Abundance, habitat and occupancy of Roosevelt Elk in the Bald Hills of Redwood National Park

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Fundamental to species management is understanding the factors that determine distribution or occupancy. We estimated occupancy in an area with two Roosevelt elk (*Cervus elaphus roosevelti*) herds that differed in abundance and hypothesized that habitat type (meadow, forest), herd, or both, influenced elk occupancy. Data were gathered from 12 repeated surveys of 47 stations conducted from May to August. At each 1-ha sign station, we surveyed for the presence or non-presence of elk sign 0–4 days old, recorded habitat type as forest or meadow, and noted which herd occupied the area. We tested the assumption of constant residence status and examined the influence of habitat and abundance on occupancy with nine single- and multi-season occupancy models. The most parsimonious model was a multi-season model where both herd and habitat type influenced occupancy and extinction. Both herds had lower occupancy of forest but complete occupancy of meadow. The herd with lower abundance had lower occupancy of forest, with occupancy declining over the 12 weeks. Roosevelt elk abundance likely influenced occupancy of forest but not meadow because forest provided less forage.

Keywords**:** abundance, California, *Cervus elaphus,* occupancy, forest, meadow, Roosevelt elk

Abundance is often used to make inferences about population persistence, however, estimates of abundance are usually costly. Therefore, some have suggested that estimating distribution or occupancy can be used as a surrogate for abundance (MacKenzie et al. 2002, 2003, 2006; Royle et al. 2005). Though it seems intuitive that larger abundances should result in higher occupancy rates, there is limited research on this relationship (Gaston et al. 2000; Freckleton et al. 2005). In spite of the limited information on abundance-occupancy relationships there is evidence that occupancy is linked to abundance but the relationship might be complicated by habitat (Freckleton et al. 2005; McLoughlin et al. 2006).

Habitat type may influence species occupancy (Gaston et al. 2000; Freckleton et al. 2005; MacKenzie et al. 2002, 2003, 2006). Thus, any consideration of the relationship between occupancy and abundance must also consider the relationship between occupancy

and habitat use of a given species. An increasing abundance may increase occupancy of marginal or lower quality habitat merely because high quality habitat is already occupied (Battin 2004; McLoughlin et al. 2006). A relationship of this nature will result in marginal habitats occupied at higher rates at high abundance and at lower rates at low abundance.

Roosevelt elk (*Cervus elaphus roosevelti*) in the Bald Hills of Redwoods National Park in northern California present an opportunity for exploring abundance and habitat influences on occupancy. Two elk herds of differing abundances occur along a north to south gradient in the Bald Hills (Starns et al. 2015; Kolbe and Weckerly 2015). In addition, Weckerly (2005) and Weckerly and Ricca (2000) reported that elk occupy meadows more frequently than forests presumably because meadows contain most of the forage in north coastal California. Yet, abundance was not considered in either study. Our objective was to estimate the influence of habitat type and abundance on occupancy by Roosevelt elk.

Materials and Methods

Study Area.—The Bald Hills area of Redwood National Park, Humboldt County, California (41˚ 11' N, 123˚ 56' W), was grazed by domestic livestock while under private ownership from about 1850 until 1977-1978 when it was acquired by the National Parks Service (Mandel and Kitchen 1979). The Bald Hills had a mild, continental climate with cool, wet winters and dry, warm summers broken by occasional fog (Weckerly and Ricca 2000; Kolbe and Weckerly 2015; Starns et. al 2015). Rain was the predominant form of precipitation with mean annual precipitation varying between ~1,200 and 1,800 mm (Weckerly and Ricca 2000). Additional precipitation was in the form of winter snow that can persist for 1–2 weeks and reach depths up to 40 cm (Starns et al. 2015). The mean summer and winter temperatures ranged from 24 ˚C to 27˚C and 3˚C to 5˚C respectively (Kolbe and Weckerly 2015).

