CALIFORNIA FISH AND GAME

"Conservation of Wildlife Through Education"

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California Fish and Game

Contents

Change in Editorship

With this issue, Armand Gonzales, special advisor with the Department of Fish and Wildlife, assumes the duties of editor-in-chief of *California Fish and Game*. Mr. Gonzales' assumption of the editorship follows the department's policy of rotating the editorship between staff members representing the Marine, Fisheries, Wildlife and Water branches. Under his guidance, the journal will continue its policy of presenting to the public the results of scientific investigations as they relate to management programs and the conservation of California fish and wildlife resources. Mr. Gonzales will strive to maintain and enhance the excellent reputation the journal has earned over the past 101 years.

To Dr. Vernon Bleich, editor-in-chief over the past six years, we wish to express our appreciation for a job well done. Dr. Bleich guided the journal through its 100 year anniversary, a milestone for the longest continuously published journal in California.

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

Notes from the Editor

It is a great honor to assume the duties of editor-in-chief of *California Fish and Game*, a role that has been fervently held for the past six years by Dr. Vernon Bleich. Just as Vern did, I will strive to maintain the journal's high standards of professionalism, integrity and relevance, which have made the journal an internationally recognized publication. Vern came out of retirement to be the editor of the journal and was most proud of being able to oversee publication of the 100th volume of the journal, a monumental and prestigious accomplishment. This together with the conversion to online publication, the rising submission as well as rejection numbers validated the importance and significance of the journal, which was distinctly improved by Vern's leadership. Thank you, Vern, for all you did and all you accomplished.

Another significant goodbye and thank you goes to Dr. Eric Loft, who retired at the end of April 2016. Eric was the editor-in-chief of the journal from 1990-1994. Since 2006, Eric has been the chief of the department's Wildlife Branch, where he oversaw programs related to lands management and restoration; nongame species management, threatened and endangered species, and special status species and their conservation; game species management and conservation; resource assessment, and disease/health investigations related to wildlife and humans. Prior to his role as branch chief, he was the lead for the department's resource assessment program and before that the statewide coordinator for the deer program, where he likely had his most fun. None of us choose this occupation for the money; it is truly for the love of nature that we devote our lives to this work of conserving our wildlife resources for the benefit of generations to come. For this, Eric has been recognized many times for his leadership and excellence in science, which is reiterated here. So, thank you, Eric, for all your hard work and dedication. We hope you enjoy your retirement and time with family.

   This 102nd volume of the journal comes late and is perhaps diminutive in comparison to recent issues. This is in large part due to the changes made in the editorship and the time needed to get up-to-speed on the intricacies of publication. Small as it may be, the content of this edition is a powerhouse of science, containing what might be one of the most important climate-related papers published in California. Wright et al. describes changes being seen and measured right now in high-elevation tree species that are correlated to a warming climate. Their outstanding work adds to the body of scientific literature that will help us tell the story of climate change and help us plan for the future. Bliss and Weckerly's study area and research subjects are excellent examples of beauty and majesty in nature. It's what gives us hope.

   With the change in editorship, there is an opportunity to consider other changes that may help improve the presentation and utility of the journal for its readers, authors, and editorial board alike. Some examples that have been kicked around are to offer more page fee waivers, especially to students, state and federal agency scientists, scientists working for non-profit organizations, and international submissions. Another thought is to use one edition per volume to publish the department's annual report from the branches. There are a number of technical reports produced each year by department staff that are posted to the department's document library, but few people outside the department know about them or know how to find them. It might be worthwhile to publish excerpts with location information so readers have the ability to find and read the full report if desired. Still another idea is to publish updates on significant accomplishments made by the department such as the recent completion of the State Wildlife Action Plan 2015 update (https://www.wildlife.ca.gov/SWAP). I'd like to ask you to help shape the future of the journal by sending me your thoughts or suggestions about what we can do to improve the journal content, readability or presentation.

   With this issue, there are some changes in the editorial board. I'd like to thank Kevin Shaffer (Fisheries Branch), who is resigning after many years as an associate editor and who specialized in anadromous fish. Kevin is being replaced by Dr. Russ Bellmer (Fisheries Branch), who came highly recommended and is also an anadromous fish expert. Returning to the editorial board is Kevin Flanders, from the Habitat Conservation and Planning Branch, who specializes in all things Bay-Delta. So, many thanks to Kevin for all the time and effort he has put into the journal, and welcome to Russ and Kevin. Your willingness to contribute to making the journal highly respected and professional is much appreciated.

   Finally, in accordance with the directions for contributors provided in Bleich 2014 and Bleich et al. 2011, please submit manuscripts by email or postal mail to the Journal Editor, Armand Gonzales, Department of Fish and Wildlife, 1416 Ninth Street, Suite 1221A, Sacramento, CA 95814, USA. Email: armand.gonzales@wildlife.ca.gov; telephone: 916-445-3379.

Armand Gonzales
Editor-in-Chief
California Fish and Game

Bleich, V. 2014. Information for contributors. *California Fish and Game* 100:757.
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Habitat use by male and female Roosevelt elk in northwestern California

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The female substitution hypothesis proposes that sexual selection influences intersexual resource use. In forage habitat, females may exhibit increases in reproductive success if there are more females than males. In such a circumstance, males may evolve a broader feeding niche that allows females to use prime foraging habitat. For grazing species, a broader forage niche could manifest as males using a wider range of forage habitats than females. Redwood National and State Parks, California, USA, is home to a non-migratory Roosevelt elk (*Cervus elaphus roosevelti*) population that inhabits a landscape in which forage habitat is divided into meadow and forest matrices. These categories are defined by high- and low-quality forage, respectively, based on forage quantity and forage species composition. Surveys of naturally marked male and female elk were conducted during January and February from 1997 to 2015 to provide data to estimate the probability of meadow use and forest use by each sex. When group size and whether or not prescribed burning occurred was statistically controlled, our analysis demonstrated that males were less likely than females to use meadows. Both male and female elk used meadows more frequently following prescribed burns. Our results demonstrating intersexual variation in habitat use by Roosevelt elk in winter are consistent with the female substitution hypothesis.

Key words: behavior, *Cervus elaphus roosevelti*, foraging ecology, large herbivores, Redwood National and State Parks, sexual segregation, ungulates, zero inflated binomial models

The differential use of space between males and females is pervasive in size-dimorphic large herbivores (Bowyer 2004, Ruckstuhl 2007, Singh et al. 2010). Hypotheses to explain intersexual differences in space use often invoke differences in body size between males and females because body size is coupled with diet selection and niche partitioning in ruminants (Bell 1971, Jarman 1974, Clutton-Brock et al. 1982, McCullough 1999, Barboza and Bowyer 2000). Browsers such as giraffes (*Giraffa camelopardalis*) can display vertical

separation whereby the sexes often feed in the same habitat but the taller males feed in higher strata of shrubs and trees than do females (Ginnett and Demment 1997). Males and females of grazing species, on the other hand, are more or less constrained to forage in the same vertical stratum and often consume the same species (Harper 1962). If males and females partition resources in such a setting, there should be horizontal segregation, which often manifests as differential use of habitats by the sexes.

Sex-specific differences in body size of large herbivores result in sex-specific differences in metabolic requirements and digestive processes, both of which affect foraging niches (Beier 1987, Kie and Bowyer 1999, Barboza and Bowyer 2000, Weckerly 2013). The larger body size of males likely evolved in response to sexual selection and, as a result, forage niche partitioning could also be influenced by size differences between the sexes. As a result, males could have a broader feeding niche whereby females can use prime foraging habitat (Geist and Petocz 1977). This possibility was called the female substitution hypothesis (McCullough 1999). Specifically, unlike female ungulates, males can sustain themselves on large quantities of low-biomass forage due to their greater gut capacity. Further, a gastrocentric model suggests that males, more so than females, suffer from digestive upset when diet quality changes rapidly (Barboza and Bowyer 2000). Therefore, the broader feeding niche of a male ungulate—an element of the gastrocentric model—is potentially consistent with the female substitution hypothesis. A broader foraging niche of males potentially reduces intersexual competition for resources, an outcome that should increase carrying capacity for females in prime forage habitat. In a polygynous mating system, resulting increases in habitat carrying capacity also increases the fitness of some males relative to others (McCullough 1999) because successful males experience the highest reproductive success when female abundance also is high.

