BioOne COMPLETE

Resource Selection and Movements by Female Mule Deer Odocoileus hemionus: Effects of Reproductive Stage

Authors: Long, Ryan A., Kie, John G., Terry Bowyer, R., and Hurley, Mark A.

Source: Wildlife Biology, 15(3) : 288-298

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/09-003

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Wildl. Biol. 15: 288-298 (2009)
DOI: 10.2981/09-003
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage

Ryan A. Long, John G. Kie, R. Terry Bowyer & Mark A. Hurley

Recent declines of mule deer *Odocoileus hemionus*, ostensibly a result of low rates of recruitment, highlight the importance of understanding relationships between parturient females and their critical habitats. We estimated timing of parturition for 20 mule deer in northeastern Oregon, USA, using movement data from global positioning system (GPS) collars in 2005 and 2006. We then evaluated patterns of resource selection by female mule deer during late gestation, the week of parturition, and subsequent lactation to determine how different stages of reproduction influenced habitat selection. Movement rates of all but one deer declined sharply between late-May and mid-June, when female mule deer give birth in northeastern Oregon. Patterns of resource selection also varied substantially relative to the estimated time of parturition. Prior to parturition, female mule deer selected gentle south-facing slopes dominated by ponderosa pine *Pinus ponderosa* and avoided permanent water sources. Parturient females also selected areas used concurrently by elk *Cervus elaphus*. Following parturition, however, females selected steep north-facing slopes dominated by fir *Abies* spp., avoided elk and selected habitat located close to permanent water sources. Stage of reproduction clearly influenced choice of habitat by female mule deer. Mule deer management plans should consider potential seasonal variability in the relative importance of forage, risk of predation and competition.

Key words: forage, GPS collars, movement, Odocoileus hemionus, risk of predation, resource selection, timing of parturition

Ryan A. Long & R. Terry Bowyer, Department of Biological Sciences, 921 South 8th Avenue, Stop 8007, Idaho State University, Pocatello, Idaho 83209, USA - e-mail addresses: longryan@isu.edu (Ryan A. Long); bowyterr@isu.edu (R. Terry Bowyer)
John G. Kie, Department of Biological Sciences, 921 South 8th Avenue, Stop 8007, Idaho State University, Pocatello, Idaho 83209, USA, and USDA Forest Service, Pacific Northwest Research Station, La Grande, Oregon 97850, USA - e-mail: kiejohn@isu.edu
Mark A. Hurley, Idaho Department of Fish and Game, 99 Highway 93 N, Salmon, Idaho 83467, USA - e-mail: mhurley@idfg.idaho.gov

Corresponding author: Ryan A. Long

Received 6 January 2009, accepted 4 April 2009

Associate editor: Marco Festa-Bianchet

Life-history strategies of ungulates have been shaped by multiple factors, including the need to acquire energy while avoiding predation (Stearns 1992, Kie 1999). Ungulates frequently face environmental constraints on their ability to survive and reproduce (Berger 1991, Kie 1999), and females, in particular, must balance energy invested in current offspring against the probability of surviving to reproduce again (Trivers 1974, Roff 1992, Stearns 1992). Consequently, females occupying heterogeneous landscapes often are forced to choose among environmental factors affecting the acquisition and investment of energy (Hamel & Côté 2008). For example, a positive spatial correlation between risk of predation and forage quality or abundance may necessitate trade-offs between predator avoidance

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

and forage acquisition (Bowyer et al. 1998, 1999, Rachlow & Bowyer 1998, Barten et al. 2001, Hamel & Côté 2007).

Stage of reproduction influences patterns of resource selection, space use and movement in female ungulates (Berger 1991, Rachlow & Bowyer 1998, Barten et al. 2001). Energetic investment in the developing fetus peaks during the last third of gestation (Barboza & Bowyer 2000, 2001), and susceptibility to predation is lowest for females without young at heel (Berger 1991). As a result, females should select habitat that provides ample forage during gestation. Conversely, susceptibility of neonates to predation is highest in the first few weeks following parturition (Bowyer et al. 1998, Ballard et al. 2001, Pojar & Bowden 2004). In addition, nutritional requirements of parturient females begin to increase shortly after parturition with the onset of lactation, and typically peak roughly 4-6 weeks following birth of young (Sadleir et al. 1982, Clutton-Brock et al. 1989). This simultaneous increase in nutritional requirements of the mother and vulnerability of young to predation following parturition imposes a significant constraint on the ability of females to provision and rear young (Bowyer et al. 1999), and understanding how females cope with such constraints behaviourally can provide important insights into the evolution of ungulate life-history strategies.

Behaviour represents one of the primary mechanisms by which animals cope with environmental constraints on survival and reproductive success (Krebs & Davies 1997). Accordingly, female ungulates often modify their behaviour in response to the different nutritional demands and degrees of susceptibility to predation imposed by gestation, parturition and lactation. Previous studies have documented effects of reproductive stage on the use of space (Clutton-Brock et al. 1982, Bleich et al. 1997, Ciuti et al. 2006), foraging strategy (Ruckstuhl & Festa-Bianchet 1998, Neuhaus & Ruckstuhl 2002), antipredator behaviour (Barten et al. 2001) and social interactions (Clutton-Brock & Guinness 1975, Bertrand et al. 1996) for a variety of ungulates. Few studies, however, have simultaneously considered effects of landscape features such as topography, distance to roads, distance to water and canopy cover on behaviour of female ungulates relative to their stage of reproduction.

