

CALIFORNIA FISH AND GAME

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Notes from the Editor

*Come gather 'round people, wherever you roam,
and admit that the waters around you have grown...
For the times, they are a-changin'.*

Bob Dylan, 1963

The Times, They are A-changin'

Indeed, some important changes to *California Fish and Game* have occurred in the editorial and publication processes over the past six years. First, we revised the format for manuscripts that are intended for this journal. We also have a rejection rate that is on an upward trajectory; in the past, many authors merely viewed *California Fish and Game* as a “last ditch” journal in which to publish material that had been rejected by at least one (and likely, several other) more “prestigious” professional journals. The Associate Editors and I have worked very hard to counter that trend, and we believe substantial progress has been made.

Following direction provided by higher authorities, we have successfully initiated electronic publication of the journal, and it is now available at no cost to scientists and other interested parties throughout the world. As part of that process, we have obtained an ISSN (International Standard Serial Number) for the electronic version of the journal, in addition to our existing print ISSN. Both ISSNs ensure that *California Fish and Game* will continue to be indexed by literature search services on an international scale.

In addition, the journal now sports color covers portraying one or more images of a species or habitat that is the subject of a paper in the current issue. Further, several new Associate Editors joined the editorial staff, and were invited because of their areas of expertise and abilities to network with potential reviewers, as well as their willingness to make objective recommendations regarding the merit of manuscripts that are received. Among those that have assisted this editor in the capacity of Associate Editor are Walter Beer, Cheryl Burton, Liam H. Davis, James Harrington, Paul Hofmann, Peter Kalvass, Nina Kogut, Dave Lentz, Scott Osborn, Steve Parmenter, Laura Patterson, Kevin Shaffer, Levi Souza, Joel Trumbo, and Jeff Villepique. These individuals have worked in a concerted effort to enhance the quality of material published in the journal. As AEs, they have been responsible for seeking reviewers, distributing manuscripts, evaluating reviewer comments, synthesizing those comments, and making recommendations as to the acceptability of the manuscripts they handle. Ultimately, the final decision on acceptance rests with the Editor-in-Chief, but those decisions are greatly facilitated by input from the AEs.

A major change occurred with the retirement of Ms. Debra Hamilton who, over the past six years, served as Production Editor for *California Fish and Game*. After 27 years of state service, Debra retired on 3 September. She was a stickler for detail, and she and I worked diligently to provide the most error-free issues of the journal that we thought were possible, albeit none were ever perfect. Debra also dedicated her skills to enhancing the quality and appearance of the journal, and her interest and endeavors made it possible to move forward with electronic publication. Thank you, Debra, for your efforts, your professional approach to publication of *California Fish and Game*, and for all of the exploratory work you did on behalf of electronic publication

and the concept of print-on-demand, which I am hoping will become the norm.

Concomitant with this issue, Ms. Carol Singleton has replaced Debra as Production Editor. Carol is employed as a Marketing Specialist in the Office of Communications, Education, and Outreach, and has extensive familiarity with the technology and software used to produce the journal. Carol and I have worked to streamline the protocol for processing manuscripts that Debra and I established, and Carol has made a number of meaningful suggestions that will facilitate the process of turning an edited manuscript into a formal publication. Thank you, Debra, for a great run and thank you, Carol, for stepping up to support the continued production of *California Fish and Game*.

Finally, this will be the last issue published under my editorship. Together, the Associate Editors, the Production Editor, and the supervisors and managers within the Office of Communications, Education, and Outreach have strived for excellence in the production of the journal. I am optimistic that the incoming editor will continue in that tradition, and that he or she will be able to move forward with initiating print-on-demand and further facilitating electronic publication. Print-on-demand technology will enable individuals interested in obtaining hard copies of the journal to do so at no cost to the Department of Fish and Wildlife. Electronic publication has been much more difficult to implement than originally anticipated by its early advocates within the Department. Nevertheless, that technology facilitates the more rapid release and dissemination of information, although the process is more complicated than originally anticipated.

I have enjoyed serving as Editor-in-Chief and working to help resolve the many challenges that have arisen over the past several years. It has been a good run, and I wish the incoming Editor-in-Chief every success in ensuring that *California Fish and Game* remains California's longest-running, continuously published scientific journal.

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

ABOUT THE COVERS

FRONT.—Controversies surrounding the natural distribution of beavers (*Castor canadensis*) are abundant, but interest in the role of those large rodents in ecosystem function is increasing rapidly. On pages 281–240 of this issue, Jeff Baldwin explores the potential for beaver populations to play a meaningful role in mitigating climate-driven changes in California's highlands. Photograph courtesy of Steve Hersey.

BACK.—Water, always a subject of interest in California, has been the subject of many recent contributions to the literature on salmonid life histories. On pages 241–266, Michael Wallace and his coauthors explore the importance of stream-estuary ecotones in Humboldt Bay, California, to juvenile coho salmon (*Oncorhynchus kisutch*). The upper photograph is of tidal brackish-water habitat in Lower Freshwater Creek Slough; the center-left image is of the freshwater stream-estuary ecotone in Martin Slough; an incoming tide from Freshwater Creek Slough at the mouth of Wood Creek is pictured in the center right-image; and in the lower photograph, a California Department of Fish and Wildlife and Pacific States Marine Fisheries Commission field crew is pictured seining tidal freshwater habitat in Martin Slough. Photographs courtesy of Michael Wallace, California Department of Fish and Wildlife.

Home-range overlap of Roosevelt elk herds in the Bald Hills of Redwood National Park

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We examined whether seasonal changes in food supply or social familiarity could explain seasonal dynamics of home-range overlap between two Roosevelt elk (*Cervus elaphus roosevelti*) herds in northwestern California. Elk location data were obtained from GPS transmitters and food supply was estimated from remotely sensed normalized difference vegetation indices (NDVI). Home-range overlap averaged 11 percent. The NDVI values were positively related to home-range overlap and greater social attraction between elk herds. Seasonal patterns of home-range overlap were consistent with changes in food supply and not social familiarity.

Key words: *Cervus elaphus roosevelti*, forage, space use, normalized difference vegetation index, half weight association index, social behavior

Home-range overlap of individuals or herds has been repeatedly documented in bovids and cervids (Harper 1967, Franklin and Lieb 1979, Jenkins and Starkey 1982, Cornelis et al. 2011, Scillitani et al. 2013). Home range is defined as ‘that area traversed by the individual during its activities of food gathering, mating, and caring for young over a given time period’ (Burt 1943). Overlap in home range between herds or individuals tends to occur in landscapes with large patches of forage habitat that varies spatially and temporally (Scillitani et al. 2013). Jenkins and Starkey (1982) observed a roughly 20 percent overlap in annual home ranges between two elk herds. For female elk from the northern herd in Yellowstone National Park, Craighead et al. (1973) also documented a similar degree of overlap between herds at the end of the winter and through post-parturition. Little work, however, has examined seasonal variation in home-range overlap. Although most studies of home-range overlap are conducted at the temporal scale of a year, examining seasonal variation in home-range overlap might be useful to help understand the degree to which home-range overlap occurs. Food resources are not consistently abundant throughout the year, thus altering competition for such resources among herds. Measuring changes in food supply and home-range overlap on a seasonal scale can provide insight into mechanisms of association. Furthermore, Roosevelt elk in Redwood National Park express unique

population dynamics among herds (Julian et al. 2013). Because of unique herd dynamics, management is probably most effective at the herd level. What is unclear is whether spatial boundaries of herds are likely to be constant or if they are likely to vary. An understanding of the mechanisms responsible for maintaining herd boundaries is needed to assess if those boundaries are constant or if they are likely to change.

Home-range overlap may be associated with seasonal changes in food supply and social structure. During the growing season—when food is more plentiful than in other seasons—there should be less partitioning of food between adjacent herds and, consequently, greater overlap in home ranges (Jenkins and Starkey 1982). Conversely, during seasons when food supplies are more limited, home-range overlap should be less because of resource partitioning between adjacent herds (Franklin et al. 1975, Bowyer 1981, Anderson et al. 2005).

Social familiarity among individuals might also explain variation in home-range overlap as well as seasonal changes in overlap. Adult females, their juvenile offspring, and sub-adult males can display strong social bonds in gregarious species of cervids, such as elk (Franklin et al 1975, Weckerly 1999). Thus, herds comprised of socially bonded individuals might be reluctant to associate with adjacent groups comprised of unfamiliar individuals regardless of seasonal fluctuations in food supply (Rutberg 1983, Thouless et al. 1985).

The objectives of this study were (1) to estimate seasonal home-range overlap of the two Roosevelt elk herds in the Bald Hills region of Redwood National Park, Humboldt County, California; and (2) to determine if forage abundance or social familiarity influence home-range overlap of the two herds. If forage abundance is associated with home-range overlap, then the extent of overlap and association between elk from different herds should be greater when food supplies are abundant. If social familiarity is driving home-range overlap then there should be no relationship, or an inverse relationship, between forage abundance and home-range overlap, and an elk herd should avoid the areas that are currently occupied by the adjacent herd.

MATERIALS AND METHODS

Study area.—This study was conducted in the Bald Hills region of Redwood National Park, Humboldt County, California (41° 11' N, 123° 56' W). The Bald Hills are a series of meadows that range in size from 10–300 ha and total about 1,000 ha (Weckerly and Ricca 2000, Starns et al. 2015). The meadows are situated along a southwest-facing ridge of Redwood Creek. The region was purchased by the National Park Service during 1977–1978 (Mandel and Kitchen 1979). Before then the area known as the Bald Hills was privately owned and was grazed by sheep and cattle.

The climate in the region has wet, cool winters, and dry summers during which precipitation is mostly limited to occasional fog (Starns et al. 2015). Average annual precipitation varies from approximately 1,200 to 1,800 mm and occurs mostly as rain (Hektner et al. 1983). Ninety percent of this precipitation falls between the months of October and April. Snow is common during the winter months (November–February) in some years but rarely remains on the ground beyond a week. Precipitation data between October 2002 and April 2003 were obtained from the RAWS USA Climate Archive (<http://www.raws.dri.edu>). Mean summer temperatures range from 24 to 27°C and mean winter temperatures range from 3 to 5°C. Elevations range from 360 to 1,050 m. The landscape is comprised of meadows (24%), oak (*Quercus* spp.) woodlands (10%), and second-growth

and old-growth redwood-conifer stands (66%) that are dominated by coast redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*; Weckerly and Ricca 2000). Oak woodlands are comprised of Oregon white oak (*Q. garryana*) and California black oak (*Q. kelloggii*). Grassland meadows have a mix of perennial and annual grasses including California oatgrass (*Danthonia californica*), sweet vernal grass (*Anthoxanthum odoratum*), deer vetch (*Lotus micranthus*), and English plantain (*Plantago lanceolata*).

During 2002, a total of 204 Roosevelt elk was counted in the Bald Hills region of Redwood National Park (Starns et al. 2015). These 204 animals were divided between two spatially distinct herds. Herd 1 was located in the northern reaches of the Bald Hills, and herd 2 was located in the southern end.

Capture.—In December 2002 and January 2003, personnel from the California Department of Fish and Game and the National Park Service conducted helicopter darting and free range darting to capture adult female elk in the Bald Hills. Two adult females were captured from herd 1 and four adult females were captured from herd 2. Captured animals were immobilized with carfentanil citrate (Miller et al. 1996). Legs of immobilized elk were hobbled and eyes covered. Animals were fitted with neck collars housing VHS and GPS transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA). To antagonize carfentanil citrate immobilization, naltrexone hydrochloride was administered intravenously. Each GPS collar was programmed to record a location at six-hour intervals for one year. Animals were captured in compliance with agency guidelines and were approved by the Texas State University institutional animal care and use committee (KSMJK6_02).

Analyses.—The 2-D and 3-D locations with position dilution of precision readings >5 were removed to avoid the use of imprecise locations due to the influences of satellite positioning, terrain, or dense vegetation (Lewis et al. 2007). This resulted in each individual having 80–130 locations per month. Four of the six GPS collars were recovered following remotely triggered detachment in March, 2004. One collar was recovered from an animal in herd 1 and the remaining three were recovered from animals in herd 2. The locations of animals in herd 2 cannot be assumed to be independent from each other. Roosevelt elk express strong social bonds throughout most of the year that allow for protection against predation as well as increased knowledge of prime foraging locations from mature individuals within the herd (Weckerly 1999). Movements by one animal are assumed to be representative of the herd's movements due to the aggregated structure of Roosevelt elk throughout the year. Thus, one animal was randomly selected from herd 2 and used in subsequent analyses, and the location data from the remaining animals in herd 2 were discarded. Hereafter, the single animal in herd 1 will be referred to as animal A and the single animal randomly selected from herd 2 will be referred to as animal B.

The fixed kernel (FK) estimator with an *ad hoc* smoothing parameter was used to estimate 95% home-range sizes for both animals A and B for each month from January to December (Seaman and Powell 1996, Kie 2013). Numerous home-range distribution estimates have used various smoothing parameters to estimate home range depending upon the objective and data availability. The FK estimator method was used to allow for contiguous polygon calculations and reduced bias given the variation in time between data point locations and multimodal animal locations (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999, Horne and Garton 2006, Kie 2013). This estimator and smoothing parameter also accounts for multimodal animal locations and does not assume normally distributed animal locations. The kernel density tool in the Spatial Analysis package in ArcMap 10.2 (ESRI 2014) was used to calculate the home range of each animal. Monthly

FK home-range estimates for each animal were plotted and estimated.

To measure home-range overlap, the FK estimate for animal A and animal B was loaded into ArcMap 10.2 for the same month. If an area of overlap existed, the area was determined to the nearest hectare. Every location in the overlap area was then placed into one of two groups: days when locations of only one of the two animals occurred within the area of overlap, and days when locations of both animals occurred within the area of overlap. To quantify association between animals, the half-weight association index (HAI) was calculated as

$$\text{HAI} = \frac{n_{\alpha\beta}}{n_{\alpha\beta} + \frac{(a + b)}{2}}$$

where n is the number of occasions that animal A and animal B were located within the area of overlap together, a is the number of occasions that animal A was located in the area of overlap unaccompanied by animal B, and b is the number of occasions that animal B occurred within the area of overlap unaccompanied by animal A (Brotherton et al. 1997).

The HAI value ranges from 0 to 1. Values closer to 0 indicate avoidance and values closer to 1 indicate attraction between the two animals. Plant biomass in meadows was indexed with the normalized difference vegetation index (NDVI; Chander et al. 2009). The NDVI measures the ratio of near infrared to red light reflected by vegetation, and is positively correlated with vegetation biomass (Anderson et al. 1993, Elmore et al. 2000).

To estimate NDVI, Landsat 5 Thematic Mapper images, obtained at 16-day intervals, were downloaded from USGS Earth Explorer (<http://earthexplorer.usgs.gov>) from January 1989 to November 2011. These images have a pixel resolution of 30 m², an area that is adequate for measuring plant biomass in meadows used by elk. Approximately 200 images were free of cloud cover. Monthly mean NDVI readings from 1989 to 2011 were used due to the lack of cloud-free images for all months in 2003. Each cloud-free image was corrected for top-of-atmospheric reflectance using the methods described by Chander et al. (2009) prior to deriving estimates. Images were then clipped down to the Bald Hills meadows. Pixels with NDVI values < 0.1 were then re-classified as “null” since they most likely were bare ground, water, or snow (Starns et al. 2015). In months where two images were available, the average of the NDVI means between the two images was used in analyses (Starns et al. 2015). All image processing was carried out using ERDAS Imagine 2013 (Intergraph Corporation 2013). An *a posteriori* two-tailed *t*-test comparing monthly rainfall accumulation in 2003 to the monthly average rainfall for the remaining years was conducted to assess if precipitation in 2003 deviated from that recorded during the other years.

Scatter plots of the data were first observed to assess whether relationships between NDVI and home-range overlap, and between NDVI and HAI, were linear. After viewing these scatter plots, two simple linear regressions were estimated between NDVI and home-range overlap, and between NDVI and HAI (Sokal and Rohlf 2012). Statistical analyses were conducted in program R (R Development Core Team 2014).

RESULTS

The Bald Hills received 1,016 mm of precipitation between the months of October 2002 and April 2003. When we compared 2003 monthly rainfall data (= 9.81 cm) and averaged monthly rainfall for the remaining years of 1989 to 2002 and 2004 to 2011 (= 11.21 cm) we found no differences ($t=-0.898$, $df=11$, $P=0.388$) suggesting that 2003 was

an average year for monthly precipitation. Home-range size for animal A fluctuated from a minimum of 33 ha in January to a maximum of 3,975 ha in August. The average monthly home-range size for animal A was 2,192 ha (± 472) ha. Animal B had a minimum home range of 1,051 ha in April and a maximum home-range size of 4,059 ha in August. Average monthly home-range size for animal B was 2,793 ha (± 494) ha. There was no overlap in home-ranges between these two elk in January, February, September and October. In the remaining months, the mean overlap area was 464 ha (± 157) ha with a minimum of 28 ha in November and a maximum of 1,417 ha in August. Taking the mean monthly overlap (309 ha) and dividing by mean monthly home-range sizes resulted in a mean home-range overlap of 11 percent (Figure 1). There was a positive relationship ($R^2 = 0.49$, $F_{1,10} = 3.129$, $P = 0.011$) between NDVI and home-range overlap (Figure 2). There was also a positive relationship between NDVI and HAI ($R^2 = 0.41$, $F_{1,10} = 2.627$, $P = 0.025$; Figure 2).

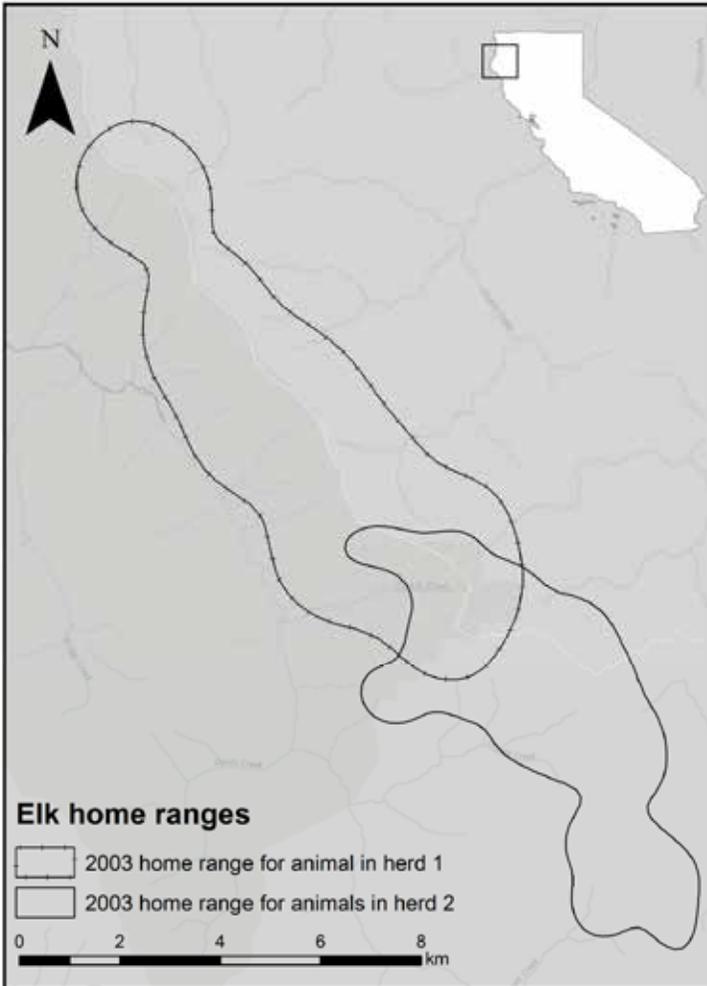


FIGURE 1.—Fixed kernel (FK) estimate for the single Roosevelt elk (*Cervus elaphus roosevelti*) in herd 1 and the FK estimate for the three elk in herd 2 of the Bald Hills of Redwood National Park, Humboldt County, California, 2003.

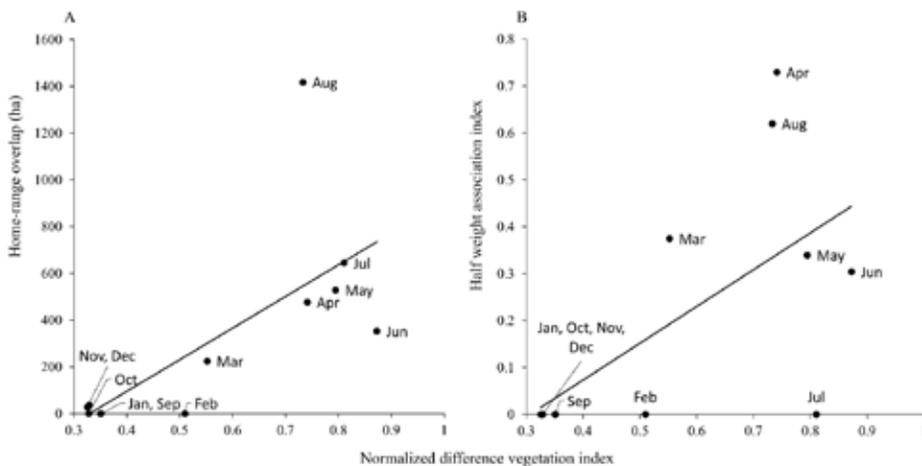


FIGURE 2.—Scatter plots with regressions of A) normalized difference vegetation index (NDVI) and home range area of overlap and B) NDVI and half-weight association index for Roosevelt elk in the Bald Hills of Redwood National Park, Humboldt County, California, 2003.

DISCUSSION

We tested two hypotheses to explain drivers of home-range overlap between elk herds. Our findings suggest seasonal changes in home-range overlap were associated with seasonal changes in food supply, and we found no evidence that home-range overlap was associated with social familiarity. When food supplies increased during the growing season, primarily April to June, there was an increase in home-range overlap. This suggests overlap occurs between animals from different herds due to increased food availability rather than social attraction. These findings are contrary to what was expected with the social familiarity hypothesis.

The positive relationships between NDVI, home-range overlap and HAI were evident but not strong. One possible reason for the weaker relationships was that we had to average NDVI between 1989 and 2011 because we did not have monthly NDVI for every month in 2003. Precipitation in the wet season from October 2002 to April 2003 appears to be on the low end (1,016 mm vs. typically 1,080 – 1,620 mm). Although the *t*-test suggested there was not a statistical difference in precipitation between 2003 and other years, the lower precipitation might have resulted in lower NDVI values and food supplies. The average NDVI values we used in the analyses might have added a source of heterogeneity to our regression analyses that we were unable to capture.

The generally larger home ranges in the late spring and summer months and the increased home-range overlap between adjacent herds probably reflects the concomitant increase in food supply and energetic demands of reproduction. Pregnant females in late spring are known to distance themselves from other animals during times of parturition to decrease chances of predation on neonates. Such dispersion can result in an enlarged

home range and more home-range overlap between adjacent herds. Immediately after parturition mothers also face the energetic demands of lactation (Cook et al. 1996, 2004), which corresponds with seasonal peaks in food supply (Phillips et al. 1973, Georgii 1980). Thus, the greater home-range overlap in late spring and summer is, to some extent, due to reproductive activities; yet, those reproductive activities probably evolved to coincide with the period during which food is most plentiful. Regardless of whether the observed patterns in home-range overlap are associated with seasonal food supply, reproductive activities, or both, these results are consistent with past observations in elk that found overlapping home ranges during seasons when vegetation is growing (Craighead et al. 1973, Jenkins and Starkey 1982, Cornelis et al. 2011).

Social bonding among females in herds is well documented in Roosevelt elk from northern California to northern Washington (Lieb 1973, Jenkins and Starkey 1982, Franklin et al. 1975, Weckerly 1999, Julian et al. 2013). Previous work examining social bonding has addressed the role of aggression in social bonding (Rutberg 1983, Thouless et al. 1985, Weckerly 1999). Understanding the drivers of seasonal changes in overlapping home ranges is useful to understanding the ecological role of social bonding. When seasonal food supplies are more limited and there is less overlap in home ranges, strong social bonding probably benefits younger animals in food acquisition. Older animals are probably more familiar than young elk with areas that contain more abundant food resources because, in part, these areas have received little or no foraging pressure by members of adjacent groups (Craighead et al. 1973, Georgii 1980, Cornelis et al. 2011).