The Bald Hills are a diverse landscape of forests and meadows. The region was approximately 4,000 ha in size (Weckerly and Ricca 2000). Meadows of 10–300 ha make up about 1,000 ha of the region while, oak woodlands, second growth, and old growth redwood (*Sequoia sempervirens*) conifer make up 76% of habitat (Weckerly and Ricca 2000; Kolbe and Weckerly 2015). The habitat in the Bald Hills generally varied with elevation which ranged from 360–930 m. Meadows generally occurred along ridgetops and contained several herbaceous species such as deervetch (*Lotus micranthus*), English plantain (*Plantago lanceolata*), California oatgrass (*Danthonia californica*), and sweet vernal grass (*Anthoxanthum odoratum*) (Weckerly and Ricca 2000; Kolbe and Weckerly 2015; Starns et. al 2015). Oak woodlands were dominated by white oak (*Quercus garryana*) and black oak (*Q. kelloggii*) while coast redwood and Douglas fir (*Pseudotsuga menziesii*) dominated second growth and old-growth redwood conifer forests (Weckerly and Ricca 2000; Kolbe and Weckerly 2015; Starns et. al 2015).

Roosevelt elk were non-migratory in the Bald Hills (Weckerly and Ricca 1995; Weckerly and Ricca 2000). In January, 2003, 204 elk were counted in the Bald Hills during systematic surveys and divided into two herds (Kolbe and Weckerly 2015; Starns et. al 2015). One herd was distributed in the northern Bald Hills while the other was distributed in the southern Bald Hills (Kolbe and Weckerly 2015). The northern herd had approximately 56 elk while the southern herd had about 148 elk (see Starns et al. 2015 for estimation methods). These herds consisted of adult females, juveniles, and sub-adult males (Kolbe and Weckerly 2015).

Methods.—Forty seven sign stations were surveyed weekly from the late May to early August, 2003, for a total of 12 surveys. All surveys were conducted by the same surveyor. Sign stations were 1-ha circular plots along roads with ≥0.8 km between stations (Weckerly and Ricca 2000). Thirteen sign stations included the area occupied by the southern herd and 34 included areas inhabited by the northern herd (Kolbe and Weckerly 2015). Oak woodlands, second growth and old growth confer stands were grouped into one habitat type, forest. There were 31 stations in forest habitat of which six were in areas that could be used by the southern herd and 25 that could be used by the northern herd. There were 16 stations in meadow habitat, seven stations in areas that could be used by the southern herd and nine stations that could be used by the northern herd. It took two days to survey all sign stations.

The surveyor searched for elk sign that was either hoof prints or feces between 0–4 days old. Sign that was ≤4 days old reduced errors in classifying sign as recent or old (Weckerly and Ricca 2000). Feces that were 0–4 days old were odious and moist and tracks that were 0–4 days old had limited plant detritus and track definition that had not be degraded by wind and moisture.

We estimated occupancy with nine single- and multi-season models in program PRESENCE (Hines 2014). We considered the entire 12 surveys a season in single-season models. To test the assumption of constant resident status, (i.e. no extinction or colonization across all surveys) we also considered multi-season models where the primary seasons were months and the secondary seasons were the four surveys conducted in each month (MacKenzie et al. 2006; Longoria and Weckerly 2007). We treated habitat as a binomial covariate where meadow was the reference category. We also considered abundance to be a binomial covariate with sign stations in the more abundant herd (the southern herd) coded as the reference category. Detection probability was kept constant in each of the nine models. The detection probability was the estimated probability of detecting elk sign during a survey when elk had actually visited the station. A preliminary analysis indicated that neither habitat type nor abundance influenced detection of sign. Colonization was set to zero in the multi-season models because no sign was detected in a primary season that had not been detected in a previous primary season. We considered five single-season models where habitat, abundance, both or neither influenced occupancy. We then considered these influences on occupancy in four multi-season models. We assessed model fit by ΔAIC_C where AIC_C was Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002). The ΔAIC_C was the difference in AIC_C between a given model and the model with the smallest AIC_C.

RESULTS

We selected the multi-season occupancy model where habitat and herd influenced both occupancy and extinction (Table 1). All other multi-season and single-season models had $\Delta AIC_C > 3.0 \, AIC_C$ units. In both herds meadows were completely occupied (1.0) throughout the 12 weeks (Table 2, Figure 1). Forest occupancy by the southern herd in the first month was similar to meadow occupancy but then declined in remaining months. The northern herd had lower forest occupancy that declined from the first to last month. The estimated detection probability was 0.36 (SE = 0.03).

Table 1. Model selection summary for occupancy by Roosevelt elk in the Bald Hills of Redwood National Park, Humboldt County, California, USA. Parameters estimated were occupancy ($\widehat{\psi}$), extinction ($\widehat{\varepsilon}$), and detection probability ($\hat{p}$). Covariates were habitat and herd. Reported in the table are the model parameters, number of parameter estimates (k), deviance (-2 log-likelihood), and ΔAICc for each model.