Mule deer *Odocoileus hemionus* populations have declined recently, ostensibly a result of low rates of recruitment (Unsworth et al. 1999, Pojar & Bowden 2004). These declines underscore the importance of understanding relationships between mule deer, particularly parturient females, and their habitat requirements. We conducted post-hoc analyses of a location data set for female mule deer collected at the Starkey Experimental Forest and Range in northeastern Oregon to evaluate patterns of resource selection by female mule deer relative to estimated time of parturition. Cervids exhibit substantial reductions in movement immediately following parturition (Bertrand et al. 1996, Bowyer et al. 1999, Vore & Schmidt 2001, Carstensen et al. 2003, Ciuti et al. 2006). Consequently, we hypothesized that movement rates of female mule deer could be an index to timing of parturition. The retrospective nature of our data set prevented us from testing this hypothesis by directly observing births. Instead, we evaluated several important predictions from the hypothesis that movement rates reflect timing of parturition. If female mule deer in our study reduced movements immediately following parturition, then: 1) the mean date of the reduction in movement rates should occur between late-May and mid-June, when female mule deer typically give birth at latitudes comparable to our study area (Steigers & Flinders 1980); 2) synchrony of the reduction in movement rates among deer should match published data on synchrony of parturition in mule deer; and 3) because pregnancy rates in mule deer typically are high when population density is low (Connolly 1981), at least 80% of the collared deer in our study should significantly reduce movement rates at the appropriate time of year, because density of deer in our study area is low relative to carrying capacity (Johnson et al. 2000). We also hypothesized that stage of reproduction would influence resource selection and movement patterns of female mule deer because gestation, parturition and lactation each impose different energetic demands (Barboza & Bowyer 2000, 2001) and susceptibility to predation (Bleich et al. 1997).

Material and methods

Study area

We conducted research at the Starkey Experimental Forest and Range in northeastern Oregon, USA (hereafter Starkey; 45°13'N, 118°31'W). Starkey encompasses 101 km^2 and is managed by the U.S. Forest Service. The area is surrounded by a 2.4-m high fence, which prevents immigration and emi-

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

gration of large herbivores (Rowland et al. 1997). Predators of mule deer fawns at Starkey include coyotes *Canis latrans*, mountain lions *Puma concolor* and black bears *Ursus americanus*. We collected data on locations of female mule deer in one main study area of 78 km^2, which was representative of habitats of the Blue Mountains of northeastern Oregon and Washington, USA. Habitat choices available to mule deer were comparable to those outside Starkey, and traffic levels, recreational activities (including hunting of mule deer and elk in autumn and winter) and timber management were similar to those on surrounding public lands (Rowland et al. 1997).

Elevations at Starkey range from 1,120 m to 1,500 m; common plant associations include bunchgrasses of the species *Festuca idahoensis*, *Poa secunda* and *Pseudoroegneria spicata*, ponderosa pine *Pinus ponderosa*, Douglas-fir *Pseudotsuga menziesii*, grand fir *Abies grandis* and lodgepole pine *Pinus contorta*. Botanical nomenclature follows U.S. Department of Agriculture, Natural Resources Conservation Service (2007). Total precipitation at La Grande, Oregon, USA (40 km from the study site), was 34 cm in 2005 and 36 cm in 2006; mean annual temperature was 9.0°C in 2005 and 9.5°C in 2006 (Western Regional Climate Center). Approximately 500 cow-calf pairs of cattle were introduced to the main study area around 15 June and removed again by 15 October during each year of our study.

Animal handling and locations of deer

Female mule deer (adults $\geq$2 years of age) were captured by project personnel at Starkey during the winters of 2004 and 2005 with panel traps baited with hay (Rowland et al. 1997). Following capture, deer were fitted with Global Positioning System (GPS) collars (model 4400M, Lotek Wireless, Inc., Newmarket, Ontario, Canada) and released back into the study area. Collars were recovered the following winter and most individual deer were monitored for only one year. Deer locations were stored on each GPS collar and retrieved at programmed intervals via an automated retrieval system (Wisdom et al. 2006). A computer queried each of eight cellphone modems located at high points in the study area at regular intervals. Each modem was connected to an ultra-high frequency (UHF) modem at the same location, and every time a connection was established, the UHF modem was directed to retrieve all data stored on GPS collars within line-of-sight of that location (Wisdom et al. 2006). Mean positional error of GPS collars was $\leq$10 m (Wisdom et al. 2006). We obtained location data for 20 female mule deer (10 in 2005 and 10 in 2006) at 50-90 minute intervals 24 hour/day for the duration of our study, giving a total of 27,041 locations.

Adult female elk *Cervus elaphus* also were captured and fitted with GPS collars during 2005 and 2006 to account for the effects of elk on resource selection by mule deer (Johnson et al. 2000, Stewart et al. 2002, 2006). Elk were lured onto a winter feeding ground beginning in mid-December, where they could be maneuvered easily into a nearby handling facility (Rowland et al. 1997). Individual females were fitted with GPS collars in early spring before being released back into the main study area. We obtained data on locations at 50-90 minute intervals for a total of 31 individual elk (eight in 2005 and 23 in 2006) during our study, giving a total of 68,831 locations. All capture and handling procedures were in accordance with protocols approved by an established Institutional Animal Care and Use Committee (Wisdom et al. 1993) and were in compliance with guidelines adopted by the American Society of Mammalogists Animal Care and Use Committee (Gannon et al. 2007).

Timing of parturition

We estimated timing of parturition at 1-week intervals from movement rates (km/hour) of female mule deer. Although we did not directly observe mule deer fawns during our study, cervids commonly exhibit a marked (i.e. $\geq$50%) decline in movement rates immediately following parturition; this well-documented change in behaviour can be used to estimate timing of parturition (Bertrand et al. 1996, Bowyer et al. 1999, Vore & Schmidt 2001, Carstensen et al. 2003, Ciuti et al. 2006). At latitudes comparable to Starkey, female mule deer typically give birth between late-May and mid-June (Steigers & Flinders 1980), and thus substantial reductions in movement rates of female deer during that period serve as an index to the timing of parturition. One female whose movement rates did not change significantly over time based on overlapping 95% confidence intervals was excluded from subsequent analyses of resource selection. After identifying the estimated week of parturition for each individual, we set that week equal to time 0 for each deer to evaluate weekly patterns of resource selection. In addition, we compared synchrony of parturition

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

among female mule deer at Starkey with previous studies of mule deer by calculating a mean date of birth and associated SD from data on estimated week of parturition using the methods of Johnson et al. (2004), which provide a robust approach to dealing with grouped (binned) data.