Examining seasonal dynamics in home-range overlap has implications for understanding population dynamics and social boundaries of Roosevelt elk. Female groups proximate to each other can display population dynamics that are uncoupled or not in synchrony (Julian et al. 2013). Distinctly different population dynamics seem to be maintained by elk groups avoiding areas that might be used by adjacent herds when food supplies are limited. As the area of overlap is rather small in relation to the size of the home range used by a herd, each herd has a slightly different set of food supplies as well as other conditions (e.g., poaching, predation) that should influence herd size. When food is most limited in autumn and winter, herds should display the least overlap in home ranges. If there is considerable overlap in home ranges between adjacent herds in autumn and winter that might be a cue that herd spatial boundaries have changed. Furthermore, seasonal change in home-range overlap influences management strategies. When overlap in home range occurs, population density in the overlap area increases. As a result, competition for resources available in the area of overlap is enhanced, potentially limiting availability of nutrients per individual. Periods of home-range overlap suggest a need to alter management strategies as herds associate and population dynamics change.

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Potential mitigation of and adaptation to climate-driven changes in California's highlands through increased beaver populations

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Climate models forecast significant changes in California's temperature and precipitation patterns. Those changes are likely to affect fluvial and riparian habitat. Across the American West several researchers and civil society groups promote increased beaver (*Castor canadensis*) presence as a means to moderate such changes. This study reviews three literatures in an effort to evaluate the potential for beaver to adapt to and to mitigate anticipated changes in California's higher elevation land- and waterscapes. First, I provide a synopsis of modeled changes in temperatures and precipitation. Forecasts agree that temperatures will continue to increase, to 1.5–4.0° C by 2060; however, forecasts for precipitation are more variable in sign and among models. Second, researchers anticipate climate-driven changes in stream and riparian areas and project that snowpacks and summer flows will continue to decline, winter and spring flood magnitudes will increase, spring stream recession will likely continue to occur earlier and more quickly, and highland fires will be more extensive. Each of these changes has important implications for wildlife and public lands managers. A third focus reviews beaver natural histories and finds that where beaver dams are persistent, they may sequester sediment and create wet meadows that can moderate floods, augment early summer baseflows, sequester carbon in soils and standing biomass, decrease ecological problems posed by earlier spring stream recession, and potentially help cool early summer and post-wildfire stream temperatures. However, due in part to currently limited habitat suitability and to conflicts with other human interests, mitigation would likely be most meaningful on local rather than statewide scales.

Key words: beaver, *Castor canadensis*, climate forecasts, California highlands, hydrological changes, mitigation, wetland restoration

In California, meteorological and hydrological records indicate that the state is already experiencing changes attributable to anthropogenic climate change (Barnett et al. 2008, Pierce et al. 2008, Bonfils et al. 2008, Das et al. 2009, Hidalgo et al. 2009). As a result, the State's snowpacks are melting earlier (Kapnick and Hall 2009), and winter precipitation is falling increasingly as rain rather than snow (Hayhoe et al. 2004, Cayan et al. 2008). Several groups in the American West (King County in Washington, The Beaver Advocacy Committee in Oregon, and in California The Beaver Work Group and Martinez Beavers) are exploring increased beaver (*Castor canadensis*) presence as a way to restore fluvial and riparian habitat and increase resilience against the effects of climate change (Apple et al. 1985, Trimble and Albert 2000, Pollock et al. 2012, DeVries et al. 2012).

This article focuses on California's highlands (the Sierra Nevada and northern coastal ranges, and the Lassen, Shasta, and Trinity regions) as that is the site of most of the State's precipitation and nearly all snowfall that currently provides about one-third of all consumed water (Gasith and Resh 1999). Furthermore, because much of the land in the areas is publicly held, population expansion and damage caused by beaver works can be effectively managed. The paper reviews extant literature towards three ends. First I introduce climate models, the scenarios for future greenhouse gas (GHG) emissions they employ, and then present forecast changes in temperatures and precipitation. Next, I extend those forecasts to examine anticipated effects on fluvial and riparian form, function, and habitat that could potentially be affected by increased beaver populations. Finally, I review what is known of beaver natural history in an effort to characterize the potential adaptations and mitigations an increased beaver population could provide. California's highlands offer somewhat unique climate and geology. Findings from studies conducted east of the Pacific Rim are treated accordingly.

CLIMATE MODELS AND FORECAST

Model ensembles and scenarios.—Following best practices established by the Intergovernmental Panel on Climate Change (IPCC) the studies reviewed here create ensemble forecasts using between 3 and 16 global circulation models (GCMs). Those models can be adjusted to provide varying spatial resolution. At their coarsest, each cell includes three degrees of longitude and three degrees of latitude, and so treats areas 160 by 330 kilometers as homogenous. Required computing power increases rapidly as resolution is increased. As a compromise researchers may use statistical resolution that compares projections made by numerous models and creates a probability distribution for more localized areas of interest. Alternatively, dynamical resolution treats the parcels surrounding the area of interest as boundary conditions and then increases resolution only for the study area. Most of the studies reviewed here have been downscaled (i.e., increased resolution) using one or both of these methods.

In order to minimize global climate response uncertainty (Costa-Cabral et al. 2013), modelers use representative CO₂ concentration pathways (RCPs)—these are referred to as scenarios. The models referenced in the following discussion employ two business-as-usual, high GHG scenarios; either the A2 scenario published in 2002 that projects atmospheric carbon equivalent to reach 800–830 ppm in the year 2100, or the more recent AR5 8.5 scenario that places CO₂ equivalent at 1250–1380 ppm in 2100.

Modelled forecasts for temperature and precipitation.—Models are more consistent

in temperature forecast than those for changes in precipitation. Together, increased warming in winter and spring is already causing diminished summer streamflow across the West (Stewart et al. 2004, 2005), a phenomenon modeled to continue (Hamlet et al. 2005, Barnett et al. 2008). Diffenbaugh et al. (2015) reported that even though rainfall anomalies have not increased in California over the past two decades, warming temperatures have decreased water availability significantly, and forecast increased drought conditions as a result.

Models agree that highland temperatures will rise through the end of the century (Table 1; Pierce et al. 2013). This is the most vigorous study published at the time of writing this review. Pierce et al. (2013) employed the SRES A2 GHG scenario and employed both statistical and dynamical downscaling to forecast changes for the 2060s relative to a 1985–1994 base period.

Precipitation changes forecast by Pierce et al. (2013) and Walsh et al. (2014) are presented in Table 2. The latter used the updated and higher greenhouse gas AR5 8.5 scenario.

TABLE 1.—Forecast increases in mean seasonal temperature (°C) of highland regions of California for the period 2060–2069 when compared to the relative historic base period of 1985–1994. The model used the high CO₂ scenario (SRES – A2; from Pierce et al. 2013).

Highland Region of California				
Season	Sierra Nevada	Shasta Region	North Coast	Central and South Coast
Winter	1.5–2.1	1.7	1.5–2.2	1.8
Spring	2.0–3.0	1.9	1.4–2.0	2.1
Summer	3.0–4.0	2.9	2.0	2.3

Highland Region	Season		
	Winter	Spring	Summer
Northern California ^a	0 ⇔ + 10	-10 ⇔ -20 N ⇔ S	- 30 ⇔ - 10 N ⇔ S
Southern California ^a	0 ⇔ - 10 N ⇔ S	- 30 ⇔ - 40 N ⇔ S	0 ⇔ +10
Shasta Region ^b	+ 9	- 11	- 29
North Coast ^b	+ 7 ⇔ - 2 N ⇔ S	- 10 ⇔ - 18 N ⇔ S	- 32 ⇔ - 13 N ⇔ S
Sierra Nevada ^b	- 5	- 11 ⇔ - 19 N ⇔ S	- 23 ⇔ + 59 N ⇔ S
Central and South Coast ^b	+ 1 ⇔ - 5 N ⇔ S	- 19	- 13 ⇔ +50 N ⇔ S

TABLE 2.—Percent changes in seasonal precipitation forecast to occur in the highland regions of California under high CO₂ scenarios (data interpreted from Piece et al 2013, Walsh et al. 2014; N= north, S=south).

^aForecast under the AR5 8.5 high CO₂ scenario for 2070–2100 compared to the relative historic base period of 1970–2000 without downscaling (from Walsh et al. 2014).

^bForecast percent increase in mean seasonal temperature by highland region for the 2060s compared to the relative historic base period of 1985–1994. The model uses the high CO₂ scenario (SRES – A2) and statistical and dynamical downscaling (from Pierce et al. 2013; N= north, S=south)

That group forecast changes for the period 2070–2100 relative to the historic base period 1970–2000. Though not downscaled, these results are similar in sign to findings by Pierce et al. (2013); however, the Walsh et al. study generally forecast a greater increase in winter precipitation and a less-marked decrease in spring and summer precipitation.

CLIMATE-DRIVEN CHANGES IN FLUVIAL AND RIPARIAN AREAS

These forecast changes in climatic boundary conditions will likely cause changes in several landscape aspects that beaver could potentially moderate. The following discussion reviews the extant literature on climate driven changes to stream flow timing and magnitude, channel morphology, stream temperatures, fire regimes, and meadows above 1,200 meters in elevation.

Snow to rain.—California's snowpacks provide about one-third of the water consumed in that state while also supplying stream flows that are critically important to dry-season habitats. Several studies have sought to quantify the magnitude of snow water equivalent (SWE) loss. Modeling by Cayan et al. (2008) suggested that the greatest diminution of snowpack will occur at elevations below 1,300 meters. Using the SRES A2 high emissions scenario (830 ppm), the modelers used data from the 1990s as a base period. The model forecast that SWE on April 1 (historically the beginning of spring melt) will decline by 37–42% by mid-century and 70–80% by 2100, thereby decreasing spring spate and summer streamflow.

A study by Das et al. (2011) suggested that warmer winters and springs will increase evapotranspiration and that sublimation may further diminish snowpacks and spring runoff. Using an ensemble of 16 GCMs, assuming a 3°C temperature increase and holding precipitation constant, they forecast that these in situ losses of snowpack would decrease April–September flows in the northern and southern Sierra Nevada by 1.8 and 3.6%, respectively, and October–March flows by 2.1% and 3.1%. Illustrating the effects of model variability, Costa-Cabral et al. (2012) ran a similar simulation and reported no relation between temperature and sublimation-evapotranspiration due to earlier snowmelt-runoff.

Beyond a diminution of this natural water reservoir, shifts from snow to increased rain suggest two related sets of problems: increased flooding and issues related to earlier snowmelt recession (Kapnick and Hall 2009). Each of these processes in turn has direct and indirect effects on ecological and human systems.

Flooding.—Hydrographic records indicate that flood magnitudes in California have increased since the 1920s. In a national study Peterson et al. (2013) found that decadal high flow magnitudes have increased at average decadal rates of 9% in northern California, 8% in the southern Sierra Nevada, and 3% on the central coast and the central Sierra Nevada. Several investigators examined increased flood magnitude under higher GHG accumulation. Cayan and Riddle (1992) reported that in California the largest floods are associated with winter-spring circulation over the central and eastern Pacific, and are specifically caused by atmospheric rivers (see also Ralph et al. 2006, Neiman et al. 2007). Again, atmospheric conditions over the Pacific are influenced by numerous factors and model ensemble results are not in strong agreement on forecast conditions. As discussed above, however, models strongly agree on the sign and trend of temperatures in the region and uniformly forecast warming. As a result, storms will be warmer and will produce less snow and more rain (Knowles et al. 2006, Das et al. 2009), producing greater flood magnitudes, particularly during rain-on-snow events.

Several other teams have modeled future flood characteristics. Das et al. (2011) used three GCMs calibrated through precasting (forecasting past flooding given historic climatic parameters) and then input results through a variable infiltration capacity hydrologic model. All three models forecast significant increases in flood magnitudes. While one model forecast decreased flood frequency, two found increased frequency. In 2012, Wehner reported that adding elevation data to a coordinated eight regional model ensemble significantly improved its precast performance. The newly parameterized ensemble compared conditions for North America in the period 2038–2070 to a 1968–1999 base period, and forecast a 5–10% increase in winter, a 10–20% decrease in spring precipitation, a 0–5% increase in winter, and a 0–15% decrease in spring maximum daily precipitation (i.e., flood magnitude).

In 2013, Dominguez et al. employed an ensemble of 8 GCMs to model changes in winter precipitation for the western United States. Comparing forecasts for the period from 2038–2070 with a base period from 1968–1999, they found a 12.6% increase in the magnitude of 20-year floods and an increase of 14.4% in 50-year floods. More generally, however, the models rendered a high probability forecast for a 7.5% decrease in average winter precipitation for the Sierra Nevada and southern California, and slight increases in precipitation for northern coastal California.

Using an ensemble of 16 GCMs and a high carbon emission SRES A2 scenario Das et al. (2013) found that flood magnitudes in the western Sierra Nevada will increase regardless of trends in mean precipitation (see also Maurer et al. 2007). The investigators found that magnitudes would increase beyond current variability as early as 2035. Compared with simulated historic 50-year flood events, the ensemble forecasts progressive increases of flood magnitude of 30–90% in the northern Sierra Nevada and 50–100% in the southern Sierra Nevada by 2100.

Again employing an ensemble of 16 GCMs and both statistical and dynamical downscaling, Pierce et al. (2013) forecast changes in three day accumulation for 100-year flood events (Table 3). Though the forecasts manifest an expected degree of variability, they produced a consensus of sign regarding flood magnitude, which is forecast to increase. There is little consensus regarding trends in total annual rainfall among California's various highland regions. An increase of winter flood events will increase the geomorphic dynamism of stream channels on a decadal scale.

TABLE 3.—Forecast changes in maximum three-day precipitation events in California's highland regions for the period 2060–2069 when compared to the base period of 1985–1994 (data interpreted from Pierce et al. 2013).

Highland Region	Current Accumulation (mm)	Forecast Accumulation (mm)	Increased Accumulation (mm)
Sierra Nevada	280	370	90
NE California	90	180	90
Shasta	180	300	120
North Coast	240	360	120
Central Coast	165	220	55
South Coast	160	190	30

Recession.—On an annual scale, spring spates were forecast to occur earlier and to decrease in magnitude and duration. Many species are adapted to the specific timing of the spate (Jager et al. 1999, Marchetti and Moyle 2001, Lytle and Poff 2004, Jowett et al. 2005), and exploit a typically slowly retreating moist fluvial margin (Kupferberg 1996, Freeman et al. 2001). More rapid recession will decrease riparian seeding (Shafroth et al. 1998) and nutrient loading (Rood et al. 1995, Langhans and Tockner 2006), decrease primary productivity (Acs and Kiss 1993) and arthropod abundance (Paetzold et al. 2008), decrease salmonid spawning activity (Moir et al. 2006), and weaken other trophic chains (Nakano et al. 1999, Yarnell et al. 2010). Geomorphically, rapid recession is expected to produce steeper bars and so decreased moist transitional area, increased water temperatures, and increased stranding of young amphibians (Kupferberg et al. 2008).

The corollary condition, decreased magnitude of peak spring flow, is expected to decrease the area of aquatic habitat through channel narrowing and loss of wetted side channels (Ligon et al. 1995, Van Steeter and Pitlick 1998) leading to decreases in diversity and abundance of macro-invertebrates and algal production (Peterson 1996, Jowett et al. 2005), which are important food sources for higher trophic levels. Decreased erosion and deposition will decrease lateral channel migration, decreasing channel elevation—and so habitat—variability (Parker et al. 2003, Shields et al. 2000), which may enhance riparian encroachment by woody vegetation (Lind et al. 1996, Shafroth et al. 2002). In addition, earlier melt will result in increased water temperatures, thereby favoring species adapted to warm water and diminishing cold water adapted species such as salmonids (Kupferberg 1996, Jager et al. 1999).

Stream temperatures.—Sub-alpine streams are also expected to warm as a result of atmospheric temperature shifts. Null et al. (2013) employed a regional equilibrium temperature modeling approach that incorporated mechanistic heat exchange between atmosphere and water to model changes in the Feather River as it flows west from the northern Sierra Nevada. The investigators found that at elevations below 1,000 and above 3,000 meters, stream temperatures rise about 1.5°C for each 2°C increase in mean average annual atmospheric temperature. Streams between 1,000 and 3,000 meters responded more strongly at about 1.8°C for each 2°C increase in atmospheric temperature; this is due largely to decreases in snowpack. Currently, July temperatures in the Feather River exceed 21°C in only the lower 30 km (20%) of that stream. However, Null et al. (2013) reported that with atmospheric temperature increases of 2, 4, and 6°C, that threshold is exceeded in 57%, 91%, and 99.3% of the stream, respectively. The authors also noted that the effect of increased atmospheric temperatures are moderated in that watershed through extensive basalt layers underlying the stream that produce significant hyporheic flows that help cool stream temperatures.

Fish.—For salmonids (anadromous and resident trout and salmon) these changes in temperature and flow regime pose particular problems. The upper end of the optimal temperature range for these indicator species is 19°C. The maximum sustained water temperature tolerated by anadromous salmonids is 24°C (Eaton and Scheller 1996). However, at certain stages of their life cycle—eggs and alevin—these fish require lower temperatures (Myrick and Cech 2001), and salmonids exhibit stress at sustained temperatures above 21°C (McCullough 1999, Myrick and Cech 2001). Null et al.'s (2013) forecast has much of the Feather River exceeding 21°C by 2070–2099.

The forecast geomorphic changes are also expected to affect fish habitats. Mantua et al. (2010) examined the effects of expected higher winter and lower summer streamflows

on anadromous salmonids in Washington State. They noted that for young Coho the two most important hydrological factors in survival are first year summer temperatures and more importantly, refuges from winter high streamflows in their second winter. Those refuges are commonly found in side channels that several studies suggested will diminish under forecast flow regimes (Ligon et al. 1995, Van Steeter and Pitlick 1998, Shields et al. 2000, Parker et al. 2003, Pollock et al. 2003).

Dam reservoir management.—Changes in precipitation, snowmelt recession, and flood regimes in highland areas pose particular problems for the management of winter and spring pool levels in California's dam system, both for flood control and for power generation (Moser et al. 2012). Das et al. (2013) observed that increased probability of larger flood events will require dams to maintain lower pools in the future to accommodate potential floods. However, should a flood not occur, dam systems will begin the dry season with pools potentially much below maximum storage. Warmer summers will increase electrical demand while summer flows into reservoirs are forecast to decrease.

Fire.—As the West warms, wildfires may become more frequent or more extensive, or both. Westerling et al. (2011) developed a three-model wildfire ensemble to forecast fire extent for California. Contrasting the optimistic SRES B1 scenario with the higher A2 emission pathway against a 1970s base period they found only moderate differences between the two scenarios and for year 2020 forecast an increase of statewide area burned at 10–20%. For 2050 and 2085 the B1 scenario forecast increases of only about 5% for each interval. However, the A2 scenario yields increases up to 38% in 2050 and 40–70% in 2085. While these increases seem somewhat moderate, a closer look at sub-regions of California yields more meaningful results. All models forecast little or no increase in area burned south of Monterey, Kings, Tulare, and Inyo counties, the Central Valley, and the mountains of the central coast. However, across the forested areas of the Sierra, all of northern California including the coastal mountains north of Marin County, the area burned is forecast to increase by 100–300%.

Increased fire extent suggests increased sediment mobilization and stream temperatures. Ice et al. (2004) reported that stream sedimentation and nutrient mobilization (with the exception of phosphorus which may volatilize) increase with fire severity (temperature and duration) and landscape gradient. They concluded that, "Long-term erosion rates in fire prone landscapes may be higher than often believed, and post-fire sediment pulses can have both positive [increased downstream channel complexity in later years] and negative effects" (Ice et al. 2004:20). The latter are related to the mobilization of fine gained sediment that can degrade spawning areas and alter trophic chains. Regarding stream temperature changes, Brown and Krygier (1970) studied two comparable streams in western Oregon, one well shaded and relatively undisturbed, the other flowed through an area that was first clear-cut then slash burned. In the second stream they observed summer temperatures rising from a mean average 13°C prior to treatment to 28°C (range 26–30°C). During the treatment summer the control stream recorded temperatures of 14–15°C. In a similar study in southwestern Oregon, Amaranthus et al. (1989) reported that small stream temperatures increased from about 14°C to 21°C following shade-removing wildfires.

High meadows.—High-elevation meadows present an additional area for consideration. A wetter climate regime beginning between 2,500 and 1,200 years BP raised water tables in high meadows that favored hydric plant communities dominated by sedges, rushes, herbs, dwarfed shrubs, and grasses (Wood 1975). Unique faunal communities subsequently adapted to live in these areas. In the later 1800s and early 1900s these meadows

were widely exploited by commercial pastoralists. As a result of grazing, road grading, intentional drainage, and grass crop cultivation many meadow streams have become incised and water tables have dropped so that mesic and xeric floral communities now dominate (Loheide et al. 2009). Climate change will further stress meadow hydrologies by changing mean annual flows, shifting spring spates earlier, and produce a lengthier low-flow period (Null et al. 2011). Loheide et al. (2009) suggested that earlier and shorter snowmelt recession and reduced daily fluxes in snowmelt-related streamflows will reduce groundwater recharge. Viers et al. (2013) noted that meadows between 1,500 and 3,000 meters will be most affected, and that because northern meadows generally are at lower elevations they are more vulnerable. Beaver populations in some of these areas were also reduced in the nineteenth century (James and Lanman 2013). Central to the current discussion, meadow restoration projects on the Feather River in northeastern California are providing some of the best opportunities for research into the potential for beaver to mediate some of the aforementioned changes in California's highland waterscapes.

BEAVERS AND CLIMATE CHANGE MITIGATION AND ADAPTATION IN CALIFORNIA

As the following review indicates, scientific studies are limited, first in applicability and so in number, and second in quality. Most scientific study is focused on areas of North America shaped by continental or extensive alpine glaciation, or by monsoonal or otherwise moist summer seasons, and so may not provide analogs for California's highland hydrologies. Furthermore, several widely cited studies from the western United States are somewhat anecdotal and, thus, problematic.

It is important to stress that habitat initially suitable to persistent beaver occupation is limited by certain factors (Baldwin 2013). Beaver dams are more persistent when situated in wider valleys on reaches with gradients less than 6%. Although they are generalists, beavers build more dams in areas where hardwoods grow within 30 meters of stream channels. Though cross-channel dams are most typical on 1st–4th order streams, beaver also dam side channels on larger streams. No statewide suitability study has been published. Yet, as this review suggests, some of those local benefits are potentially significant.

The following discussion addresses several processes through which beavers might moderate the climate driven changes identified in the previous section. Among these are water storage, streamflow seasonality, sediment flows and storage, nutrient flows and stocks, riparian vegetation, flood events, changes in spring stream recession, and wildfire.

Water storage.—Beaver works cause water to be stored both in surface ponds and wetlands, and in subsurface or hyporheic flows. Studies indicate that the amount of storage is highly variable. Westbrook et al. (2006), for example, recorded two dams on the upper Colorado River that inundated 5.8 and 12.0 ha of the nearby flood plain, primarily by diverting streamflow onto terraces downstream from the dams. However, working in eastern Washington, Scheffer (1938) recorded average pond storage to be 86 m³ among 22 dams in one reach of Mission Creek; in that same study the author reported a single year-old dam on Ahtanum Creek stored 2,603 m³ and that storage expanded to 6,170 m³ the following summer. Because beaver colonies tend to build several dams, aggregate pond storage is often more meaningful than single dam storage capacity. Studies found a wide range of colony and dam density in the West. Clearly the amount of water stored in these systems is highly variable (Table 4).

TABLE 4.—Numbers of beaver dams, or beaver colonies, per kilometer of stream channel at various locations in high mountain environments of the western United States.

Authority	Location	Average number/km
Yeager and Hill (1954)	Southern Colorado	30 active and former dams
Butler and Malanson (1994)	Rocky Mountains (Montana)	25
Bates (1963)	Wasatch Range (Utah)	24
Smith (1980)	Wyoming	1.3
Busher et al. (1983)	Eastern Sierra Nevada	0.75 to 1.5 colonies

Dams also divert surface flows to slower hyporheic flows. However, due to the impermanence of extant dams and the unpredictability of new dams, related sub-surface flows are difficult to study and quantify. In Westbrook et al.'s (2006) study the team was able to quantify dam-related hyporheic storage lost. In that case, a monitoring station 670 meters below the failed dam indicated that within a week of the breach, water levels dropped from 21 cm above to 41 cm below ground surface. While the effect is clear, in order to calculate storage one must characterize local soil water-holding capacity. Other findings are less circumstantial and are more suggestive. Studying 10 dams on first order streams in low gradient glacial valleys in Glacier National Park, Meentenmeyer and Butler (1999) reported that three dams completely diverted all streamflow to aquifers.