The objective herein was to estimate habitat use by male and female Roosevelt elk (*Cervus elaphus roosevelti)* in Redwood National and State Parks, California, USA, and determine if males used forest habitat more often than females. In our study area, the mild climate makes it unlikely that inclement weather influences habitat use and elk were less vulnerable to succumbing to predation in meadows (Weckerly et al. 2001). Also, because the landscape composition of habitats is relatively simple: forage habitat can be divided into meadow and forest that are defined by high- and low-quality forage based on forage quantity and forage species composition (Weckerly 2005). Meadows were the habitat with the greatest amount of high-quality forage (Franklin et al. 1975, Weckerly 2007). If the female substitution hypothesis holds then males should use a broader range of forage habitats, which should result in greater forest use than females.

MATERIALS AND METHODS

Study area.—The study population of Roosevelt elk occupied about 10 km² of forest and meadows in the Prairie Creek drainage in Redwood National and State Parks, Humboldt County, California, USA. We surveyed the Davison meadows (≈50 ha), Boyes meadow (≈51 ha), and meadows (≈19 ha) along the Highway 101 bypass. The climate was maritime and mild: high temperatures in the summer were rarely greater than 25° C, and the mean minimum temperature in winter was 2° C (Starns et al. 2014). Precipitation was in the form of rain in winter and fog in summer. Mean annual precipitation was >150 cm, most of which fell between October and May. Meadow forage habitat was characterized by flat terrain that supported perennial and annual grasses such as California oat grass (*Danthonia*

californica), soft chess (*Bromus hordeaceus*), redtop (*Agrostis alba*), and some forbs such as hairy cat's ear (*Hypochoeris radicata*), narrow-leaved plantain (*Plantago lancelata*), and bracken ferns (*Pteridium sp.*) (Harper et al. 1967). In the more mesic meadows, reed canary grass (*Phalaris arundinacea*) was prevalent (Starns et al. 2015). Germination and growth of grasses began with the onset of rain in autumn and ceased when rainfall diminished in spring.

Meadows were surrounded by forests dominated by redwood (*Sequioa sempervirens)* and other conifer species (Douglas fir [*Pseudotsuga menziesii*], Sitka spruce [*Picea sitchensis*], and red alder [*Alnus rubra*]). In the Prairie Creek drainage, elk were habituated to human presence and thus easily observed (Harper et al. 1967, Weckerly 1999). Prescribed fires were conducted in the same meadow (Boyes) in September 1996, 2000, 2005, 2006, 2008, and 2013.

Habitat use.—Ten meadow surveys were conducted at dawn in January or February 1997 and from 2000 to 2015; in 1998 and 1999, only five surveys were conducted. Surveys began at dawn along a predetermined route that was driven in a vehicle (Weckerly et al. 2004, Weckerly 2007). When elk were encountered, the observer could exit the vehicle to count and classify elk into age-sex categories and record marked elk. We used natural marks (antler and pelage anomalies, slits or notches in ears, and scars that remained throughout each survey season) to identify individual animals (Weckerly 1996). Two types of social groups were defined: male groups consisted entirely of ≥1 adult male (branched antlers) and female groups. Female groups had juveniles, sub-adult males, and females. Sub-adult males and juvenile individuals were grouped with females because they were most frequently observed in female groups (>99% of observations). Sometimes female groups contained a small proportion of adult males. When adult males associated with females (22% of female groups, $SE = 2\%$, $n=19$ years) they comprised about 9% ($SE = 0.7\%$, $n=172$ groups) of female groups (Weckerly et al. 2001, Peterson and Weckerly *in review*). Because elk were habituated to the presence of humans, the animals could be viewed for sufficient time (>15 min) and at distances (20–200 m) that reduced the likelihood of misidentifying marked animals.

Across the surveys we conducted each year, we tallied the number of times we sighted animals with natural marks. This information was used to estimate the probability of meadow use with three, zero-inflated binomial models estimated in program PRESENCE (Weckerly 2007). Due to the simplicity of the landscape, habitat use was assumed to be mutually exclusive. Elk are primarily grazers and if an elk was not sighted in a meadow during a daily survey it was assumed to be foraging in the forest. Furthermore, during January and February, all age and sex classes of elk are taller than the height of meadow vegetation and, thus, are easily observed. The natural markings of individual animals did not usually persist across years. Hence, the naturally marked elk in one year differed from individually recognizable elk in another year.

We built models to assess the influence of sex and the potentially confounding influences of group size, whether a meadow had been burned that previous autumn (no – 0, yes – 1), and combinations of these predictors for a total of three models. A preliminary analysis suggested that there was a threshold relationship between group size and probability of meadow use, so we used the natural logarithm of typical group size as a predictor variable. Typical group size was calculated by summing the square of observed group sizes divided by the sum of observed group sizes (Jarman 1974). As a measure of gregariousness, typical group size is an animal-centered measure that is more resistant to the influence of solitary animals than is the arithmetic mean of group size (Heard 1992). To select the model that

best summarized meadow use we used the Akaike Information Criterion corrected for small size (AIC_c) and reported AIC_c and ΔAIC_c, the difference in AIC_c between a model and the model with the lowest AIC_c. The model with the lowest AIC_c was selected as the best model.

Results

Our analysis included 90 males and 36 females across the yearly surveys conducted from 1997 to 2015. The number of marked elk ranged from two to ten males, and one to six females each year. Group sizes for males were on average less than group sizes for females. Male group size ranged from 1 to 20 (median = 5) and female group size ranged from 8 to 52 (median = 26). Based on the model with the lowest AIC_c, meadow use was dependent on group size, sex, and prescribed fire in one meadow the previous September (Table 1). The selected model also estimated reasonably precise parameters and indicated that group size, sex, and prescribed fire all had a positive influence on meadow use (Table 2). The probability of meadow use by females ranged from 0.80 for a group size of 5 to 0.95 for a group size of 52 (Figure 1). Use of meadows by males was less than by females but was more variable, ranging from 0.41 for a group size of 1 to 0.88 for a group size of 52.

TABLE 1.—AIC*c*, delta (Δ) AIC*c*, number of parameters estimated (K), and deviance (-2 x log-likelihood) of three models to estimate meadow use of Roosevelt elk in Redwood National State Park, Humboldt County, California, USA, 1997–2015. The natural log of the typical group size is coded as "lntypgs"

Model	AIC_c	ΔAIC_c	K	Deviance
lntypgs,sex,burn	1135.70	0	4	1127.37
lntypgs,sex	1145.53	9.83	3	1139.33
lntypgs	1174.42	38.72	2	1170.32

TABLE 2.—Parameter coefficients and standard errors (SE) of the selected model estimating meadow use of Roosevelt elk in Redwood National State Park, Humboldt County, California, USA, 1997–2015.

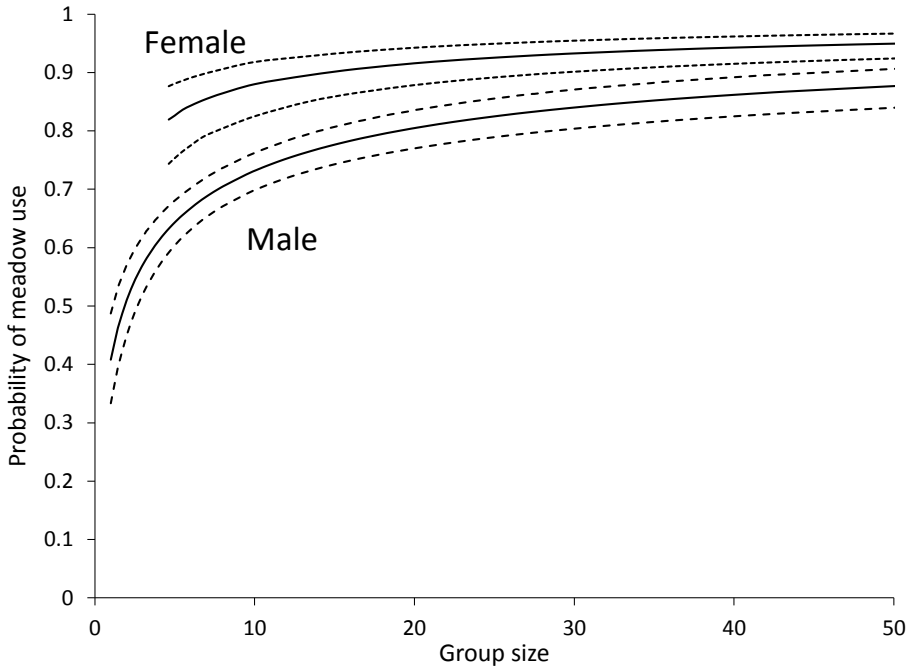| Parameter	Coefficient	SE
Intercept	-0.361	0.161
ln(typical group size)	0.593	0.069
Sex (0-Male, 1-Female)	0.980	0.229
Burn (0-No, 1-Yes)	2.410	1.024

Figure 1.—Probability of meadow use by group size and sex of Roosevelt elk in Redwood National and State Park, 1997–2015. Regressions for each sex were controlled for prescribed fire. The regressions are solid lines, and the 95% confidence intervals are shown by dashed lines.