Predictor variables

We included predictor variables in our analyses that are thought to influence patterns of resource selection and space use by female mule deer at Starkey (Johnson et al. 2000, Stewart et al. 2002). We obtained the following variables from the habitat database at Starkey (Rowland et al. 1998): slope (in %), convexity (a measure of topographical complexity; Johnson et al. 2000), aspect (transformed with sine and cosine functions to measure eastness and northness of aspect, respectively), distance to open (open to public access) and restricted (access restricted to authorized personnel) roads (in m), distance to permanent water (in m) and elevation (in m a.s.l.). We obtained values of each habitat variable for every 30 m^2 pixel in the study area.

In addition to variables obtained from the habitat database, we incorporated data on total canopy closure (in %) and habitat type (vegetation association) into our analyses. Those data were derived at a 30-m^2 resolution from 1:12,000 colour aerial photos of the study area taken in 2000. We used the categorization of Kie et al. (2005) as a basis for defining habitat types: 1) dry grassland, 2) wet meadow-riparian, 3) mesic forest dominated by grand fir or Douglas-fir, 4) xeric forest dominated by ponderosa pine, and 5) xeric forest dominated by lodgepole pine. In addition, each forested type was divided into two subtypes based on tree size: 1) small trees (canopy closure $\geq 40\%$ in trees ≤ 10.2 cm diameter at breast height = 1.37 m), or 2) large trees (canopy closure of small trees $< 40\%$).

We also included probability of use by elk as a predictor variable in our analyses. We estimated probability of use with utilization distributions (UDs) derived from elk locations. We produced 95% fixed kernel UDs on a weekly basis for the population of radio-collared elk at Starkey using the Home Range Tools extension for ArcGIS (Rogers et al. 2007). Rather than using a mathematical optimization routine to select the appropriate bandwidth for each UD, we fixed the bandwidth at 183 m for all UDs. This value represents an estimate of the perception distance of elk in semi-open terrain (Reynolds 1966), and thereby provides a biological basis for selecting the bandwidth. In addition, we used a 30-m^2 grid structure for estimating UDs to match the resolution of our habitat layers.

Modeling

We evaluated patterns of resource selection by female mule deer from six weeks prior to six weeks after the estimated period of parturition. As a result of relatively small sample sizes within years, we pooled data from 2005 and 2006 to calculate resource selection functions (RSFs) at the population level for each of 13 weeks (six weeks prior to parturition and six weeks post-parturition). We estimated RSFs based on a matched-case design (Hosmer & Lemeshow 2000, Manly et al. 2002, Boyce 2006). Locations from individual deer represented used points, each of which was assigned to the appropriate 30-m^2 pixel within the study area to determine values of associated habitat variables. We also joined the estimated probability of use by elk (UD height) associated with each pixel to all deer locations occurring in that pixel during the appropriate week. Finally, we cast three random locations within the study area for every used location and assigned random locations to the appropriate pixels to quantify habitat availability and weekly probability of use by elk for each individual deer. The fence boundary at Starkey represented the spatial extent of our analyses, and thus weekly RSFs reflected the influence of habitat and probability of use by elk on where female mule deer chose to establish home ranges within that area (second-order selection; Johnson 1980).

We estimated RSFs using conditional logistic regression (Compton et al. 2002, Boyce 2006). We considered the individual mule deer as a stratified variable to control for variation among individuals, and the logistic model for each week was conditioned upon that variable. Prior to conducting formal modeling procedures, we evaluated collinearity among continuous predictor variables using a correlation matrix (PROC CORR; SAS Institute, Cary, North Carolina). When two variables were highly correlated ($|r| \geq 0.60$), we retained the variable with the greatest potential to influence space use by female mule deer based on results of past research (Johnson et al. 2000, Stewart et al. 2002). In addition, we used the dry grassland habitat type as the basis for comparison of use among all habitat types, because use was near equal to availability. Consequently, parameter estimates for each habitat

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

type represent contrasts between use of that type and use of the dry grassland type.

We used an information-theoretic approach for model selection and, following evaluation of the initial correlation matrix, we placed remaining variables into one of five effect categories based on their potential to influence space use by female mule deer (Long et al. 2008a): 1) topography (slope, aspect), 2) proximity to roads (distance to open and restricted roads), 3) proximity to water (distance to permanent water), 4) vegetative characteristics (canopy closure and habitat type), and 5) interspecific interactions (probability of use by elk). We modeled all possible combinations of the five effect categories for each week, which resulted in a total of 31 models in each of the 13 model sets. For each model we recorded Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c and the Akaike weight (w_i), and we selected a 95% confidence set of models from each complete set based on w_i values (Burnham & Anderson 2002). Using only models from the 95% confidence set for each week, we then calculated weighted model-averaged parameter estimates and unconditional standard errors (SE) for each predictor variable (Burnham & Anderson 2002). We concluded that model-averaged parameter estimates differed significantly from 0 if a 95% confidence interval around the mean (based on the unconditional SE) did not contain 0. For each continuous variable, positive parameter estimates indicated that probability of use by female mule deer increased with increasing values of that variable (selection), whereas negative parameter estimates indicated the opposite relationship (avoidance).

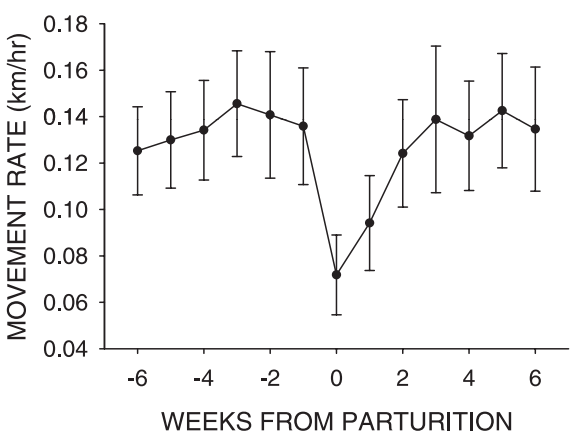


Figure 1. Mean weekly movement rates of 19 female mule deer from six weeks prior to six weeks after the estimated week of parturition (0) at the Starkey Experimental Forest and Range, Oregon, USA, during 2005-2006. Error bars show 95% confidence intervals.