Several other studies provide more definitive findings. Working on Bridge Creek in central Oregon, Lowry (1993) found that the riparian water table associated with a small beaver dam closely reflected pond surface levels laterally up to 50 meters from the pond, and estimated ground water storage at 90 m³. Working on Currant Creek in a semi-arid area in southwestern Wyoming, Apple et al. (1985) studied the effects of re-introduced beaver. They found that within two years, seven beavers had created three dam complexes that raised adjacent water tables by 0.3 to 1.0 meters. Researching a 320 meter reach of Red Canyon Creek, a second order stream in the semi-arid Wind River Range of Wyoming, Lautz et al. (2006) found that about 30% of the stream volume entered hyporheic flows above beaver dams. Those flows raised water tables as far as 50 meters to one side of the stream. Water tables reflected pond surface levels and were maintained at 20–40 cm below the pond surface. The authors also reported that various portions of the study reach alternatively gained water and lost water to hyporheic flows depending on very local conditions confounding quantifications of streamflow.

Generally water storage both in ponds and in aquifers seems to be a function of a few key factors. Low valley gradient (with accordant low stream power) and broad valley floors both allow greater storage in dams and in aquifers (Pollock 2007). Sediment pore space and depth to impermeable substrate suggests reservoir capacity. Finally, the availability of woody dam-building material controls the size, efficacy, and permanence of dams. Thus, in California the most promising areas for water storage by beaver works probably rest among high meadows on headwater streams and amid side channels on lower elevation rivers.

Emmons (2011) estimated that should all currently incised meadows in the Sierra Nevada have their groundwater storage potential restored, about 80 million additional cubic meters of water would be cached. Some portion of that storage would transfer to the

atmosphere through increased evapotranspiration (Hammersmark 2008, Hoffman et al. 2013). The increased flow is not significant statewide, but local habitat benefits might be.

Extending summer flows.—Evidence for augmentation of summer flows is perhaps the weakest aspect in the scientific research into potential benefits by beavers. Numerous review articles suggest that beaver dams and ponds augment low summer baseflows; however, studies relevant to California are largely anecdotal. Peer reviewed studies from the Pacific Northwest by Finley (1937) and Scheffer (1938) both reported significant decreases and increases in baseflow following beaver removal and re-colonization, respectively. However, neither study controlled for changes in precipitation nor land cover; further, Scheffer's (1938) results are not clearly confirmed by my analysis of relevant stream gauge records (see author forthcoming for further discussion).

As research into meadow hydrologies in California has found, it is very difficult to control all variables relevant to baseflow augmentation. Studies seeking to quantify the effects of beaver are confounded by multiple uncontrollable variables: they tend not to stay where they are released, making before and after studies nearly impossible; decadal scale climate trends, land use changes, topologies specific to study sites may also alter stream flow.

Plug-and-pond meadow restoration projects in upper reaches of the Feather River in northeastern California provide a potentially useful analog regarding potential modification of baseflows by beaver colonies. There, several stream reaches were re-directed to their former shallow, sinuous, non-incised channels, and the former channels converted to series of hyporheically connected ponds (Hoffman et al. 2010). Above-and-below seepage studies on several treated reaches indicated some aquifer absorption of high flows (Tague et al. 2008) and some augmentation of baseflows, but only into July (Cawley 2011, Hill et al. 2011). Several investigators reported that even where 48.3 ha of meadow were treated, base flow was not increased in August and September (Freeman 2010, Cawley 2011, Hoffman et al. 2013). Thus, widespread meadow restoration resulting from beaver activity may help blunt floods and increase stream flow in June and into July.

Sediment flows and storage.—Because dams decrease stream velocity, their associated ponds and overbank flows may allow sediment sequestration and accumulation (Westbrook et al. 2010). Several studies characterized the variability of sedimentation related to beaver works. In Yellowstone, Persico and Meyer (2009) reported that dams on small streams more effectively sequestered sediment. Butler and Malanson (1995) noted that low-gradient streams have lower suspended and bed loads, and so sedimentation rates also decrease. Studies agree that sediment accumulation decreases with pond age while volume increases with size (Table 5).

Some have argued that beaver-driven sediment accumulation may make significant changes in western landscapes. Working among headwater creeks in Colorado, Ives (1942:198) wrote that, "Detailed field studies indicate that water levels have been raised as much as two feet [0.6 meters], during the past 20 years, in about one-fifth of the beaver occupied area ... As pond-filling proceeds at about the same rate as the elevation of water levels, but with the lag of several years, it may be assumed, from these figures, that valley floor elevation, as a result of beaver work, proceeds at a rate approximating one quarter inch per year." While the studies themselves were not included, Ives suggested that the "false senility" of streams—mature features such as meanders, oxbows, and peat bogs, all the result of low gradient—provide further evidence of valley-wide aggradation. Ives (1942) argued that beaver ponds normally transition to meadows following pond filling and that process

repeats continually, as beavers move to new sites. Though somewhat anecdotal, this study is cited by 98 scholarly sources identified in Google Scholar's database.

TABLE 5.—Sediment accumulation rates, and volumes of sediment accumulated by younger and older, and smaller and larger beaver dams in Montana and Oregon, USA.

Authority	Location	Sedimentation Accumulation Rate (cm/yr) Younger <=> Older	Accumulated Volume of Sediment (m ³) Smaller <=> Larger
Butler and Malanson (1995)	Glacier NP Montana	27.9 <=> 2.1	
Meentenmeyer and Bulter (1999)	Glacier NP Montana	45 <=> 30	~ 9.4 <=> 267
Bigler et al. (2001)	Glacier NP Montana	43 <=> 19	
Pollock et al. (2007)	Bridge Ck Oregon	45 <=> 7.5	17 <=> 533
Westbrook et al. (2010)	Glacier NP Montana		Maximum of 750

In a more empirical study, Pollock et al. (2007) reported significant sediment deposition upstream from dams and argued that long-term occupation by beavers decreases bed slope and increases the area likely to be wetted during over-bank flows. Again, variability of landscape response to beaver activity is evidenced by the contrasting results of Meentenmeyer and Butler (1999), who reported that repeat field visits and aerial photo survey indicated that ponds seldom become meadows in Glacier National Park, Montana. Viers (2013) reported that where ponds do fill with sediment and transition to meadows, beaver works may provide important refugia for a host of native California species.

Nutrient flows and stocks.—As beaver works may slow and accumulate sediment, so too may they affect flows of nutrients. In their study of a 320 meter reach of Red Canyon Creek, a second order stream in the semi-arid Wind River Range of Wyoming, Lutz et al. (2006) reported that hyporheic exchange decreased total solute flow velocity by about 30%. Working on Currant Creek in southwestern Wyoming, Maret et al. (1987) reported that during high flows suspended solids, total phosphorous (but not ortho-phosphate), and nitrogen decreased in beaver ponds.

While decreases in suspended sediment are attributable to decreases in velocity, decreases in dissolved nutrients are due to adsorption to fine clays accumulated in the pond bottom sediments (Naiman and Melillo 1984). As a result, pond sediments tend to be very fertile. Naiman et al. (1994) measured available soil nitrogen in beaver meadows at 29.8 kg/ha compared to 6.8 kg/ha in a nearby dry forest. Other investigators reported that total organic carbon is also elevated in pond or meadow soils. Westbrook et al. (2010) analyzed the soil sequestered behind a failed dam and found relatively abundant nutrients: carbon

was 24.1 g/kg of soil, total nitrogen 1.5 g/kg soil, and total phosphorous 0.9 g/kg soil (see also Klotz 1998). Naiman et al. (1986) reported that organic carbon turnover time in pond sediments was about 161 years, compared to 24 years for a nearby riffle, and that the pond's stream metabolism index of ecosystem efficiency was over five times higher for the pool than in the riffle.

Nutrient sequestration suggests that high meadows might serve as significant carbon sinks. Norton et al. (2014) suggested that southern Sierra Nevada wet meadows contain about 54.3 mg/ha of soil organic carbon, or about 12.3% of all such carbon sequestered in the Sierra Nevada. In addition, these rich soils encourage further carbon sequestration in new standing biomass.

Vegetation.—As Yeager and Hill (1954) observed under certain conditions, beavers may denude riparian vegetation and “scalp” top soils from pond edges and may also cultivate riparian deciduous and wetland herbaceous production. They may accomplish this through several processes. First, beavers increase water availability both spatially across valley bottoms through hyporheic flows, through overbank flows, and through canals excavated in order to more effectively move cut wood to the dams (Seton 1953), and temporally by providing water further into summer dry seasons. Apple et al. (1985) illustrated the effect upon riparian vegetation: three summers after beavers were re-introduced on Currant Creek in southwest Wyoming willow had colonized and grown up to 2.0 meters in height in spaces where water tables had been raised by beaver ponds to within 40 cm of the surface. In the downstream reach where aquifers were not charged by beaver ponds, willows had not recovered. On the Colorado Plateau in New Mexico, Trimble and Albert (2000:91) noted the addition of “extensive riparian habitat, especially willows” 6–14 years after re-introduction. Other authors reported that aspen, alder and cottonwood also responded well to the wetter habitats created by beavers (Ives 1942, Baker 2003).

The results of several studies suggest that willows and aspen live mutualistically with beavers. Working in Rocky Mountain National Park, Baker et al. (2005) simulated the effect of beaver browse on riparian willow with and without elk browsing. With elk herbivory, willows produced fewer and longer roots and displayed a higher percentage of dead biomass. Pruning followed by elk exclusion resulted in shorter, but far more numerous shoots; total stem biomass after three years was 10 times greater without elk browsing and those plants recovered 84% of their pre-cut biomass after only two growing seasons. With browsing by elk, however, plant biomass recovery was only 6%. Thus, under certain conditions, beavers may cultivate the development of bank stabilizing willow carrs, but only where elk browsing is limited. Because elk hunting licenses constitute an important revenue source for the California Department of Fish and Wildlife, reducing populations may require further budgetary support from the State. In Yellowstone, re-introduced wolf populations effectively moved elk away from streams and allowed both willow re-growth and subsequent re-occupation of streams by native beaver populations (Ripple and Larsen 2000).

Beavers may affect other changes in riparian forests. By taking down more mature trees, either through cutting or by drowning roots, and especially of conifers, beaver works may create light gaps that allow the growth of early successional species such as alder and willow, creating a diverse ecotone at the margin of their browsing zone 30–50 meters from the edge of their ponds (Donkor and Fryxell 2000). Several investigators noted that sedges and other wetland plants often colonized the saturated margin of beaver ponds (Johnston and Naiman 1987, Pollock et al. 1998, Westbrook et al. 2010). Clearing of riparian canopies

may also result in problematically warmer stream temperatures.

Flood events.—Several review articles suggested that beaver works may attenuate flood events (e.g., Parker 1986). Hillman (1986) and Ehrman and Lamberti (1992) reported evidence of this in low-gradient landscapes. Working in mountainous northern Idaho, DeVries et al. (2012) documented the hydrological effects of anthropogenic structures that emulate beaver dams and found that check dams increased the frequency of overbank flows that worked to dissipate flood crests (see also DeBano and Heede 1987). Taking a different approach, Beedle (1991) modeled flood behavior amid glacially carved valleys on Kuiu Island in southeast Alaska. His model assumed that all dams were at capacity at the time of the flood, so that much of the attenuation resulted from deflection away from channels. He found that any one dam decreased flows by only about 5 percent, but that a series of five large dams reduced the peak flow of a two-year flood event by 14 percent, and reduced the peak of a 50-year event by four percent. These are small, but potentially meaningful, changes.

Beaver dam failures figure prominently in this literature. Working in a desert environment on the Bill Williams River in Arizona, Andersen and Shafroth (2010) reported that over 50 percent of beaver dams were damaged in a relatively large flood pulse of about 60m³/sec, and that a pulse as low as 5 m³/sec caused significant damage. On a 32-km reach of Bridge Creek in semi-arid central Oregon, Gibson and Olden (2014) reported over a period of 17 years that no dam persisted longer than 7 years and that most breached within two years. However, in agreement with Demmer and Beschta's earlier study (2008), the authors found that these dams did attenuate high flows through their ability to divert high flows to local terraces and by creating greater sinuosity and valley bottom heterogeneity. In Glacier National Park, Westbrook et al. (2010) also reported that extant and breached beaver dams increased riparian drainage complexity, and also increased vegetation capable of flood attenuation. Two groups of investigators added anchoring structures and noted that anchoring significantly increased dam durability (Apple et al. 1985, Pollock et al. 2012).

In some contexts, beaver-enhanced riparian vegetation may play an important role in flood mitigation. Smith (2007) offered an extensive study on the role and capacity of willow carrs to slow flood waters, and that is particularly relevant given the ability of beavers to cultivate these thickly branched willow stands. Those investigators reported that where stem spacing is less than 30 cm, vegetative stalks up to 2 meters in height, whether flexible or rigid, are able to reduce boundary shear stress to allow sediment deposition even if over-topped. In short, thick willow stands not only protect terraces from erosion, but also trap new sediment even during flood events. This vegetative aspect of beaver ecology could, thus, attenuate anticipated increased floods and sediment mobilization in California.

Changes in spring recession and ecotones.—As discussed above, for many plant, invertebrate, and aquatic species, the recession of high spring flows produces a vital, yet transient and moving, ecotone. The altered timing and decreased availability of these wetted margins promises to stress certain species of riparian plants and invertebrates. Both intact and broken beaver dams can create similar habitat. Breached dams expose nutrient-rich and sometimes bare soils. Because beavers typically use soil to seal leaks in dams, the structures themselves may offer moist spaces available for colonization by invertebrates or plants, or by both. Mature dams often host willow, cottonwood, and aspen samplings, young trees whose roots can help to further consolidate dams (Bigler et al. 2001).

Wildfire.—Thus far few studies have been conducted into the relationship between beavers and wildfires. In his encyclopedic *Lives of Game Animals*, Seton (1953:455) wrote

that “by conserving the water supply, the Beaver keeps little brooks running all year, instead of only freshets, so the forest is helped by irrigation. . . . Its ponds provide valuable fireguards.” However, he did not offer evidence supporting these assertions.

More careful studies offer insights into beaver-wildfire interactions. Working in areas formerly covered by continental glaciers, two studies reported rather different interactions between beaver presence and fire. In Mount Desert Island, Maine, Little et al. (2012) used aerial surveys to assess beaver response to a fire in 1947 following beaver re-introduction in 1921. Following the fire, the researchers reported that dams increased rapidly in the burnt areas, but decreased from 60 to 10 in unburned areas by 1970. They also documented a decline in dams in the burned areas from about 100 in 1980 to fewer than 40 in 1990. Interestingly, ponds in this environment were observed to become meadows.

Hood et al. (2007), working in Elk Island National Park in Canada, studied beaver lodge occupation in relation to prescribed fires. They reported that lodges were nearly uniformly abandoned following first burns, and completely abandoned following subsequent fires; they also reported that if the area does not burn again over the following 20–30 years, pond creation increases. The authors suggested that trembling aspen (*Populus tremuloides*) regenerates well after fire. Bailey and Whitham (2002) reported that aspen regenerated 10 times more biomass following a severe burn. However, when elk are present, browsing decreased standing aspen biomass 90-fold, and so severely limited beaver re-colonization following fires.

Wildfires can also increase sediment mobilization that can be problematic for human and wild habitats. Once stripped of vegetative cover, slopes are exposed to sheet flow and gully. Ice et al. (2004) reported that the potential for soil mobilization increased with the severity of fires. In very intense fires soil can become mineralized and nearly impermeable, forcing any runoff to flow rapidly down-slope, entraining soil particles along the way. Beaver dams may help sequester sediment in this context as well. Christian’s (2014) comparative aerial surveys of eastern Glacier National Park found that prior to a large fire upstream pond sizes were variable year to year with changes of 40% typical. Following the fire, ponds steadily decreased in size, indicating sequestration of some portion of increased sediment flows.

As noted previously, wildfires will tend to increase stream temperatures. Beaver works, through increasing residence time in ponds and through decreasing shading gallery forest canopy, may also increase stream temperatures. Where stream temperatures are very cold, this may benefit certain native species; however, in many contexts this increase in stream temperatures may be problematic to salmonids. Dams can also work, however, to cool mid-summer stream temperatures when cold spring flows diverted to aquifers re-join streams 1–3 months later (Lowry and Beschta 1994). This retention and delayed release of cooler spring water might more generally buffer increasing summer stream temperatures.

Thus, following wildfires beaver dams may help sequester sediment, very locally decrease seasonal stream temperatures, and enhance riparian revegetation. However, the persistence of beaver colonies following wildfires seems highly variable and dependent in part, upon low elk abundance and subsequent browsing.

DISCUSSION

Recent climate models forecast decreased snowpacks and summer streamflows, earlier and shorter spring spates, increased flood magnitudes, higher stream temperatures,

and increased area of wildfire amid California's highlands—all with implications for habitat alteration. Few geographically analogous studies on beavers have been published, several of those original studies are somewhat anecdotal, and their claims apparently are at times exaggerated. However, several valid studies do suggest that on some of California's headwater streams beaver dams may work to recharge aquifers, augment baseflows for several weeks into summer dry seasons, sequester sediment and nutrients, encourage restoration of meadow vegetation and willow carrs that can ameliorate some of the problematic aspects of floods and wildfires, and supplement decreasing recessional riparian ecotones.

In short, beavers cannot mitigate all of the anticipated climate related changes in California's highland hydrologies. However, as this literature review suggests, beavers potentially offer meaningful local benefits. Unlike human-engineered projects, the effects of beavers on local hydrologies and habitats are variable and uncertain, and further investigations particular to California's highlands is warranted.

Extant studies suggest experimental designs to study hydrologies and habitat changes. As before and after studies are highly problematic due to subject mobility and variable boundary conditions, a simultaneous investigation of two analogous streams or watersheds, one with and one without beavers, would obviate problems posed by inter-annual precipitation and temperature variability and avoid re-introduction issues specific to California. Ideally, study meadows would not be connected to adjacent watersheds hyporheically, thus allowing accurate quantification of the effect of beaver works on timing of flows leaving the meadow. The stream reach seepage studies conducted amid the plug-and-pond meadow restoration projects on the Feather River offer an alternative design for studying water storage and baseflow augmentation. Such studies could align with on-going efforts to restore meadowlands in California. A nascent wetland restoration grant program funded through California's carbon market and administered by the California Department of Fish and Wildlife might prove a reliable source of financial support.

Several of the studies reviewed here indicate that the ecosystem services provided by beavers are increased as colony density increases on streams and in watersheds. The extent of additive benefit is not well quantified, but a controlled study of beaver re-introduction on a watershed scale is currently under way in the Methow Valley in eastern Washington. There, the Methow Conservancy project—a partnership between Washington Department of Ecology, Washington Department of Fish and Wildlife, The US Forest Service, and the Pacific Biodiversity Institute—is engaged in a watershed scale, before-and-after study of the hydrological, geomorphic, and ecological effects of beavers. They have installed 6 flow and 32 temperature stations to monitor changes. Their experimental design calls for a three-year pre-study period prior to beaver introduction and a 3–5 year post-introduction monitoring period. The protocol has been confounded by beavers not staying or succeeding in the pre-monitored release sites. As of 2013, introduced beavers had successfully inhabited only one-third to one-half of the 45 release sites. Results thus far are also confounded by environmental variability. The strength of findings will also be subject to changing boundary conditions (wetter, drier, warmer, cooler seasons) that may coincide with re-introductions and so confuse causation. The group plans to begin publication of results as early as 2018. Due to topography, results there may be most directly applicable to California's Cascade Range and coastal ranges.

Though able to create their preferred environment to a degree, beaver persistence requires low-gradient and wide stream plains. Even when well established, they apparently are also subject to long-term drought. Persico and Meyer (2009) found in Yellowstone

National Park that beaver have been endemic throughout the Holocene; however, during two notably dry periods, from 2200–1800 and from 950–750 years BP, beavers were absent from the area. Beavers may not be able to persist into California's drier future.

Finally, though advocates often portray beavers as a very low cost means of stream restoration or climate change mitigation because they tend to interact with built infrastructure, they also require management. Publications such as the Oregon Department of Fish and Wildlife's monograph detail techniques for live-management; that activity would require resources beyond the current budgets of many wildlife or public land management agencies, but holds the potential to provide benefits beyond costs.

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Importance of the stream-estuary ecotone to juvenile coho salmon (*Oncorhynchus kisutch*) in Humboldt Bay, California

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Recent studies have shown the broad role estuaries plays in juvenile coho salmon (*Oncorhynchus kisutch*) life history; however, most of these studies were limited to the Pacific Northwest and did not include information from the southern end of its range in California. We sampled the stream-estuary ecotone (SEE) of numerous Humboldt Bay tributaries from 2003 to 2011 to document use by juvenile coho salmon. We sampled fish using seine nets and baited minnow traps and found that young-of-the-year (YOY) and yearling plus (1+) coho salmon reared primarily in freshwater or tidal freshwater habitat in the SEE. We detected three basic life history strategies employed by juvenile coho salmon regarding their use of the SEE. The first group were YOY fish that arrived in the spring and resided mostly in mainstem channel habitat in the summer and early fall; the second group of nearly 1+ fish arrived after the first large stream flow event in the fall and resided extensively in smaller tributary and off-channel habitat during the winter and spring; and finally a third group of stream-reared 1+ coho salmon emigrated through the SEE quickly during the following spring. Juvenile coho salmon resided in the SEE an average of one to two months but some individuals reared there for over a year. We found that about 40% of the coho salmon smolt production from Freshwater Creek, Humboldt Bay's largest tributary, originated

from the SEE. Juvenile coho salmon rearing in the SEE were larger than their cohorts rearing in stream habitat upstream of the SEE. Our results demonstrate that juvenile coho salmon utilize portions of the Humboldt Bay SEE in ways similar to those reported in Pacific Northwest estuaries, and suggest that the SEE of Humboldt Bay provides quality rearing habitat—especially over winter rearing habitat—for those juveniles. By incorporating this knowledge into habitat restoration plans we can design effective habitat restoration projects to improve habitat conditions and non-natal rearing for juvenile coho salmon.

Key words: coho salmon, estuaries, Humboldt Bay, *Oncorhynchus kisutch*, over winter rearing habitat

Estuaries have long been known as important habitat for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) (Reimers 1971, Healey 1982, Kjelson et al. 1982, Simenstad et al. 1982, Healey 1991) and coastal cutthroat trout (*Oncorhynchus clarki clarki*) (Northcote 1997, Trotter 1997) but until recently have not been thought to be important to coho salmon (*Oncorhynchus kisutch*). Though coho salmon were shown to use estuarine habitat in limited geographic areas (Tschaplinski 1982), the traditional model of their life cycle was that juveniles were born and resided in freshwater for a year or more, migrated quickly through the estuary to the sea as smolts, reared there for 18 months or more, and then returned to their stream of origin as adults to spawn and die (Sandercock 1991). Recently biologists have begun to appreciate the broader role that estuarine habitat plays among juvenile coho salmon over much of their range (Miller and Sadro 2003, Koski 2009, Craig 2010, Jones et al. 2014). However, estuarine habitat use by coho salmon has not been described at the southern end of their range in California where the species is listed as threatened under both state and federal endangered species acts (Federal Register 1997, CDFG 2002).

Simenstad et al. (1982) hypothesized that estuaries provided an advantage to rearing juvenile salmonids by providing a productive foraging area, refuge from predators, and an area to gradually shift from freshwater to marine habitats. For salmonids other than coho salmon, faster growth in the estuary and larger size at ocean entrance has been shown to account for increased marine survival (Nicholas and Hankin 1989, Northcote 1997, Percy 1997, Trotter 1997, Bond et al. 2008). For example, California steelhead trout (*Oncorhynchus mykiss*) populations use estuarine habitats for months at a time primarily to acclimate, forage, and grow (Bond et al. 2008). Holtby et al. (1990) reported, however, that size at ocean entry can be particularly important for coho salmon during periods of low ocean productivity. Potential survival benefits to coho salmon have largely been inferred from these studies, but coho salmon have substantially different life histories and, therefore, estuary use patterns that potentially differ from those of other salmonid species.

Recent studies have identified the importance of the greater transition zone, or ecotone (Odum 1971), between fresh and brackish water to juvenile salmonids (Miller and Sadro 2003, Koski 2009, Jones et al. 2014). Miller and Sadro (2003) defined this stream-estuary ecotone (SEE), and we adapt their definitions, to include the area of low gradient stream extending from stream entrance to the wide valley floor, through the upper limit of tidal influence downstream to the area where the channel becomes bordered by tidal mudflats.

This definition of the SEE includes all side channels, off channel ponds, tidal channels, and fringing marsh habitats that are accessible to fish for at least some portion of the tidal cycle.

Habitat quality is best defined as the benefit to survival or reproduction that an organism receives from using the habitat (Rosenfeld et al. 2005), and is often evaluated relative to other potential or available habitats. Understanding of the quality of differing habitats and its relative abundance on the landscape is requisite for informed resource management and targeted restoration. This is especially true for the freshwater rearing phase of juvenile coho salmon, where rearing areas can be dynamic over both time and space within a watershed, and multiple life history pathways potentially contribute differentially to the reproductive population (Jones et al. 2014, Nordholm 2014).

