

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

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23

24 Abstract

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26 Recent declines of mule deer (*Odocoileus hemionus*), ostensibly a result of low rates of
27 recruitment, highlight the importance of understanding relationships between parturient
28 females and their critical habitats. We estimated timing of parturition for 20 mule deer in
29 northeastern Oregon, USA, using movement data from global positioning system (GPS)
30 collars in 2005 and 2006. We then evaluated patterns of resource selection by female mule
31 deer during late gestation, the week of parturition, and subsequent lactation to determine
32 how different stages of reproduction influenced habitat selection. Movement rates of all
33 but 1 deer declined sharply between late-May and mid-June, when female mule deer give
34 birth in northeastern Oregon. Patterns of resource selection also varied substantially
35 relative to the estimated time of parturition. Prior to parturition, female mule deer selected
36 gentle south-facing slopes dominated by ponderosa pine (*Pinus ponderosa*) and avoided
37 permanent water sources. Parturient females also selected areas used concurrently by elk
38 (*Cervus elaphus*). Following parturition, however, females selected steep north-facing
39 slopes dominated by fir (*Abies* spp.), avoided elk, and selected habitat located close to
40 permanent water sources. Stage of reproduction clearly influenced choice of habitat by
41 female mule deer. Mule deer management plans should consider potential seasonal
42 variability in the relative importance of forage, risk of predation, and competition.

43

44 Introduction

45

46 Life-history strategies of ungulates have been shaped by multiple factors, including the

47 need to acquire energy while avoiding predation (Stearns 1992, Kie 1999). Ungulates
48 frequently face environmental constraints on their ability to survive and reproduce (Berger
49 1991, Kie 1999), and females, in particular, must balance energy invested in current
50 offspring against the probability of surviving to reproduce again (Trivers 1974, Roff 1992,
51 Stearns 1992). Consequently, females occupying heterogeneous landscapes often are
52 forced to choose among environmental factors affecting the acquisition and investment of
53 energy (Hamel and Côté 2008). For example, a positive spatial correlation between risk of
54 predation and forage quality or abundance may necessitate tradeoffs between predator
55 avoidance and forage acquisition (Bowyer et al. 1998, 1999; Rachlow & Bowyer 1998;
56 Barten et al. 2001; Hamel and Côté 2007).

57 Stage of reproduction influences patterns of resource selection, space use, and
58 movement in female ungulates (Berger 1991, Rachlow & Bowyer 1998, Barten et al. 2001).
59 Energetic investment in the developing fetus peaks during the last third of gestation
60 (Barboza & Bowyer 2000, 2001), and susceptibility to predation is lowest for females
61 without young at heel (Berger 1991). As a result, females should select habitat that
62 provides ample forage during gestation. Conversely, susceptibility of neonates to predation
63 is highest in the first few weeks following parturition (Bowyer et al. 1998, Ballard et al.
64 2001, Pojar & Bowden 2004). In addition, nutritional requirements of parturient females
65 begin to increase shortly after parturition with the onset of lactation, and typically peak
66 roughly 4–6 weeks following birth of young (Sadleir et al. 1982, Clutton-Brock et al.
67 1989). This simultaneous increase in nutritional requirements of the mother and
68 vulnerability of young to predation following parturition imposes a significant constraint on
69 the ability of females to provision and rear young (Bowyer et al. 1999), and understanding

70 how females cope with such constraints behaviourally can provide important insights into
71 the evolution of ungulate life-history strategies.

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

84 Mule deer (*Odocoileus hemionus*) populations have declined recently, ostensibly a
85 result of low rates of recruitment (Unsworth et al. 1999, Pojar & Bowden 2004). These
86 declines underscore the importance of understanding relationships between mule deer,
87 particularly parturient females, and their habitat requirements. We conducted post-hoc
88 analyses of a location dataset for female mule deer collected at the Starkey Experimental
89 Forest and Range in northeastern Oregon to evaluate patterns of resource selection by
90 female mule deer relative to estimated time of parturition. Cervids exhibit substantial
91 reductions in movement immediately following parturition (Bertrand et al. 1996, Bowyer et
92 al. 1999, Vore & Schmidt 2001, Carstensen et al. 2003, Ciuti et al. 2006). Consequently,

93 we hypothesized that movement rates of female mule deer could be an index to timing of
94 parturition. The retrospective nature of our dataset prevented us from testing this
95 hypothesis by directly observing births. Instead, we evaluated several important
96 predictions from the hypothesis that movement rates reflect timing of parturition. If female
97 mule deer in our study reduced movements immediately following parturition, then: 1) the
98 mean date of the reduction in movement rates should occur between late-May and mid-
99 June, when female mule deer typically give birth at latitudes comparable to our study area
100 (Steigers & Flinders 1980); 2) synchrony of the reduction in movement rates among deer
101 should match published data on synchrony of parturition in mule deer; and 3) because
102 pregnancy rates in mule deer typically are high when population density is low (Connolly
103 1981), at least 80% of collared deer in our study should significantly reduce movement
104 rates at the appropriate time of year, because density of deer in our study area is low
105 relative to carrying capacity (Johnson et al. 2000). We also hypothesized that stage of
106 reproduction would influence resource selection and movement patterns of female mule
107 deer because gestation, parturition, and lactation each impose different energetic demands
108 (Barboza & Bowyer 2000, 2001) and susceptibility to predation (Bleich et al. 1997).