Discussion

Using zero inflated binomial models to estimate meadow use, we uncovered differences between male and female forage habitat use in a sample population that ranged from 37 to 133 individuals across a period of 19-years (Weckerly 2007, Starns et al. 2015). Although the majority of all elk were sighted in meadows, males were less likely to be sighted in meadow habitat and, thus, more likely than females to use forest habitat. This horizontal niche partitioning is consistent with the female substitution hypothesis; males were more likely to use forests that were likely to have lower quantities of forage biomass than meadows, and thus probably had a broader forage niche (Weckerly 2005).

Differential habitat use by male and female *C. elaphus* is the standard and not the exception (Clutton-Brock et al. 1982, McCorquodale 2001, Long et al. 2009). Differential use of habitat in ungulates is frequently attributed to differences in predation risk tolerance between males and females or sex-specific severe weather tolerance. The predation risk hypothesis posits that male and female ungulates exhibit differential habitat use because of sex-specific differences in predation risk (Bleich et al. 1997, Main et al. 1996). In settings where abundant forage is also where predation risk is great, males use areas with abundant forage, despite an increase in predation risk, to increase their fitness by augmenting body condition and size. The possible fitness gain for males is higher than the predation risk. Females, in contrast, use areas with lower predation risk to reduce risks to offspring, in spite of costs to forage acquisition. Inclement weather has also been shown to affect habitat

use (Conradt et al. 2000). Due to larger body size and larger surface area, males are more vulnerable to lower temperatures and high winds. This vulnerability allows smaller bodied females to use prime forage that is located in areas open to severe weather.

The female substitution hypothesis enabled us to predict the direction of change in habitat use between male and females. This resident population is ideal for studying intersexual variation in habitat use due to the relatively simple environmental setting. Roosevelt elk are grazers during winter and, therefore, are more likely to display horizontal segregation or intersexual differences in habitat use (Harper 1962, Harper et al. 1967). Furthermore, during January and February Roosevelt elk are not involved in reproductive activities but still maintain sexual segregation. Thus, habitat use in winter is probably driven by resource use and not complicated by seasonal reproductive activities (Weckerly 1999). Additionally, landscape composition in our study area was very simple. In many landscapes, habitat provides a heterogeneous mix of shelter from weather and predators, and there are only subtle differences among habitats in quantities of nutrient rich and digestible forages (Stewart et al. 2015). Across the simple landscape of this study, however, meadows in winter provide the bulk of forage and are a habitat in which elk probably have low vulnerability to natural predators (Atwood et al. 2009); as a result, we assumed risk of predation to be less in meadows than in forested areas. Previous investigators have reported that forage in forested areas supplements, rather than complements, forage available in meadows (Weckerly 2005). Thus, the forest is not providing a resource that the male elk cannot find in the meadow. Moreover, owing to the mild winter climate, habitat use for the purpose of thermal regulation likely plays an inconsequential role in affecting habitat use.

Another feature affecting intersexual meadow use was the group size in which an individual occurred. In our study sex and group size were confounded. Male groups tended to be smaller than female groups, a phenomenon widely reported in *C. elaphus* throughout their geographic range (Clutton-Brock et al. 1982, Weckerly 2001). Females occurring in large groups might be constrained to forage in meadows because meadows provide abundant forage necessary to sustain a large group (Weckerly 2007). If we had not considered group size, we would not have been able to rigorously test whether males and females differed in meadow use.

The positive, nutritional benefits associated with prescribed fire are well-documented (Van Dyke and Darragh 2007, Allred et al. 2011). In our study males and females that used the meadow burned the previous autumn increased use of both the burned meadow and unburned meadows the following winter, but the reason for this is unclear. Presumably, unburned meadows should have lower quantities of nutrient rich and readily digestible forage (i.e., high-quality forage) than burned meadows (Anderson et al. 2007, Van Dyke and Darragh 2007).

Male groups used meadows less often than female groups across the spectrum of group sizes in this study. The nonlinear, threshold relationship suggests that large groups were more likely to use meadows, where forage biomass was most abundant (Weckerly 2005). One alternative explanation for intersexual differences in habitat use in our study landscape was the lower gregariousness of males (Weckerly 2007). Owing, in part, to the role of aggression in male dominance hierarchies, males aggregate with fewer males (Weckerly et al. 2004). Smaller group sizes, in turn, could use forest habitat that has less forage and where it plausible to expect that per capita forage might be comparable to per capita forage of large groups in meadows. Our results, however, suggest that is not a viable

explanation. Regardless of group size, males were observed in meadows less frequently than were females. Because males were overall less likely to use meadows, subtle influences of body size on food intake, processing, and digestion are a more likely explanation than male gregariousness for the differences in habitat use between the sexes (Ginnett and Demment 1997, Barboza and Bowyer 2000, Weckerly 2013).

One of the criticisms of previous explanations of males leaving habitats with abundant forage where females congregated (Geist and Petocz 1977) was that group selection is necessary to explain that behavior (Main and Coblentz 1990, Bleich et al. 1997). The female substitution hypothesis does not require group selection and probably was proposed to, in part; circumvent the pitfalls associated with a group selection argument (McCullough 1999). The simplified landscape and mild winter conditions inhabited by our study population facilitated our determination of the direction of intersexual habitat use. Our evidence, moreover, is consistent with the female substitution hypothesis in that males used the habitat with the greatest availability of forage less frequently than did females.

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Upward shifts in recruitment of high-elevation tree species in the northern Sierra Nevada, California

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We compared presence or absence of tree species recruitment in 381 recent random plots in the northern Sierra Nevada of California with 2160 Vegetation Type Map project plots of the 1930s. Of 12 tree species with adequate sample sizes for analysis, we found a significant upward elevation shift in recruitment in three species over this 80-year interval: red fir, western white pine, and mountain hemlock. A marginally significant upward shift was seen in lodgepole pine. All four species are higher elevation conifers in our study area. A few significant latitudinal shifts were also observed, but in a direction counter to the expectation of poleward shift. We believe this reversal is because more northerly latitudes in our study area have lower maximum elevations, whereas the more southerly latitudes have high mountains. One especially high-elevation species, mountain hemlock, became rare to lacking in the northern parts of our region, where the elevations at which it was formerly found may no longer be cool enough for the species. Because our measure of recruitment integrates over multiple years of seed germination and seedling and sapling survival, we believe these changes in small trees may reflect ongoing climatic changes in the Sierra Nevada, foreshadowing changes in plant communities and wildlife habitats.

Key words: Elevation shift, trees, conifers, latitude, climate change, *Abies magnifica*, *Pinus monticola*, *Tsuga mertensiana*, *Pinus contorta*, VTM

The Vegetation Type Map project of the 1920s and 1930s (VTM), headed by Albert Wieslander for the U.S. Forest Service, produced a vast store of data from tens of thousands of forest plots, representing a unique resource for judicious comparisons with past conditions (Wieslander 1935; Thorne et al. 2008; Dolanc et al. 2012, 2014a,b). A far-seeing effort by the Universities of California, Berkeley and Davis, has made the historical data readily available in digital and geospatial forms (Kelly et al. 2005, 2008; http://vtm.berkeley.edu).

When we began a long-term montane biodiversity monitoring project in 2009, we therefore planned our sampling to allow direct comparison with VTM data, such as by replicating VTM plot sizes and tree measurement categories. Our Ecoregional Biodiversity

Monitoring project (EBM, formerly Sierra Monitoring Project), now in its eighth year in the California Department of Fish and Wildlife (Department) North Central Region (NCR), uses a stratified random design to produce a scientifically valid sample of the Sierra Nevada landscape. The intent of our project is to establish a baseline and to test for trends in species, communities or habitats, and to relate those trends to environmental variables such as land use and climate change. The project was begun in the Department's Northern Region in 2002 (Furnas and Callas 2015) and later extended to the NCR, where we initiated the effort to compare with VTM data. Because the VTM project established certain vegetation baseline data in the 1930s, we have a unique opportunity to test for changes over an 80 year time interval, even while it is still too early for the EBM project to detect most gradual trends.