Generally, to consider the Humboldt Bay SEE as relatively high quality habitat for coho salmon one or more of the following should be true: coho salmon have prolonged residence in the SEE; multiple life stages of coho salmon use the SEE; a substantial portion of the population uses the SEE; the SEE provides productive foraging, resulting in increased growth rates or larger size; and the SEE supports coho salmon during stressful periods (i.e., summer, periods of drought, or winter high flows). We provide information to infer relative habitat quality of the SEE in tributaries of the Humboldt Bay watershed by presenting information regarding juvenile coho salmon movement and residence times (Winker et al. 1995), size at time or individual growth (Holtby et al. 1990), and habitat use (Rosenfeld 2003), and comparing this to similar information from riverine habitats upstream of the SEE. The goal of this paper is to describe the use of portions of the Humboldt Bay SEE by coho salmon and to demonstrate their patterns of estuarine use are similar to other populations in the Pacific Northwest as described by other researchers such as Miller and Sadro (2003) and Koski (2009).

MATERIALS AND METHODS

Study area.—Humboldt Bay is located 442 km north of San Francisco, California, and its watershed area is 578 km² (HBWAC 2005). The two largest tributaries entering Humboldt Bay are Freshwater Creek with a drainage area of 9,227 ha² and Elk River with a drainage area of 8,632 ha² (HBWAC 2005). Many smaller tributaries, sloughs, and tidal streams contribute to a complex and dynamic hydrological regime in drainages around the bay (Figure 1). We defined sloughs as bodies of water with very low flow velocities and very low gradients regardless of tidal influence. We also characterized areas that experience changes in tidal heights, but are upstream of the influence of saltwater, as tidal freshwater. Tide gates are common on tributaries and sloughs entering Humboldt Bay, with 79 identified from a recent U.S. Fish and Wildlife Service (USFWS 2007) inventory. The lower portions of most streams entering Humboldt Bay flow through agricultural lands (primarily cattle grazing) and are characterized by low gradient, tidal ranges of 2–3 m, limited riparian vegetation, and confinement within levees. Physical conditions in Humboldt Bay tributaries such as saltwater intrusion show a high degree of annual, seasonal, and daily variation due to changes in stream flow and tidal inundation. The lower 2–4 km of Freshwater Creek and Elk River sloughs experience fluctuations in tidal height up to 3 m, and brackish water (25–30 ppt) is usually present from late spring through the early fall. Water temperatures of 20–25°C occur during the summer in the lower portion of Freshwater Creek Slough due to water heating up while on the mudflats during low tides, and limited tidal circulation

(Wallace 2006, Wallace and Allen 2015).

The tidal freshwater portions of most of the tributaries have water temperatures <18° C, and are maintained within confined channels (some within levees) having dense stands of riparian vegetation dominated by willow (*Salix* sp.) and alder (*Alnus* sp.). Lack of water turbulence and wind mixing in the freshwater-saltwater interface zone commonly results in a stratified water column with freshwater near the surface overlaying a wedge of brackish water near the bottom (Wallace 2006, Wallace and Allen 2015). Freshwater Creek Slough and Elk River Slough contain tidal slough habitat as they near Humboldt Bay, non-tidal low gradient stream habitat flowing through broad valleys upstream of the estuaries and higher gradient streams in steep canyons in the upper part of the watersheds (Figures 1 and 2). In Freshwater Creek the upstream end of the SEE is near the Howard’s Heights

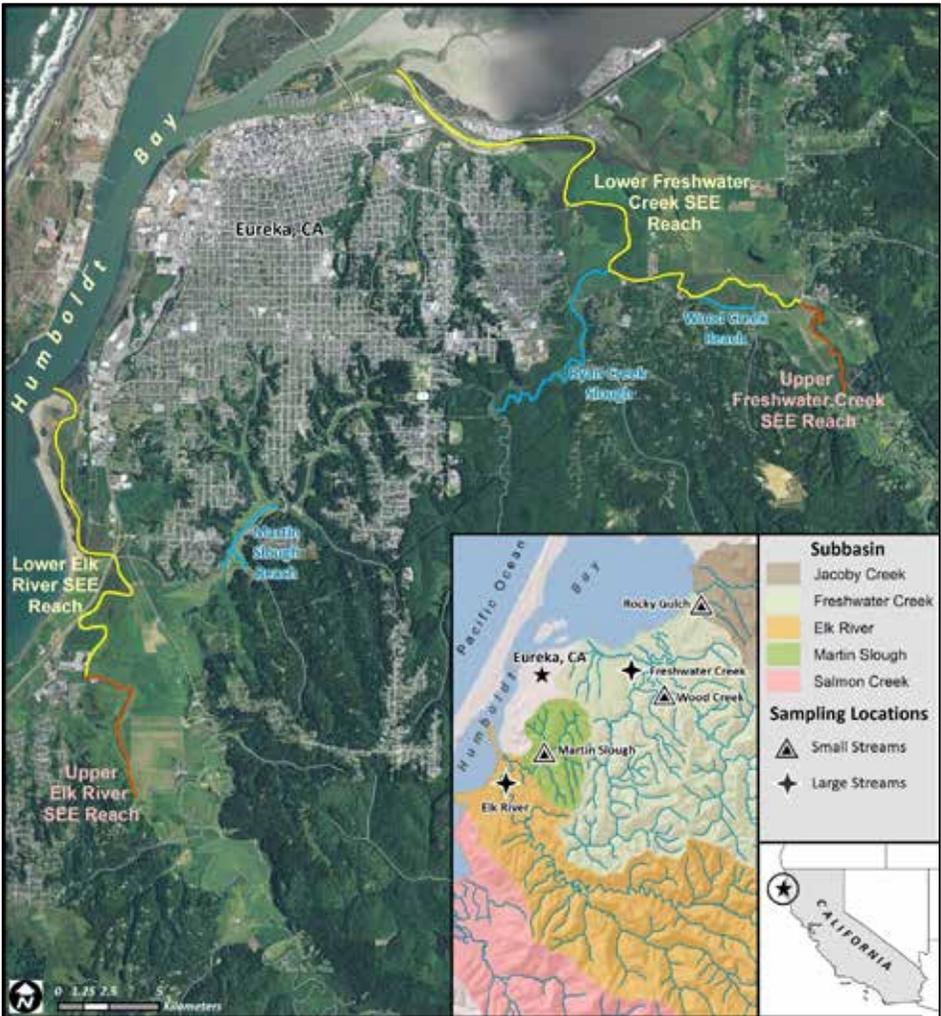


FIGURE 1.—Location of Humboldt Bay tributaries including demarcations of lower vs. upper sloughs in Freshwater Creek and Elk River along with Martin Slough and Wood Creek sampling areas Humboldt County, California. Lower and upper Freshwater Creek and Elk River sloughs are shown in yellow and red, respectively, and Martin Slough, Wood Creek, and Ryan Creek Slough are shown in blue.

downstream migrant trap (Figure 2). Smaller tributaries included in this study include Wood Creek, Martin Slough, and Rocky Gulch. These tributaries are within or proximal to Freshwater Creek, Elk River, and Jacoby Creek, respectively (Figures 1 and 2), which are the primary source populations of coho salmon in the Humboldt Bay watershed. Habitat conditions and land use of the small tributaries are similar to those described above. The largest tributary entering Freshwater Creek Slough is Ryan Creek (Figure 2). We did not sample this stream, but we did detect coho salmon tagged by Green Diamond Resources Company (described below) that emigrated from Ryan Creek into the lower Freshwater Creek watershed.

Seining and minnow trapping.—We sampled two large and three small Humboldt Bay tributaries, with a variety of gear, sampling frequencies, and time periods from 2003

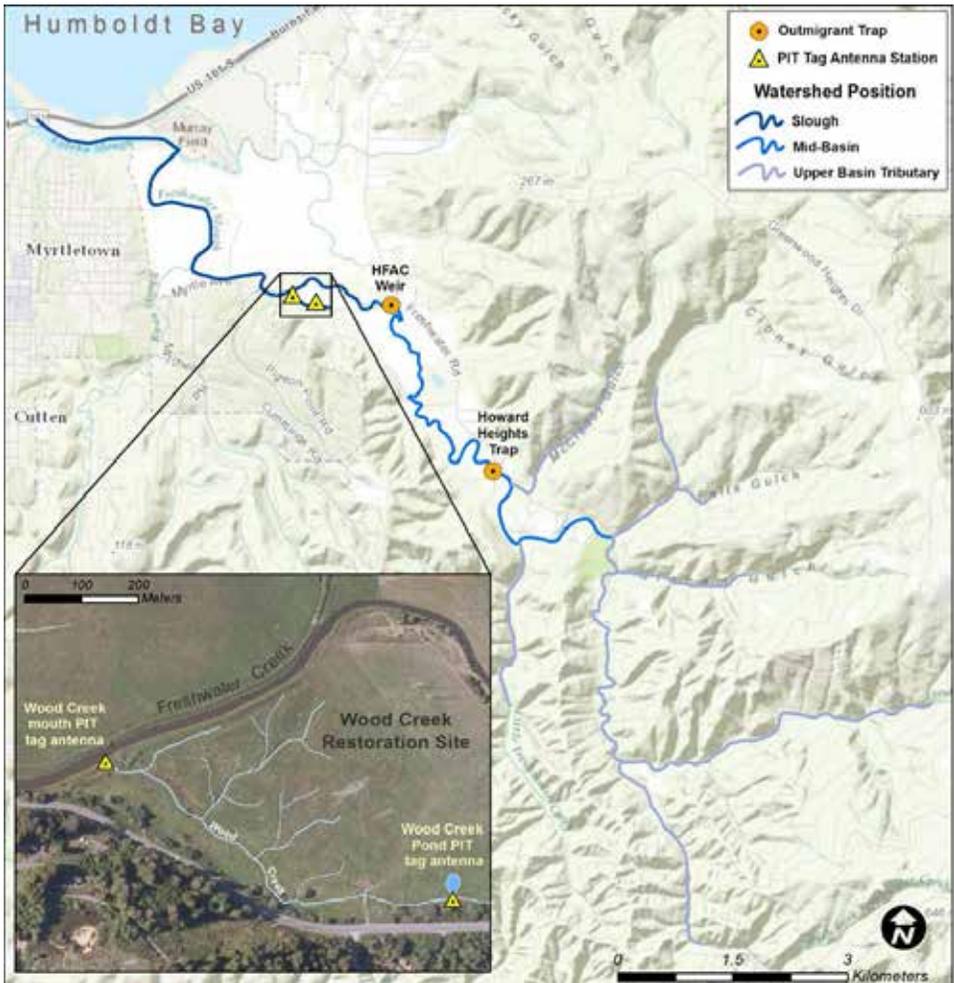


FIGURE 2.—Freshwater Creek basin showing locations of major tributaries, Howard Heights downstream migrant traps at the head of the broad valley floor, the Humboldt Fish Action Council (HFAC) fish trap in the stream-estuary ecotone, and PIT-tag antennas on Wood Creek, Humboldt County, California. Upstream extent of the SEE is located between Howard Heights Trap and McCready Gulch.

to 2011 (Table 1). In the slough portions of Freshwater Creek and Elk River we stratified sampling between the upper and lower sloughs due to differences in water salinity and the need to use different types of gear in the two sections of those sloughs. The stratification was necessary due to the presence of heavy riparian vegetation in the upper sloughs that required field crews to use a smaller seine net than that used to sample the larger water area in the lower sloughs. This is also the general area where riparian vegetation started to appear, representing a boundary between primarily estuarine and tidal freshwater habitat.

TABLE 1.—Sampling locations, methods, frequency, and duration conducted by this project in Humboldt Bay tributaries, Humboldt County, California, 2003–2011.

Location	Method	Frequency	Duration
Large streams			
Freshwater Creek			
upper	9-m seine	weekly	2003–2011
lower	30-m seine	weekly	2003–2009
Elk River			
upper	9-m seine	weekly	2005–2010
lower	30-m seine	weekly	2005–2010
Small streams			
Rocky Gulch	9-m seine; minnow trap	monthly	2007–2010
Wood Creek	minnow trap	monthly	2007–2011
Wood Cr. Pond	30-m seine	monthly	2009–2011
Martin Slough	9- & 30-m seines; minnow trap	monthly	2007–2010

We located sites to sample the slough continuum from the mouth to the upstream end of tidal influence. We chose individual seine sites based on the ability to pull a seine net through them and minnow trap sites in areas having perceived fish cover. We established six sampling sites in the upper slough of Freshwater Creek and four sites in upper Elk River Slough; those sloughs were 1.3 km and 1.7 km in length, respectively. Field crews made two hauls per sampling site using a 9.1 m × 1.8 m × 6.4-mm mesh beach seine. We established seven sampling sites in the lower slough of Freshwater Creek and five sites in lower Elk River Slough, and they were 8.5 km and 5.5 km in length respectively. Field crews made one seine haul per site using a 30.5 m × 2.4 m beach seine (mesh size of the wings was 19.1 mm and the bag was 1.5 m deep with 6.4-mm mesh) deployed by hand or boat. In the small tributaries we used a variety of sampling gear (Table 1). In Rocky Gulch, crews made two hauls at one site with the 9.1-m seine and deployed minnow traps baited with frozen salmon roe for 30 to 210 min at locations where seine hauls were precluded due to steep banks and heavy vegetation. In Wood Creek we deployed baited minnow traps for 30 to 210 min at sites. We made one to two hauls with the 30.5-m seine in a constructed pond connected to the Wood Creek channel. In Martin Slough we used the 30.5-m seine set by hand or kayak to sample a large pond, the 9.1-m seine to sample the slough channel, and baited minnow traps were deployed for 30 to 210 min where seine hauls were precluded due to steep banks and heavy vegetation.

Fish processing.—Field crews anaesthetized, identified, counted, and examined all juvenile coho salmon for marks and tags and determined life stage (i.e., parr, pre-smolt, smolt) of yearling plus (1+) coho salmon. We designated coho salmon as young-of-the-year (YOY) until the end of the calendar year after which we designated them as 1+. We distinguished 1+ from YOY coho salmon based on their greater fork length (FL). Crews

measured FL to the nearest mm and weight to the nearest 0.1 g for all juvenile coho salmon except for the rare occasions when the number of fish captured (i.e., >100 fish/site) or environmental conditions, such as high water temperatures or high winds made it dangerous for the fish or for field crews to process the fish.

All fish with tags or marks were measured for FL, weighed, and their mark or tag number was recorded. We applied Passive Integrated Transponder (PIT) tags to untagged juvenile coho salmon by making a small incision along the ventral surface and inserting the tag into the body cavity. All coho salmon ≥ 70 mm FL received an 11.5 mm HDX PIT-tag. Starting in 2008, all coho salmon ≥ 55 mm and ≥ 69 mm FL received an 8.5 mm FDX PIT-tag. We also encountered and processed coho salmon containing PIT-tags applied by other fish monitoring projects in the Freshwater Creek basin (see below in *Data Analysis*). Once processed, the fish were allowed to fully recover for 10–30 min and then released at the sampling site.

Downstream migrant trapping.—In 2007 and 2008 we operated two downstream migrant traps on Freshwater Creek from early March to June to estimate coho salmon smolt production above each site and partition smolt production into that occurring above and between trap placements. The upstream trap was a floating inclined plane trap placed in the mainstem of Freshwater Creek 12.5 km upstream of the mouth where the stream exited steep canyons and entered low stream gradient habitat flowing through broad valley floor (Howards Heights Trap in Figure 2). The downstream trap was a modified adult salmon weir originally installed by the Humboldt Fish Action Council (HFAC) fitted with a pipe trap located in the lower coastal plain 8.5 km above the mouth (HFAC Weir in Figure 2). At this point the stream is usually freshwater but its elevation is strongly influenced by daily tidal cycles and brackish water extends up to this point at high tides during summer and early fall. Captured fish were processed with the same protocol as the SEE sampling, but all PIT-tagged fish were transported above the traps and released to help establish period-specific trap efficiency estimates that were used to expand total catch as an estimate of smolt production (Bjorkstedt 2005, Ricker and Andersen 2014).

PIT-tag antennas.—We installed two PIT-tag antenna arrays on Wood Creek, a small tributary entering Freshwater Creek Slough (Figure 2) to document the residence times and origin of PIT-tagged salmonids residing in, or passing by, Wood Creek. The first was placed at the entrance of the newly constructed off-channel pond on 29 January 2010 and the second was installed at the mouth of Wood Creek in the tide gate structure on 22 February 2010; both were operated throughout the length of this study. We installed two independent antennas at each site to discern directional movement in and out of the pond and creek. Each PIT-tag antenna array consisted of a multiplex transceiver (Mauro Engineering) and data logger powered by two 12V batteries that were continuously charged by a solar panel. Antennas were constructed of copper tubing and sealed inside PVC pipe. At the pond site we attached the two antennas to wooden posts driven into the substrate. At the tide gate site we attached wooden tracks to the concrete tide gate structure and slid the antennas into the tracks.

Data analysis.—To assess residency time and growth in the SEE, we included all fish marked either in the SEE, or upstream in the greater basin and later recaptured in the SEE (Figure 2). We calculated length of SEE residence for PIT-tagged fish by combining fish captures and antenna recordings to determine the number of days between tagging or first detection in the SEE and last recapture or detection date. Calculated growth rates were

simply the change in FL between date of tagging or first capture and date of last recapture divided by the number of days at large between first and last encounter. Mean residence times were not calculated for YOY or 1+ coho salmon when sample sizes were composed of <10 individuals to limit the influence of the occasional individual exhibiting extreme residence time. Growth rates were not calculated for fish-at-large ≤ 12 days to minimize short-term tagging effects on growth rate calculations. The lower downstream migrant trap (HFAC Weir; Figure 2) was also operated as an adult salmonid counting weir by CDFW to obtain annual adult coho salmon run size estimates using mark-recapture techniques (Ricker and Anderson 2011).

We used analysis of variance (ANOVA) to investigate spatial and temporal differences in the mean fork length of coho salmon rearing in different portions of the SEE during the spring, and between the SEE and upper stream network during the fall. Residual plots and length-frequency histograms were examined to detect outliers and to test for violations of ANOVA assumptions (i.e., homoscedasticity and normality).

To analyze differences in 1+ coho salmon FLs in spring, we compared the data collected annually between March 1 and May 29 by basin (freshwater elk), year, and location (slough type) within the SEE. For the fall, we only analyzed Freshwater Creek YOY coho salmon length data because we did not collect any size data from fish upstream of the SEE in Elk River. Furthermore, we collected length data from YOY coho salmon rearing in upper Freshwater Creek basin streams, and in the mid-basin upstream of the SEE, allowing us to compare mean fall fork length throughout the entire stream network from the SEE to headwater reaches. To analyze differences in YOY coho salmon FLs in fall, we compared the data collected annually between September 9 and November 11 by basin, year, and location within SEE. Significance levels were set at $P < 0.05$ and all post-hoc comparisons of groups were performed using Tukey-Kramer multiple comparisons (Zar 1999).

RESULTS

Juvenile coho salmon were widely distributed throughout the sampled portion of the Humboldt Bay SEE. Catches of juvenile coho salmon varied between years and life stage in upper Elk River and Freshwater Creek sloughs (Figure 3). Young-of-the-year coho salmon were present in these large tributaries from roughly April to December with peak catches in June and July, while 1+ coho salmon were present mostly January to June with peak catches in April and May (Figure 3). In upper Freshwater Creek Slough, where we had the longest time series, we used our June catch-per-unit-effort (CPUE) of YOY coho salmon as an index of relative abundance between years and detected large variations in their annual abundance in the SEE (Table 2). We also found that June CPUE of YOY coho salmon was positively correlated ($r^2 = 0.87$) with adult coho salmon escapement from the previous winter (Figure 4).

Seasonality of peak juvenile coho salmon catches also varied between tributary size and life stage. In the larger tributaries, YOY coho salmon comprised a majority of the catches and usually peaked in spring and summer (Table 3) while in small tributaries catches of primarily 1+ coho salmon peaked in the winter when stream flows were high (Table 4). Conversely, the lowest seasonal catches of coho salmon in large streams usually occurred in the winter while the lowest catches of coho salmon in small streams occurred primarily in the summer and fall (Tables 3 and 4). This resulted in a dyssynchronous seasonal pattern of juvenile coho salmon occupation between large and small tributaries (Figure 5).

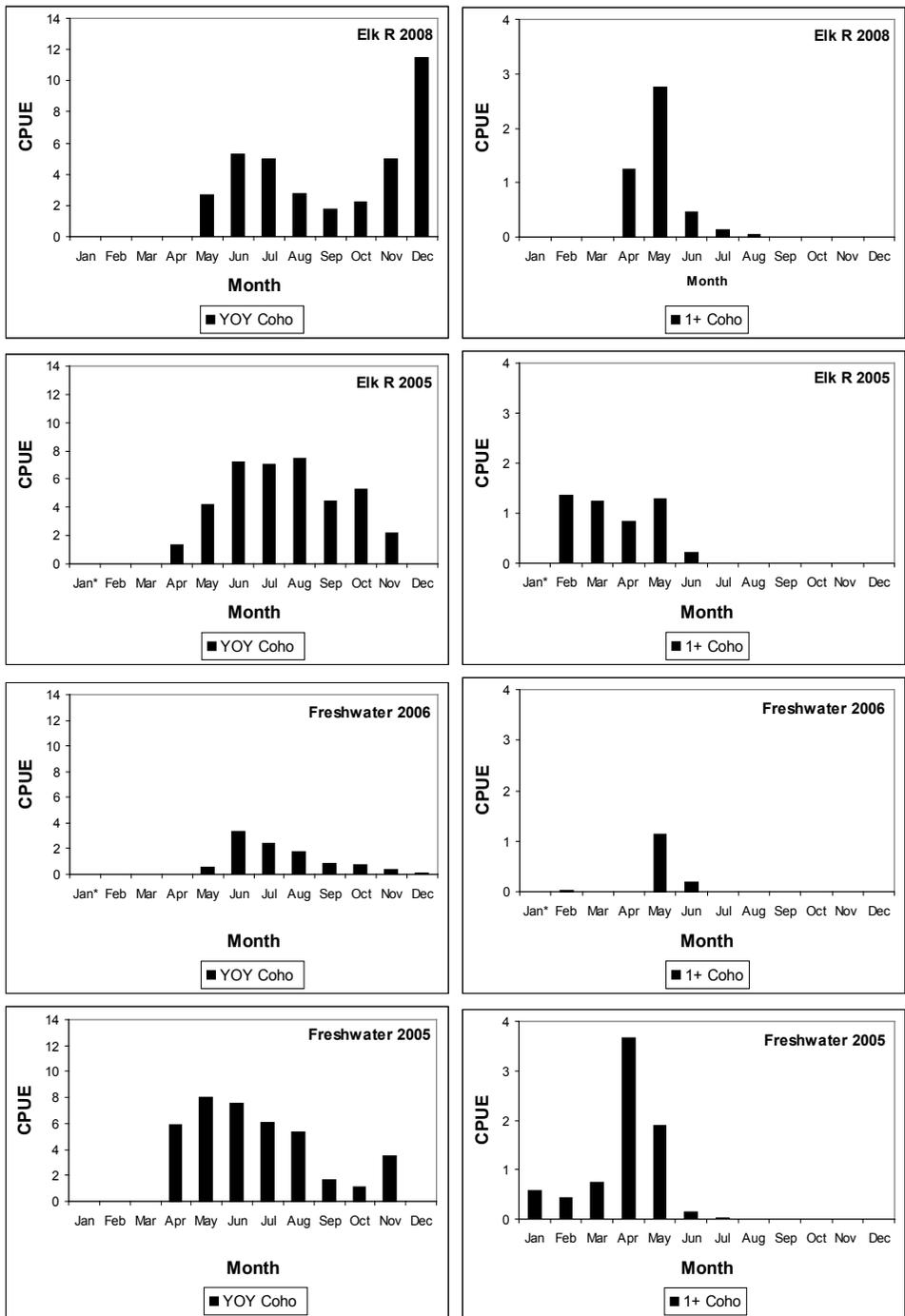


FIGURE 3.—Catch-per-unit-effort (# of fish/seine haul) of young-of-the-year (YOY) and yearling plus (1+) coho salmon from upper Freshwater Creek and Elk River sloughs, Humboldt County, California, for selected years.

TABLE 2.—Effort, number captured, and catch-per-unit-effort (CPUE) of young-of-the-year coho salmon in upper Freshwater Creek Slough, Humboldt County, California, during the month of June, 2003–2011.