109

110 **Materials and methods**

111

112 **Study area**

113 We conducted research at the Starkey Experimental Forest and Range in northeastern
114 Oregon, USA (hereafter Starkey; 45°13'N, 118°31'W). Starkey encompasses 101 km² and
115 is managed by the U.S. Forest Service. The area is surrounded by a 2.4-m-high fence,

116 which prevents immigration and emigration of large herbivores (Rowland et al. 1997).
117 Predators of mule deer fawns at Starkey include coyotes (*Canis latrans*), mountain lions
118 (*Puma concolor*), and black bears (*Ursus americanus*). We collected data on locations of
119 female mule deer in main study area (78 km²), which was representative of habitats of the
120 Blue Mountains of northeastern Oregon and Washington, USA. Habitat choices available
121 to mule deer were comparable to those outside Starkey, and traffic levels, recreational
122 activities (including hunting of mule deer and elk in fall and winter), and timber
123 management were similar to those on surrounding public lands (Rowland et al. 1997).

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

134

135 **Animal handling and locations of deer**

136 Female mule deer (adults ≥ 2 yrs-of-age) were captured by project personnel at Starkey
137 during winters of 2004 and 2005 with panel traps baited with hay (Rowland et al. 1997).
138 Following capture, deer were fitted with Global Positioning System (GPS) collars (model

139 4400M, Lotek Wireless, Inc., Newmarket, Ontario, Canada) and released back into the
140 study area. Collars were recovered the following winter and most individual deer were
141 monitored for only 1 yr. Deer locations were stored on each GPS collar and retrieved at
142 programmed intervals via an automated retrieval system (Wisdom et al. 2006). A computer
143 queried each of 8 cell-phone modems located at high points in the study area at regular
144 intervals. Each modem was connected to an ultra-high frequency (UHF) modem at the
145 same location, and every time a connection was established the UHF modem was directed
146 to retrieve all data stored on GPS collars within line-of-sight of that location (Wisdom et al.
147 2006). Mean positional error of GPS collars was ≤ 10 m (Wisdom et al. 2006). We
148 obtained location data for 20 female mule deer (10 in 2005, 10 in 2006) at 50 to 90 min
149 intervals 24 hr/day for the duration of our study, for a total of 27,041 locations.

150 Adult female elk (*Cervus elaphus*) also were captured and fitted with GPS collars
151 during 2005 and 2006 to account for the effects of elk on resource selection by mule deer
152 (Johnson et al. 2000; Stewart et al. 2002, 2006). Elk were lured onto a winter feeding
153 ground beginning in mid-December, where they could be maneuvered easily into a nearby
154 handling facility (Rowland et al. 1997). Individual females were fitted with GPS collars in
155 early spring before being released back into main study area. We obtained data on
156 locations at 50 to 90 min intervals for a total of 31 individual elk (8 in 2005, 23 in 2006)
157 during our study ($n = 68,831$ locations). All capture and handling procedures were in
158 accordance with protocols approved by an established Institutional Animal Care and Use
159 Committee (Wisdom et al. 1993) and were in compliance with guidelines adopted by the
160 American Society of Mammalogists Animal Care and Use Committee (Gannon et al. 2007).
161

162 Timing of parturition

163 We estimated timing of parturition at 1-week intervals from movement rates (km/hr) of
164 female mule deer. Although we did not directly observe mule deer fawns during our study,
165 cervids commonly exhibit a marked (i.e., $\geq 50\%$) decline in movement rates immediately
166 following parturition; this well-documented change in behaviour can be used to estimate
167 timing of parturition (Bertrand et al. 1996, Bowyer et al. 1999, Vore & Schmidt 2001,
168 Carstensen et al. 2003, Ciuti et al. 2006). At latitudes comparable to Starkey, female mule
169 deer typically give birth between late-May and mid-June (Steigers & Flinders 1980), and
170 thus substantial reductions in movement rates of female deer during that period serve as an
171 index to timing of parturition. One female whose movement rates did not change
172 significantly over time based on overlapping 95% confidence intervals was excluded from
173 subsequent analyses of resource selection. After identifying the estimated week of
174 parturition for each individual, we set that week equal to time 0 for each deer to evaluate
175 weekly patterns of resource selection. In addition, we compared synchrony of parturition
176 among female mule deer at Starkey with previous studies of mule deer by calculating a
177 mean date of birth and associated SD from data on estimated week of parturition using the
178 methods of Johnson et al. (2004), which provide a robust approach to dealing with grouped
179 (binned) data.

180

181 Predictor variables

182 We included predictor variables in our analyses thought to influence patterns of resource
183 selection and space use by female mule deer at Starkey (Johnson et al. 2000, Stewart et al.
184 2002). We obtained the following variables from the habitat database at Starkey (Rowland

185 et al. 1998): slope (%); convexity (a measure of topographical complexity; Johnson et al.
186 2000); aspect (transformed with sine and cosine functions to measure eastness and
187 northness of aspect, respectively); distance to open (open to public access) and restricted
188 (access restricted to authorized personnel) roads (m); distance to permanent water (m); and
189 elevation (m). We obtained values of each habitat variable for every 30 m² pixel in the
190 study area.

