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

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

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

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

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

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

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

Materials and Methods

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

The climate in the region has wet, cool winters, and dry summers during which precipitation is mostly limited to occasional fog (Starns et al. 2015). Average annual precipitation varies from approximately 1,200 to 1,800 mm and occurs mostly as rain (Hektner et al. 1983). Ninety percent of this precipitation falls between the months of October and April. Snow is common during the winter months (November–February) in some years but rarely remains on the ground beyond a week. Precipitation data between October 2002 and April 2003 were obtained from the RAWS USA Climate Archive (http://www.raws.dri.edu). Mean summer temperatures range from 24 to 27°C and mean winter temperatures range from 3 to 5°C. Elevations range from 360 to 1,050 m. The landscape is comprised of meadows (24%), oak (*Quercus* spp.) woodlands (10%), and second-growth and old-growth redwood-conifer stands (66%) that are dominated by coast redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*; Weckerly and Ricca 2000). Oak woodlands are comprised of Oregon white oak (*Q. garryana*) and California black oak (*Q. kelloggii*). Grassland meadows have a mix of perennial and annual grasses including California oatgrass (*Danthonia californica*), sweet vernal grass (*Anthoxanthum* odoratum), deer vetch (*Lotus micranthus*), and English plantain (*Plantago lanceolata*).

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

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

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

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

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

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

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

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

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

To estimate NDVI, Landsat 5 Thematic Mapper images, obtained at 16-day intervals, were downloaded from USGS Earth Explorer (http://earthexplorer.usgs.gov) from January 1989 to November 2011. These images have a pixel resolution of 30 m^2, an area that is adequate for measuring plant biomass in meadows used by elk. Approximately 200 images were free of cloud cover. Monthly mean NDVI readings from 1989 to 2011 were used due to the lack of cloud-free images for all months in 2003. Each cloud-free image was corrected for top-of-atmospheric reflectance using the methods described by Chander et al. (2009) prior to deriving estimates. Images were then clipped down to the Bald Hills meadows. Pixels with NDVI values < 0.1 were then re-classified as "null" since they most likely were bare ground, water, or snow (Starns et al. 2015). In months where two images were available, the average of the NDVI means between the two images was used in analyses (Starns et al. 2015). All image processing was carried out using ERDAS Imagine 2013 (Intergraph Corporation 2013). An *a posteriori* two-tailed *t*-test comparing monthly rainfall accumulation in 2003 to the monthly average rainfall for the remaining years was conducted to assess if precipitation in 2003 deviated from that recorded during the other years.

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

Results

The Bald Hills received 1,016 mm of precipitation between the months of October 2002 and April 2003. When we compared 2003 monthly rainfall data (= 9.81 cm) and averaged monthly rainfall for the remaining years of 1989 to 2002 and 2004 to 2011 (= 11.21 cm) we found no differences (t=−0.898, df=11, P=0.388) suggesting that 2003 was an average year for monthly precipitation. Home-range size for animal A fluctuated from a minimum of 33 ha in January to a maximum of 3,975 ha in August. The average monthly home-range size for animal A was 2,192 ha (±472) ha. Animal B had a minimum home range of 1,051 ha in April and a maximum home-range size of 4,059 ha in August. Average monthly home-range size for animal B was 2,793 ha (±494) ha. There was no overlap in home-ranges between these two elk in January, February, September and October. In the remaining months, the mean overlap area was 464 ha (±157) ha with a minimum of 28 ha in November and a maximum of 1,417 ha in August. Taking the mean monthly overlap (309 ha) and dividing by mean monthly home-range sizes resulted in a mean home-range overlap of 11 percent (Figure 1). There was a positive relationship ($R^2 = 0.49$, $F_{1,10} = 3.129$, $P = 0.011$) between NDVI and home-range overlap (Figure 2). There was also a positive relationship between NDVI and HAI ($R^2 = 0.41$, $F_{1,10} = 2.627$, $P = 0.025$; Figure 2).