Year	Seine Hauls (<i>n</i>)	Fish Caught (<i>n</i>)	CPUE (fish/haul)
2003	48	478	9.96
2004	60	335	5.58
2005	59	447	7.58
2006	48	161	3.35
2007	48	64	1.33
2008	44	4	0.09
2009	34	106	3.34
2010	10	2	0.20
2011	24	33	1.38

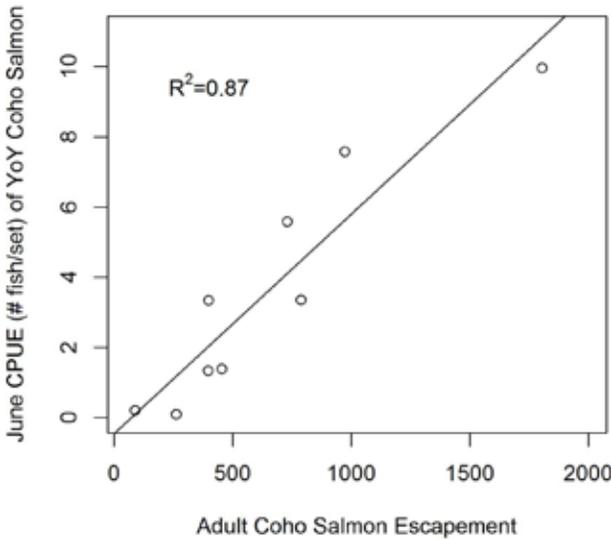


FIGURE 4.—Relationship between adult coho salmon escapement and subsequent catch-per-unit-effort (CPUE) of young-of-the-year (YOY) coho salmon progeny captured in upper Freshwater Creek Slough, Humboldt County, California, the following June.

TABLE 3.—Catch-per-unit-effort of young-of-the-year (YOY) and yearling plus (1+) coho salmon captured in Freshwater Creek Slough and Elk River Slough, Humboldt County, California, by season, 2007–2010. Winter is January to March, Spring is April to June, Summer is July to September, and Fall is October to December.

Season	Freshwater Creek Slough		Elk River Slough		Combined Sloughs	
	1+	YOY	1+	YOY	1+	YOY
Winter 2007	0.20	0.00	0.00	0.00	0.14	0.00
Spring 2007	1.44	0.92	1.19	2.35	1.35	1.43
Summer 2007	0.01	0.37	0.03	2.97	0.02	1.39
Fall 2007	0.00	0.38	0.00	1.18	0.00	0.70
Winter 2008	0.00	0.00	0.00	0.00	0.00	0.00
Spring 2008	0.27	0.06	1.36	2.43	0.75	1.10
Summer 2008	0.03	0.04	0.07	3.50	0.04	1.39
Fall 2008	0.00	0.02	0.00	4.31	0.00	1.53
Winter 2009	0.04	0.00	0.64	0.00	0.30	0.00
Spring 2009	0.36	1.57	5.02	3.18	2.31	2.24

TABLE 4.—Number of young-of-the-year (YOY) and yearling plus (1+) coho salmon captured in Wood Creek, Martin Slough, and Rocky Gulch, Humboldt County, California, by season, 2007–2010. Winter is January to March, Spring is April to June, Summer is July to September, and Fall is October to December.

Season	Wood Creek		Martin Slough		Rocky Gulch		Combined	
	1+	YOY	1+	YOY	1+	YOY	1+	YOY
Winter 2007	86	0	4	0	68	0	158	0
Spring 2007	27	2	71	0	33	1	131	3
Summer 2007	1	16	0	17	0	0	1	33
Fall 2007	0	17	0	24	0	1	0	42
Winter 2008	125	0	68	0	20	0	213	0
Spring 2008	50	0	70	0	16	0	136	0
Summer 2008	0	1	0	13	0	0	0	14
Fall 2008	1	4	0	37	0	0	1	41
Winter 2009	46	0	435	0	28	0	509	0
Spring 2009	19	3	246	1	3	0	268	4
Summer 2009	1	3	17	31	0	0	18	34
Fall 2009	1	3	8	8	0	1	9	12
Winter 2010	140	0	198	0	76	0	414	0
Spring 2010	19	3	83	0	38	0	140	3

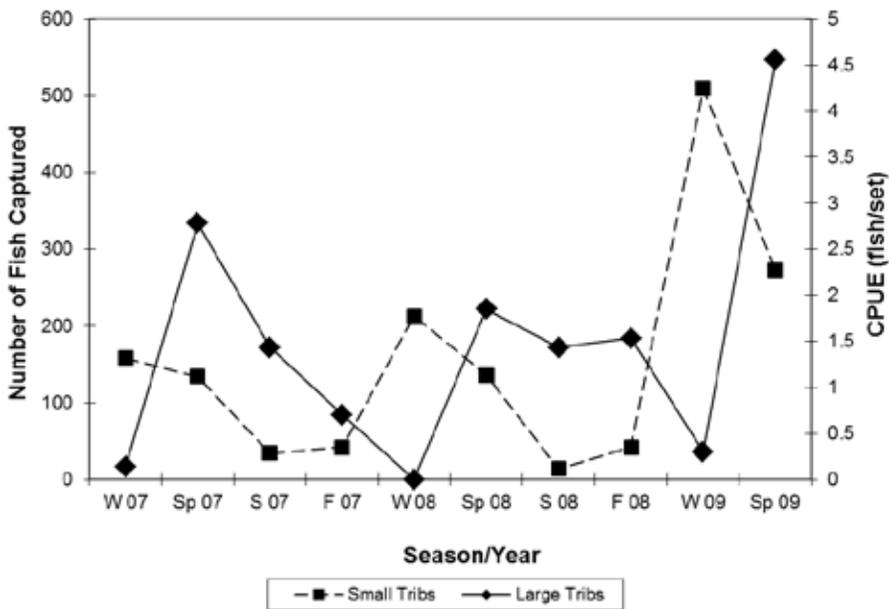


FIGURE 5.—Comparison of the number of yearling plus (1+) and young-of-the-year (YOY) coho salmon captured in minnow traps by season in Rocky Gulch, Wood Creek, and Martin Slough (small tributaries) and combined catch-per-unit-effort (CPUE) of 1+ and YOY coho salmon captured by seining in upper Freshwater Creek and Elk River sloughs (large tributaries), Humboldt County, California, 2007–2009. W= winter, Sp= spring, S= summer, and F= fall.

Both YOY and 1+ coho salmon reared for extended periods in the sampled portions of the Humboldt Bay SEE. YOY coho salmon resided primarily in the upper sloughs of the larger streams during the spring and summer. The mean residence times of PIT-tagged YOY coho salmon that were tagged and recaptured as YOY ranged from one to two months, but individual fish reared for up to six months (Table 5); some individual fish tagged as YOY

TABLE 5.—Summary of residence times in days at liberty (DAL) and growth rates (GR) in mm/day of young-of-the-year coho salmon in Freshwater Creek Slough, Elk River Slough, Martin Slough, Wood Creek, Rocky Gulch, and Ryan Creek, Humboldt County, California, 2005–2010. Mean days at liberty were not calculated for fish with sample sizes less than 10 individuals and mean growth rates were not calculated for fish at large ≤ 12 days except where noted.

Basin	Year	<i>n</i>	Mean DAL	Range DAL	Mean GR	Range GR
Freshwater	2010	12	41	16-113	0.23	0.12-0.48
	2009	69	60	13-175	0.20	0.00-0.68
	2008	0	-	-	-	-
	2007	12	68	6-167	0.17	0.12-0.45
	2006	57	33	5-106	0.15	0.00-0.29
	2005	112	32	4-128	0.17	0.00-0.43
Elk	2009	19	17	13-27	0.46	0.31-0.64
	2008	104	58	6-168	0.29	0.04-0.68
	2007	55	44	5-124	0.16	0.00-0.38
	2006	41	39	6-128	0.19	0.07-0.39
	2005	121	34	4-110	0.13	0.00-0.38
Martin	2010	0	-	-	-	-
	2009	4	-	28-126	-	0.21-0.43
	2008	0	-	-	-	-
	2007	4	-	30-58	-	0.27-0.33
Wood	2010	1	-	29	-	0.14
	2009	1	-	58	-	0.17
	2008	0	-	-	-	-
	2007	4	-	26-129	-	0.03-0.22
Rocky Gulch	2010	0	-	-	-	-
	2009	0	-	-	-	-
	2008	0	-	-	-	-
	2007	0	-	-	-	-
Ryan	2010	0	-	-	-	-

and recaptured as 1+ reared in the SEE for over a year (Table 6). The 1+ coho salmon reared mostly during the winter in both the larger and smaller streams and the mean residence times of PIT-tagged 1+ coho salmon ranged from a few weeks to nine months (Table 6). In the more brackish, lower sloughs of Freshwater Creek and Elk River, the presence of YOY and 1+ coho salmon was confined mostly to spring (Wallace 2006, Wallace and Allen 2009, Wallace and Allen 2012).

Young-of-the-year coho salmon were captured only in the lower sloughs during spring freshets and did not rear extensively in lower Freshwater Creek Slough but some did move into Wood Creek, which enters Freshwater Creek in the lower slough. Coho salmon categorized as 1+ were consistently captured in the lower sloughs from April to June. The residence times of 1+ coho salmon in the lower sloughs were much shorter than in the areas upstream of brackish water, but some fish were found to rear for one to four weeks in lower Freshwater Creek Slough (Wallace 2006; Wallace and Allen 2009, 2012; Pinnix et al. 2012).

TABLE 6.— Summary of residence times in days at liberty (DAL) and growth rates (GR) in mm/day of yearling 1+ coho salmon in Freshwater Creek Slough, Elk River Slough, Martin Slough, Wood Creek, Rocky Gulch, and Ryan Creek, Humboldt County, California, 2005–2010. Mean days at liberty were not calculated for fish species or life stage with sample sizes less than 10 individuals and mean growth rates were not calculated for fish at large ≤ 12 days except where noted. The table also includes fish tagged as young-of-the-year (YOY) and recaptured the following year.

Basin	Year	<i>n</i>	Mean DAL	Range		
				DAL	Mean GR	Range GR
Freshwater	2010	0	-	-	-	-
	2009	1	-	-	-	-
	2008	1	-	-	-	-
	2007	22	21	5-224	0.43	0.23-0.60
	2006	4	-	5-11	-	-
	2005	20	20	2-81	0.42	0.21-0.56
	Tagged YOY	2	-	170-245	-	0.15-0.17
Elk	2009	18	19	13-42	0.30	0.00-0.54
	Tagged YOY	5	-	133-349	-	0.14-0.18
	2008	19	14	5-25	0.37	0.17-0.72
	Tagged YOY	1	-	294	-	0.10
	2007	8	-	7-258	-	0.09-0.50
	2006	7	-	6-282	-	0.18
	2005	3	-	9-94	-	0.11-0.33
Martin	2010	17	50	27-119	0.41	0.21-0.76
	Tagged YOY	3	-	64-310	-	0.14-0.25
	2009	33	42	23-126	0.32	-0.04-0.67
	Tagged YOY	5	-	67-270	-	0.13-0.20
	2008	14	34	25-60	0.32	0.16-0.51
Wood	2007	1	-	39	-	1.03
	2010	6	-	9-153	-	0.11-0.73
	2009	5	-	23-91	-	0.03-0.35
	2008	7	-	28-57	-	0.05-0.32
	Tagged YOY	3	-	110-449	-	0.10-0.17
	2007	5	-	35-70	-	0.13-0.43
Rocky Gulch	Tagged YOY	2	-	213-251	-	0.12-0.12
	2010	13	43	28-94	0.33	0.12-0.45
Ryan	Tagged YOY	1	-	90	-	0.21
	2009	4	-	43-69	-	0.09-0.26
	2008	2	-	30-30	-	0.10-0.13
	2007	6	-	10-37	-	0.27-0.41
2010	22	49	14-90	0.46	0.20-0.75	

Typically, in the upper sloughs of Freshwater Creek and Elk River the monthly mean FL of captured YOY coho salmon increased from around 40 mm in early spring to 80–110 mm by the end of the year (Table 7). The mean monthly FL of 1+ coho salmon captured in the upper sloughs was typically around 80 mm in the winter and increased to 105–115 mm during April and May (Table 7). The monthly mean FL of the small numbers of YOY coho salmon in the lower sloughs was around 40 mm in early spring and 65–85 mm by the end of the year (Table 8). The mean monthly FL of 1+ coho salmon captured in the lower slough was typically 65–80 mm in the winter and increased to 110–120 mm during the spring and early summer (Table 8).

Yearling (1+) coho salmon captured in the lower sloughs of Freshwater Creek and Elk River were significantly larger (mean FL = 114 mm, SE = 0.54 mm) than those captured in the upper sloughs (mean FL = 106 mm, SE = 0.41 mm); ANOVA, $F_{1,1479} = 90.86, P < 0.001$

TABLE 7.—Monthly mean fork length (FL) and size range in millimeters of young-of-the-year (YOY) and yearling plus (1+) coho salmon in upper Freshwater Creek Slough and upper Elk River Slough, Humboldt County, California, for selected years.

Month	Freshwater Creek Slough											
	2005				2007				2009			
	YOY Coho		1+ Coho		YOY Coho		1+ Coho		YOY Coho		1+ Coho	
	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range
Jan	-	-	77	64-86	-	-	-	-	-	-	-	-
Feb	-	-	80	70-100	-	-	-	-	-	-	-	-
Mar	-	-	81	67-96	-	-	83	67-100	-	-	-	-
Apr	40	33-50	104	81-133	42	34-47	100	85-134	34	34-34	110	90-127
May	43	31-61	102	79-123	54	39-67	100	76-127	42	35-48	106	93-114
Jun	57	29-96	106	92-136	65	31-75	101	82-111	64	40-85	106	100-110
Jul	66	51-99	98	98	79	69-91	123	123	77	66-90	-	-
Aug	73	56-93	-	-	86	80-97	-	-	80	63-94	106	96-115
Sep	77	59-95	-	-	88	85-94	-	-	83	71-95	-	-
Oct	82	70-101	-	-	86	63-105	-	-	87	70-99	-	-
Nov	79	57-113	-	-	85	76-101	-	-	90	70-103	-	-
Dec	-	-	-	-	-	-	-	-	-	-	-	-

Month	Elk River Slough											
	2005				2007				2008			
	YOY Coho		1+ Coho		YOY Coho		1+ Coho		YOY Coho		1+ Coho	
	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range
Jan	-	-	-	-	-	-	-	-	-	-	-	-
Feb	-	-	80	64-100	-	-	-	-	-	-	-	-
Mar	-	-	82	62-93	-	-	-	-	-	-	-	-
Apr	41	37-53	113	98-129	-	-	-	-	39	39	111	80-125
May	41	35-67	114	97-142	54	34-70	109	80-139	53	39-63	107	87-125
Jun	59	43-81	107	88-119	62	45-82	104	86-125	63	45-79	106	94-116
Jul	68	51-90	-	-	73	52-95	105	100-114	74	58-97	118	101-141
Aug	71	57-94	-	-	80	65-100	-	-	84	67-102	118	118
Sep	75	63-95	-	-	90	84-97	-	-	90	74-101	-	-
Oct	80	67-97	-	-	86	54-97	-	-	94	76-111	-	-
Nov	78	60-93	-	-	78	58-100	-	-	96	86-112	-	-
Dec	-	-	-	-	-	-	-	-	111	80-124	-	-

(Figure 6). No interactions were found between basin and slough type, indicating the lower sloughs of both basins contained larger yearling coho salmon; ANOVA, $F_{1,1474} = 1.05$, $P = 0.31$. Overall, year had a significant effect on mean yearling coho salmon FLs for both basins; Tukey post-hoc comparisons indicated the 2005 coho salmon were much smaller and the 2006 coho salmon were much larger than those measured from 2007 to 2009; ANOVA, $F_{4,1480} = 38.00$, $P < 0.001$ (Figure 6). However, the interaction between year and slough type on mean coho salmon FLs was not significant, indicating mean FLs were consistently larger in lower sloughs regardless of their annual size or basin of origin; ANOVA, $F_{4,1470} = 1.47$, $P = 0.21$. The interaction of year and basin was significant indicating annual differences in mean coho salmon FLs were largely basin-specific instead of a regional trend; ANOVA, $F_{4,1475} = 10.49$, $P < 0.001$. Last, yearling coho salmon captured during the spring from 2005 to 2009 were slightly larger on average in Elk River (mean FL = 111 mm, SE = 0.44 mm) than in Freshwater Creek (mean FL = 105 mm, SE = 0.62 mm); ANOVA, $F_{1,1484} = 12.12$, $P < 0.001$; the 6-mm size difference is, however, unlikely to be biologically meaningful.

Young-of-the-year coho salmon in the Freshwater Creek SEE were larger than their cohorts rearing upstream and their FLs increased from the upper tributaries to the mid-basin to the SEE (Figure 7). Young-of-the-year coho salmon captured in Freshwater Creek during the fall of 2009 and 2010 were significantly larger in the mid-basin than those captured in upper tributaries; ANOVA, $F_{2,2218} = 97.94$, $P < 0.001$. Mean FLs were 87 mm (SE = 0.67

TABLE 8.—Monthly mean fork length (FL) and size range in millimeters of young-of-the-year (YOY) and yearling plus (1+) coho salmon in lower Freshwater Creek Slough and lower Elk River Slough, Humboldt County, California, for selected years.

Month	Freshwater Creek Slough											
	2005				2007				2008			
	YOY Coho		1+ Coho		YOY Coho		1+ Coho		YOY Coho		1+ Coho	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Jan	-	-	-	-	-	-	-	-	-	-	-	-
Feb	-	-	-	-	-	-	-	-	-	-	-	-
Mar	39	39	83	62-127	-	-	-	-	-	-	-	-
Apr	39	33-45	113	86-125	-	-	105	83-151	-	-	113	105-127
May	49	32-60	117	90-146	42	42	107	95-118	-	-	114	101-124
Jun	65	60-70	104	94-112	-	-	-	-	-	-	122	122
Jul	-	-	-	-	-	-	-	-	-	-	94	94
Aug	76	74-78	-	-	-	-	-	-	-	-	-	-
Sep	80	77-83	-	-	-	-	-	-	-	-	-	-
Oct	-	-	-	-	-	-	-	-	-	-	-	-
Nov	77	62-94	-	-	-	-	-	-	-	-	-	-
Dec	-	-	-	-	-	-	-	-	-	-	-	-

Month	Elk River Slough											
	2005				2007				2008			
	YOY Coho		1+ Coho		YOY Coho		1+ Coho		YOY Coho		1+ Coho	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Jan	-	-	64	60-68	-	-	-	-	-	-	72	55-89
Feb	-	-	82	60-105	-	-	-	-	-	-	-	-
Mar	39	39	90	76-117	-	-	113	108-119	-	-	-	-
Apr	41	35-46	110	73-136	-	-	127	109-139	-	-	119	94-143
May	47	37-71	107	74-133	42	42	119	91-183	-	-	109	90-133
Jun	64	62-69	110	95-126	-	-	109	86-125	-	-	120	101-143
Jul	-	-	129	129	-	-	-	-	-	-	128	111-141
Aug	-	-	-	-	-	-	-	-	-	-	-	-
Sep	87	86-87	-	-	-	-	-	-	-	-	-	-
Oct	-	-	-	-	-	-	-	-	-	-	-	-
Nov	-	-	-	-	-	-	-	-	-	-	-	-
Dec	66	61-70	-	-	-	-	-	-	-	-	-	-

mm) for the slough (SEE) locations, 80 mm (SE = 0.46 mm) for the mid-basin locations, and 72 mm (SE = 0.32 mm) for the upper tributary locations. Also, overall FLs of YOY coho salmon rearing throughout Freshwater Creek were substantially larger in 2010 (2010 mean FL = 79 mm, SE = 0.31 mm) than in 2009 (2009 mean FL = 71, SE = 0.45 mm); ANOVA, $F_{1,2217} = 1255.11, P < 0.001$ (Figure 7). No interaction was detected between watershed position and year, indicating mean FLs were progressively larger in the lower watershed than in the upper watershed regardless year (Figure 7); ANOVA, $F_{2,2215} = 0.77, P < 0.001$.

Annual mean growth rates of PIT-tagged YOY coho salmon rearing in the SEE ranged from 0.13 to 0.46 mm/day, but individual fish grew up to 0.68 mm/day (Table 5). Annual mean growth rates of PIT tagged 1+ coho salmon ranged from 0.30 to 0.46 mm/day, but individual fish grew up to 1.03 mm/day (Table 6).

The PIT-tag antennas at Wood Creek detected PIT-tagged juvenile coho salmon originally tagged throughout the Freshwater Creek watershed; in some cases those fish were from many kilometers upstream (Table 9). The antennas detected juvenile salmonids moving into Wood Creek and the pond to rear over winter during high stream flows. The pond PIT-tag antenna detected 46 coho salmon originally tagged by CDFW personnel in and upstream of the SEE in 2010, and 28 in 2010–2011 (Table 9).

A large portion of coho salmon smolt production uses the Freshwater Creek SEE. California Department of Fish and Wildlife calculated smolt production estimates entering

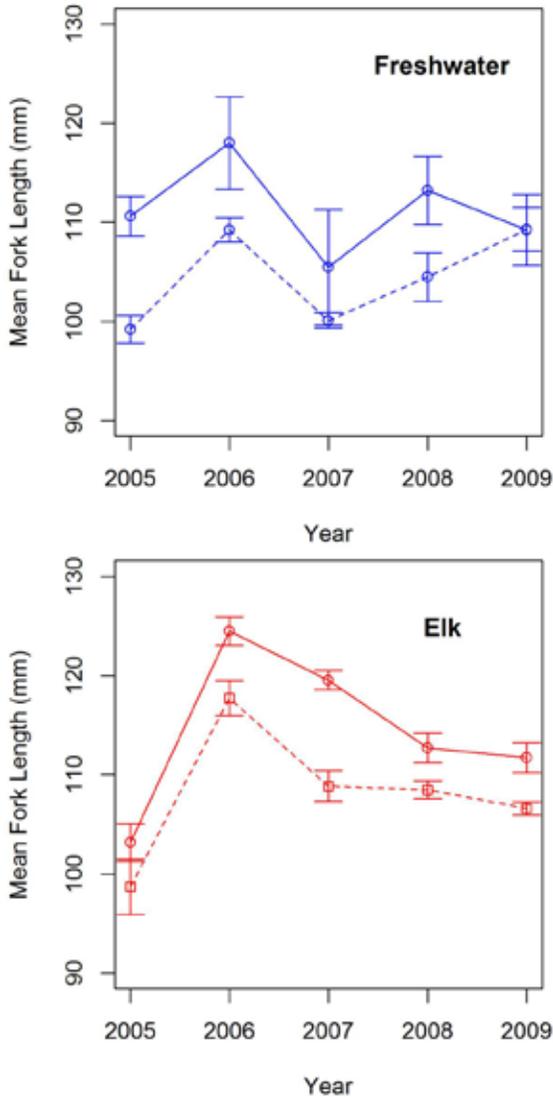


FIGURE 6.—Comparison of the annual mean fork lengths and standard errors of age 1+ coho salmon from upper Freshwater Creek and Elk River sloughs (dotted lines) and lower Freshwater Creek and Elk River sloughs (solid lines), Humboldt County, California, 2005–2009.

the SEE and within the SEE in 2007 and 2008. The 2007 coho salmon smolt estimates were $3,685 \pm 266$ at the Howards Heights Trap at the upstream end of the SEE (Figure 2) and $5,888 \pm 503$ at the HFAC Weir within the SEE. In 2008, the coho salmon smolt estimates were $3,096 \pm 154$ at the Howard Heights Trap and $4,945 \pm 232$ at the HFAC Weir (Ricker and Anderson 2011). These smolt estimates indicate ~40% of the coho smolt production in these two years were already present in this 4-km section of the SEE compared to ~60% residing in the 21 km of coho salmon habitat upstream of the Howard Heights Trap.

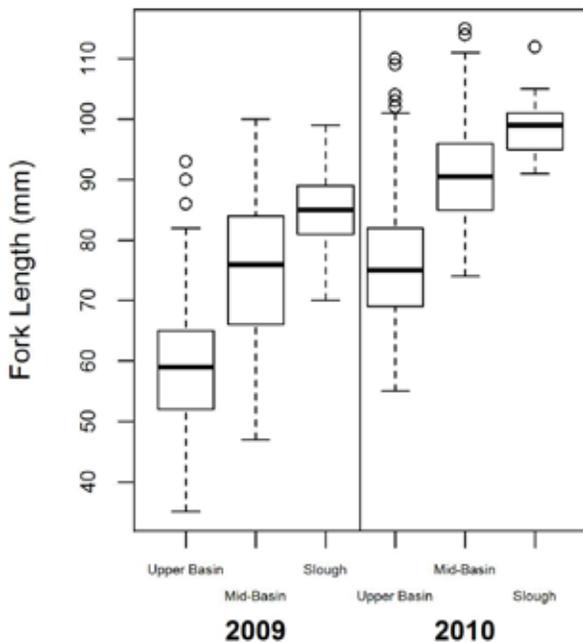


FIGURE 7.—Box plots comparing mean fork lengths of young-of-the-year coho salmon captured in the slough (stream-estuary ecotone), mid-basin, and upper basin portions of Freshwater Creek, Humboldt County, California, in the fall of 2009 and 2010. Boxes depict the 25th, 50th, and 75th percentiles, whiskers depict 5th and 95th percentiles, and points indicate outliers.