191 In addition to variables obtained from the habitat database, we incorporated data on
192 total canopy closure (%) and habitat type (vegetation association) into our analyses. Those
193 data were derived at a 30-m² resolution from 1:12,000 colour aerial photos of the study area
194 taken in 2000. We used the categorization of Kie et al. (2005) as a basis for defining
195 habitat types: 1) dry grassland, 2) wet meadow-riparian, 3) mesic forest dominated by
196 grand fir or Douglas-fir, 4) xeric forest dominated by ponderosa pine, and 5) xeric forest
197 dominated by lodgepole pine. In addition, each forested type was divided into 2 subtypes
198 based on tree size: 1) small trees (canopy closure $\geq 40\%$ in trees ≤ 10.2 cm diameter at breast
199 height = 1.37 m); or 2) large trees (canopy closure of small trees $< 40\%$).

200 We also included probability of use by elk as a predictor variable in our analyses.
201 We estimated probability of use with utilization distributions (UDs) derived from elk
202 locations. We produced 95% fixed-kernel UD's on a weekly basis for the population of
203 radiocollared elk at Starkey using the Home Range Tools extension for ArcGIS (Rogers et
204 al. 2007). Rather than using a mathematical optimization routine to select the appropriate
205 bandwidth for each UD, we fixed the bandwidth at 183 m for all UD's. This value
206 represents an estimate of the perception distance of elk in semi-open terrain (Reynolds
207 1966), and thereby provides a biological basis for selecting the bandwidth. In addition, we

208 used a 30-m² grid structure for estimating UDs to match the resolution of our habitat layers.

209

210 **Modeling**

211 We evaluated patterns of resource selection by female mule deer from 6 weeks prior to 6
212 weeks after the estimated period of parturition. As a result of relatively small sample sizes
213 within years, we pooled data from 2005 and 2006 to calculate resource selection functions
214 (RSFs) at the population level for each of 13 weeks (6 weeks prior to parturition and 6
215 weeks post-parturition). We estimated RSFs based on a matched-case design (Hosmer &
216 Lemeshow 2000, Manly et al. 2002, Boyce 2006). Locations from individual deer
217 represented used points, each of which was assigned to the appropriate 30-m² pixel within
218 the study area to determine values of associated habitat variables. We also joined the
219 estimated probability of use by elk (UD height) associated with each pixel to all deer
220 locations occurring in that pixel during the appropriate week. Finally, we cast 3 random
221 locations within the study area for every used location and assigned random locations to the
222 appropriate pixels to quantify habitat availability and weekly probability of use by elk for
223 each individual deer. The fence boundary at Starkey represented the spatial extent of our
224 analyses, and thus weekly RSFs reflected the influence of habitat and probability of use by
225 elk on where female mule deer chose to establish home ranges within that area
226 (second-order selection; Johnson 1980).

227 We estimated RSFs using conditional logistic regression (Compton et al. 2002,
228 Boyce 2006). We considered the individual mule deer as a stratified variable to control for
229 variation among individuals, and the logistic model for each week was conditioned upon
230 that variable. Prior to conducting formal modeling procedures, we evaluated collinearity

231 among continuous predictor variables using a correlation matrix (PROC CORR; SAS
232 Institute, Cary, North Carolina). When 2 variables were highly correlated ($|r| \geq 0.60$), we
233 retained the variable with the greatest potential to influence space use by female mule deer
234 based on results of past research (Johnson et al. 2000, Stewart et al. 2002). In addition, we
235 used the dry grassland habitat type as the basis for comparison of use among all habitat
236 types, because use was near equal to availability. Consequently, parameter estimates for
237 each habitat type represent contrasts between use of that type and use of the dry grassland
238 type.

239 We used an information-theoretic approach for model selection and, following
240 evaluation of the initial correlation matrix, we placed remaining variables into 1 of 5 effect
241 categories based on their potential to influence space use by female mule deer (Long et al.
242 2008a): 1) topography (slope, aspect); 2) proximity to roads (distance to open and restricted
243 roads); 3) proximity to water (distance to permanent water); 4) vegetative characteristics
244 (canopy closure and habitat type); and 5) interspecific interactions (probability of use by
245 elk). We modeled all possible combinations of the 5 effect categories for each week, which
246 resulted in a total of 31 models in each of the 13 model sets. For each model we recorded
247 Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c , and the
248 Akaike weight (w_i), and we selected a 95% confidence set of models from each complete
249 set based on w_i values (Burnham & Anderson 2002). Using only models from the 95%
250 confidence set for each week, we then calculated weighted model-averaged parameter
251 estimates and unconditional standard errors (SE) for each predictor variable (Burnham &
252 Anderson 2002). We concluded that model-averaged parameter estimates differed
253 significantly from 0 if a 95% confidence interval around the mean (based on the

254 unconditional SE) did not contain 0. For each continuous variable, positive parameter
255 estimates indicated that probability of use by female mule deer increased with increasing
256 values of that variable (selection), whereas negative parameter estimates indicated the
257 opposite relationship (avoidance).