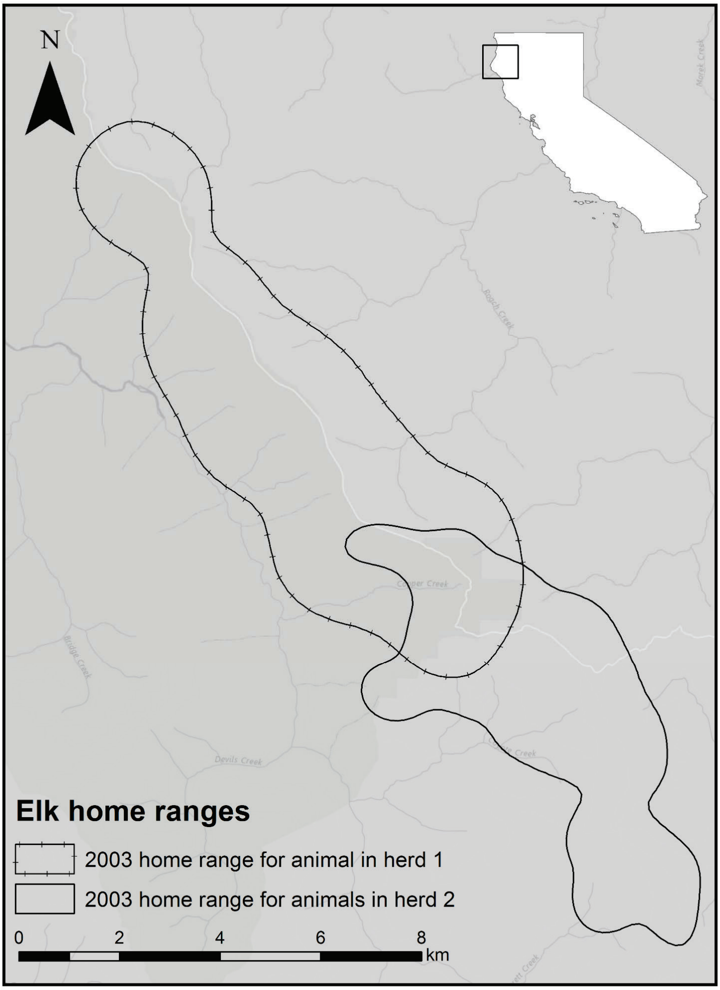

FIGURE 1.—Fixed kernel (FK) estimate for the single Roosevelt elk (*Cervus elaphus roosevelti*) in herd 1 and the FK estimate for the three elk in herd 2 of the Bald Hills of Redwood National Park, Humboldt County, California, 2003.

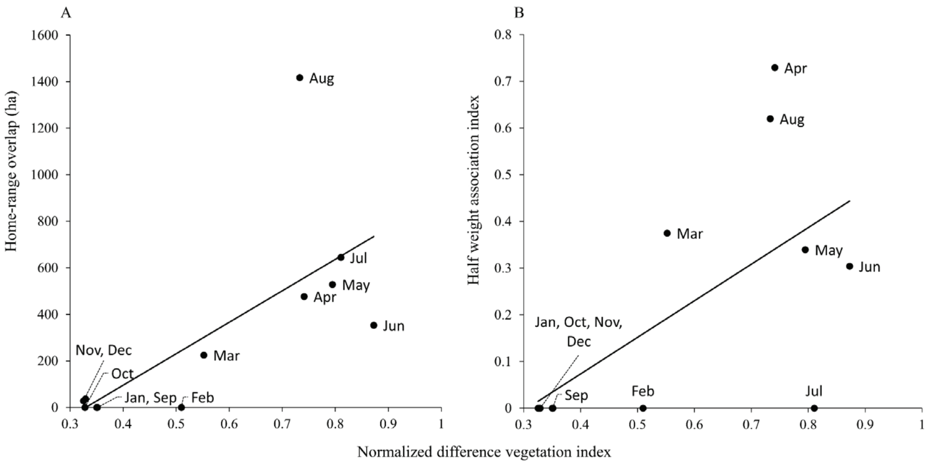

Figure 2.—Scatter plots with regressions of A) normalized difference vegetation index (NDVI) and home range area of overlap and B) NDVI and half-weight association index for Roosevelt elk in the Bald Hills of Redwood National Park, Humboldt County, California, 2003.