Results

Movement rates

Most (19 of 20) collared female mule deer significantly reduced rates of movement between late-May and mid-June (Fig. 1). In 2005, three deer reduced movements during 22-28 May, four during 29 May-4 June and three during 12-18 June. Estimated mean date of birth (±SD) in 2005 was 30

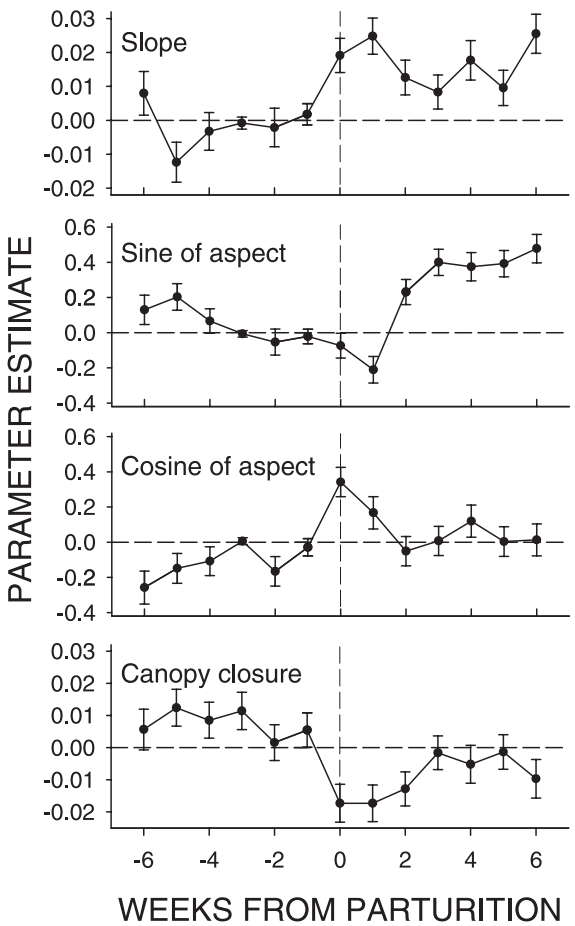


Figure 2. Parameter estimates for slope, sine (eastness) and cosine (northness) of aspect, and canopy closure obtained from resource selection functions (RSFs) for 19 female mule deer at the Starkey Experimental Forest and Range, Oregon, USA. For each habitat variable, positive parameter estimates indicate that probability of use by mule deer increased with increasing values of that variable (selection), whereas negative parameter estimates indicate the opposite relationship (avoidance). Conditional logistic regression was used to estimate weekly RSFs from six weeks prior to six weeks after the estimated week of parturition (0) based on location data collected during 2005-2006. Error bars show 95% confidence intervals.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

May ± 7.3 days. In 2006, three deer reduced movements during 28 May-3 June, five during 4-10 June and one during 11-17 June. Estimated mean date of birth (± SD) in 2006 was 1 June ± 3.2 days. The overall change (mean ± SD) in mean rate of movement from one week prior to parturition to the estimated week of parturition was 0.06 ± 0.02 km/hour, a 47% reduction in movement rates (see Fig. 1).

Resource selection

Patterns of resource selection by female mule deer at Starkey varied with stage of reproduction as estimated by patterns of movement. Prior to parturition, weekly parameter estimates either were negative or non-significant for percent slope (with one exception), positive or non-significant for sine of aspect and negative or non-significant for cosine of aspect. These parameter estimates indicate that deer selected gentle to moderate slopes with south to southeasterly aspects during late gestation (Fig. 2). In addition, parameter estimates for canopy closure were consistently positive prior to parturition, indicating that female mule deer selected habitats that provided a moderate to high degree of canopy cover during late gestation (see Fig. 2). Female mule deer also selected habitat close to both open and restricted roads, but avoided habitat close to permanent water sources during gestation (Fig. 3). Weekly parameter estimates for probability of use by elk prior to parturition either were positive or non-significant, indicating that mule deer often selected areas also used by elk during late gestation (see Fig. 3).

Prior to parturition, female mule deer generally used mesic forest significantly less than dry grasslands, and use of mesic stands dominated by large trees consistently was greater than use of stands dominated by small trees (Fig. 4). In contrast, mule deer regularly used xeric forest dominated by ponderosa pine more than dry grasslands prior to parturition, and stands of ponderosa pine dominated by small trees were used more than stands dominated by large trees (see Fig. 4). Female mule deer occasionally were located in xeric forest dominated by lodgepole pine. Prior to parturition, no female deer were located in lodgepole stands dominated by small trees, and lodgepole stands characterized by large trees were used significantly less by mule deer than dry grasslands four and two weeks prior to parturition (see Fig. 4). Female mule deer never were located in the wet meadow-riparian type, likely because that type comprised <0.5% of the study area.

Patterns of habitat selection changed markedly following parturition. Female mule deer selected significantly steeper slopes in the weeks during and after parturition than during the six weeks prior to parturition (see Fig. 2). Similarly, mule deer selected northwesterly aspects during and in the first week after parturition and easterly aspects from 2-6 weeks after parturition, as opposed to south to southeasterly aspects prior to parturition (see Fig. 2). In addition, deer switched from selecting habitats that provided at least a moderate degree of canopy cover