There is overwhelming evidence that average temperature has increased and is increasing globally (Rajaratnam et al. 2015), but to what extent has climate changed within our study area? Cordero et al. (2011) found that, statewide, California mean minimum (Tmin) and maximum (Tmax) temperatures have increased significantly since 1918; and at an increased rate since 1970. This was true in their Sierra Region (encompassing our EBM study area) especially for Tmin; changes in Tmax were not significant. In the Sierra Nevada, the change in Tmin was about + 0.6 deg C per 100 yrs, and was greatest in summer Tmin (June-July-August: +1.3 deg C per 100 yrs). East slope ("Northeast") increases were more pronounced (n=3 stations). Cordero et al. (2011) found long-term temperature changes in California consistent with greenhouse gas forcing. Declining snowpack in the northern Sierra Nevada including our EBM study area was described by Mote et al. (2005). These results are generally echoed by recent National Forest Service analyses for National Forests within our study area (Merriam et al. 2013, Meyer et al. 2013, Mallek et al. 2014), which also report declines in numbers of months with average Tmin below freezing.

Here we examine the question of whether comparing current with historical tree data shows any elevational changes in species distributions, as have been predicted and increasingly found to occur due to climate change (Beckage et al. 2008, Kelly and Goulden 2008, Kullman 2002, Lenoir et al. 2008). In order to test this question, we elected to examine a measure of recruitment of young trees into the forest, hypothesizing that this would be the first and most sensitive index of change for tree species (Kullman 2002). If climate change is causing habitable zones for montane tree species to move upward in elevation as has been predicted, we would expect upward shifts in recruitment over the 80-year interval between VTM and our study.

Methods

Study region.—We focused on a nine-county area of the northern Sierra Nevada range, from Alpine and Calaveras County on the south to Butte and Plumas County in the north (Figure 1), and within the Sierra Nevada Ecoregion (USDA, http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327836). Habitats above 914 m elevation (3000 feet) were considered.

VTM data.—We downloaded data from the VTM Project website (http://vtm.berkeley.edu/) and extracted plots that fell within our study region. VTM plot data in our region were mainly collected from 1934-1935. We accepted VTM plots without a digitally mapped latitude and longitude if the original datasheet cited an elevation and a township/range/section with a centroid within our study area (532 plots). We did not analyze treeless
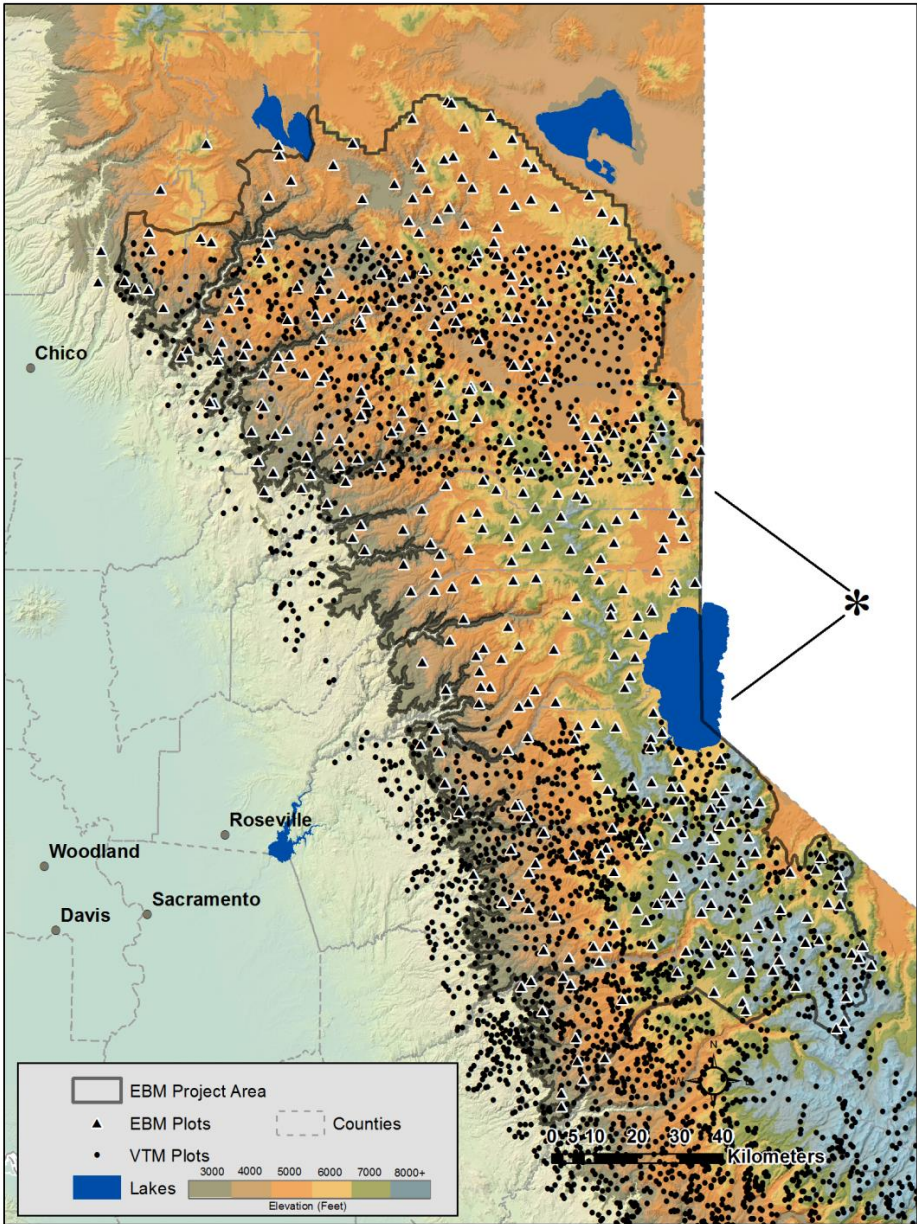
Figure 1 — Study area: the northern Sierra Nevada ecoregion, California, USA, above 914 m elevation (3000 feet). Lake Tahoe is at right-center. Black triangles show EBM sample points; small black dots show VTM plots. *The asterisk denotes an area where VTM data were available but not precisely mapped. We were able to incorporate 532 VTM plots from this area because it included elevations and township-range-section data from which we could accurately estimate latitude. A true gap in VTM data was present in the northernmost extent of the study area, from which VTM data have not been found. Elevation strata for EBM sampling are shown in color bands.

plots out of concern that the VTM project's commercial timber bent might have biased sampling of such plots. See Appendix I for additional discussion of error-checking and processing of VTM data.

EBM sampling.—Plots for sampling for our EBM project were randomly generated in a geographic information system (GIS), in equal numbers within 6 elevation strata across the study region (914-1218 m, 1219-1523 m, 1524-1828 m, 1829-2133 m, 2134-2438 m, and above 2438 m) (3000-3999, 4000-4999, 5000-5999, 6000-6999, 7000-7999, and 8000+ feet). Plots were constrained to be 1) terrestrial, i.e., not in water, 2) non-urban, 3) more than 100 m from a road, and 4) not within an area of less than 10 hectares "islanded" by surrounding roads. We also rejected potential plots with slopes steeper than 35 degrees or requiring more than five hours hiking time to complete. Subsequent random plots were rejected if they fell within a Forest Inventory and Analysis (FIA) (Bechtold and Patterson 2005) 5.26-km hexagon containing a previously selected plot, or within 400 m of a previous plot in a different hexagon: this resulted in some spatial dispersion of plots (Figure 1).

The present analysis includes EBM plots sampled during 2009-2015. The majority of land ownership in our study region is public – mainly US Forest Service – and ultimately the great majority of our plots were on public lands. In practice, we found it necessary to eliminate or randomly relocate a handful of plots that were too close to residences or other development, or inaccessible due to private property restrictions. Field protocols included a procedure for offsetting such plots in a manner that would result in an unbiased plot location.

At each random plot location, we recorded all trees to species and in size categories within a 0.0809 ha plot (circular in EBM, equal in area to 0.2-acre rectangular plots in VTM). Our EBM plot locations broadly sampled the region from which we selected VTM plot data (Figure 1). For comparison with the VTM plots, we omitted 14 treeless EBM plots with no burn history within 35 years of the time of sampling from analysis. Data from our EBM sampling are freely available on the CDFW website, "BIOS" geographic database (http://www.dfg.ca.gov/biogeodata/bios/).

