California Fish and Game 102(1):8-16; 2016

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

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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 km^2 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

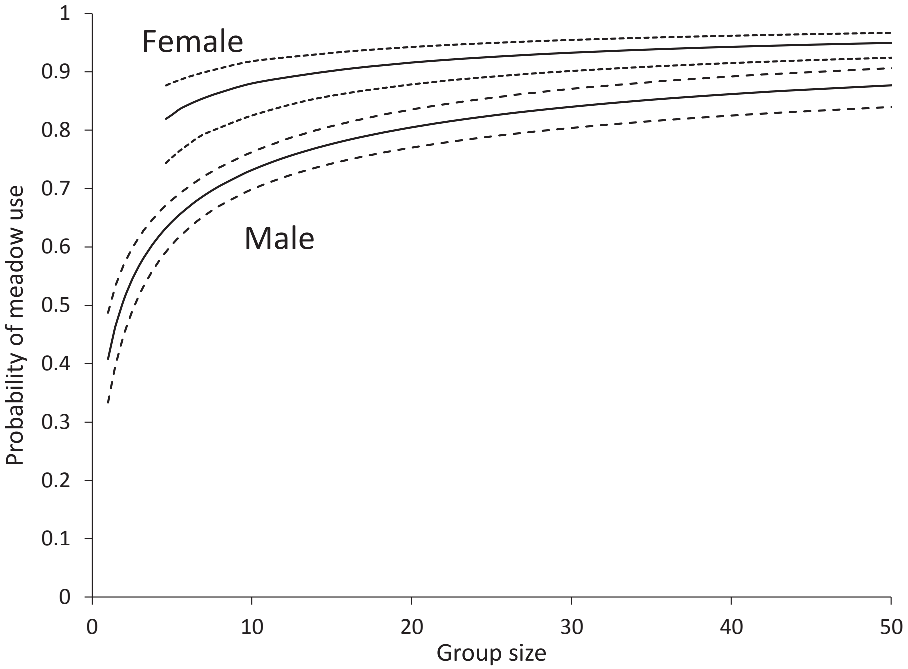

Figure 1.—Probability of meadow use by group size and sex of Roosevelt elk in Redwood National and State Park, 1997–2015. Regressions for each sex were controlled for prescribed fire. The regressions are solid lines, and the 95% confidence intervals are shown by dashed lines.

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.

Acknowledgments

We thank the many students and local experts who helped with this project over its 19 years. In particular, we thank: A. Duarte, R. Keleher, N. Kolbe, J. Hunt, D. Lancaster, M. Longoria, R. Luna, K. McFarland, M. O'Dell, L. Peterson, M. Ricca, K. Richardson, S. Robinson, K. Schmidt, S. Shelton, H. Starns, G. Street, and D. Wolcott. We are also very thankful for the assistance and support we received from Redwood National and State Parks. Funding was provided by the California Department of Fish and Wildlife, National Science Foundation, Redwood National Park, Rocky Mountain Elk Foundation, Alamo Safari Club, Granite Bay Safari Club, Houston Safari Club, and Texas State University.

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Received 16 October 2015
Accepted 23 February 2016
Associate Editor was J. Villepique