Discussion

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

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

The generally larger home ranges in the late spring and summer months and the increased home-range overlap between adjacent herds probably reflects the concomitant increase in food supply and energetic demands of reproduction. Pregnant females in late spring are known to distance themselves from other animals during times of parturition to decrease chances of predation on neonates. Such dispersion can result in an enlarged home range and more home-range overlap between adjacent herds. Immediately after parturition mothers also face the energetic demands of lactation (Cook et al. 1996, 2004), which corresponds with seasonal peaks in food supply (Phillips et al. 1973, Georgii 1980). Thus, the greater home-range overlap in late spring and summer is, to some extent, due to reproductive activities; yet, those reproductive activities probably evolved to coincide with the period during which food is most plentiful. Regardless of whether the observed patterns in home-range overlap are associated with seasonal food supply, reproductive activities, or both, these results are consistent with past observations in elk that found overlapping home ranges during seasons when vegetation is growing (Craighead et al. 1973, Jenkins and Starkey 1982, Cornelis et al. 2011).

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

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

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Literature Cited

Anderson, D. P., J. D. Forester, M. G. Turner, J. L. Frair, E. H. Merrill, D. Fortin, J. S. Mao, and M. S. Boyce. 2005. Factors influencing female home range size in elk (*Cervus elaphus*) in North American landscapes. Landscape Ecology 20:257-271.

Anderson, G. L., J. D. Hanson, and R. H. Haas. 1993. Evaluating landsat thematic mapper derived vegetation indices for estimating above-ground biomass on semiarid rangelands. Remote Sensing of Environment 45:165-175.

Bowyer, R. T. 1981. Activity, movement, and distribution of Roosevelt elk during rut. Journal of Mammalogy 62:574-582.

Brotherton, P. N., M., J. M. Pemberton, P. E. Komers, and G. Malarky. 1997. Genetic and behavioral evidence of monogamy in a mammal, Kirk's dik-dik (*Madoqua kirkii*). Canadian Journal of Zoology 81:1589-1597.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Chander, G., B. L. Markham, and D. L. Helder. 2009. Summary of current radiometric calibration coefficients for landsat MSS, TM, ETM+, and EO-1 ALI sensors. Remote Sensing of Environment 111:893-903.

Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1996. Nutrition-growth relations of elk calves during late summer and fall. Journal of Wildlife Management 60:528-541.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1-61.

Cornelis, D., S. Benhamou, G. Janeau, N. Morellet, M. Ouedraogo, and M. Visscher. 2011. Spatiotemporal dynamics of forage and water resources shape space use of West African savanna buffaloes. Journal of Mammalogy 92:1287-1297.

Craighead, J. J., F. C. Craighead, Jr., R. L. Ruff, and B. W. O' Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison Drainage herd as determined by biotelemetry. Wildlife Monographs 33:1-50.

Elmore, A. J., J. F. Mustard, S. J. Manning, and D. B. Lobell. 2000. Quantifying vegetation change in semiarid environments: precision and accuracy of spectral mixture analysis and the normalized difference vegetation index. Remote Sensing of Environment 73:87-102.

ESRI (Environmental Science Research Institute). 2014. ArcGIS Desktop 10.2. Environmental Science Research Institute, Redlands, California, USA.

Franklin, W. L., A. S. Mossman, and M. Dole. 1975. Social organization and home range of Roosevelt elk. Journal of Mammalogy 56:102-118.

Franklin, W. L., and J. W. Lieb. 1979. The social organization of a sedentary population of North American elk: a model for understanding other populations. North American elk: ecology, behavior and management. Pages 185-198 *in* M. S. Boyce and L. D. Hayden-Wing, editors. University of Wyoming, Laramie, USA.