Data analysis.— To assess recruitment of trees, we used the 10-30 cm, "extra-small" size category (4-11-inch in VTM, diameter at breast height [dbh]) as an index of recruitment into the plot over the recent past. In some instances a tree less than 30.5 cm dbh in the Sierra Nevada may be more than 75 years old (FEIS 2013, USDA-FS 1990), but in most cases an extra-small tree in the present was recruited to that size category sometime after the period of VTM sampling. On the other hand, a tree of this size can be a few decades old, so our use of extra-small trees as an index of recruitment integrates conditions affecting seed germination and survival and growth of seedlings and saplings over multiple seasons.

For valid comparison with the VTM data, we sought a recruitment variable that would be insensitive to possible biases. For example, we might suspect that VTM field workers tended to select plots "representative" of vegetation types, or tended (perhaps unconsciously) to select more open or more mature plots. We elected to use simple presence of at least one "extra-small" (10-30 cm) stem of a species as our response variable, reasoning that the presence or absence of one small tree would be unlikely to have influenced VTM workers in selecting or avoiding a plot. This rudimentary variable will still be sensitive to distributional shifts over time, especially into areas where the species was not recruiting previously or loss of recruitment from areas where it formerly occurred.

For each tree species, we compared the project means (VTM vs. EBM) of elevation of plots where extra-small stems were present, testing for statistical significance by t-test. Tests for latitude shifts were conducted similarly. We used Welch's t-test for comparison

of samples with unequal variances for all comparisons because unequal variances were evident in some tests (Levene 1960, Zimmerman 2004). Since our working hypothesis was that tree species distributions might be shifting upward, we applied a one-tailed significance test. We also tested for latitudinal shifts, but since changes in climate across latitude may be more complex (such as possible spatially varying precipitation changes: Merriam et al. 2013, Mallek et al. 2014), we applied a two-tailed test.

RESULTS

Elevation shift.—We were able to compare data on 381 recent EBM plots with 2160 historical VTM plots. Both EBM and VTM sampled broadly across forested elevations (Figure 1). Plots in the recent EBM study averaged slightly higher in elevation than VTM plots (+28 m), due to more equal stratification across elevation zones (Figure 2a), but this difference was not statistically significant (t = 1.01, 2-tailed, P > 0.30). Note that more plots were sampled than contained recruitment of any individual tree species, therefore slightly differing total plot distribution across elevations between EBM and VTM time periods is
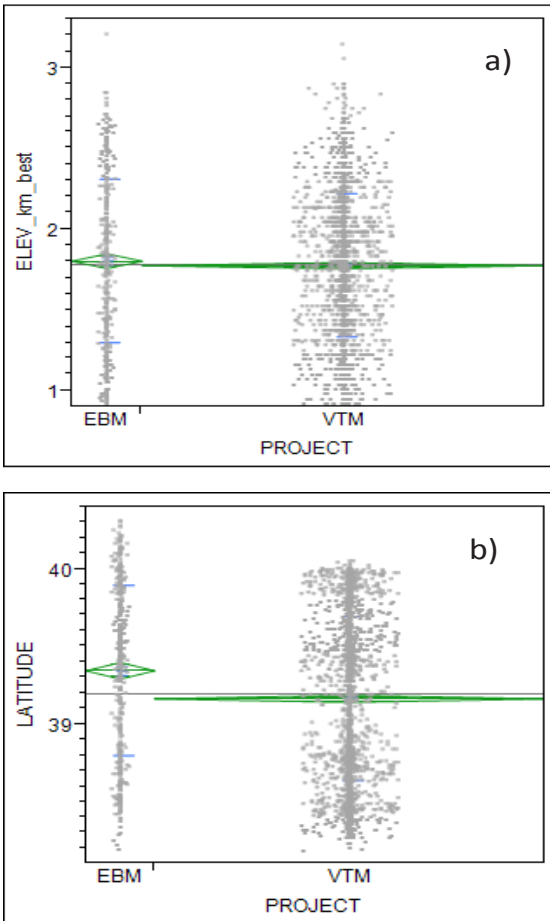

FIGURE 2 — a) Elevation distribution of plots sampled, VTM and EBM (elevation in km; "best" means datasheet-reported elevations were used for VTM and 10-m digital GIS elevations for EBM; gray points represent plot elevations jittered around the vertical project line; green diamonds center on the mean, extend to the upper and lower confidence limits of the mean, and have width proportional to sample size). EBM plots averaged 28 m higher than VTM; this difference was not significant (P > 0 .30). Both projects broadly sampled across northern Sierra Nevada elevations; b) Latitudinal distribution of plots sampled, VTM and EBM (latitude in degrees north; symbols as above). VTM data from north of 40° remain missing within our study area (Kelly et al. 2005); EBM samples ranged significantly further north (P < 0.0001).

unlikely to constrain the average elevation of plots with recruitment, discussed below.

Three of 12 tree species with adequate sample sizes for analysis showed significant upward shifts in elevation of recruitment between the 1930s and recent sampling: red fir (*Abies magnifica*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga mertensiana*) (t = 4.49, 2.78, 3.68, respectively, all P < 0.005 one-tailed; Figure 3). The average elevation of plots with mountain hemlock recruitment shifted upward by 119 m, red fir by 147 m, and western white pine by 112 m. In addition, a fourth species, lodgepole pine, showed a suggestive upward trend (t = 1.45, P = 0.075 one-tailed; Figure 3d), with an average upward shift in recruitment of 75 m. These four coniferous species are the highest-elevation common species in our study (EBM median elevations of occurrence, all stem sizes included: red fir 2310 m, western white pine 2450 m, mountain hemlock 2600 m, lodgepole pine 2390 m).
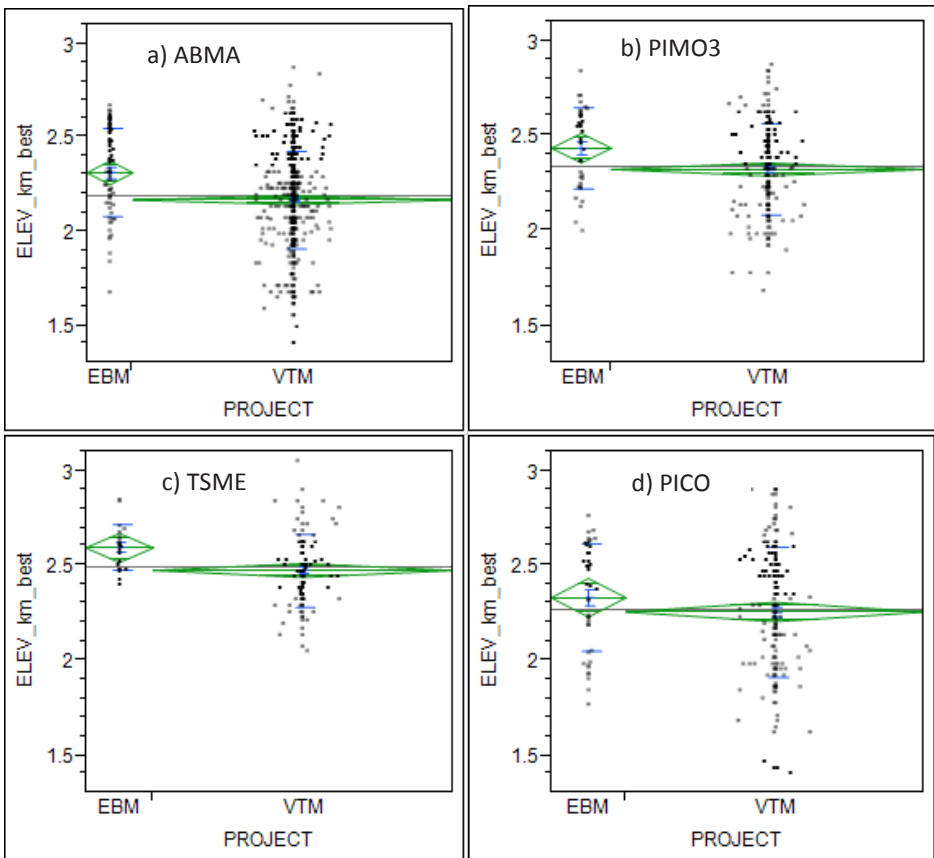
Figure 3—Elevation distribution of historical (VTM) and recent (EBM) plots containing recruitment of four high-elevation conifers: a) red fir (*Abies magnifica*), b) western white pine (*Pinus monticola*), c) mountain hemlock (*Tsuga mertensiana*), and, d) lodgepole pine (*Pinus contorta*). Points represent individual plots; green diamonds center on the mean and extend to its 95% confidence limits. Differences between EBM and VTM are significant for red fir (P < 0.0001), western white pine (P = 0.0038), and mountain hemlock (P = 0.0003); and are marginally significant for lodgepole pine (P = 0.0755) (Welch's t-test, all one-tailed).