Model	k	-2 Log-likelihood	ΔAIC$_c$
$\widehat{\psi}$(Herd^1 + Habitat^2), $\widehat{\varepsilon}$(Herd + Habitat), $\hat{p}$(.)	7	577.11	0.00
$\widehat{\psi}$(Herd + Habitat),$\widehat{\varepsilon}$(.),$\hat{p}$(.)	5	584.15	3.04
$\widehat{\psi}$(Habitat),$\widehat{\varepsilon}$(.),$\hat{p}$(.)	4	589.16	6.05
$\widehat{\psi}$(Herd),$\widehat{\varepsilon}$(.),$\hat{p}$(.)	4	591.21	8.10
$\widehat{\psi}$(Herd + Habitat), $\hat{p}$(.)	4	591.90	8.79
$\widehat{\psi}$(Habitat), $\hat{p}$(.)	3	597.10	11.99
$\widehat{\psi}$(.),ε(.),$\hat{p}$(.)	3	597.94	12.83
$\widehat{\psi}$(Herd),$\hat{p}$(.)	3	599.24	14.13
$\widehat{\psi}$(.),$\hat{p}$(.)	2	606.39	19.28

Table 2. Untransformed parameter estimates and standard errors (SE) of the selected multi-season occupancy model of Roosevelt elk in the Bald Hills of Redwood National Park, Humboldt County, California, USA. Parameters in the multi-season model were occupancy ($\widehat{\psi}$), extinction ($\widehat{\varepsilon}$), and detection probability ($\hat{p}$). Covariates were habitat type and herd. Reference categories were meadow habitat and the more abundant herd. The $\hat{\beta}_0$ is the constant or intercept.

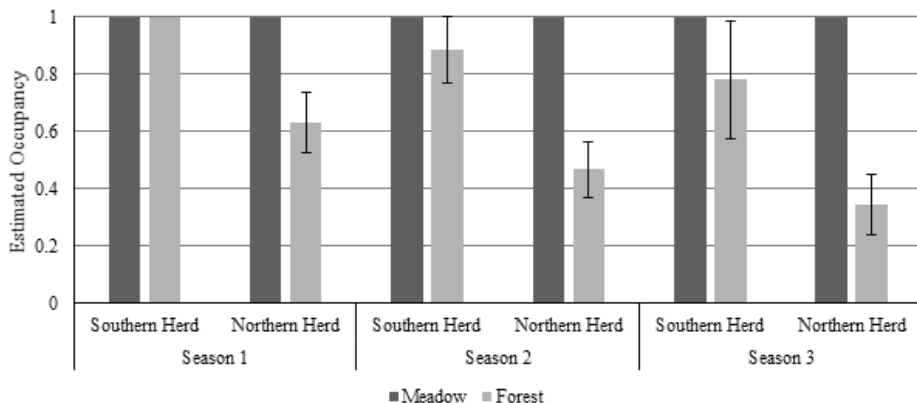| Coefficients	Estimate	SE
$\widehat{\psi}_{\hat{\beta}_0}$	61.973	1.634
$\widehat{\psi}_{\text{Herd}}$	-31.891	2.493
$\widehat{\psi}_{\text{Habitat}}$	-29.538	2.528
$\widehat{\varepsilon}_{\hat{\beta}_0}$	-42.236	18.732
$\widehat{\varepsilon}_{\text{Herd}}$	0.995	1.237
$\widehat{\varepsilon}_{\text{Habitat}}$	40.208	18.768
$\hat{p}_{\hat{\beta}_0}$	-0.561	0.110

FIGURE 1.—Estimates of occupancy from sign surveys conducted for Roosevelt elk in the Bald Hills of Redwood National Park, Humboldt County, California, USA. Reported are the three secondary-season occupancy estimates with SE bars. Estimates are divided into northern and southern herds that had different abundances. The southern herd had the highest abundance. The dark gray bars are meadow and light gray bars are forest.