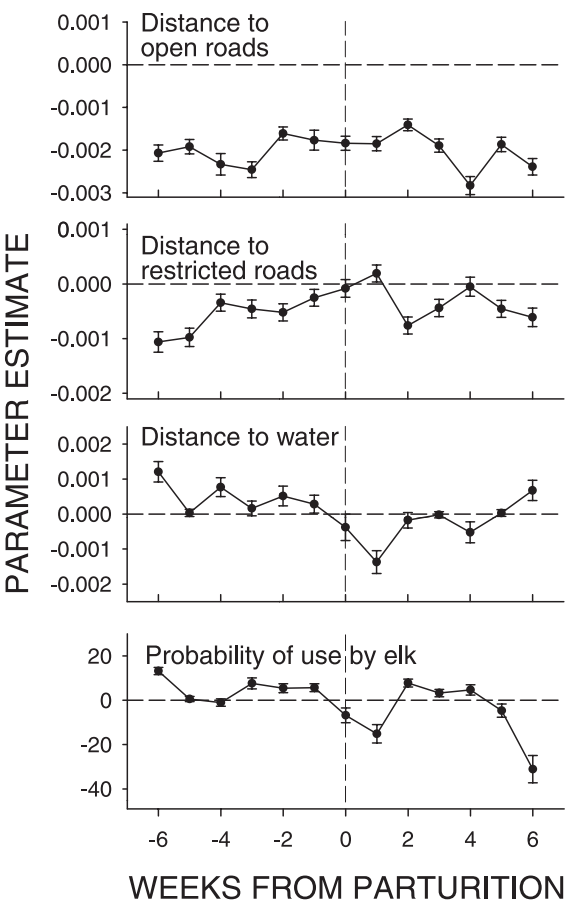


Figure 3. Parameter estimates for distances to open roads, restricted roads and water, as well as probability of use by elk, obtained from resource selection functions (RSFs) for 19 female mule deer at the Starkey Experimental Forest and Range, Oregon, USA. For each habitat variable, positive parameter estimates indicate that probability of use by mule deer increased with increasing values of that variable (selection), whereas negative parameter estimates indicate the opposite relationship (avoidance). Conditional logistic regression was used to estimate weekly RSFs from six weeks prior to six weeks after the estimated week of parturition (0) based on location data collected during 2005-2006. Error bars show 95% confidence intervals.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

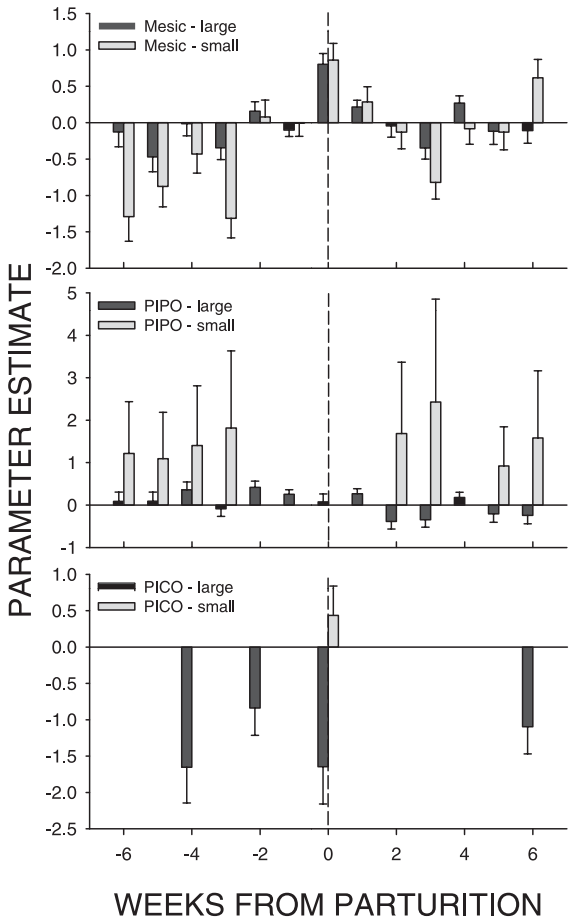


Figure 4. Parameter estimates for six habitat types obtained from resource selection functions (RSFs) for 19 mule deer at the Starkey Experimental Forest and Range, Oregon, USA. Conditional logistic regression was used to estimate weekly RSFs from six weeks prior to six weeks after the estimated week of parturition (0) based on location data collected during 2005-2006. Broad vegetation types were: 1) mesic forest dominated by grand fir or Douglas-fir (Mesic), 2) xeric forest dominated by ponderosa pine (PIPO), and 3) xeric forest dominated by lodgepole pine (PICO). Each vegetation type was further divided into two subtypes dominated by either small or large trees. Parameter estimates represent contrasts between use of dry grassland by mule deer and each of the other six habitat types. Missing values for a habitat type indicate that no mule deer were located in that type during that particular week. Error bars show 95% confidence intervals.

prior to parturition to relatively open-canopy habitats during and after parturition (see Fig. 2). Mule deer also changed from avoiding permanent water sources during late gestation to selecting habitat located close to water sources during and in the first week after parturition (see Fig. 3). Parameter estimates for distance to water 2-6 weeks after parturition were comparable to estimates from the six weeks prior to parturition (see Fig. 3). Conversely, female mule deer typically selected habitat close to roads throughout our study, with the exception of the first week following parturition when deer showed some selection for habitat located away from restricted roads (see Fig. 3). Negative parameter estimates for probability of use by elk were first obtained from models for the week of and the week after parturition (see Fig. 3), indicating that mule deer avoided areas used by elk during that period. Parameter estimates for probability of use by elk returned to positive values from two weeks to four weeks after parturition, then declined sharply to the lowest values observed from five to six weeks after parturition (see Fig. 3), indicating strong avoidance of elk in mid- to late-summer.

Selection of habitat types by female mule deer also changed dramatically relative to estimated time of parturition. With only two exceptions, mule deer used mesic forest less than dry grasslands prior to and from two to six weeks after parturition (see Fig. 4). Conversely, mule deer used mesic stands significantly more than dry grasslands during the week of and in the first week after parturition (see Fig. 4). In addition, use of mesic forest by female mule deer during and shortly after parturition did not differ between stands dominated by small versus large trees (see Fig. 4). Use of xeric stands dominated by ponderosa pine also changed relative to time of parturition. Female mule deer used ponderosa pine stands dominated by small trees more than dry grasslands from three to six weeks before and from two to six weeks after parturition, but no mule deer were located in those stands from two weeks prior to one week after parturition (see Fig. 4). In addition, stands of ponderosa pine dominated by large trees typically were used slightly more than dry grasslands by female mule deer from six weeks prior to one week after parturition, but were used less than dry grasslands from two to six weeks after parturition (see Fig. 4). Finally, the only instance in which mule deer were located in xeric forest dominated by small lodgepole pine trees was during the week of parturition, and in that instance, deer used lodgepole stands more than dry grasslands (see Fig. 4).