For these four high-elevation conifers with significant or suggestive upward shifts in recruitment, evidence was primarily for a loss at lower elevations and upward redistribution of recruitment in middle elevations, with lesser or no expansion of recruitment at higher elevations (Table 1; Figure 3). Minimum and maximum elevations are suggestive of the same trends (Figure 3), although minima and maxima are subject to more sampling variation and are affected by sample size, which was smaller for EBM than VTM.

TABLE 1.—Historic versus recent elevations at lower and upper percentiles of elevation distribution of recruitment, for four high-elevation conifer species in the northern Sierra Nevada, California, USA. Entries show VTM / EBM elevations and the change, in meters (e.g., the lower 10th percentile elevation of red fir recruitment plots in VTM was 1829 m / in EBM was 1980 m, a change of +151 m). All four species lost more distribution at lower elevations than they gained at the highest elevations.

Species	Percentile			
	10%	25%	75%	90%
Red fir	1829/1980 +151	2012/2145 +133	2332/2529 +197	2499/2601 +102
Western white pine	1990/2136 +146	2134/2244 +110	2499/2602 +103	2621/2684 +63
Mountain hemlock	2225/2436 +211	2316/2477 +161	2598/2675 +77	2743/2798 +55
Lodgepole pine	1835/1929 +94	1981/2045 +64	2530/2577 +47	2682/2638 -44

The remaining eight species did not show significant upward change in elevation of recruitment between time periods (white fir–*Abies concolor*; incense cedar–*Calocedrus decurrens*; sugar pine–*Pinus lambertiana*; Jeffrey pine–*P. jeffreyi*; Ponderosa pine–*P. ponderosa*; Douglas fir–*Pseudotsuga menziesii*; canyon live oak–*Quercus chrysolepis*, black oak–*Q. kelloggii*). Power to detect change may have been less for these species other than white fir because the lower portion of their elevation ranges was not sampled by this study–they extend below the 914 m elevation sampling boundary. As was seen for the four highest-elevation conifer species, the lower elevation range margin may be important in reflecting elevation shifts.

Latitude shift.—VTM data from the northern portion of our study area have never been found (Kelly et al. 2005, Dolanc et al. 2014), whereas EBM did sample at latitudes north of 40° (Figure 2b). Omitting EBM samples north of 40° latitude from analysis, EBM samples averaged 0.07° (6.7 km) poleward of the VTM mean latitude, a small but significant difference (t = 2.36, P < 0.02 two-tailed). If anything, this might be expected to predispose results toward finding recent northward shifts of species. Working with the same subset of the data (truncated to ≤40°; n = 333 EBM, 2160 VTM), we found a variety of patterns including both northward and southward shifts. These results will be addressed in more detail separately; but notably, the same three species with significant upward elevation shifts also showed significant *southward* shifts in latitude (mean latitude difference EBM-VTM: red fir, -0.14°, t = 2.34, P = 0.022; western white pine, -0.15°, t= 2.14, P = 0.037; mountain

hemlock, -0.22°, t = 3.01, P = 0.004, all tests two-tailed).

      We believe these southerly recruitment shifts by species which have also displayed upward elevation shifts result from the fact that more northerly latitudes have lower maximum elevations and thus warmer temperatures than the southern portions of our study area (Figure 1). Consequently, if recruitment of these species is tracking changing temperatures to higher, cooler elevations, areas where recruitment may be found are more rapidly lost in the northern portions of our study area than in the south.

      For example, a substantial zone of distribution of mountain hemlock below 2380 m was completely absent during the EBM sample period (Figure 3c), which was also expressed as a significant loss of latitudinal distribution (Figure 4). A remaining outpost of mountain hemlock recruitment at approximately 39.4° (Figure 4) corresponds to higher-elevation areas of Nevada County. North of Nevada County, elevations in excess of 2400 m (7880 ft) are rare, relatively low (none over 2700 m), and small in areal extent. Consequently, cool, high elevation refugia for species like the mountain hemlock are limited in number and extent within our study region north of Nevada County.
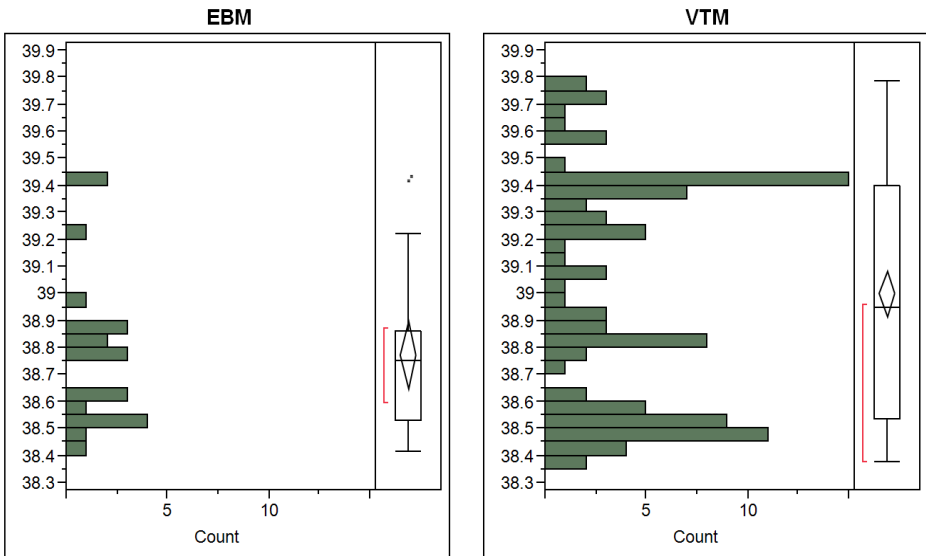

FIGURE 4 — Latitude in degrees north versus number of plots containing one or more "extra-small" (10-30-cm dbh) mountain hemlock stem (*Tsuga mertensiana*): EBM, n = 22; VTM, n = 100. There has been a noticeable reduction of distribution of the species northward of 39° latitude in our study area.

DISCUSSION

Northern Sierra Nevada tree species that shifted upward in this study were all higher elevation species – they are the four highest-occurring species that we recorded with any frequency. Whitebark pine (*Pinus albicaulis*) does occur at even higher median elevation but was not well enough represented in the data to analyze. All four species that shifted in our analysis also prefer cool microhabitats within our region, as indicated by their preference for more northeasterly as opposed to southerly slope aspects (this study: unpublished data). All are conifers, as are all more common tree species in the Sierra Nevada above 2000 m.

This report of upward shift of higher-elevation tree recruitment across a large region is one of relatively few studies to date documenting such shifts by tree species across large spatial scales. Lenoir et al. (2008) reported 41 significant upward shifts among 171 forest plant species from six mountain ranges in western Europe. Woody species were less likely to show a significant shift, but one coniferous (*Abies alba*) and six deciduous tree species were identified as shifting up; one deciduous tree species shifted down (*Quercus pubescens*) (Lenoir et al. 2008 including supplemental online materials). The longer life-spans and survival capacity of woody plants and particularly trees seem likely to make detection of overall-population changes more difficult. Recruitment or mortality may respond more quickly to environmental changes. Examining establishment in former snowfields, invasion of meadows, branch growth, and upright stem development in high-elevation Sierra Nevada conifers, including western white pine and lodgepole pine, Millar et al. (2004) found these ecological responses were broadly correlated with increases in minimum temperature. Van Mantgem, Lutz, Stephenson and others (van Mantgem et al. 2009, Lutz et al. 2009) have reported large-scale observations of increased tree mortality rates, apparently in response to rising temperatures and increasing water deficits. Lutz et al. (2009) and McIntyre et al. (2015) found declines in large-diameter trees since the VTM surveys, correlated with changes in water availability due to warming climate. For *Pinus jeffreyi*, *P. lambertiana*, and *P. ponderosa*, the decline of large trees was greatest in lower elevation habitats of their ranges within Yosemite National Park (centered 50 km south of our study region; Lutz et al. 2009). Thorne et al. (2008) and McIntyre et al. (2015) found large-scale shifts in vegetation types including tree dominance in the Sierra Nevada since the VTM project. They concluded that some conifers were losing low and mid-elevation distribution or abundance and being replaced by oaks.