258

259 **Results**

260

261 **Movement rates**

262 Most (19 of 20) collared female mule deer significantly reduced rates of movement
263 between late-May and mid-June (Fig. 1). In 2005, 3 deer reduced movements during 22–28
264 May, 4 during 29 May–4 June, and 3 during 12–18 June. Estimated mean date of birth (\pm
265 SD) in 2005 was 30 May \pm 7.3 days. In 2006, 3 deer reduced movements during 28 May–3
266 June, 5 during 4–10 June, and 1 during 11–17 June. Estimated mean date of birth (\pm SD) in
267 2006 was 1 June \pm 3.2 days. The overall change (mean \pm SD) in mean rate of movement
268 from 1 week prior to parturition to the estimated week of parturition was 0.06 ± 0.02 km/hr,
269 a 47% reduction in movement rates (Fig. 1).

270

271 **Resource selection**

272 Patterns of resource selection by female mule deer at Starkey varied with stage of
273 reproduction as estimated by patterns of movement. Prior to parturition, weekly parameter
274 estimates either were negative or nonsignificant for percent slope (with 1 exception),
275 positive or nonsignificant for sine of aspect, and negative or nonsignificant for cosine of
276 aspect. These parameter estimates indicate that deer selected gentle to moderate slopes

277 with south to southeasterly aspects during late gestation (Fig. 2). In addition, parameter
278 estimates for canopy closure were consistently positive prior to parturition, indicating that
279 female mule deer selected habitats that provided a moderate to high degree of canopy cover
280 during late gestation (Fig. 2). Female mule deer also selected habitat close to both open
281 and restricted roads, but avoided habitat close to permanent water sources during gestation
282 (Fig. 3). Weekly parameter estimates for probability of use by elk prior to parturition either
283 were positive or nonsignificant, indicating that mule deer often selected areas also used by
284 elk during late gestation (Fig. 3).

285 Prior to parturition, female mule deer generally used mesic forest significantly less
286 than dry grasslands, and use of mesic stands dominated by large trees consistently was
287 greater than use of stands dominated by small trees (Fig. 4). In contrast, mule deer
288 regularly used xeric forest dominated by ponderosa pine more than dry grasslands prior to
289 parturition, and stands of ponderosa pine dominated by small trees were used more than
290 stands dominated by large trees (Fig. 4). Female mule deer occasionally were located in
291 xeric forest dominated by lodgepole pine. Prior to parturition, no female deer were located
292 in lodgepole stands dominated by small trees, and lodgepole stands characterized by large
293 trees were used significantly less by mule deer than dry grasslands 4 and 2 weeks prior to
294 parturition (Fig. 4). Female mule deer never were located in the wet meadow-riparian type,
295 likely because that type comprised <0.5% of the study area.

296 Patterns of habitat selection changed markedly following parturition. Female mule
297 deer selected significantly steeper slopes in the weeks during and after parturition than
298 during the 6 weeks prior to parturition (Fig. 2). Similarly, mule deer selected northwesterly
299 aspects during and in the first week after parturition and easterly aspects from 2–6 weeks

300 after parturition, as opposed to south to southeasterly aspects prior to parturition (Fig. 2).
301 In addition, deer switched from selecting habitats that provided at least a moderate degree
302 of canopy cover prior to parturition to relatively open-canopy habitats during and after
303 parturition (Fig. 2). Mule deer also changed from avoiding permanent water sources during
304 late gestation to selecting habitat located close to water sources during and in the first week
305 after parturition (Fig. 3). Parameter estimates for distance to water from 2 to 6 weeks after
306 parturition were comparable to estimates from the 6 weeks prior to parturition (Fig. 3).
307 Conversely, female mule deer typically selected habitat close to roads throughout our study,
308 with the exception of the first week following parturition when deer showed some selection
309 for habitat located away from restricted roads (Fig. 3). Negative parameter estimates for
310 probability of use by elk were first obtained from models for the week of and the week after
311 parturition (Fig. 3), indicating that mule deer avoided areas used by elk during that period.
312 Parameter estimates for probability of use by elk returned to positive values from 2 to 4
313 weeks after parturition, then declined sharply to the lowest values observed from 5 to 6
314 weeks after parturition (Fig. 3), indicating strong avoidance of elk in mid- to late-summer.

315 Selection of habitat types by female mule deer also changed dramatically relative to
316 estimated time of parturition. With only 2 exceptions, mule deer used mesic forest less
317 than dry grasslands prior to and from 2 to 6 weeks after parturition (Fig. 4). Conversely,
318 mule deer used mesic stands significantly more than dry grasslands during the week of and
319 in the first week after parturition (Fig. 4). In addition, use of mesic forest by female mule
320 deer during and shortly after parturition did not differ between stands dominated by small
321 versus large trees (Fig. 4). Use of xeric stands dominated by Ponderosa pine also changed
322 relative to time of parturition. Female mule deer used ponderosa pine stands dominated by

323 small trees more than dry grasslands from 3 to 6 weeks before and from 2 to 6 weeks after
324 parturition, but no mule deer were located in those stands from 2 weeks prior to 1 week
325 after parturition (Fig. 4). In addition, stands of ponderosa pine dominated by large trees
326 typically were used slightly more than dry grasslands by female mule deer from 6 weeks
327 prior to 1 week after parturition, but were used less than dry grasslands from 2 to 6 weeks
328 after parturition (Fig. 4). Finally, the only instance in which mule deer were located in
329 xeric forest dominated by small lodgepole pine trees was during the week of parturition,
330 and in that instance, deer used lodgepole stands more than dry grasslands (Fig. 4).

