Book).

KIRKWOOD, S., AND E. MEYERS. 2012. America's national parks: an insider's guide to unforgettable places and experiences. Time Home Entertainment, Inc., New York, New York, USA. 208 pages. $24.95 (hard cover).

LOVE, M. S. 2011. Certainly more than you want to know about the fishes of the Pacific coast: a postmodern experience. Really Big Press, Santa Barbara, California, USA. 650 pages. $29.95 (soft cover).

INFORMATION FOR CONTRIBUTORS

California Fish and Game is a peer-reviewed, scientific journal focused on the biology, ecology, and conservation of the flora and fauna of California or the surrounding area, and the northeastern Pacific Ocean. Authors may submit papers for consideration as an article, note, review, or comment. The most recent instructions for authors are published in Volume 97(1) of this journal (Bleich et al. 2011), and are accessible through the California Department of Fish and Wildlife web site (www.dfg.ca.gov/publications).

Planning is in progress to provide an avenue for authors to submit manuscripts directly through the web site, and to enable restricted and confidential access for reviewers. In the meantime, manuscripts should be submitted by e-mail following directions provided by Bleich et al. (2011). The journal standard for style is consistent with the Council of Science Editors (CSE) Style Manual (CSE 2006). Instructions in Bleich et al. (2011) supersede the CSE Style Manual where differences exist between formats.

Authors of manuscripts that are accepted for publication will be invoiced for charges at the rate of $50 per printed page at the time page proofs are distributed. Authors should state acceptance of page charges in their submittal letters. The corresponding author will receive a PDF file of his or her publication without additional fees, and may distribute those copies without restriction. Plans are underway to make the complete series of *California Fish and Game* available as PDF documents on the California Department of Fish and Wildlife web site.

LITERATURE CITED

BLEICH, V. C., N. J. KOGUT, AND D. HAMILTON. 2011. Information for contributors to *California Fish and Game*. California Fish and Game 97:47-57.

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The Scientific Journal *California Fish and Game* celebrates its 100th Anniversary with four special collector editions.

The California Department of Fish and Wildlife (CDFW) has published the highly respected scientific journal *California Fish and Game* continuously for an entire century. To commemorate the Centennial Anniversary of the journal, CDFW is publishing four special issues in Volume 100.

Promoting "Conservation of Wildlife Through Education", *California Fish and Game* is an internationally recognized, peer-reviewed research publication of interest primarily to scientists active in the fields of conservation, ecology, and natural resource management. It focuses on the wildlife of western North America and the eastern North Pacific Ocean, but occasionally includes material from elsewhere.

This is the third of four special issues scheduled to be published this year, and includes the results of research on wildlife ecology conducted CDFW scientists, scientists in additional resource management agencies, and others representing academic institutions or non-governmental organizations. Subject matter varies from historical accounts to papers reporting the results of original research. All contributions to *California Fish and Game* are peer-reviewed and represent conservation science at its best.

"I'm proud to have been the editor of this important scientific journal for the past five years, and to guide it through publication of its centennial volume," said Dr. Vern Bleich, Editor-in-Chief. "Material published in the journal represents the important work that scientists, both within CDFW and elsewhere, are doing on behalf of conservation."

The Special Wildlife Issue features an introduction by Anthony Rendon, Chair of the Assembly Water, Parks, and Wildlife Committee, and additional remarks co-authored by CDFW Director Charlton H. Bonham and R. Terry Bowyer of Idaho State University. The first issue of volume 100 focused on research and conservation of the vegetation resources in California; the second focused on marine ecology and management, and the remaining 100th Anniversary Issue will focus on the ecology of freshwater organisms. It, too, will be introduced by prominent Californians and scientists involved in the conservation of the flora and fauna of western North America.

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