Several studies of smaller areas have shown trees' upward shifts or other plant species trends consistent with warming climate. Kullman (2002) found a shift in recruitment across elevation and +120 to +375 m increases over a 50-year interval in the upslope range margins of five tree taxa in southern Sweden. Along an elevation transect established in 1964 in the northeastern USA (Green Mountains, Vermont), Beckage et al. (2008), reported upward elevation changes of several conifer and hardwood tree species. Kelly and Goulden (2008) revisited precise sites in Deep Canyon, Santa Rosa Mountains, California, USA and found upward shifts of white fir (*Abies concolor*) and other species over a 30-year interval. Species and community shift over a 57-year interval since Whittaker's (1960) classic study, toward plants more typical of warmer, drier conditions, was described by Damschen et al. (2010). Lutz et al. (2010) modeled past, present, and future climatic water deficit and judged western white pine (*P. monticola*) and mountain hemlock (*T. mertensiana*) – two of the species showing significant upward shift in recruitment in our study – most likely to be

affected by climate change in Yosemite National Park, just south of our study region.

Despite multiple examples and rich results in the literature from such studies, trends over time are minimally resolved by examining only a single, albeit 80-year, interval; yet those are the data available to us. In the future, we anticipate expanding this study in multiple ways, not the least of which is continued EBM sampling to detect trends within the continuously sampled EBM record, now approaching its 8th year of sampling in NCR and a 15-year continuous record in CDFW Northern Region (Furnas and Callas 2015).

While VTM data were collected for the specific purpose of supporting a vegetation mapping effort and were not a rigorously randomized sample of forest conditions of the time, like many researchers before us we have found the scope, intensity and consistency of the VTM sampling presents opportunities for careful comparisons with current datasets. We believe concerns about the potential for sampling bias in the VTM data must be addressed (Keeley 2004, Bouldin 2009); therefore we chose a conservative metric – presence of at least one "extra-small" size tree – as our test measure for changes in recruitment. Another reason we believe our analysis is robust to possible bias in VTM sampling is that the test of interest is not of the main effect of the project period (mean VTM recruitment presence vs. mean EBM recruitment presence) but of the interaction between project period and elevation: namely, difference in the elevation distribution of recruitment between VTM and EBM samples. We might well suspect that VTM crews consciously or unconsciously tended to select plots with more mature trees, likely to support fewer extra-small trees [though Dolanc et al. (2014a) reported comparable spread of tree density across VTM and FIA plots]. However, to produce the requisite interaction effect, any bias of VTM sampling would have had to differ at different elevations. For example, for a VTM bias to explain our analysis results, one would have to posit stronger VTM bias against including extra-small trees at higher elevations than at lower elevations, for western white pines, mountain hemlocks, and red firs but not for white fir or other species. We consider such a strained bias hypothesis to be unrealistic; the data are more simply explained by true elevation shifts by a few species.

We find climate change in the Sierra Nevada to be a leading contender among possible causes for the significant elevation shifts we documented. The large spatial scale of our study implies a large-scale effect like climate change. Of the three species most affected, all are higher-elevation species, and western white pine and mountain hemlock were both identified by Lutz et al. (2010) as species at risk from climate change at their lower elevation margin. In a Bayesian logistic regression distribution-modeling study, Bell et al. (2014) found that projected change in climatic envelopes for high-elevation conifers, including lodgepole pine, are likely to result in substantial loss and upward shift of habitable area. Climate in our study area has been measurably changing, resulting in fewer freezing days, lower snowpack, earlier snowmelt, warmer nighttime temperatures, and greater water-deficit values (Cordero et al. 2011, Lutz et al. 2010), especially at low to middle elevations. At high elevations there may be some tendency to increased precipitation (Mallek et al. 2014) and warmer temperatures may yet be below freezing at night, creating opportunities for upslope establishment by some higher elevation tree species (Millar et al. 2004, Dolanc et al. 2013).

Fire and logging are two other often-discussed catalysts of forest change in the Sierra Nevada (Dolanc et al. 2014b, McIntyre et al. 2015, Naficy et al. 2010). Because they occur in patchworks, they appear less likely to cause clear patterns over very large scales, though they may do so on average. While beyond the scope of this paper, we did amass data

on fire and logging history for our plots which will be analyzed elsewhere. Particularly at the elevations and in the habitats occupied by western white pine and mountain hemlock, fire and harvest are relatively less frequent than at lower elevations (Caprio and Swetnam 1995, Skinner and Chang 1996) – for example, we found no history of fire in mountain hemlock plots. Within our study area at higher elevations there are substantial areas of designated wilderness where no logging may occur. Thus even where forest-stand effects of timber harvest and fire are expected to have been weak, we observed upward shifts of high-elevation tree species. Schwartz et al. (2015) reported increasing frequency of fire over time at higher elevations in the Sierra Nevada, suggesting that the limited effects of fire within the highest portions of our study area may expand over time. Whether increased fire frequency would facilitate or impede tree elevation shifts remains to be seen and is likely to be species-specific.

Coniferous trees in the Sierra Nevada are major establishers of habitats and habitat types, and produce seed that is food for numerous species of mammals and birds (Mayer and Laudenslayer 1988). Our results suggest that, with trees moving up, stands of vegetation forming habitats will move up as well, with a range of implications for multiple wildlife species. Well developed habitats will take time to establish on cool, rocky slopes. Another widely appreciated aspect of such upward shifts is that there is less area available at higher elevations – because mountains are roughly cone-shaped – therefore subalpine habitats and the wildlife they support are likely to be confined to reduced and fragmented areas over time (Dullinger et al. 2012, Bell et al. 2014).

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APPENDIX I

While the VTM database compiled online is a uniquely valuable resource, users should examine the data carefully for errors before drawing conclusions from it. Here we catalog some edits we found necessary.

Incorrect codes (or, regional differences in the codes that VTM allowed that were not preserved in the historical information available to the University of California VTM Project):

VTM code	Nominal code species	Likely species intended in our study area	Comments, per our study area
Ld	incense cedar (*Calocedrus (Libocedrus) decurrens*): also I, IC	tan oak (*Lithocarpus densiflora*): codes Lde, T	Ld code co-occurs in data with I code, suggesting Ld used for Lde
R	coast redwood (*Sequoia sempervirens*)	red fir (*Abies magnifica*): code R1	Coast redwood does not occur. Elevation and data notations confirm red fir. We interpreted R as a code for red fir where a tree was indicated.
SP	Bishop pine (*Pinus muricata*)	sugar pine (*Pinus lambertiana*): code S	Bishop pine does not occur. Data notations and elevations consistent with sugar pine. We interpreted SP as sugar pine.
W	Interior live oak (*Quercus wislizeni*)	white fir (*Abies concolor*): code W1	Elevation and notations suggest white fir. We did not include these occurrences in our analysis.

Incense cedar and tan oak were not analyzed, in part due to these ambiguities. We did not analyze potential shifts of interior live-oak because a complete absence in recent sampling (0/381) and 57/2160 samples in VTM suggested miscoding in the VTM data that we could not resolve.

We used verbatim elevations reported by VTM surveyors for VTM plots rather than digital elevations derived from estimated latitude and longitude in a GIS. A regression analysis showed no substantial deviation of VTM elevation estimates from the digitized estimates, and we found occasional errors in the GIS locations. For EBM, we used digital elevations (10-m resolution) calculated using geographic positioning system (GPS) averaged waypoints obtained in the field and compared with pre-planned plot locations.

Book Review

Closer to the ground

Tomine, D. 2012. Patagonia, Ventura, California, USA. 255 pages. Soft cover. $17.95. ISBN: 978-1-938340-50-5

The author, Dylan Tomine, has written a delightful account of island life on the Puget Sound. With his family—wife and two kids—he chronicles his adventures over the course of a year, conveniently dividing the book into four sections, one section per season. Each section is split further up to eight chapters addressing a specific aspect of his daily struggles and triumphs. From chanterelle (*Cantharellus cibarius*) hunting to splitting fire wood—Tomine's writing is humorous and a pleasure to read.