331

332 **Discussion**

333

334 Although we did not directly observe parturition, our results are consistent with the
335 hypothesis that movement rates of female mule deer can be used as an index to timing of
336 parturition. We know of no other life-history characteristic or event that could have
337 resulted in the consistent, significant reductions in movement among female deer in late
338 spring observed during our study. Moreover, timing of parturition was nearly identical
339 between years. In addition, reductions in movement were highly synchronous, and the
340 degree of synchrony was consistent with previous results reported for synchrony of
341 parturition in female mule deer (Bowyer 1991).

342 Our hypothesis that stage of reproduction would influence patterns of resource
343 selection and movement among female mule deer was supported. Although we could not
344 determine whether all parturient females successfully reared young to ≥ 6 weeks of age,
345 consistency in patterns of selection and variance estimates associated with regression

346 coefficients from 2 to 6 weeks after parturition indicate that loss of young likely had a
347 limited effect on our analyses. Female mule deer likely selected gentle, south-facing slopes
348 prior to parturition to increase nutritional gain during gestation (Barboza & Bowyer 2000,
349 2001). Green-up of forage following winter typically occurs first on south-facing slopes,
350 and forage is more abundant in those areas than on north-facing slopes in early spring (pers.
351 obs.). In addition, energetic costs of locomotion are substantially greater in steep than in
352 gentle terrain, and by using gentle to moderate slopes, mule deer reduce energy expenditure
353 of movements (Parker et al. 1984). In contrast, selection of steep slopes with northwesterly
354 aspects by female mule deer during the week of and in the first week after parturition might
355 have reflected a strategy of predator avoidance, as well as spatial separation by maternal
356 dams. Although senescence of forage plants typically occurs later on north- than
357 south-facing slopes, forage quality and abundance on south-facing slopes at Starkey
358 generally remain high until early July (Long et al. 2008b), well after parturition has
359 occurred. Consequently, movements of female mule deer from south- to north-facing
360 slopes during the estimated week of parturition likely were not driven by the need to
361 acquire better forage. Similarly, at a constant rate of movement, the overall energetic cost
362 of locomotion increases as percent slope increases (Parker et al. 1984), and as a result, the
363 switch to selection of steep slopes by female mule deer likely increased energy expenditure
364 of movements.

365 Coursing predators, such as coyotes and black bears often favour easily traversable
366 terrain (Bowyer 1987, Farmer et al. 2006), and other studies have documented use of
367 moderate to steep slopes by female mule deer and their young as a means of reducing
368 predation risk (Riley & Dood 1984, Fox & Krausman 1994). Nevertheless, an alternative

369 hypothesis for use of steep slopes by female mule deer in our study during and in the first
370 week after parturition relates to selection of habitat located close to water during those
371 weeks. Water requirements of female deer increase substantially with the onset of lactation
372 (Bowyer 1984, Boroski & Mossman 1996), and most permanent water available at Starkey
373 is located in 2 creek drainages that bisect the study area. Much of the steepest terrain on
374 the study site also is located in those drainages, and consequently parturient females
375 moving closer to water following parturition might be expected to utilize relatively steep
376 slopes. In contrast to our hypothesis of predator avoidance, however, a hypothesis of
377 selection for water fails to explain why female deer in our study continued to use steep
378 slopes 6 weeks after parturition, but stopped selecting areas near water beginning 2 weeks
379 after birth.

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

388 We hypothesize that use of stands of ponderosa pine by female mule deer prior to
389 parturition was related to selection of topographic features that were favourable for
390 foraging in spring, as discussed previously. Xeric forest occurs almost exclusively on
391 south- and east-facing slopes at Starkey, whereas mesic forest occurs on north-facing slopes

392 (Stewart et al. 2006). Although mesic stands of forest at Starkey are more productive on an
393 annual basis (Stewart et al. 2006), earlier green-up of forage in xeric stands on south-facing
394 slopes may attract deer to those areas during spring, when energetic demands of late
395 gestation are increasing and deer are recovering from the physiological stresses of winter
396 (Barboza & Bowyer 2000). In addition, 75% of xeric forest at Starkey is dominated by
397 ponderosa pine, which helps explain why deer selected those stands, but only occasionally
398 used xeric stands dominated by lodgepole pine during gestation. Why female mule deer
399 primarily selected the most closed-canopy portions of ponderosa stands during gestation,
400 however, is less clear. One explanation for this phenomenon stems from the relationship
401 between habitat selection and spatial scale. Strategies used by ungulates to meet nutritional
402 requirements often vary with both spatial and temporal scale (Parker 2003), and thus
403 patterns of resource selection and space use tend to be highly sensitive to scale (Bowyer &
404 Kie 2006). We hypothesize that female mule deer selected ponderosa pine on south-facing
405 slopes to increase access to high-quality forage prior to parturition, but then selected areas
406 within those stands that provided a high degree of concealment cover to reduce risk of
407 predation while foraging.