TABLE 9.—Origin of PIT-tagged juvenile coho salmon tagged in Freshwater Creek basin, Humboldt County, California, detected at Wood Creek pond and tide gate antennas during January to September 2010 and during October 2010 to June 2011.

Fish Origin	Pond 2010	Pond 2010/11	Tide Gate 2010	Tide Gate 2010/11
Stream-Estuary Ecotone	7	1	9	30
Lower Mainstem	11	6	11	49
Middle Mainstem	-	11	-	79
Upper Mainstem	7	6	10	59
Little Freshwater Cr	12	-	13	-
Cloney Gulch	9	4	8	45
South Fork Freshwater Cr	-	0	-	13
Freshwater Creek (total)	46	28	51	275
Wood Cr Pond	74	8	33	2
Wood Cr (tagged 2011)	-	6	-	17
Wood Cr (tagged 2010)	26	3	47	5
Wood Cr (tagged 2009)	1	0	1	0
Ryan Sl/Cr	0	0	26	5
Freshwater Sl (tagged 2011)	-	0	-	2
Freshwater Sl (tagged 2010)	0	0	2	8
Freshwater Sl (tagged 2009)	5	0	9	0
HFAC Weir (tagged 2011)	-	0	-	122
HFAC Weir (tagged 2010)	0	0	161	1
HFAC Weir (tagged 2009)	1	0	1	0
Grand Total	153	45	331	437

DISCUSSION

Craig (2010) provided an excellent description of the various coho salmon life history patterns, moving from the traditional almost exclusively “stream-type” life history pattern (Sandercock 1991) to appreciating the multiple life history patterns exhibited by coho salmon where the SEE plays an important role in their development. These diverse patterns include, but are not limited to arriving and rearing in the SEE during spring and summer as fry (Miller and Sadro 2003, Wallace 2006, Jones et al. 2014); coho salmon parr arriving in the fall to rear during winter in the SEE (Koski 2009, Jones et al. 2014), or even moving into the marine environment as YOY fish (Bennett et al. 2015). Rearing fry and parr may over winter in the SEE or move into adjacent non-natal streams (Craig 2010, Jones et al. 2014, this study) or exhibit the “nomad” life history of moving back upstream to overwinter (Miller and Sadro 2003, Koski 2009).

A review by Koski (2009) showed juvenile coho salmon rear in the SEE from southwestern Alaska to southern Oregon. The redistribution and use of non-natal streams by juvenile coho salmon has been briefly noted in California streams including the Smith River (Parish and Garwood 2015), Klamath River (YTFP 2009), Redwood Creek (Bob Pagliuco, NOAA Restoration Center, personal communication November 2014), Eel River (Renger and Blessing 2014), and Russian River (SCR 2014). Our results indicate this life history strategy is prominent in multiple tributaries entering Humboldt Bay, California (Figure 8).

The SEE around Humboldt Bay appears to meet criteria for classification as

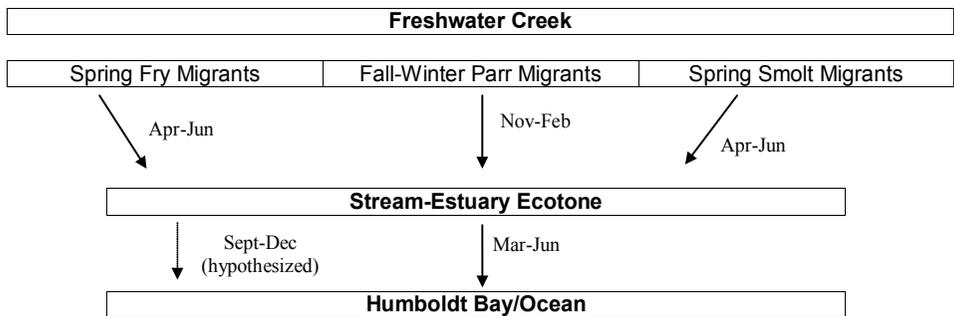


FIGURE 8.—Diagram of juvenile coho salmon life history pattern in Freshwater Creek watershed, Humboldt County, California (modified from Craig 2010).

relatively high quality habitat for juvenile coho salmon as outlined in the introduction. We found that the SEE (1) provided non-natal rearing habitat for prolonged residence by juvenile coho salmon (Tables 5 and 6); (2) supported multiple life stages (i.e. summer YOY and winter 1+) of coho salmon; (3) supported a substantial portion (~40%) of the coho salmon smolt population from throughout the basin (Table 9); (4) allowed juvenile coho salmon to obtain a larger size (Figures 6 and 7), and presumably grow faster than their stream dwelling conspecifics; and (5) provided slow-water habitat that appears to be limited in the upper stream channels during a stressful period due to high winter stream flows.

Young-of-the-year coho salmon moved to the SEE of Freshwater Creek and Elk River during spring and resided there throughout the summer. This pattern is similar to that observed in other Pacific Northwest estuaries (Tschaplinski 1987, Miller and Sadro 2003, Koski 2009). We do not know the underlying cause of this movement, but other researchers

have suggested density dependent factors upstream (Chapman 1962, Hartman et al. 1982), high flushing stream flows (Tschaplinski 1987), or expressions of genotypic or phenotypic variation (Healey 2009, Waples et al. 2009). Regardless of the reasons for their movement into the SEE, once there coho salmon resided almost exclusively in the freshwater portion of the SEE. Furthermore, based on our PIT-tag data, most YOY coho salmon moved very little during the summer, with >90% of recaptured fish being caught at the same location at which they had been marked (Wallace and Allen 2007, 2009, 2012). Similar individual site fidelity has also been documented in studies in other Pacific Northwest estuaries (Tschaplinski 1987, Miller and Sadro 2003).

We found tidal and salinity influences on the SEE were most dynamic during the summer and we often observed coho salmon residing in the surface freshwater layer when the water column is stratified and the more dense brackish water is present along the bottom. Coho salmon residing here were more silvery in appearance and had much less pronounced parr marks than their conspecifics upstream in typical stream habitat, indicating they may occasionally be exposed to salt water. Later in the summer and early fall we captured small numbers of YOY coho salmon in brackish water. These fish were >70 mm FL and may have reached a size adequate to be able to adapt to saltwater. Other investigators have shown that salinity tolerances were a function of size, rather than age, in coho salmon (Conte et al. 1966; Weisbart 1968 as cited by Koski 2009). Other investigators documented sub-yearling coho salmon enter the marine environment, survive, and return as spawning adults, especially when they are ≥ 70 mm FL (Bennett et al. 2015). Most YOY coho salmon rearing in the Humboldt Bay SEE were ≥ 70 mm FL by the end of their first summer, and some may take on the sub-yearling ocean entry life history.

Abundance of YOY coho salmon usually peaked in Freshwater Creek and Elk River sloughs during June and July and then declined to low levels in late summer and early fall (Figure 3), likely as a result of mortality and seasonal movement in the SEE. During the subsequent winter and spring we recaptured fish tagged the previous summer in the vicinity of where they were originally marked or further downstream in tidal tributaries including Wood Creek in the Freshwater Creek watershed and Martin Slough in the Elk River watershed. Although we did detect juvenile coho salmon moving upstream in tributaries entering the SEE, we never detected any substantial upstream movement in the main stem of Freshwater Creek and Elk River sloughs. For example, during the six years of operation we never captured a fish tagged in the SEE at the Howard Heights Trap (approximately 4 km upstream of our SEE sample sites). Therefore, it appears that YOY coho salmon that rear in the sampled portion of the Humboldt Bay SEE during the summer stay in place, have a net downstream movement to over winter in lower mainstem portion or small tributaries of the SEE, perish, or enter the ocean as sub-yearling fish. Other than moving back upstream to over winter, these life history patterns are similar to those reported in Pacific Northwest estuaries (Miller and Sadro 2003, Koski 2009, Jones et al. 2014).

Coho salmon moved from stream habitat downstream to the SEE of Freshwater Creek during the first large stream flows in the fall and winter. Relatively large numbers of 1+ coho salmon moved into small and low gradient non-natal tributaries surrounding Humboldt Bay such as Martin Slough, Wood Creek, and Rocky Gulch (Table 4). These small tributaries were generally unsuitable for juveniles during summer and fall due to high water temperature and salinity, but provided good over winter rearing habitat with refuge from high stream flows. In Freshwater Creek our PIT-tag antennas documented movement of PIT-tagged juvenile coho salmon from throughout the watershed and downstream to

Wood Creek (Table 9). Rebenack et al. (2014) estimated that from 8% to 25% of juvenile coho salmon marked in the upper basin emigrated to the SEE in Freshwater Creek prior to March, and the majority of movement occurred in or about December. There was no tagging program in place upstream of the SEE in Elk River or Jacoby Creek, but we observed the same pattern of new fish arriving in Martin Slough and Rocky Gulch as we observed in Wood Creek, and are confident this illustrates that juvenile coho salmon from Elk River and Jacoby Creek have similar life history patterns to fish from Freshwater Creek.

One of the traits attributed to nomadic coho salmon is their propensity to rear in non-natal streams. Little to no coho salmon spawning takes place in Wood Creek, Martin Slough, or Rocky Gulch, yet we captured juveniles rearing in these areas during the winter and spring. Based on our PIT-tag detections and recoveries, these over wintering coho salmon tend to move around the SEE more than YOY individuals in the summer. For example, we originally tagged juvenile coho salmon in upper Elk River Slough and at specific sites in Martin Slough, and then recaptured them throughout the entire Martin Slough sampling area. We also detected tagged fish moving throughout the Freshwater-Ryan Creek SEE (Table 9). Furthermore, we documented occasional movement between adjacent watersheds by recapturing two 1+ coho salmon in Rocky Gulch one spring that were originally tagged in Jacoby Creek the preceding December. These fish either entered Humboldt Bay to move between watersheds or had been able to traverse over pasturelands during high winter flows. We have even recaptured coho smolts originally tagged in Freshwater Creek in the lower kilometer of Elk River Slough, likely an example of coho salmon moving into tidal slough habitat to forage while rearing in Humboldt Bay on their way to the ocean. Increased connectivity between tributaries and other types of seasonal habitats have been shown to improve winter growth and survival of juvenile coho salmon (Ebersole et al. 2006). It is almost certain that the ability of juveniles to move throughout the SEE of Humboldt Bay has been greatly reduced by levee construction and tide gate installations, both of which have resulted in loss of watershed connectivity and rearing habitat. In some Oregon estuaries it is thought that loss of habitat and connectivity has resulted in the loss of life history diversity (Bottom et al. 2005).

Juvenile coho salmon captured in the SEE of Freshwater Creek were larger than their upstream cohorts at every life stage. Ricker and Anderson (2011) noted that juveniles were larger at their sampling sites in the SEE than at their traps farther upstream during both fall and spring sampling. Other investigators reported juvenile coho salmon being larger in the SEE compared to those in streams (Tschaplinski 1987, Miller and Sadro 2003, Craig 2010). Also, larger juvenile coho salmon had higher over winter survival than smaller fish (Tschaplinski 1982, Heifetz et al. 1989, Ebersole et al. 2006). The larger size of fish in the SEE is thought to be due to increased food, warmer water temperatures, and lower bioenergetic demands due to low water velocity in these low-gradient ecotones compared to stream habitats. Rebenack et al. (2014) reported that in Freshwater Creek, juvenile coho salmon from the mid-basin were more likely to move to the SEE than were fish from the upper basin. Since fish in the mid-basin were on average larger than those in the upper basin (Figure 7), this movement pattern might have contributed to the larger size of juveniles found in the SEE.

We also noted the average size of YOY coho salmon in the SEE was smaller in years of high YOY coho CPUE (Wallace and Allen 2015), indicating that high density may adversely affect growth in the SEE. This result suggests that restoring historic rearing habitat

in the SEE could increase the size of YOY coho salmon rearing in the SEE by lowering density and thereby increasing their overwinter survival. Larger sized salmonid smolts have been shown to have a higher marine survival rate than smaller smolts (Pearcy 1997). Therefore, juvenile coho salmon that have reared in the SEE may survive in the ocean at a higher rate than their stream dwelling cohorts.

The SEE produced a substantial portion of the coho salmon smolts emigrating from Freshwater Creek watershed in 2007 and 2008. Mark-recapture studies carried out by CDFW personnel in the Freshwater Creek SEE during those years indicated the low-gradient 4 km area between the HFAC weir and the Howards Heights trap produced ~40% of the coho salmon spring smolts (Wallace and Allen 2009, Ricker and Anderson 2011). In some other years the majority of smolts originated in the SEE. Additionally, estimates of spring smolt abundance increased at each subsequent downstream counting station. Although Ricker and Anderson (2011) expected this to be the case, the magnitude of increase was not proportional to the linear stream length added by each trap; as a result, smolt estimates increased by up to eight-fold when the SEE was included. Ricker and Anderson (2011) hypothesized that winter was the limiting period for coho smolt production in the stream portion of Freshwater Creek and the SEE was populated after stream carrying capacity is reached. We observed similar life history patterns in the other Humboldt Bay tributaries such as Elk River-Martin Slough and Jacoby Creek-Rocky Gulch. We do not have empirical data demonstrating that the same portions of the SEEs were used by coho salmon smolts. However, based on the relatively large catches of coho salmon in Rocky Gulch—and especially Martin Slough—we suspect substantial portions of smolt production occurs in the SEE of these streams as well.

In Freshwater Creek we detected a positive relationship between adult escapement and subsequent CPUE of YOY coho salmon in the upper slough (Figure 4). The linear relationship with the Y-intercept near zero suggests a density-independent movement rate and we would expect more juvenile coho salmon in the SEE subsequent to years of high adult escapement. The widespread utilization of the SEE by juveniles leads to a number of life history and management considerations. First, the SEE will likely be sparsely populated in the summer by YOY coho salmon following years of low adult escapement, similar to what occurred in the Freshwater Creek SEE in 2008 and 2010 (Table 2). When assessing the success of habitat restoration projects in the SEE after low escapement years, care must be taken to not misinterpret low juvenile coho salmon abundance at the restored sites as indicating project failure when, in reality, it may be due to a lack of seeding. Second, for coho salmon populations that are recovering, it is necessary to take full advantage of high abundance of spawning adults and subsequent offspring and a healthy, restored SEE is needed to provide adequate rearing areas. Third, large numbers of juveniles in the SEE will bias coho salmon smolt estimates low since most trapping sites used to estimate smolt abundance are located upstream of fish rearing in the SEE. Fourth, because juvenile coho salmon abundance in the SEE appears to be dependent on the magnitude of adult spawner escapement, fish abundance may not be the best metric to track trends in estuary recovery. For example, increasing SEE habitat availability or quality with habitat restoration projects could occur during a region-wide downward trend in the sizes of adult runs and result in fewer juvenile fish moving to the SEE independent of conditions occurring there. Assessing the success of these projects and the overall health of the estuary may be better served by using population-independent metrics based on changes in the SEE, such as the amount and types of available salmonid habitat, and the spatial distribution of juvenile coho salmon

relative to the availability of habitat.

Due to the extensive use of the SEE by juvenile coho salmon and the perceived benefits resulting from this behavior, numerous habitat restoration projects have been planned, initiated, and completed in the SEE around Humboldt Bay. Results from three completed sites (Wood Creek, Rocky Gulch, and Salmon Creek [the third largest tributary to Humboldt Bay]), indicated that juvenile coho salmon immediately moved into newly accessible streams and man-made off-channel ponds. Fish access to Rocky Gulch had been blocked by tide gates for decades. A new fish-friendly tide gate was installed in December 2004 (Mierau 2005), and by 2007 juvenile coho salmon were found rearing there in winter and spring (Wallace and Allen 2009). Similarly, juveniles moved into newly constructed off-channel ponds in Wood and Salmon creeks during their first opportunity with increased stream flows in late fall (Wallace 2010, Wallace and Allen 2012). The Wood Creek pond has been used by coho salmon from throughout the Freshwater and Ryan Creek basin every winter-spring season since it was built (Wallace 2010, Wallace and Allen 2015). During 2011–12, the first winter-spring season after the Salmon Creek off channel ponds were constructed, CDFW personnel captured more juvenile coho salmon than in the six previous years combined (Wallace and Allen 2015).

These results demonstrate that habitat restoration projects designed to create overwinter habitat and reconnect adjacent stream networks can immediately increase rearing habitat that likely benefits coho salmon populations in portions of the Humboldt Bay SEE, and suggest these measures could provide similar benefits to coho salmon throughout their range in California. By documenting life history strategies of coho salmon and identifying factors that limit their production we can design restoration projects that effectively improve habitat conditions and non-natal rearing potential for juvenile coho salmon.

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Habitat selection and survival of pronghorn fawns at the Carrizo Plain National Monument, California

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On the Carrizo Plain National Monument (CPNM), California, little is known about survival rates and habitat characteristics of pronghorn fawns (*Antilocapra americana*). A marked decline in pronghorn numbers on the CPNM (from approximately 200 to <30 individuals from 1989 to 2011) prompted a study of fawn habitat use and fawn survival from 2009 to 2011. Only 45 fawns were born during this period. We attached GPS collars to 44% of these fawns (<5 days-of-age). We then used the locations of collared fawns to develop two separate binary logistic regression models to explore the best combination of micro- and macrohabitat-scale environmental variables for predicting (1) fawn habitat selection and (2) fawn survival. Model results for habitat selection showed that fawn locations were associated with increased concealment at close distances (5 m and 50 m) and decreased concealment at far distances (100 m). Fawn locations were on lower sloped terrain and closer to available drinking water and saltbush (*Atriplex* spp.). Model results for fawn survival showed that increased survival time was associated with higher sloped terrain, proximity to available drinking water and saltbush, and increased distance from high-use roads. Collectively, these results demonstrate that fawn habitat selection is scale-dependent and likely influenced by the combined spatio-temporal needs of both females and their young. The results of this study can be used to inform critical management actions on the CPNM.

Key words: *Antilocapra americana*, California, Carrizo Plain, fawn, habitat, offspring, pronghorn, recruitment, selection, survival

Pronghorn (*Antilocapra americana*) in California's San Joaquin Valley were once abundant, representing one of the highest densities in the country prior to the 1800s (Newberry

1855, cited in Yoakum 2004b; Pyshora 1977). By the 1940s however, overhunting, disease, competition from livestock, and conversion of native grasslands to croplands and non-native plant assemblages had triggered a demographic collapse and pronghorn became extirpated from the region (CDFG 1982, Koch and Yoakum 2002). As part of an effort to reintroduce the species to portions of its historic range, the California Department of Fish and Game (now Wildlife; CDFW) translocated over 200 individuals in 1987, 1988, and 1990 from northeastern California to areas within and surrounding what is now the Carrizo Plain National Monument (CPNM). Initially, the translocated population increased but, following a period of prolonged drought, numbers began to fluctuate and eventually declined (Koch and Yoakum 2002, Sommer 2012). By 2012, it was estimated that fewer than 30 individuals occupied the CPNM. Small, isolated populations such as this are of particular concern to resource managers because of increased vulnerability to localized extinction.

Extinction risk is amplified for low-density populations if annual rates of recruitment are not sufficient to overcome the compounding effects associated with demographic or environmental stochasticity (Courchamp et al. 2008). For pronghorn, annual reproductive output (the number of offspring produced per adult female per year) is typically consistent, but survival of juveniles is far lower and more variable than survival of adults (Vriend and Barrett 1978, Gaillard et al. 2000, Eberhardt 2002), causing high annual variation in recruitment (Kohlman 2004). For pronghorn fawns <45 days-of-age, predation is commonly cited as a primary mortality factor (Byers 1997b, O'Gara and Shaw 2004). However, the effect of predation on recruitment has been shown to covary with habitat quality, whereby predation of fawns is high when environmental conditions are poor (Kohlman 2004). Marginal or sub-marginal habitats tend to produce costs to fitness, such as low offspring survival, which cause population size to become unstable or to decline (Vriend and Barrett 1978). On the CPNM, prior research indicated that habitat conditions for pronghorn are moderate to poor due, in particular, to low shrub cover (Longshore and Lowrey 2008).

Pronghorn fawns exhibit hiding behavior to avoid detection by predators (Byers 1997b, Yoakum 2004a). It is generally understood that fawns select individual bed-sites within a larger fawning area pre-selected by adult females (Yoakum 2004a). While the success of fawn hiding behavior is dependent upon the availability of vegetative and topographic concealment (Alldredge et al. 1991, Canon and Bryant 1997), adult females require open, relatively flat landscapes (<10% slope) with low vegetation height for long-range visibility and detection of predators (Ockenfels and Wennerlund 1994), as well as high-quality forage conditions during lactation (Yoakum 2004c). Accordingly, contrasting habitat requirements for fawns and females must be met simultaneously and at different spatial scales. At the micro-habitat scale, selection is based on the hiding requirements of fawns. At the macro-habitat scale, selection is dependent on the visibility and dietary requirements of females balanced with the needs of their offspring.

Pronghorn on the CPNM are at risk of extirpation and adequate rates of recruitment are necessary to prevent further decline. A conservation strategy that aims to reverse that downward trend requires site-specific knowledge of the factors influencing fawn survival, information that has been largely unavailable for this population. Here, we use Global Positioning System (GPS) collars to investigate how pronghorn fawns on the CPNM select specific environmental features at variable spatial scales, and how that selection influences fawn survival. Results from this study can be used to inform management actions on the CPNM and surrounding region.

MATERIALS AND METHODS

Study area.—The Carrizo Plain National Monument is located within the coast range in southeastern San Luis Obispo County, California (Goodwin Education Center: 35° 11' 24" N, 119° 51' 48" W). The monument contains one of the largest remnants of the San Joaquin Valley grassland ecosystem (Schiffman 2000), encompassing 102,639 hectares co-managed by CDFW, Bureau of Land Management (BLM) and The Nature Conservancy (TNC). Topography within the monument is primarily a broad plain bordered by two mountain ranges: the Temblor Range along the northeast border and the Caliente Range along the southwest border. Elevation along the valley floor averages 615 m, and the highest elevation is Caliente Peak (1,556 m). Annual precipitation occurs primarily between December and April and can be highly variable among years (\bar{x} = 24.56 cm, SE = 2.31 cm). During this study, annual precipitation was 17.58 cm in 2009, 48.39 cm in 2010 and 23.52 cm in 2011. Runoff from rainfall sustains the ephemeral Soda Lake, a shallow, alkali terminal lake in the center of the valley floor (Penrod et al. 2010). Mean minimum daily temperature ranges between 5° C and 24° C.

Historically, the area was used for dry-land wheat farming. While most farming activities have ceased, some livestock grazing continues. Due to past agricultural practices, much of the grassland habitat on the CPNM is now dominated by non-native annual grasses, notably brome (*Bromus* spp.) and wild oats (*Avena* spp.). Alkali sink vegetation, including spiny saltbush (*Atriplex spinifera*) and iodine bush (*Allenrolfea occidentalis*), is found at the lowest elevations. Juniper-oak, cismontane woodland, and cismontane juniper woodland and scrub are found in the higher elevations. For a more detailed description of vegetation on the CPNM refer to Stout et al. (2013).

Fawn capture and monitoring.—Fawns were captured using methods described by O'Gara et al. (2004) and Gregg et al. (2001) in accordance with safe handling guidelines (Sikes et al. 2011). Pronghorn fawns (≤ 5 days-of-age) were outfitted with GPS collars each year during April and May of 2009–2011. Collars were designed to be lightweight (≤ 120 g), to expand comfortably as fawns developed in size (i.e., the use of Velcro in place of traditional threaded stitching), and to detach at approximately 90 days-of-age (i.e., neck circumference = 30 cm; O'Gara 2004). For fawns whose birth was not observed, birth date was estimated by behavioral criteria, condition of pelage, hoof and dental development, and desiccation of the umbilical cord (see O'Gara et al. 2004).