DISCUSSION

Our results suggest that Roosevelt elk occupancy is influenced by abundance and habitat type. Occupancy was highest in meadows and lowest in forests. Meadows were occupied by elk at the highest possible rate (1.0) although abundance differed greatly. Forest habitat was occupied at a lower rate than meadow habitat and at an even lower rate when abundance was low. Thus, elk occupy marginal habitat when quality habitat is already occupied but it is conditional on elk abundance. Elk occupied forest more frequently when abundance was high. Our results contrasted with those of Gaston et al. (2000), who suggested that differences in habitat quality would not influence abundance-occupancy relationships at large spatial scales. However, this may be a product of the study taxa. Gaston et al. (2000) discussed abundance and occupancy relationships of songbirds not elk. In Europe individual *C. elaphus* used habitat in a manner consistent with an ideal-free distribution (McLoughlin et al. 2006) whereas songbirds generally follow an ideal-despotic distribution (Holmes et al. 1996). The smaller body size and despotic behavior displayed by songbirds might affect habitat use in relation to abundance differently than elk. Elk range over a larger area and often occupy multiple kinds of habitat with marginal habitat used more frequently during high abundance. Songbirds often use one kind of habitat and adjust territory size according to habitat quality (Warren et al. 2013). In high quality habitat territory size is smaller than in marginal habitat. The result can be that songbird occupancy is similar in low and high quality habitat.

Occupancy of forest habitats by elk decreased in both herds across the 12 weeks of surveys, a period when food resources in forests may have declined. Meadows, in contrast, maintained the same occupancy throughout the 12 weeks. The heterogeneity in occupancy across months suggests that elk distribution can change across months (MacKenzie et al.

2006; Longoria and Weckerly 2006). The higher occupancy rate and lower extinction rate in meadows is in line with previous studies of habitat influences on Roosevelt elk distribution (Weckerly and Ricca 2000; Weckerly 2005; Starns et al. 2015; Kolbe and Weckerly 2015). Extinction may have been influenced by abundance as it was in the top model; however, the standard error of the herd coefficient was high. The imprecision of extinction coefficients might be affected by the small sample size in relation to the number of parameters estimated by the model.

The estimated probability of detection (0.36) was surprisingly low. Weckerly and Ricca (2000) reported an estimated detection probability (0.96) that was almost three times higher. Our surveys were conducted in the summer and not winter when other sign surveys were conducted (Weckerly and Ricca 2000; Weckerly 2005). Weckerly and Ricca (2000) also did not estimate the detection probability using occupancy estimators. Nonetheless, the warm, dry climate of the Bald Hills in the summer could have dried the feces resulting in misclassifications (i.e., 0-4 day old feces classified as >4 day old feces). Similarly hoof prints made in moist substrate in winter are likely to be readily detectable, while hoof prints on a dry substrate may be less detectible and denude more quickly. Thus the difference in our estimated detection probability could be a product of missing sign and misclassifying young sign as old. If error in aging sign did occur then it might have been more extensive in forests than in meadows. Forests receive less direct sun light and are generally moister than meadows. The misclassification in age of sign would not negate our findings, however, because the misclassification would likely result in estimates that were biased low in meadows and high in forests. Yet, we still estimated lower occupancy in forests. Future studies that consider summer occupancy of elk should consider measuring covariates such as precipitation, number of dry days, and weekly average wind speeds because they might denude signs and make them less likely to be detected.

Our analysis suggests that Roosevelt elk occupancy is driven by both habitat type and abundance. Our findings are in accord with the ideal-free distribution. Roosevelt elk use habitats of high quality most often and low quality habitat less often. Roosevelt elk habitat use is analogous to the findings of McLoughlin et al. (2006) who found that as density increased red deer selected a wider range of habitats. In the same way, Bald Hill forests were occupied at a higher rate by the more abundant southern herd than by the northern herd. In contrast, the higher quality meadows were occupied at the same rate for both herds. Additionally, Kolbe and Weckerly (2015) found that the home-ranges of the two Bald Hills herds were similar in size. Yet, the southern herd had an abundance that was roughly 3 times greater than the northern herd. One way for both herds to have similar home range sizes is for the more abundant herd to occupy marginal habitat more often. Our study suggests that abundance and habitat influence occupancy of Roosevelt elk.

Logistical burdens are usually high when estimating elk abundance because population surveys often are conducted from aircraft or by intense ground surveys. We have shown that sign surveys, which are relatively less costly, present a viable alternative for monitoring elk populations. Moreover, occupancy or distribution of elk can be estimated accommodating imperfect detection of sign. Because elk are distributed in the manner of an ideal-free distribution, changes in occupancy of quality and marginal habitat should also shed insight into changes in elk abundance.

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