408 Selection of relatively open portions of fir stands by female mule deer during and
409 shortly after parturition also may reflect effects of scale. Mesic forest at Starkey, whether
410 dominated by small or large trees, has the highest average canopy cover and tree densities
411 of all forest types on the study site (Long et al. 2008b). Consequently, the abrupt switch
412 from selection of ponderosa pine by mule deer to selection of fir stands in the week of
413 parturition may represent a predator-avoidance strategy, because canopy cover and tree
414 density ostensibly are inversely related to risk of predation (Bowyer et al. 1999). Locations

415 within fir stands that have the lowest total canopy cover, however, are likely to have the
416 highest level of understory productivity as a result of increased penetration of light and
417 water to the understory (Long et al. 2008b). We hypothesize that at a broad spatial scale
418 (i.e., within the study area) female mule deer selected fir stands during and shortly after
419 parturition to reduce risk of predation on neonates, but within those stands, deer selected
420 areas with lower-than-average canopy cover to increase access to high-quality forage.

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

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

438

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444

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599 **Figure captions**

600

601 **Figure 1.** Mean weekly movement rates of 19 female mule deer from 6 weeks prior to 6
602 weeks after the estimated week of parturition at the Starkey Experimental Forest and
603 Range, Oregon, USA, during 2005-2006. Error bars are 95% confidence intervals.

604 **Figure 2.** Parameter estimates for slope, sine (eastness) and cosine (northness) of aspect,
605 and canopy closure obtained from resource selection functions (RSFs) for 19 female mule
606 deer at the Starkey Experimental Forest and Range, Oregon, USA. For each habitat
607 variable, positive parameter estimates indicate that probability of use by mule deer
608 increased with increasing values of that variable (selection), whereas negative parameter
609 estimates indicate the opposite relationship (avoidance). Conditional logistic regression
610 was used to estimate weekly RSFs from 6 weeks prior to 6 weeks after the estimated week
611 of parturition based on location data collected during 2005-2006. Error bars are 95%
612 confidence intervals.

613 **Figure 3.** Parameter estimates for distances to open roads, restricted roads, and water, as
614 well as probability of use by elk, obtained from resource selection functions (RSFs) for 19
615 female mule deer at the Starkey Experimental Forest and Range, Oregon, USA. For each
616 habitat variable, positive parameter estimates indicate that probability of use by mule deer
617 increased with increasing values of that variable (selection), whereas negative parameter
618 estimates indicate the opposite relationship (avoidance). Conditional logistic regression
619 was used to estimate weekly RSFs from 6 weeks prior to 6 weeks after the estimated week
620 of parturition based on location data collected during 2005-2006. Error bars are 95%
621 confidence intervals.

622 **Figure 4.** Parameter estimates for 6 habitat types obtained from resource selection
623 functions (RSFs) for 19 mule deer at the Starkey Experimental Forest and Range, Oregon,
624 USA. Conditional logistic regression was used to estimate weekly RSFs from 6 weeks
625 prior to 6 weeks after the estimated week of parturition based on location data collected
626 during 2005-2006. Broad vegetation types were: 1) mesic forest dominated by grand fir or
627 Douglas-fir (Mesic); 2) xeric forest dominated by ponderosa pine (PIPO); and 3) xeric
628 forest dominated by lodgepole pine (PICO); each type was further divided into 2 subtypes
629 dominated by either small or large trees. Parameter estimates represent contrasts between
630 use of dry grassland by mule deer and each of the other 6 habitat types. Missing values for
631 a habitat type indicate that no mule deer were located in that type during that particular
632 week. Error bars are 95% confidence intervals.