All pronghorn fawns known to occur on the CPNM (both collared and uncollared) were monitored daily. Individual collared fawns were identified by their unique VHF telemetry signal. The propensity of neonatal siblings to bed together allowed for observation of uncollared fawns when siblings were collared. We further used individual pelage characteristics of the mother (Byers 1997a) and location of the general fawning area as identifying characteristics for uncollared fawns. Fawns that lived >90 days were considered to have been recruited into the population based on abundant evidence that 95% of fawn mortality takes place at <18 days-of-age (Gregg et al. 2001). Results for survival rates were compared to 18 other studies conducted within 10 different states as reported by O'Gara and Shaw (2004). Deceased fawns were recovered as quickly as possible to determine whether death was due to predation and, if so, to identify the species of predator according to the criteria of O'Gara and Shaw (2004). Carcasses found to be in good condition (i.e., fresh and intact) were transported to the CDFW Wildlife Investigations Laboratory for necropsy.

Statistical analyses.—Location information from collared individuals was used to develop a fawn habitat selection model and a fawn survival model. We used a combination of biotic and abiotic environmental parameters within an Akaike Information Criterion (AIC) modified for small sample size (AIC_c) and logistic regression framework to predict habitat selection and survival (Hosmer and Lemeshow 2000, Burnham and Anderson 2002). We selected model parameters based on a comprehensive review by Yoakum (2004a) that listed critical criteria for fawning areas including vegetation height and type, physiography (Einarsen 1948), availability of nutritious forage (Ellis 1970), vegetative cover (Autenrieth 1984), lack of fences (O’Gara et al. 1986), proximity to available water (Ockenfels et al. 1992), and minimal anthropogenic disturbance (U.S. Fish and Wildlife Service 1994). The log-likelihood estimates from each of the alternative logistic regression models were used to rank the set of candidate models. We eliminated models with ΔAIC_c of >2 , and used Akaike weights (w_i) and evidence ratios to assess the relative strength of evidence for each remaining model (Burnham and Anderson 2002). Statistical analyses were performed using SigmaPlot 12.3 and Geographical Information System (GIS) analyses were conducted using ArcMap 10.1 (ESRI, Inc. Redlands, California).

For the fawn habitat selection model, we compared the relationship of collared fawn locations and random locations to a suite of micro- and macrohabitat explanatory variables. We considered microhabitat characteristics to be located within a spatial scale small enough to elicit a response by individual fawns. Microhabitat was defined exclusively as the area within a 100-m radius of a fawn and included measurements of vegetation height and composition (i.e., forb, grass, shrub, bare ground), as well as adult and fawn visibility, at 70 fawn locations and 61 random locations. Measurements were made at each location and along four equidistant transects at distances of 5 m, 10 m, 20 m, 30 m, 40 m, 50 m, and 100 m. Transects were oriented by randomly selecting an aspect for one transect and then distributing the remaining three transects by a separation of 90 degrees (modified from Canon and Bryant 1997). Visibility was defined as the proportion of a 1-m measuring stick (located at the center of each plot) visible from each of the measured locations at the height of a fawn (0.5 m) and an adult (1 m).

Macrohabitat characteristics were defined as landscape-scale features that could potentially influence female habitat selection but not necessarily fawn habitat selection. Macrohabitat predictors were measured with a GIS at 30-meter resolution and included percent slope of terrain (vertical distance/horizontal distance) and linear distances to water, fences, saltbush (*Atriplex* spp.), high-use primary roads (Soda Lake Rd., Panorama Rd., Selby Rd., and Elkhorn Rd.), and all roads (i.e., high-use primary roads and low-use roads combined). Open drinking water for pronghorn on the CPNM is found primarily at man-made water sources (e.g., water troughs). We located all known water sources using a data layer provided by CDFW and then inventoried each of them for the availability of water (i.e., active or inactive). We did not consider Soda Lake or ephemeral drainages as sources of water for pronghorn. Human activity on the CPNM occurs primarily along roads, which we used as the best available measure of anthropogenic disturbance. Data layers for saltbush, roads and fences were provided by the BLM.

For the fawn survival model we compared the relationship between locations of collared fawns ≤ 17 and > 17 days-of-age and a suite of macrohabitat features including linear distances to water, fences, saltbush, high-use primary roads, and all roads combined (i.e., high-use primary roads and low-use roads), as well as the slope of terrain. We did not include microhabitat features (i.e., vegetation height and type, or visibility) in the fawn

survival model and, instead, used a subset of covariates to increase parsimony and prevent overfitting the model. We predicted fawns >17 days-of-age would have a higher expectancy for survival than fawns ≤17 days of age, and that habitat selection by fawns in these two groups would vary, based on information from Gregg et al. (2001) that the majority (95%) of fawn mortalities take place among fawns ≤17 days-of-age, as well as corresponding evidence from our survival data (see Results).

RESULTS

Fawn productivity and survival.—In total, 45 pronghorn fawns were known to have been born on the CPNM during three seasons from 2009 to 2011. The number of fawns recruited out of the total born each season was 3 of 22 (14%) in 2009, 5 of 12 (42%) in 2010, and 4 of 11 (36%) in 2011. Collars were attached to 20 of 45 fawns (44%; 7 males and 13 females) born during the study (13 fawns in 2009, 4 fawns in 2010, 3 fawns in 2011). Mean age at capture was 2.07 days ($SE = 0.33$). Survival between male and female collared fawns did not differ ($Z = -0.32, P = 0.75$). The remaining 25 uncollared fawns were monitored through systematic field observation (see description in Methods). Survivorship of collared fawns (20.0%) and uncollared fawns (32%) did not differ ($Z = -0.25, P = 0.81$). Survivorship of all fawns (both collared and uncollared; 26.7%) did not differ from that found for other populations (29.4%, $N = 995$) as reported by O'Gara and Shaw (2004) ($Z = 0.22, P = 0.82$). Annual fawn productivity and survival were variable across years (mean productivity = 15.0 fawns, $SE = 3.5$ and mean survival = 30.7%, $SE = 8.5$). Of 13 recovered collars, 10 functioned properly while deployed (i.e., they consistently recorded locations); of these 10 functioning collars, 9 were from deceased fawns. The mean number of days lived for the 9 collared fawns that died was 14.4 days ($SE = 2.9$) and all but one of these fawns died at ≤18 days of age.

Causes of mortality for the 20 collared fawns and 1 uncollared fawn included predation (28.6%; $n = 6$), health-related issues (9.5%; $n = 2$) and undetermined causes (61.9%; $n = 13$). For the 6 predator-related mortalities, evidence of coyote ($n = 6$) or golden eagle ($n = 1$) was detected. Results from laboratory necropsies performed for the two health-related mortalities indicated that death was caused by an infected umbilical cord for one individual, and a lacerated liver (possibly from being stepped on by its mother) for the other.

Fawn habitat selection model.—To model fawn habitat selection, eight candidate models were developed using 70 locations from collared individuals and 61 random locations (Table 1). The habitat parameters used in the global model are indicated at the bottom of Table 1. Two candidate models, Model 1 ($w_i = 0.56$) and Model 2 ($w_i = 0.36$), showed substantial support as the best approximating models ($\Delta AIC_c < 2$). Parameter estimates (β), standard errors (SE) of the estimates, odds ratios, and 95% confidence intervals (CI) for the odds ratios of the variables in the two models are shown in Table 2. Model 1 showed that fawn locations were negatively associated with increased vegetation height at 5 m, fawn visibility at 5 m and 50 m, slope of terrain, and distance to saltbush and water, yet positively associated with increased forb composition and fawn visibility at 100 m. Model 2 consisted of the same parameters and respective negative and positive associations as Model 1 for all variables excluding forb composition and fawn visibility at 50 m. A generalized map of fawn habitat selection within the CPNM (Figure 1) was created using Model 1 and Model 2 variables that could be measured with standard GIS layers (i.e., slope of terrain and distance to water and saltbush).

TABLE 1.—Comparison and relative ranking of candidate models for pronghorn fawn habitat selection on the Carrizo Plain National Monument, California from 2009 to 2011. Akaike's Information Criterion corrected for small sample sizes (AIC_c) was used for model selection. Included for each candidate model are values for log-likelihood, number of parameters (k), AIC_c values, ΔAIC_c values, and Akaike weights (w_i). Relative ranking of models was determined using ΔAIC_c .

Model	-2LogL	k	AIC_c	ΔAIC_c	w_i
1 dsb+dw+ps+fvis5+fvis50+fvis100+f0+ht5	98.33	8	115.51	0	0.5593
2 dsb+dw+ps+fvis5+fvis100+ht5	103.74	6	116.41	0.91	0.3552
3 dsb+dw+fvis5+fvis100+f0	109.57	5	120.05	4.54	0.0578
4 Global model ^a	83.51	17	122.93	7.42	0.0137
5 dsb+dw+fvis100	116.76	3	122.95	7.44	0.0135
6 dsb+dw+f0	123.44	3	129.63	14.12	0.0005
7 dsb+dw	128.57	2	132.66	17.16	0.0001
8 dw+ps+ht5+fvis100+f0	125.73	5	136.21	20.70	0.00002

^aGlobal model included distances to saltbush (dsb), water (dw), main roads (dmr), and fences (df); percent slope of terrain (ps); fawn visibility at fawn location (fvis0) and at distances of 5 m (fvis5), 10 m (fvis10), 50 m (fvis50) and 100 m (fvis100); forb cover at fawn location (f0), grass cover at fawn location (g0), and cover at distances of 5 m for forbs (f5), grasses (g5) and shrubs (s5); vegetation height at fawn location (ht0) and at 5 m distance (ht5).

TABLE 2.—Parameter estimates, standard errors of the estimates, odds ratios, and 95% confidence intervals for the odds ratios of the variables in the two best approximating models for pronghorn fawn habitat selection (β , SE, Odds ratio, 95% CI, respectively) on the Carrizo Plain National Monument, California, 2009–2011.

Effect	β	SE	Odds ratio	95% CI
Model 1:				
dsb	-0.002	0.001	0.998	0.996-0.999
dw	-0.001	<0.001	0.999	0.998-1.000
ps	-0.424	0.256	0.654	0.396-1.080
fvis5	-0.040	0.020	0.961	0.924-1.000
fvis50	-0.027	0.026	0.973	0.924-1.025
fvis 100	0.053	0.027	1.054	1.000-1.111
f0	0.020	0.010	1.021	1.001-1.040
ht5	-0.045	0.023	0.956	0.915-0.999
Model 2:				
dsb	-0.002	0.001	0.997	0.997-0.999
dw	-0.001	<0.001	0.998	0.998-0.999
ps	-0.225	0.191	0.550	0.550-1.161
fvis5	-0.046	0.020	0.919	0.919-0.993
fvis 100	0.031	0.012	1.011	1.011-1.054
ht5	-0.041	0.021	0.921	0.921-1.001

Variables include distance to saltbush (dsb), distance to water (dw), percent slope of terrain (ps), fawn visibility at distances of 5 m (fvis5), 50 m (fvis50) and 100 m (fvis100), forb cover at fawn location (f0), and vegetation height at 5 m (ht5).

Fawn survival model.—To model fawn survival, six candidate models were developed (Table 3) using 1,417 locations from 10 GPS-collared individuals. Two candidate models, Model 1 ($w_i = 0.55$) and Model 2 (global model; $w_i = 0.32$), showed support as the best approximating models ($\Delta AIC_c < 2$). Parameter estimates (β), standard errors (SE) of the estimates, odds ratios, and 95% confidence intervals (CI) for the odds ratios of the variables in the two models are shown in Table 4. Model 1 showed that locations of individuals that lived >17 days were positively associated with increased slope and distance to main roads, but were negatively associated with increased distance to water, fences, and all roads. Model 2, in addition to the same parameters and respective positive or negative associations as

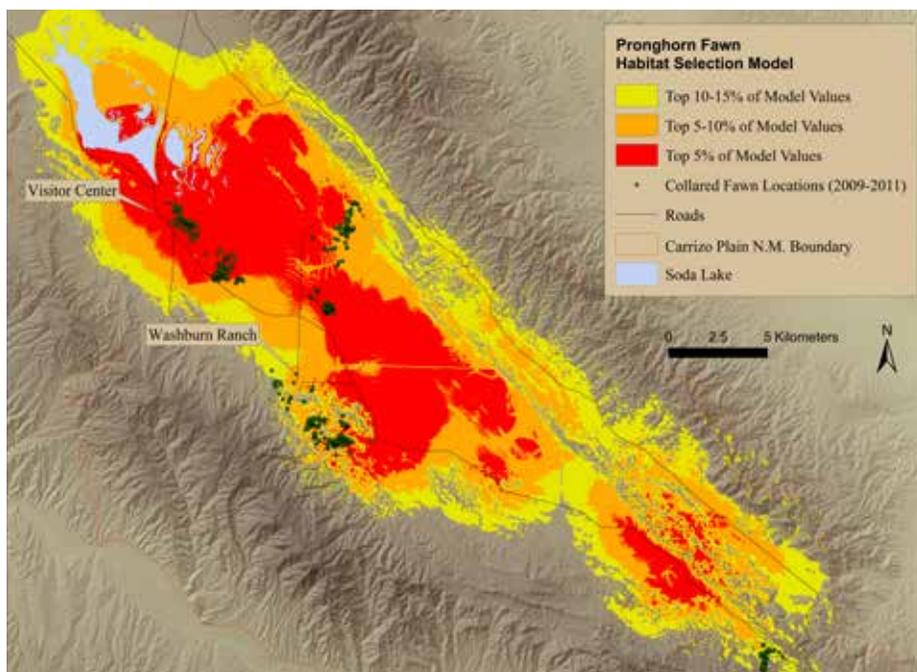


FIGURE 1.—Pronghorn fawn habitat selection model for the Carrizo Plain National Monument, California, 2009–2011. Included are variables from the best approximating binary logistic regression model for predicting fawn habitat and that could be mapped using a Geographic Information System (i.e., linear distance to water and saltbush communities and percent slope of terrain). The top 15% of model values within the boundary of the monument are indicated.

Model 1, showed a negative association with distance to saltbush. A generalized map of fawn survival within the CPNM (Figure 2) was created using Model 1 and Model 2 (the global model) variables that could be measured with standard GIS layers (e.g., slope of terrain and distance to water, saltbush, and all roads).

DISCUSSION

Fawn productivity and survival.—Pronghorn fawn survivorship on the CPNM, overall, did not differ from that reported for other populations across the geographic distribution of pronghorn based on the results of O’Gara and Shaw (2004). However, variability in offspring productivity and survivorship was observed during 2009–2011 and only three to five fawns survived during any one season. Pronghorn commonly exhibit high variability in annual recruitment (Vriend and Barrett 1978, Kohlmann 2004), and years of low offspring survival generally do not impact long-term demographics of large populations. For small or sparse populations, however, low annual recruitment, particularly during consecutive years, increases extinction risk (Courchamp et al. 2008). Increased rates of fawn survival are likely required to sustain a viable population of pronghorn at this site and management actions that increase recruitment could reduce the risk of localized extinction.

Of the four primary mortality factors (predation, starvation, exposure, disease) described by O’Gara and Shaw (2004), we detected evidence only of predation. Although predation is not generally considered to drive pronghorn population dynamics, the importance

TABLE 3.—Comparison and relative ranking of candidate models for pronghorn fawn survival, on the Carrizo Plain National Monument, California from 2009 to 2011. Akaike's Information Criterion corrected for small sample sizes (AICc) was used for model selection. Included for each candidate model are values for log-likelihood, number of parameters (k), AICc values, Δ AICc values, and Akaike weights (w_i). Relative ranking of models was determined using Δ AICc.

Model	-2LogL	k	AIC _c	Δ AIC _c	w_i
1 dmr+dar+df+dw+ps	478.20	5	488.25	0	0.5540
2 Global model ^a	477.30	6	489.36	1.12	0.3172
3 dmr +dar+df+dw	483.16	4	491.19	2.94	0.1275
4 dmr+ dar+df	494.34	3	500.35	12.11	0.0013
5 dmr + dar	508.19	2	512.19	23.95	< 0.0001
6 dmr +dw+ps	527.97	3	533.98	45.74	< 0.0001

^aGlobal model included percent slope of terrain (ps) and distances to saltbush (dsb), water (dw), main roads (dmr), all roads (dar) and fences (df).

TABLE 4.—Parameter estimates, standard errors of the estimates, odds ratios, and 95% confidence intervals for the odds ratios of the variables in the two best approximating models of pronghorn fawn survival, (β , SE, Odds ratio, 95% CI, respectively) on the Carrizo Plain National Monument, California, 2009–2011.

Effect	β	SE	Odds ratio	95% CI
Model 1:				
dmr	0.001	<0.001	1.001	1.000-1.001
dar	-0.003	0.001	0.997	0.996-0.998
df	-0.002	<0.001	0.998	0.997-0.999
dw	-0.0004	<0.001	1.000	0.999-1.000
ps	0.0403	0.019	1.041	1.004 -1.080
Model 2:				
dmr	0.001	<0.001	1.001	1.000-1.001
dar	-0.003	0.001	0.997	0.996-0.998
df	-0.002	0.001	0.998	0.997-0.999
dw	-0.0004	<0.001	1.000	0.999-1.000
ps	0.051	0.022	1.052	1.009-1.097
dsb	-0.002	<0.001	1.000	0.999-1.000

Variables include percent slope of terrain (ps) and distances to water (dw), main roads (dmr), all roads (dar), fences (df), and saltbush (dsb).

of predation increases for static or declining populations, as well as for populations occupying marginal habitats or areas where the number of predators is high in relation to the number of pronghorn (Lee et al. 1998, O'Gara and Shaw 2004). In addition, the abundance of alternative prey (e.g., lagomorphs, rodents) can alleviate predation on pronghorn fawns (Beale 1986). Mortalities related to health (infected umbilical cord and lacerated liver) appeared to be separate and unrelated events. Due to the high percentage of unknown mortality (65%), meaningful comparisons between predation on the CPNM (29%) and predation on other populations (53%; O'Gara and Shaw 2004) were not possible. The high number of undetermined causes of death was due primarily to technical malfunctions of VHF telemetry signals, which were often weak or non-existent. Poor signal quality delayed the time in which deceased fawns could be located. Often fawns were consumed entirely before being found, or only small tooth and bone fragments remained. Scavengers (e.g., vultures, corvids, coyotes) are abundant on the CPNM, and differentiating between scavenging and predation events becomes increasingly difficult with delayed recovery times (e.g., >24 hours).

Fawn habitat selection model.—Results from the fawn habitat selection model

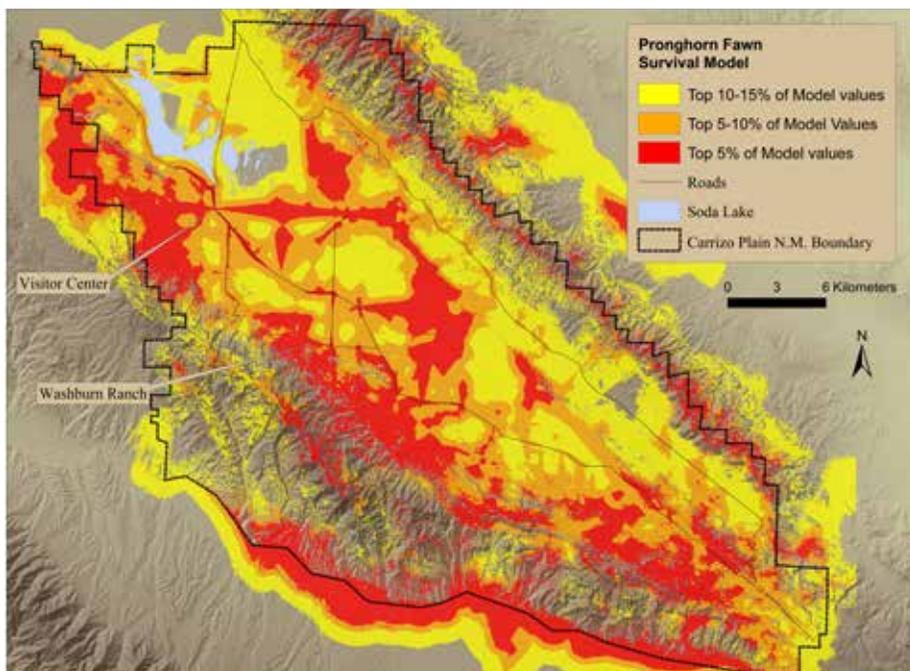


FIGURE 2.—Pronghorn fawn survival model for the Carrizo Plain National Monument, California, 2009–2011. Model parameters include slope of terrain and distances to water sources, saltbush (*Atriplex* spp.), fences, small dirt roads, and high use main roads (Soda Lake Rd., Elkhorn Rd., Panorama Rd. and Selby Rd.). The top 15% of model values within the boundary of the monument are indicated.

indicate that females and their fawns both selected for a combination of environmental parameters at both macro- and microhabitat scales. At the microhabitat scale, the negative associations for variables measured close to fawn locations and the positive associations for similar variables measured 100 m from fawns reveal that the relationship between these variables and choice of bed-sites is scale-dependent. Fawn locations had lower visibility at close distances compared to random locations. However, fawn locations within low visibility vegetation patches were, on average, located on a larger scale in open areas with greater visibility compared to surrounding habitat. Fawns appeared to choose sites in isolated patches of cover within larger areas containing less concealment from predators, rather than in continuous habitat with dense cover. Movement between those isolated patches is likely to increase the risk of detection by predators. However, pronghorn females may choose areas with higher visibility surrounding hidden fawns as a means of enhancing their own ability to detect predators.

Females with fawns exhibit increased vigilance and aggressive behavior toward predators (Byers 1997b), and fawn survival can be higher in habitat containing open areas with shorter vegetation height than in other areas (Bodie 1978, Autenrieth 1992). Additionally, our results show that fawn locations had higher forb cover than random locations. Forbs are a critically important source of nutrients for lactating females (Yoakum 2004c) and our results indicate that fawns are selecting bed-sites within areas pre-selected by females for forage quality.

At the macrohabitat scale, fawn locations, in comparison to random locations, were in areas with lower slope and closer to water sources and large saltbush shrub communities.

Flat terrain increases the ability of adult pronghorn to detect and avoid predators (Yoakum 2004a). The availability of surface drinking water for adult pronghorn can be important in arid environments such as the CPNM, particularly for lactating females (Yoakum 2004a). Ockenfels et al. (1992) suggested that water on arid grasslands is an important, if not critical, factor in determining the location of fawn bed-sites (Yoakum 2004a). We did not anticipate that proximity to saltbush would be an important habitat variable for fawns because saltbush communities on the CPNM tend to be clustered in dense stands along the valley floor with heights that are indicative of low quality habitat (>50 cm; Longshore and Lowrey 2008). Although moderate dispersion of shrubs in grassland habitats can increase fawn survival (Autenrieth 1982), sites with shrubs >75 cm in height can have higher predator-related mortality of fawns (Bodie 1978).

Fawn survival model.—Results from the fawn survival model indicate that locations of individuals who lived beyond 17 days, in comparison to those who lived ≤ 17 days, were closer to water sources, farther from high-use main roads, and on steeper terrain. Postnatal fawns acquire water strictly from nursing, and females inhabiting more mesic areas than the CPNM typically meet most of their water requirements through the consumption of succulent forage items (Yoakum 2004b). For pronghorn occupying arid ranges, however, availability and dispersion of open water sources can directly affect adult health and reproduction, as well as fawn productivity and survival (McKee and Wolf 1963, Beale and Smith 1970, Ockenfels et al. 1992).

The positive association between survival and distance from high-use main roads suggests that anthropogenic disturbance during the fawning season influences survival. Model results also indicated that these survivors were located closer to fences and all roads (small dirt roads as well as main roads). This result is most likely due to the fact that fences and dirt roads are abundant and well dispersed throughout the monument, and not because proximity to either resulted in increased survival times. It was unexpected that survival would be positively influenced by steeper terrain because pronghorn typically select habitat with the lowest slope (Ockenfels et al. 1994). Einarsen (1948) reported, however, that the best physiography for fawning sites was among basins surrounded by low ridges or hills. On the CPNM, areas with high percent slope may offer environmental conditions such as improved forage quality, increased vegetative and topographic concealment, or even the absence of human disturbance, that increase fawn survival and outweigh the risks associated with steep terrain (e.g., decreased range of predator detection).

Collectively, these findings highlight the importance of both micro- and macrohabitat-scale environmental attributes for recruitment in pronghorn. Ecological studies on recruitment, as well as conservation strategies aimed at increasing rates of recruitment, should consider the habitat requirements of females and fawns simultaneously. Methods and results reported herein, when combined with results reported by others, can be used as guidelines for conservation and management of pronghorn within the CPNM.