Discussion

Although we did not directly observe parturition, our results are consistent with the hypothesis that movement rates of female mule deer can be used as an index to timing of parturition. We know of no other life-history characteristic or event that could

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

have resulted in the consistent, significant reductions in movement among female deer in late spring observed during our study. Moreover, timing of parturition was nearly identical between years. In addition, reductions in movement were highly synchronous, and the degree of synchrony was consistent with previous results reported for synchrony of parturition in female mule deer (Bowyer 1991).

Our hypothesis that stage of reproduction would influence patterns of resource selection and movement among female mule deer was supported. Although we could not determine whether all parturient females successfully reared young to ≥ 6 weeks of age, consistency in patterns of selection and variance estimates associated with regression coefficients from two to six weeks after parturition indicate that loss of young likely had a limited effect on our analyses. Female mule deer likely selected gentle, south-facing slopes prior to parturition to increase nutritional gain during gestation (Barboza & Bowyer 2000, 2001). Green-up of forage following winter typically occurs first on south-facing slopes, and forage is more abundant in those areas than on north-facing slopes in early spring (R.A. Long, pers. obs.). In addition, energetic costs of locomotion are substantially greater in steep than in gentle terrain and, by using gentle to moderate slopes, mule deer reduce energy expended on movement (Parker et al. 1984). In contrast, selection of steep slopes with northwesterly aspects by female mule deer during the week of and in the first week after parturition might have reflected a strategy of predator avoidance, as well as spatial separation by maternal dams. Although senescence of forage plants typically occurs later on north- than south-facing slopes, forage quality and abundance on south-facing slopes at Starkey generally remain high until early July (Long et al. 2008b), well after parturition has occurred. Consequently, movements of female mule deer from south- to north-facing slopes during the estimated week of parturition likely were not driven by the need to acquire better forage. Similarly, at a constant rate of movement, the overall energetic cost of locomotion increases as percent slope increases (Parker et al. 1984) and, as a result, the switch to selection of steep slopes by female mule deer likely increased energy expenditure of movements.

Coursing predators, such as coyotes and black bears often favour easily traversable terrain (Bowyer 1987, Farmer et al. 2006), and other studies have documented use of moderate to steep slopes by female mule deer and their young as a means of reducing predation risk (Riley & Dood 1984, Fox & Krausman 1994). Nevertheless, an alternative hypothesis for use of steep slopes by female mule deer in our study during and in the first week after parturition relates to selection of habitat located close to water during those weeks. Water requirements of female deer increase substantially with the onset of lactation (Bowyer 1984, Boroski & Mossman 1996), and most permanent water available at Starkey is located in two creek drainages that bisect the study area. Much of the steepest terrain on the study site is also located in those drainages, and consequently parturient females moving closer to water following parturition might be expected to utilize relatively steep slopes. In contrast to our hypothesis of predator avoidance, however, a hypothesis of selection for water fails to explain why female deer in our study continued to use steep slopes six weeks after parturition, but stopped selecting areas near water beginning two weeks after birth.

Prior to parturition, selection by female mule deer increased as canopy cover increased. In contrast, xeric forest dominated by ponderosa pine (which, on average, had the most open canopy of all forest types on the study site) was used more frequently by mule deer during gestation than all other habitat types. Considered together, these results indicate that prior to parturition, mule deer selected stands of ponderosa pine that provided the greatest amount of canopy cover available in that habitat type. During and shortly after parturition, however, female mule deer selected relatively open portions of mesic forest dominated by fir, which had the east open canopy of all forest types on the study site.

We hypothesize that use of stands of ponderosa pine by female mule deer prior to parturition was related to selection of topographic features that were favourable for foraging in spring, as discussed previously. Xeric forest occurs almost exclusively on south- and east-facing slopes at Starkey, whereas mesic forest occurs on north-facing slopes (Stewart et al. 2006). Although mesic stands of forest at Starkey are more productive on an annual basis (Stewart et al. 2006), earlier green-up of forage in xeric stands on south-facing slopes may attract deer to those areas during spring, when energetic demands of late gestation are increasing and deer are recovering from the physiological stresses of winter (Barboza & Bowyer 2000). In addition, 75% of xeric forest at Starkey is dominated by ponderosa

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

pine, which helps explains why deer selected those stands, but only occasionally used xeric stands dominated by lodgepole pine during gestation. Why female mule deer primarily selected the most closed-canopy portions of ponderosa stands during gestation is, however, less clear. One explanation for this phenomenon stems from the relationship between habitat selection and spatial scale. Strategies used by ungulates to meet nutritional requirements often vary with both spatial and temporal scale (Parker 2003), and thus patterns of resource selection and space use tend to be highly sensitive to scale (Bowyer & Kie 2006). We hypothesize that female mule deer selected ponderosa pine on south-facing slopes to increase access to high-quality forage prior to parturition, but then selected areas within those stands that provided a high degree of concealment cover to reduce risk of predation while foraging.

Selection of relatively open portions of fir stands by female mule deer during and shortly after parturition also may reflect effects of scale. Mesic forest at Starkey, whether dominated by small or large trees, has the highest average canopy cover and tree densities of all forest types on the study site (Long et al. 2008b). Consequently, the abrupt switch from selection of ponderosa pine by mule deer to selection of fir stands in the week of parturition may represent a predator-avoidance strategy, because canopy cover and tree density ostensibly are inversely related to risk of predation (Bowyer et al. 1999). Locations within fir stands that have the lowest total canopy cover, however, are likely to have the highest level of understory productivity as a result of increased penetration of light and water to the understory (Long et al. 2008b). We hypothesize that at a broad spatial scale (i.e. within the study area) female mule deer selected fir stands during and shortly after parturition to reduce risk of predation on neonates, but within those stands, deer selected areas with lower than average canopy cover to increase access to high-quality forage.