Georgi, B. 1980. Home range patterns of female red deer (*Cervus elaphus* L.) in the Alps. Oecologia 47:278-285.

Harper, J. A., J. H. Harn, W. W. Bentley, and C. F. Yocom. 1967. The status and ecology of the Roosevelt elk in California. Wildlife Monographs 16:1-49.

Hektner, M. M., R. W. Martin, and D. R. Davenport. 1983. The Bald Hills prairies of Redwood National Park. Pages 70-78 *in* L. D. Whittig and M. L. Murphy, editors. Proceedings of the Biennial Conference of Research in California's National Parks 111:70-78.

Horne, J. S., and E. O. Garton. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70:641-648.

Intergraph Corporation. 2013. ERDAS Imagine 2013. Intergraph Corporation, Huntsville, Alabama, USA.

Jenkins, K. J., and E. E. Starkey. 1982. Habitat use by Roosevelt elk in unmanaged forests of the Hoh Valley, Washington. Journal of Wildlife Management 48:642-646.

Julian, A. E., K. Schmidt, and F. W. Weckerly. 2013. Group size dynamics of female Roosevelt elk in Redwood National and State Parks, California. California Fish and Game 99:49-54.

Kie, J. G. 2013. A rule-based *ad hoc* method for selecting a bandwidth in kernel home-range analyses. Animal Biotelemetry 1:1-13.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. Journal of Applied Ecology 44:663-671.

Lieb, J. W. 1973. Social behavior in Roosevelt elk cow groups. M.S. Thesis, Humboldt State University, Arcata, California, USA.

Mandel, R. D., and D. W. Kitchen. 1979. The ecology of Roosevelt elk in and around the Redwood National Park. Humboldt State University, Arcata, California, USA.

Miller, M. W., M. A. Wild, and W. R. Lance. 1996. Efficacy and safety of naltrexone hydrochloride for antagonizing carfentanil citrate immobilization in captive Rocky Mountain elk (*Cervus elaphus nelsoni*). Journal of Wildlife Diseases 32:234-239.

Phillips, R. L., W. E. Berg, and D. B. Siniff. 1973. Moose movement patterns and range use in northwestern Minnesota. Journal of Wildlife Management 37:266-278.

RAWS USA Climate Archive. 2015. RAWS 2015. Remote Automatic Weather Stations, Boise, Idaho, USA.

R Development Core Team. 2014. R: a language and environment for statistical computing. R Development Core Team, Vienna, Austria.

Rutberg, A. T. 1983. Factors influencing dominance status in American bison cows (*Bison bison*). Zeitschrift fur Tierpsychologie 63:206-212.

Scillitani, L., G. Darmon, A. Monaco, G. Cocca, E. Sturaro, L. Sturaro, L. Rossi, and M. Ramanzin. 2013. Habitat selection in translocated gregarious ungulate species: an interplay between sociality and ecological requirements. Journal of Wildlife Management 77:761-769.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

Sokal, R. R., and F. J. Rohlf. 2012. Biometry: the principles and practice of statistics in biological research. Third edition. W. H. Freeman and Company, San Francisco, California, USA.

Starns, H. D., F. W. Weckerly, M. A. Ricca, and A. Duarte. 2015. Vegetation changes associated with a population irruption by Roosevelt elk. Ecology and Evolution 5:109-120.

Thouless, C. R., and F. E. Guinness. 1985. Conflict between red deer hinds: the winner always wins. Animal Behaviour 34:1166-1171.

USGS EarthExplorer. 2011. U.S. Department of the Interior [Internet]. USGS EarthExplorer; Available from http://earthexplorer.usgs.gov

Weckerly, F. W. 1999. Social bonding and aggression in female Roosevelt elk. Canadian Journal of Zoology 77:1379-1384.

Weckerly, F. W., and M. A. Ricca. 2000. Using presence of sign to measure habitats used by Roosevelt elk. Wildlife Society Bulletin 28:146-153.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164-168.

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