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A potential range expansion of the coastal fisher (*Pekania pennanti*) population in California

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Fishers (*Pekania pennanti*) are a forest-specialist mesocarnivore and are a species of special concern in California (CDFW 2015a, 2015b). Fisher populations are thought to be limited due to a historical over-harvest for their fur, habitat fragmentation, and the impact of logging on their habitat (Zielinski et al. 2005, Tucker et al. 2012). There are three distinct populations of fishers in California: Sierra, Cascade, and coastal (Zielinski et al. 1995). The Sierra population appears to be peninsular and is restricted to the western slopes of the Sierra Nevada south of Yosemite National Park. Recent research indicates the Sierra population is genetically homogenous due to isolation prior to European settlement, but is stable despite possible range contractions in the last 100 years (Tucker et al. 2012). The Cascade population ranges from Plumas and Tehama Counties in the Cascade Mountains north to the California-Oregon border. The population was considered small and restricted and was augmented by translocations in the last decade (Callas and Figura 2008).

In comparison to the Sierra and Cascade populations, the coastal population is under-studied and the southern extent of its range is not clearly documented (Zielinski et al. 1995). The population is found in the Coast Range, from the northern border of California south to the Mendocino National Forest. There have been no confirmed sightings south of the Mendocino National Forest since 1941. Grinnell et al. (1937) reported anecdotal records as far south as Marin County, which was considered the historical southern limit of the population (Figure 1). It is thought that the coastal population has contracted in the last 100 years and that fishers are absent from the southern portion of their historical distribution (CDFW 2015a).

Zielinski et al. (1995) first called for surveys in the coastal population, with one

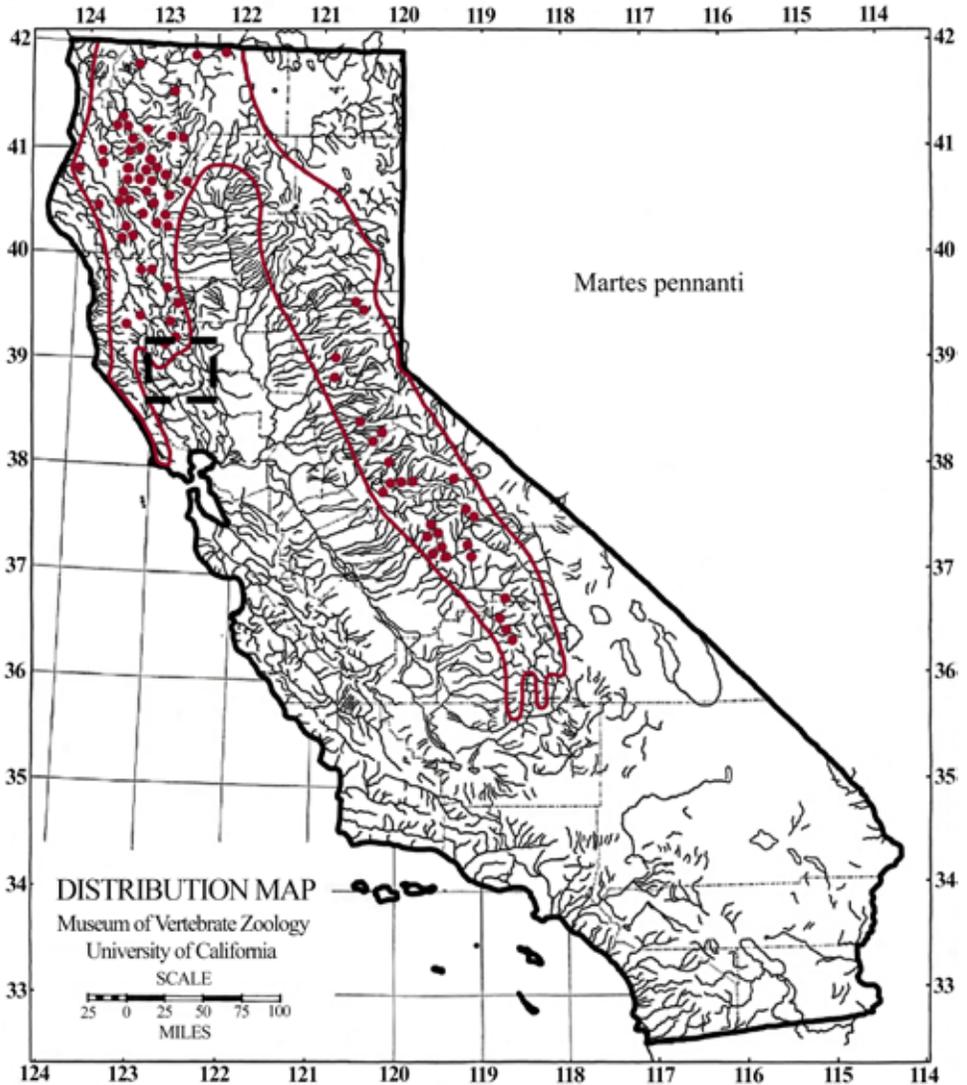


FIGURE 1.—Map of the distribution of fishers in California showing locations from 1919 to 1924 and the historic range of fishers in California as understood at the time (adapted from Grinnell et al. 1937). The inset represents the location of the smaller area detailed in Figure 3.

purpose being to determine the population’s southern boundary. Opportunistic sightings and trapper takes were documented in the Mendocino National Forest from the 1920s through 1940s (Grinnell et al. 1937, Hemphill 1952). Surveys have been completed in the last decade, with fishers detected at half of all track plate stations set for fishers and American martens (*Martes americana*) in 2006 (Slauson and Zielinski 2007). In addition, Evans et al. (2012) reported fishers present at 33% of cameras baited with deer carcasses ($n=66$) in the Mendocino National Forest, confirming what is likely a viable population there. It is unclear, however, if those surveys have clearly defined the southern boundary of the coastal population, or if individuals at the southern end of the range could be going unnoticed. Here we report a recent fisher detection substantially farther south than any other confirmed

detection this century, and its implications for the California coastal range fisher population.

A motion-triggered camera (Bushnell, Overland Park, KS, USA) was deployed on private property to document local wildlife. The camera location ($38^{\circ} 43' 33.06''$ N, $122^{\circ} 41' 51.90''$ W) was in Lake County, and was set in a stand of Douglas fir (*Pseudotsuga menziesii*) facing towards a natural spring that had been enhanced as a permanent pool of water by the landowner. The camera was set to record 10 seconds of video, with a time and date stamp for each triggered event. We compared this confirmed sighting with others from published literature including Slauson and Zielinski (2007) and Grinnell et al. (1937), as well as records from the California Natural Diversity Database (CNDDDB; particularly EO Index #78496).

On 22 April 2013 at 0705, a fisher triggered the camera twice, recording a total of 20 seconds of video as the fisher investigated the pool (Figure 2). This detection is notably farther south than any confirmed fisher sighting in the coastal population. The location is approximately 64 km farther south than any confirmed detection of fishers in the coastal range in the last decade (Slauson and Zielinski 2007), approximately 52 km farther south than any confirmed detections reported by Grinnell et al. (1937), and approximately 47 km farther south than any confirmed detection of fishers in the coastal range in the last century (Figure 3).

Grinnell et al. (1937) included anecdotal reports to suggest that fishers extended as far south as Marin County, but did not have direct evidence and these reports could



FIGURE 2.—A photo taken from the videos recorded of a fisher investigating a woodland pool of water at $38^{\circ} 43' 33.06''$ N, $122^{\circ} 41' 51.90''$ W. This location is in Lake County, California, approximately 1 km north of the Sonoma County border.

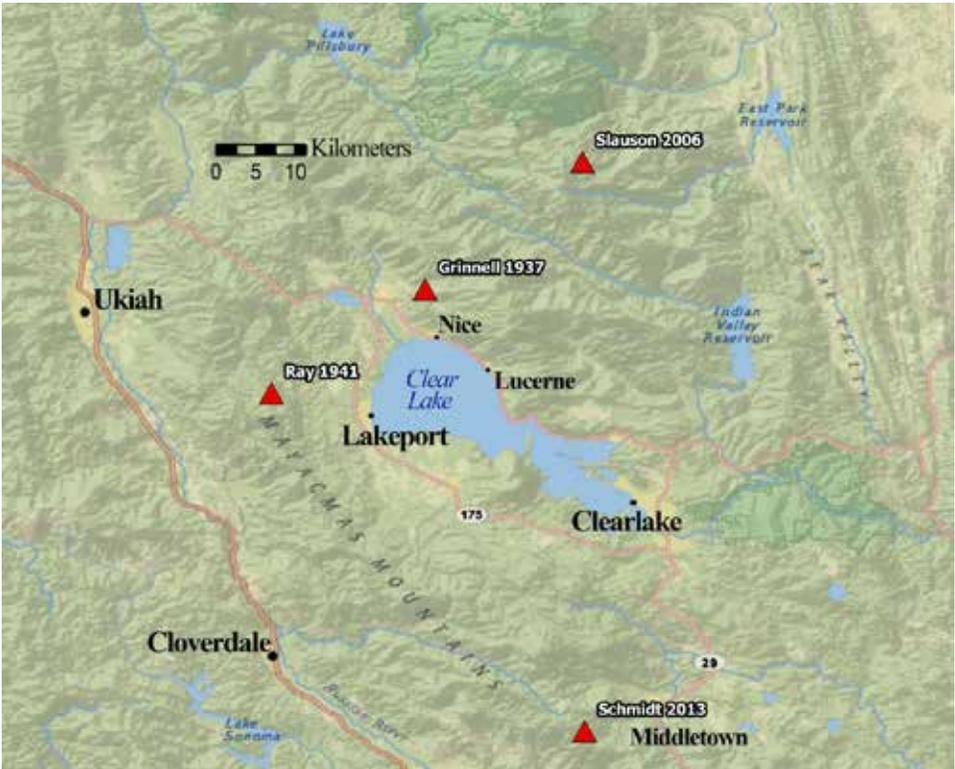


FIGURE 3.—Current and historical locations of fishers (triangles) identified in this paper, with their source and year of occurrence. The location labeled Schmidt 2013 is that described in this paper.

have been inaccurate. For example, Grinnell et al. (1937) also considered the Sierra and Cascade populations to be connected, and this has recently been proven to be incorrect by genetic data that indicate the populations have been separated since before the arrival of Europeans in North America (Tucker et al. 2012). Sightings and trapper takes have been documented in the Mendocino National Forest from the 1920s (Grinnell 1937, Hemphill 1952) and continued through the last decade (Slauson and Zielinski 2007, Evans et al. 2012). Nevertheless, this is the first verifiable documentation of a fisher south of the Mendocino National Forest and Highway 20 since 1941.

The previous detections in the Mendocino National Forest combined with the occurrence reported here indicate that one of two scenarios is likely in the coastal range during the last century: that fishers have been present in the area but have gone undetected, or that fishers are expanding back into the southern extent of their historic range. It seems unlikely that a self-sustaining population has been consistently present at the southern edge of the range and has merely escaped detection. Fishers are, however, difficult to detect (Zielinski et al. 1995), and the lack of survey efforts as far south as Sonoma County may have resulted in fishers escaping detection. Alternatively, the coastal population could be expanding and recolonizing parts of its historical distribution, as fishers are quite capable of recolonizing former parts of their range (Carr et al. 2007). If the coastal population is expanding, it could provide valuable insight into the conservation of the southern Sierra population, which also appears to be peninsular and has been thought to be contracting

in distribution. A systematic survey to determine the southern limit of the coastal fisher population would potentially improve our understanding of its distribution and dynamics, and also inform management of the species statewide. Further, the conservation status of fishers currently is under review (CDFW 2015a).

The use of motion-triggered cameras has increased greatly in the last decade, both by citizen scientists, as well as for studies of animal behavior and ecology (Locke et al. 2012). This observation has been recorded in the California Natural Diversity Database as species occurrence number 733 and EO Index 90288. We encourage the documentation of species by the public, as well as the increased use of the CNDDDB to maintain information on the current distributions of rare species.

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First record of striped mullet (*Mugil cephalus*) in Humboldt Bay, California

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On 11 June 2015 three juvenile striped mullet (*Mugil cephalus*) were collected by personnel from the California Department of Fish and Wildlife in the Salmon Creek estuary, Humboldt Bay, California (40° 40' 37.7" N, 124° 12' 15.0" W). This record represents a northward range extension of nearly 450 kilometers from the previously reported northernmost occurrence of that species in San Francisco Bay, California (Moyle 2002). All three striped mullet were collected from a brackish off-channel pond during routine surveys for juvenile salmonids in the Humboldt Bay National Wildlife Refuge. Two individuals were released at the location of capture and one was retained as a voucher specimen and deposited in the Humboldt State University Fish Collection (HSU Collection number HSU 5290). Field collections were conducted using a 9.1 m × 1.8 m × 6.4-mm mesh beach seine at a depth of 0.75 m at 0915 near a predicted 1.5-m high tide. Habitat at the collection site was mostly open water with mud substrate. The pond was stratified with a surface temperature of 18.8° C, salinity was 25.0 ppt, and dissolved oxygen was 5.15 mg/l; near the bottom those readings were 21.2° C, 30.6 ppt, and 1.90 mg/l, respectively.

Striped mullet have thick, torpedo-shaped bodies, broad flat heads, small terminal mouths, large eyes, deeply forked caudal fin, two dorsal fins that are widely separated, and translucent adipose eyelids that nearly cover the eye (Moyle 2002). All three striped mullet captured were very similar in size and appearance (Figure 1). Meristic and morphometric characteristics of the voucher specimen (fork length = 69 mm) were consistent with values reported for striped mullet (Miller and Lea 1976, Moyle 2002).

Striped mullet inhabit tropical and subtropical coastal areas around the world. In California they primarily inhabit coastal waters and estuaries in southern California and the lower Colorado River (Miller and Lea 1976, Moyle 2002, McGinnis 2006). Striped mullet



FIGURE 1.—Striped mullet (*Mugil cephalus*) captured by California Department of Fish and Wildlife personnel on 11 June 2015 in an off-channel pond in Salmon Creek Estuary, Humboldt Bay, Humboldt County, California; the scale is in millimeters.

have been reported as far north as San Francisco Bay during El Niño years, but they are rare north of Point Conception (Moyle 2002). They are sometimes among the most abundant fish captured in southern California estuaries (Horn and Allen 1981, Moyle 2002). They were once very abundant in the Salton Sea but now are rare (Moyle 2002, McGinnis 2006) or possibly extirpated (CDFW 2014). They tolerate a wide range of salinities, having been collected in water from 0 to 75 ppt, but cannot tolerate temperatures much below $\sim 15^{\circ}$ C. Striped mullet often ascend rivers and have been found many kilometers upstream of saltwater in rivers such as the Colorado River, Santa Margarita River, and Los Angeles River (Moyle 2002).

Water quality conditions in the Salmon Creek estuary on 11 June 2015 were similar to conditions typically observed in mid- to late summer during 2010–2014 (Wallace and Allen 2015). Also, ocean temperatures off the coast of California were approximately 3° C warmer than historic averages in the Fall of 2014, which ranked among the warmest conditions observed during the last 30 years (data from NOAA Northwest Fisheries Science Center; <http://www.nwafc.noaa.gov>). Numerous warm-water fishes and invertebrate species that are usually found in more southern waters have been detected off the coast of California during the past 6 to 12 months (Rogers 2014). It is plausible that the striped mullet moved northward from southern or central California and found their way into Humboldt Bay and the Salmon Creek Estuary during these warm water conditions.

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BOOK REVIEW

Desert bighorn sheep: wilderness icon

Mark C. Jorgensen with photographs by Jeff Young. 2014. Sunbelt Publications, San Diego, California, USA. 143 pages. Soft cover. \$29.95. ISBN 978-1-941384-00-8

Mark Jorgensen, who had a stellar career with the California Department of Parks and Recreation and who has spent his professional life as an advocate for desert bighorn sheep has teamed with Jeff Young—a photographer with skills second to none—to produce a book that is both scientifically sound and provides the reader with breathtaking images. Those images clearly illustrate many of the life-history traits of bighorn sheep that Mark so completely describes in the text. This book, albeit not of great length, contains some of the most impressive photographs of desert bighorn sheep, their habitat, and threats to the long-term persistence of those specialized ungulates that I have encountered during my career. Importantly, each image is accompanied by a caption that clearly describes the photograph and that very nicely complements the accompanying text.

The book begins with a brief foreword by Esther Rubin, with whom Mark—and many of us involved in the conservation of desert bighorn sheep—worked for many years; Dr. Rubin provides numerous details regarding Mark’s qualifications to write this book. In an extensive conveyance of acknowledgments, Mark then goes on to thank those individuals and organizations with whom he has worked for decades. Finally, he introduces Jeff Young, with whom he has shared his knowledge of, and passion for, desert bighorn sheep and whose images clearly illustrate the many topics presented in the text. This book is not only a compilation of biology and its implications for conservation, but a visual portrayal of the life history of desert bighorn sheep.

The first chapter, “Origins and Distribution in the United States and Mexico” not only contains information on the origins of wild sheep in North America, but provides descriptions of the relationships between that species and native peoples. Mark touches on the ways that bighorn sheep were hunted and utilized by the earliest Americans, and provides a fine summary of the widespread occurrence of bighorn sheep as subjects of early rock art, primarily in the form of petroglyphs.

The importance of habitat, and the dependency of desert bighorn sheep on it and the ways it is used, are the subjects of Chapter 2. The importance of “escape terrain” is emphasized, particularly as it relates to security. Mark also provides a good summary of the importance and availability of high-quality forage, descriptions of their food habits, a summary description of the ruminant digestive system, a brief summary of the physiological adaptations to the harsh, arid environments inhabited by desert bighorn sheep, and the importance of water to the distribution, life history, and persistence of this species. Chapter 2 is illustrated profusely with many images that more than adequately portray the subject matter.

Chapter 3, “Adaptations to a Desert Environment” contains summaries of the many adaptations of desert bighorn sheep to life in the hot, arid ecosystems of western North America. In this chapter, the author and photographer explore the ways that these animals “take advantage” of habitat conditions and further discuss the physiological adaptations introduced in Chapter 2. Along with a summary of those physiological adaptations, Mark

nically discusses the published information on the behavioral and anatomical adaptations that so clearly contribute to the life history strategies of male and female bighorn sheep.

“Life History and Behavior—A Year in the Life of a Desert Bighorn” is the title of Chapter 4, and it is aptly named. There are some statements that could be construed by some to convey misinformation in the strictest sense (e.g., “The largest, most aggressive and powerful ram is often thought to do more than his share of the breeding with receptive ewes, theoretically passing on the most dominant genetic line to the next generation”), but the point is that dominant breeding males are more apt to pass their genes on to the next generation. Nevertheless, the audience likely to benefit most from this book will understand the intended meaning.

This chapter also describes the behavior of bighorn sheep in the context of various seasons of the year, and the life-history traits associated with those seasons. From the text (and, in particular, the photographs accompanying the text), it is clear that sexual segregation, or the fact that for much of the year male and female bighorn sheep utilize different habitats, is an important life-history trait of desert bighorn sheep (and most other sexually dimorphic ungulates). The word “segregate”—or a derivative thereof—appears only once in the text, but the importance of this concept could be further emphasized, particularly in the context of conservation.

Mark presents an excellent summary of the importance of habitat connectivity to the persistence of viable populations of desert bighorn sheep across an increasingly fragmented landscape. He notes that, “Looking back over the last half of the 20th century, it has become clear that with more insight into the needs of wildlife, planning could have curtailed many of the human impacts on wildlife habitat and wildlife movement corridors.” Clearly, the message is that if we don’t break something, it won’t need fixing, and Mark emphasizes the importance of science-driven forethought and planning as important ways to minimize conflicts in the future. Although the title of the book identifies desert bighorn sheep as a “wilderness” icon, I would argue that the desert bighorn is more of an icon of wild places, and not legislated wilderness; the absence of ecological forethought in the designation of wilderness has contributed to many of the problems with which desert bighorn sheep and other large mammals are faced. Mark’s admonition regarding better planning should be heeded by developers, conservationists, agency administrators, and politicians because, in the end, it will be the actions of all of them that determine the future of bighorn sheep across much of its range.

Chapter 5 consists of an extensive discussion of the causes of mortality and threats with which desert bighorn sheep are faced. Disease, habitat fragmentation, habitat loss, resource depletion, predation, human disturbance, and other such factors are addressed in some detail, and include up-to-date assessments of ongoing episodes. Also discussed are a number of methods or activities that have had benefits to conservation. Mark is not shy about discussing the important role that hunting has played in providing funds that are used to conserve bighorn sheep or acquire habitat. Moreover, he does not shy away from discussing the importance of providing resources or habitat management actions wherever needed to help maintain existing populations, or to help reverse a trend in declining numbers in some populations. He addresses the fallacy of the importance of “pristine” wilderness areas to bighorn sheep, noting that humans have an obligation to wildlife conservation that goes beyond the status quo: part of that obligation exists in a commitment to ensure the survival of desert bighorn sheep by using the methods and technology currently available to amend mistakes that have been detrimental to desert bighorn sheep. That is a gutsy approach, but one that Mark has been an advocate for during the more than 40 years of our friendship

and professional relationship.

In the final chapter, “Hope for the Future—Maneuvering the Modern West” the author brings into clear focus the accomplishments that have occurred on behalf of the conservation of this iconic animal, the ways and means through which those accomplishments have occurred, and clearly emphasizes the importance of active management to conservation and restoration. He then presents a summary of the current status of desert bighorn sheep in the seven states and Mexico, places inhabited by that specialized ungulate. Mark, who is not only a fine scientist and an ardent conservationist, is also a very pragmatic individual, calling attention to the needs to provide resources, primarily in the form of wildlife water developments, or to restore habitat for bighorn sheep using fire, removal of exotic vertebrates or vegetation, the restoration of connectivity (and, thereby, metapopulation function), and translocation as management tools. This chapter concludes with a discussion of predator management and its potential importance in the maintenance of bighorn sheep populations, or their restoration to parts of their historical range.

In preparing this informative book, Mark has delved into the evolutionary history, biology, beauty, and the relevance of appropriate management to the conservation of one of the iconic representatives of North American wildlife. The book is well-done, and profusely illustrated, and presents up-to-the minute descriptions of the challenges with which desert bighorn sheep are faced, as well as the accomplishments that have been made on their behalf. Material presented is based on the author’s extensive experience and his familiarity with the scientific literature and that literature is summarized in language that even those without a background in science can readily appreciate. I noted a few places in the book where more thorough editing might have been helpful (for example, the ways that the verbs evade and avoid—and derivations thereof—in relation to predators and predation are used interchangeably), but these instances do not detract from the value and importance of the material contained in this book. As noted earlier, some subjects could be expanded upon in terms of their relevance to desert bighorn sheep, but these are minor points in the context of the importance of bringing an understanding of the biology and the need for conservation to the reader.

Never one to be shy when offering opinions or advice regarding the management of desert bighorn sheep, Mark has addressed the controversial topics of wildlife conservation and habitat management in legislated wilderness, trophy hunting, captive breeding, and predator management in the context of their overall benefits to the conservation of desert bighorn sheep, and is to be commended for doing so. To complement the text, Jeff Young has provided dozens of outstanding photographs that not only illustrate material being discussed in the text, but also provide insight into many aspects of the life history of this species; I consider myself fortunate to own a signed print of the image on page 55 and display it in my shabby little office.

Mark and Jeff are to be congratulated on a book that, in my opinion, is a contribution and I encourage all with an interest in desert bighorn sheep to take advantage of the information it contains and to enjoy the outstanding photos included therein. The final sentence in the book is a statement that all that read it—and perhaps more importantly those that elect to not take the opportunity to do so—must appreciate: “People have risen up to support sustainable bighorn populations, to restore habitat, and to insure the future of this majestic symbol of wild places. Their future truly is in our hands.”

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J. Wehausen	White Mountain Research Station
J. Wilcox	Sonoma Mountain Ranch Preservation Foundation
I. Woo	U.S. Geological Survey

BOOKS RECEIVED AND AVAILABLE FOR REVIEW

Copies of the following books have been received and are available for review. Anyone 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 a request to do so.

BECK, B. H., AND E. PEATMAN (editors). 2015. Mucosal health in aquaculture. Academic Press, San Diego, California, USA. 395 Pages. \$180.00 (hard cover). ISBN: 978-0-12-417186-2

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, USA. 208 pages. \$24.95 (hard cover). ISBN: 1-61893-025-7

SJAASTAD, E., AND K. E. SVENSSON. 2015. Small ambassadors: the legendary light-line fishing reels. Schiffer Publishing, Atlen, Pennsylvania, USA. 256 pages. \$45.00 (hard cover). ISBN: 978-0-7643-4866-2

TOMINE, D. 2012. Closer to the ground. Patagonia, Ventura, California, USA. 255 pages. \$17.95 (soft cover). ISBN: 978-1-938340-50-5

YANG, H., J.-F. HAMEL, AND A. MERCIER (editors). 2015. The sea cucumber *Apostichopus japonicus*: history, biology and aquaculture. Academic Press, San Diego, California, USA. 454 pages. \$180.00 (hard cover). ISBN: 978-0-12-799953-1