Previous work at Starkey has documented strong avoidance of elk by female mule deer (Johnson et al. 2000, Stewart et al. 2002). No previous studies, however, evaluated resource selection by mule deer at Starkey on a fine (e.g. weekly) temporal scale throughout the spring and summer. Our results indicate that female mule deer avoided elk primarily during and shortly after parturition, as well as in mid- to late-summer, suggesting that the negative effects of elk on female mule deer increased when females had young at heel.

Results of our study support the hypothesis that patterns of resource selection by female mule deer vary substantially relative to time of parturition. Female mule deer at Starkey likely faced tradeoffs among forage acquisition, risk of predation and competition with elk. Weekly patterns of space use by female mule deer relative to time of parturition reflected strong selection or avoidance of landscape characteristics related to topography, canopy closure, proximity to roads and water, probability of use by elk and habitat type. We suggest that management plans for mule deer would benefit by taking into account the potential for intra-annual variability in the relative importance of forage, risk of predation and competition in influencing populations of mule deer. Moreover, such effects might be especially important around parturition, and may operate at a relatively fine temporal scale.

Acknowledgements - our research was supported by the US Forest Service Pacific Northwest Research Station and the Department of Biological Sciences at Idaho State University. We appreciated the hard work and assistance of Starkey Project personnel, including B. Dick, R. Kennedy, J. Nothwang, J. Boyd and M. Wisdom. We also thank D. Freddy, K. Monteith, J. Whiting and S. Schoen for helpful comments on this manuscript.

References

Ballard, W.B., Lutz, D., Keegan, T.W., Carpenter, L.H. & de Vos, J.C. 2001: Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. - Wildlife Society Bulletin 29: 99-115.

Barboza, P.S. & Bowyer, R.T. 2000: Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. - Journal of Mammalogy 81: 473-489.

Barboza, P.S. & Bowyer, R.T. 2001: Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. - Alces 37: 275-292.

Barten, N.L., Bowyer, R.T. & Jenkins, K.J. 2001: Habitat use by female caribou: tradeoffs associated with parturition. - Journal of Wildlife Management 65: 77-92.

Berger, J. 1991: Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. - Animal Behaviour 41: 61-77.

Bertrand, M.R., DeNicola, A.J., Beissinger, S.R. & Swihart, R.K. 1996: Effects of parturition on home ranges and social affiliations of female white-tailed deer. - Journal of Wildlife Management 60: 899-909.

Bleich, V.C., Bowyer, R.T. & Wehausen, J.D. 1997: Sexual segregation in mountain sheep: resources or predation? - Wildlife Monographs 134: 1-50.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Boroski, B.B. & Mossman, A.S. 1996: Distribution of mule deer in relation to water sources in northern California. - Journal of Wildlife Management 60: 770-776.
Bowyer, R.T. 1984: Sexual segregation in southern mule deer. - Journal of Mammalogy 65: 410-417.
Bowyer, R.T. 1987: Coyote group size relative to predation on mule deer. - Mammalia 51: 515-526.
Bowyer, R.T. 1991: Timing of parturition and lactation in southern mule deer. - Journal of Mammalogy 72: 138-145.
Bowyer, R.T. & Kie, J.G. 2006: Effects of scale on interpreting life-history characteristics of ungulates and carnivores. - Diversity and Distributions 12: 244-257.
Bowyer, R.T., Kie, J.G. & Van Ballenberghe, V. 1998: Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? - Journal of Mammalogy 79: 415-425.
Bowyer, R.T., Van Ballenberghe, V., Kie, J.G. & Maier, J.A.K. 1999: Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. - Journal of Mammalogy 80: 1070-1083.
Boyce, M.S. 2006: Scale for resource selection functions. - Diversity and Distributions 12: 269-276.
Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. - Springer-Verlag, New York, USA, 496 pp.
Carstensen, M., DelGiudice, G.D. & Sampson, B.A. 2003: Using doe behavior and vaginal-implant transmitters to capture neonate white-tailed deer in north-central Minnesota. - Wildlife Society Bulletin 31: 634-641.
Ciuti, S., Bongi, P., Vassale, S. & Apollonio, M. 2006: Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. - Journal of Zoology 268: 97-107.
Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. 1989: Fitness costs of gestation and lactation in wild mammals. - Nature 337: 260-262.
Clutton-Brock, T.H. & Guinness, F.E. 1975: Behavior of red deer (*Cervus elaphus* L) at calving time. - Behaviour 55: 287-299.
Clutton-Brock, T.H., Iason, G.R., Albon, S.D. & Guinness, F.E. 1982: Effects of lactation on feeding behavior and habitat use in wild red deer hinds. - Journal of Zoology 198: 227-236.
Compton, B.W., Rhymer, J.M. & McCollough, M. 2002: Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. - Ecology 83: 833-843.
Connolly, G.E. 1981: Assessing populations. - In: Wallmo, O.C. (Ed.); Mule and black-tailed deer of North America. University of Nebraska Press, Nebraska, USA, pp. 287-346.
Farmer, C.J., Person, D.K. & Bowyer, R.T. 2006: Risk factors and mortality of black-tailed deer in a managed forest landscape. - Journal of Wildlife Management 70: 1403-1415.
Fox, K.B. & Krausman, P.R. 1994: Fawning habitat of desert mule deer. - Southwestern Naturalist 39: 269-275.
Gannon, W.L., Sikes, R.S. & the Animal Care and Use Committee of the American Society of Mammalogists 2007: Guidelines of the American Society of Mammalogists for the use of wild mammals in research. - Journal of Mammalogy 88: 809-823.
Hamel, S. & Côté, S.D. 2007: Habitat use patterns in relation to escape terrain: are alpine ungulate females trading off better foraging sites for safety? - Canadian Journal of Zoology 85: 933-943.
Hamel, S. & Côté, S.D. 2008: Trade-offs in activity budget in an alpine ungulate: contrasting lactating and nonlactating females. - Animal Behaviour 75: 217-227.
Hosmer, D.W. & Lemeshow, S. 2000: Applied logistic regression. 2nd edition. - John Wiley and Sons, New York, USA, 392 pp.
Johnson, B.K., Kern, J.W., Wisdom, M.J., Findholt, S.L. & Kie, J.G. 2000: Resource selection and spatial separation of mule deer and elk during spring. - Journal of Wildlife Management 64: 685-697.
Johnson, D.H. 1980: The comparison of usage and availability measurements for evaluating resource preference. - Ecology 61: 65-71.
Johnson, D.S., Barry, R.P. & Bowyer, R.T. 2004: Estimating timing of life-history events with coarse data. - Journal of Mammalogy 85: 932-939.
Kie, J.G. 1999: Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. - Journal of Mammalogy 80: 1114-1129.
Kie, J.G., Ager, A.A. & Bowyer, R.T. 2005: Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. - Landscape Ecology 20: 289-300.
Krebs, J.R. & Davies, N.B. (Eds.) 1997: Behavioural ecology: an evolutionary approach. 4th edition. - Blackwell Publishing, Oxford, UK, 464 pp.
Long, R.A., Rachlow, J.L. & Kie, J.G. 2008a: Effects of season and scale on response of elk and mule deer to habitat manipulation. - Journal of Wildlife Management 72: 1133-1142.
Long, R.A., Rachlow, J.L., Kie, J.G. & Vavra, M. 2008b: Fuels reduction in a western coniferous forest: effects on quantity and quality of forage for elk. - Rangeland Ecology and Management 61: 302-313.
Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. 2002: Resource selection by animals: statistical design and analysis for field studies. 2nd edition. - Kluwer Press, Massachusetts, USA, 240 pp.
Neuhaus, P. & Ruckstuhl, K.E. 2002: Foraging behaviour in alpine ibex (*Capra ibex*): consequences of reproduc-