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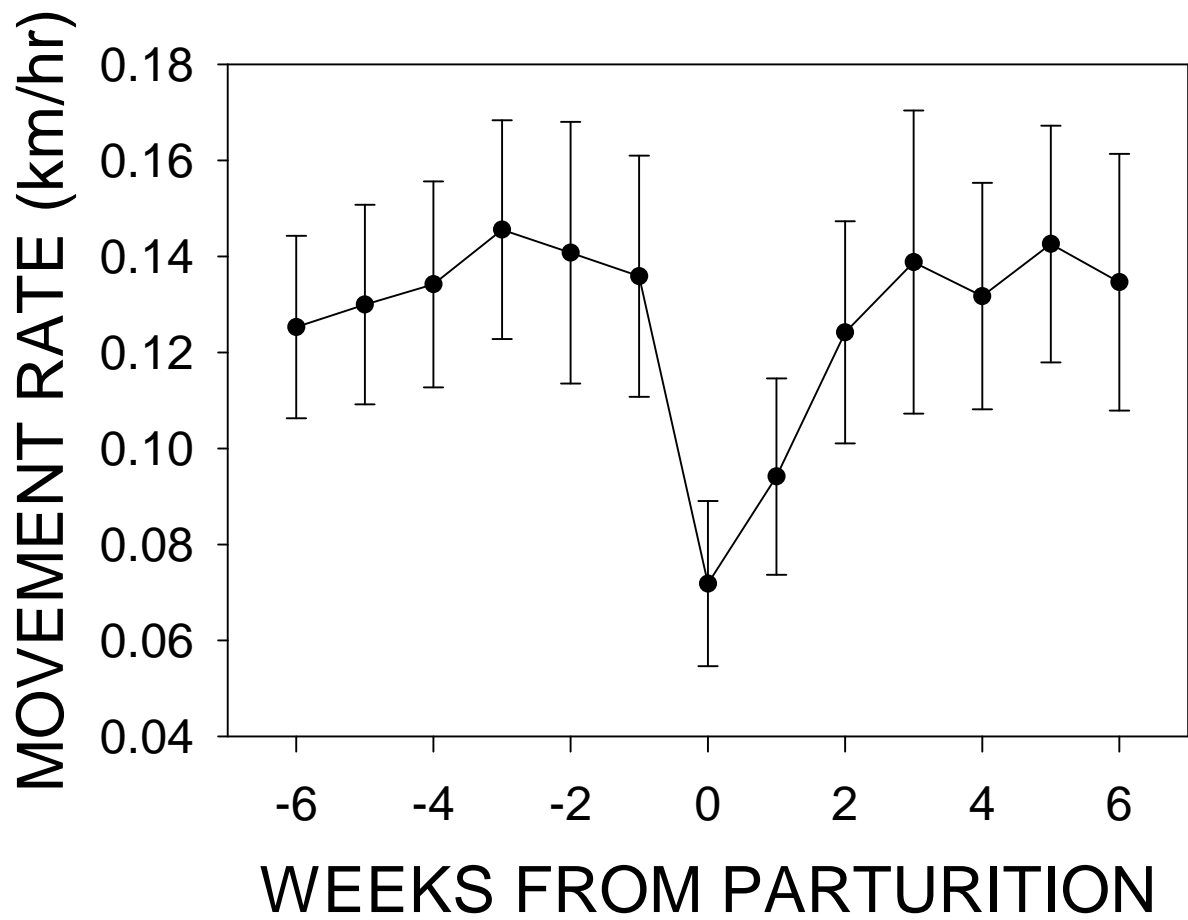
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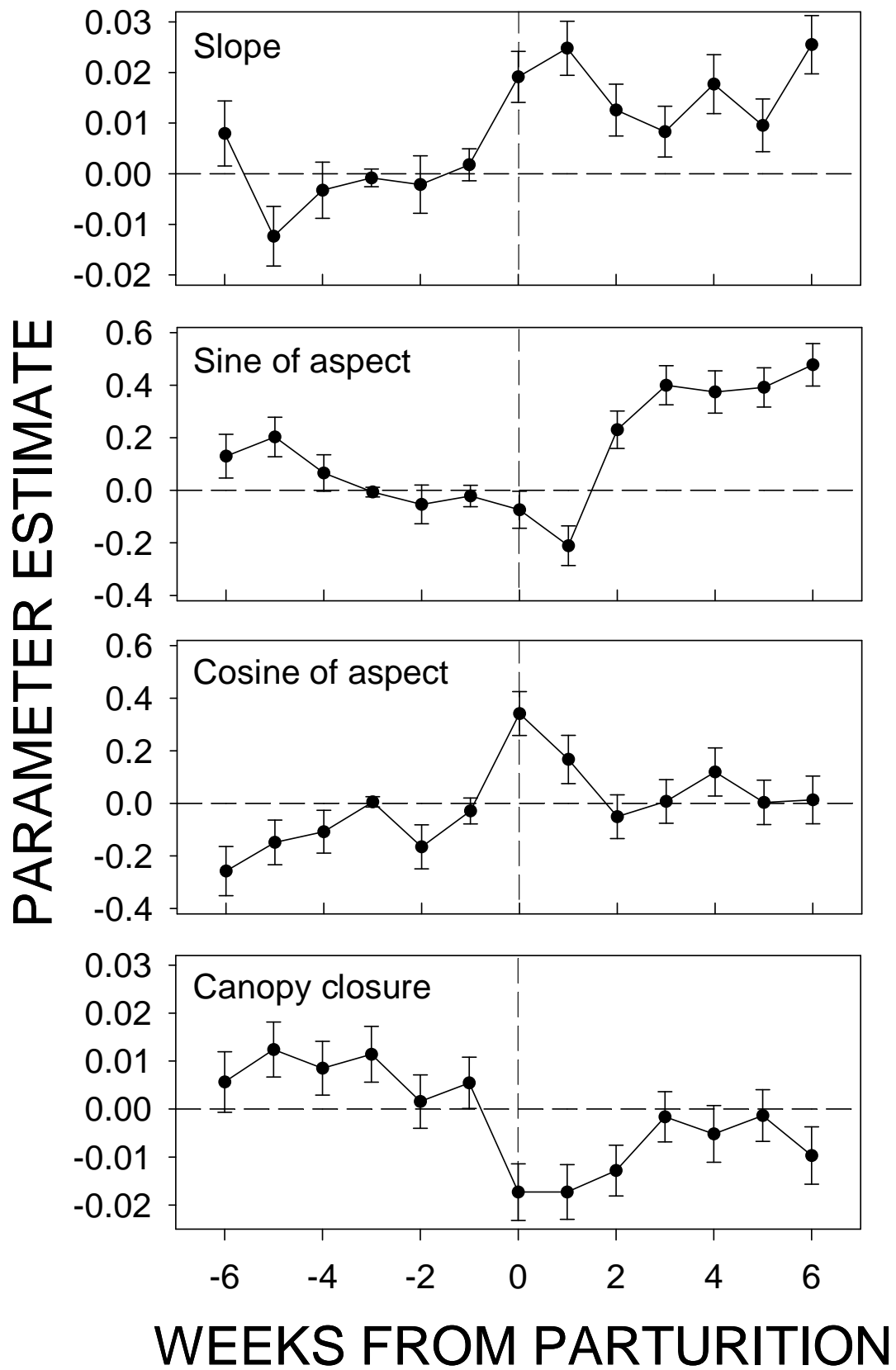