Tomine is well aware of human impact on the planet and although he realizes his carbon footprint cannot be zero, he tries his best to do what's best and reduce his impact as much as possible. He teaches his children the importance of the various actions someone can do to be a positive steward of the earth. Many times throughout the book I nod in agreement with his sound advice regarding growing food in a home garden to only collecting firewood from downed trees. He fishes with an ecological conscience and ensures that he does all he can to pass his knowledge and skills to his kids. With his Japanese cultural background, Tomine links the past to the present with the idea that the future is not far off. His journey is about growth and learning new things—and experiencing them with his family. It reminds me of my own childhood as I roamed over the countryside—exploring life in irrigation canals and trying to identify a random bird foraging in the trees. The connection we make with nature can be everlasting.

Scattered throughout the book are black and white photographs (and occasionally a few in color) of Tomine's family captured in various activities that they hold close to their heart, such as fishing, boating, harvesting the garden, crabbing and playing on the beach. His treatments of cutting, collecting and stacking firewood take on a deep personal meaning for me as I recall cutting up old almond trees for winter fires with my father.

One of the highlights I enjoyed about the book was the "significance of birds" sections—one for each season. Only a couple pages long, each section explores an aspect of avian natural history and how it relates to his life. With touching and skillful language, these sections create a personal connection with the author not often encountered in nature
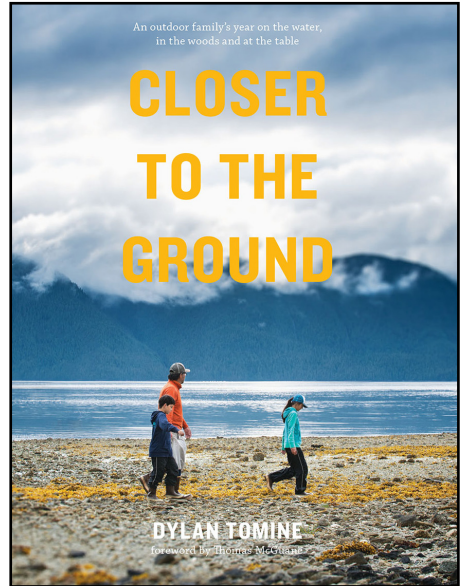
writings. Another key highlight was the several recipes added to the book's second edition. A total of 17 recipes are distributed throughout the book—with each season featuring up to five exciting dishes the Tomine family relishes with delight. Food preparation is frequently encountered in the book. Tomine expresses his lust for life through food and doesn't hesitate to entertain the reader on the ritual of food collection—such as digging for clams or fishing for salmon—to food preparation and consumption. It seems that the human day is measured by what meals are being prepared and Tomine doesn't disappoint.

      Closer to the Ground is a wonderful read. Tomine's fluid and humorous writing style makes the book a quick but insightful read. The book can easily be viewed a vehicle for personal reflection on embracing nature and showing a level of respect for our planet that needs to be more commonplace. Raising children is never easy, but a key responsibility as parents is keeping our actions with nature "closer to the ground" and fully engaging with whatever comes along. It's about the journey—not necessarily the destination.

Howard O. Clark, *Jr., Wildlife Ecologist, Garcia and Associates, Clovis, CA.*

INFORMATION FOR CONTRIBUTORS

California Fish and Game is a peer-reviewed, scientific journal focused on the biology, ecology, and conservation of the flora and fauna of California or the surrounding area, and the northeastern Pacific Ocean. Authors may submit papers for consideration as an article, note, review, or comment. The most recent instructions for authors are published in Volume 97(1) of this journal (Bleich et al. 2011), and are accessible through the California Department of Fish and Wildlife website (www.wildlife.ca.gov/publications). Planning is in progress to provide an avenue for authors to submit manuscripts directly through the website, and to enable restricted and confidential access for reviewers. In the meantime, manuscripts should be submitted by e-mail following directions provided by Bleich et al. (2011). The journal standard for style is consistent with the Council of Science Editors (CSE) Style Manual (CSE 2006). Instructions in Bleich et al. (2011) supersede the CSE Style Manual where differences exist between formats. Authors of manuscripts that are accepted for publication will be invoiced for charges at the rate of $50 per printed page at the time page proofs are distributed. Authors should state acceptance of page charges in their submittal letters. The corresponding author will receive a PDF file of his or her publication without additional fees, and may distribute those copies without restriction. Plans are underway to make the complete series of *California Fish and Game* available as PDF documents on the California Department of Fish and Wildlife website.

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About the Covers

Front.—Two Roosevelt elk browse in Prairie Creek Redwoods State Park in Humboldt County. Photo courtesy of Gerald and Buff Corsi at the California Academy of Scientists.

Back.—A gnarled mountain hemlock (*Tsuga mertensiana*) grows high on Lembert Dome in Yosemite National Park (elevation 2,860 meters). Photo courtesy of David Wright, California Department of Fish and Wildlife.
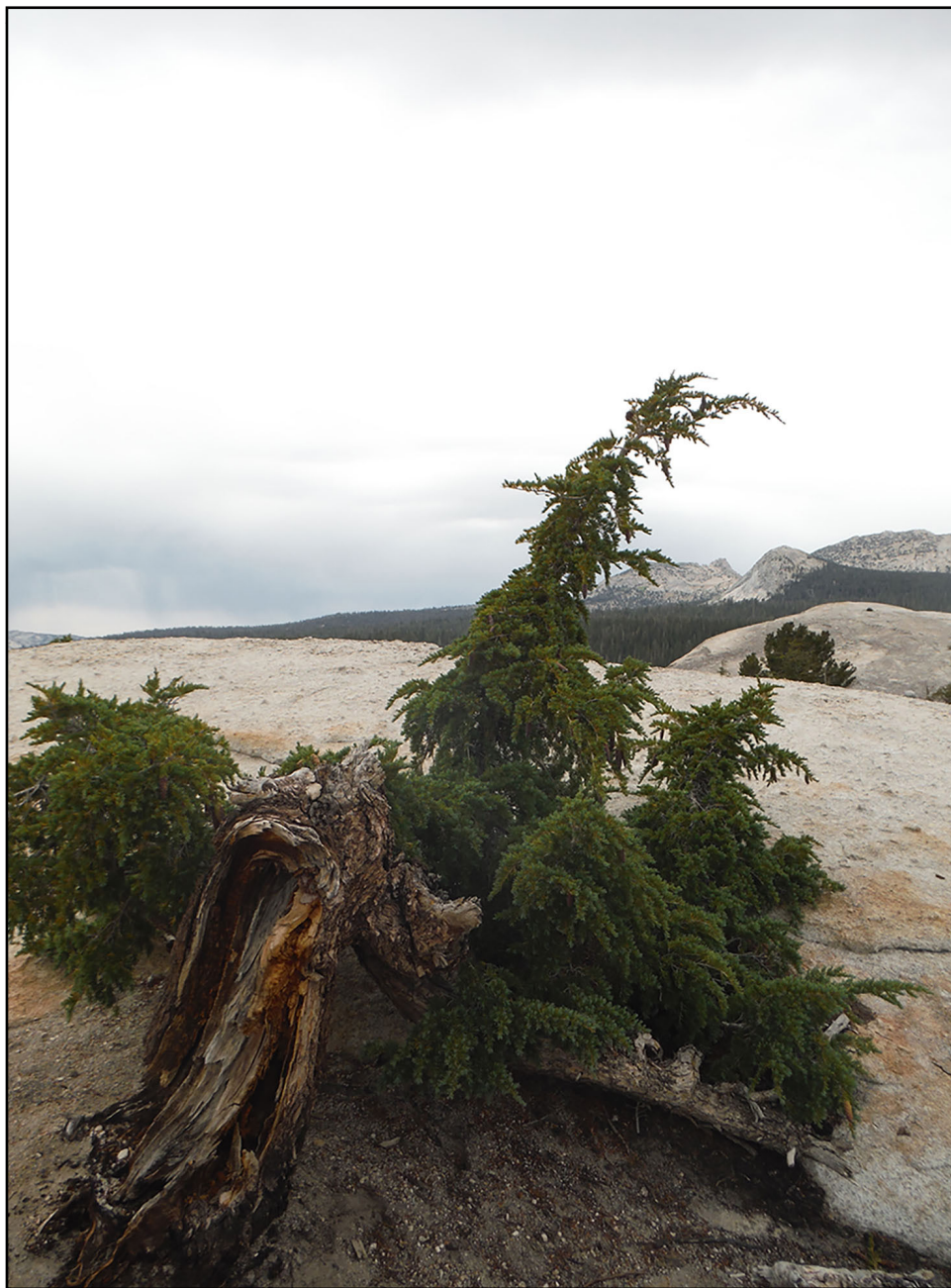
CDFW Photo by David Wright

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