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

tive status, body size, age and sex. - Ethology, Ecology and Evolution 14: 373-381.
Parker, K.L. 2003: Advances in the nutritional ecology of cervids at different scales. - Écoscience 10: 395-411.
Parker, K.L., Robbins, C.T. & Hanley, T.A. 1984: Energy expenditure for locomotion by mule deer and elk. - Journal of Wildlife Management 48: 474-488.
Pojar, T.M. & Bowden, D.C. 2004: Neonatal mule deer fawn survival in west-central Colorado. - Journal of Wildlife Management 68: 550-560.
Rachlow, J.L. & Bowyer, R.T. 1998: Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. - Journal of Zoology 245: 457-465.
Reynolds, H.G. 1966: Use of ponderosa pine forest in Arizona by deer, elk, and cattle. - U.S. Forest Service Research Note RM-63, Colorado, USA, 7 pp.
Riley, S.J. & Dood, A.R. 1984: Summer movements, home range, habitat use, and behavior of mule deer fawns. - Journal of Wildlife Management 48: 1302-1310.
Roff, D.A. 1992: The evolution of life histories: theory and analysis. - Chapman and Hall, London, UK, 548 pp.
Rodgers, A.R., Carr, A.P., Beyer, H.L., Smith, L. & Kie, J.G. 2007: HRT: Home Range Tools for ArcGIS. Available at: http://blue.lakeheadu.ca/hre/ (Last accessed on 18 January 2008).
Rowland, M.M., Bryant, L.D., Johnson, B.K., Noyes, J.H., Wisdom, M.J. & Thomas, J.W. 1997: The Starkey Project: history, facilities, and data collection methods for ungulate research. - U.S. Forest Service General Technical Report PNW-GTR-296, Oregon, USA, 62 pp.
Rowland, M.M., Coe, P.K., Stussy, R.J., Ager, A.A., Cimon, N.J., Johnson, B.K. & Wisdom, M.J. 1998: The Starkey habitat database for ungulate research: construction, documentation, and use. - U.S. Forest Service General Technical Report PNW-GTR-430, Oregon, USA, 48 pp.
Ruckstuhl, K.E. & Festa-Bianchet, M. 1998: Do reproductive status and lamb gender affect the foraging behavior of bighorn ewes? - Ethology 104: 941-954.
Sadleir, R.M.F.S. 1982: Energy consumption and subsequent partitioning in lactating black-tailed deer. - Canadian Journal of Zoology 60: 382-386.
Stearns, S.R. 1992: The evolution of life histories. - Oxford University Press, Oxford, UK, 264 pp.
Steigers, W.D. & Flinders, J.T. 1980: Mortality and movements of mule deer fawns in Washington. - Journal of Wildlife Management 44: 381-388.
Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J. & Johnson, B.K. 2002: Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. - Journal of Mammalogy 83: 229-244.
Stewart, K.M., Bowyer, R.T., Ruess, R.W., Dick, B.L. & Kie, J.G. 2006: Herbivore optimization by North American elk: consequences for theory and management. - Wildlife Monographs 167: 1-24.
Trivers, R.L. 1974: Parent-offspring conflict. - American Zoologist 14: 249-264.
Unsworth, J.W., Pac, D.F., White, G.C. & Bartmann, R.M. 1999: Mule deer survival in Colorado, Idaho, and Montana. - Journal of Wildlife Management 63: 315-326.
USDA, Natural Resources Conservation Service 2007: The PLANTS Database. Available at: http://plants.usda.gov (Last accessed on 23 November 2007).
Vore, J.M. & Schmidt, E.M. 2001: Movements of female elk during calving season in northwest Montana. - Wildlife Society Bulletin 29: 720-725.
Wisdom, M.J., Cook, J.G., Rowland, M.M. & Noyes, J.H. 1993: Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range. - U.S. Forest Service General Technical Report PNW-GTR-311, Oregon, USA, 49 pp.
Wisdom, M.J., Meczarski, L., Lekovic, D. & Cimon, N.J. 2006: A GPS-based automated telemetry system for ungulate research at the Starkey Experimental Forest and Range, northeast Oregon, USA. - U.S. Forest Service Unpublished Report, Oregon, USA, 15 pp.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use