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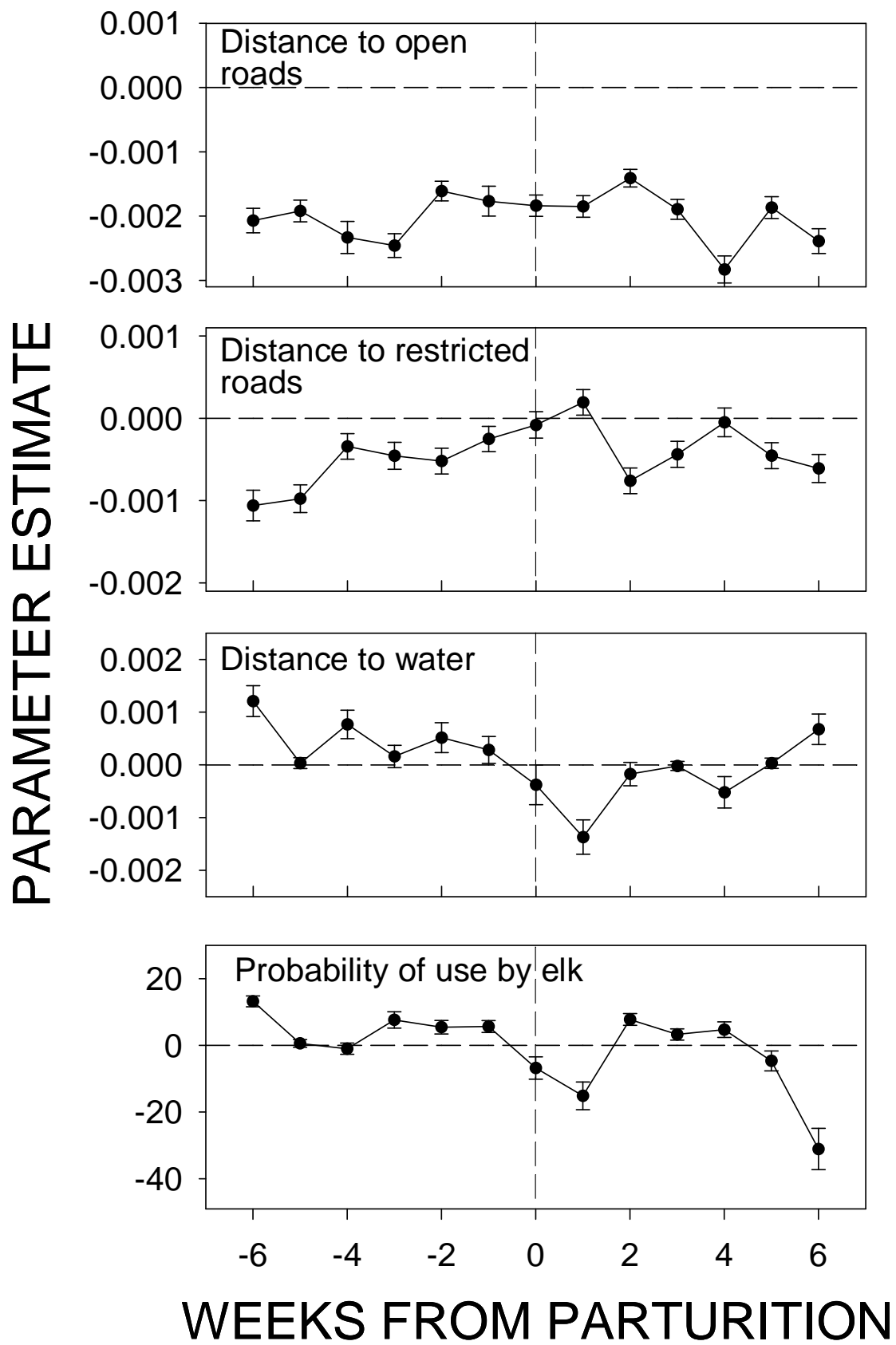
Long et al. Figure 1



Long et al. Figure 2



Long et al. Figure 3



Long et al. Figure 4

