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# HABITAT SELECTION BY NEONATAL BLACK-TAILED DEER: CLIMATE, FORAGE, OR RISK OF PREDATION?

R. TERRY BOWYER, JOHN G. KIE, AND VICTOR VAN BALLEMBERGHE

*Institute of Arctic Biology, and Department of Biology and Wildlife, University of Alaska Fairbanks,  
Fairbanks, AK 99775-7000 (RTB)*

*United States Forest Service, Pacific Southwest Research Station, 2081 East Sierra Avenue,  
Fresno, CA 93710 (JGK)*

*United States Forest Service, Pacific Northwest Research Station, 3301 C Street,  
Suite 200, Anchorage, AK 99503 (VVB),*

*Present address of JGK: United States Forest Service, Pacific Northwest Research Station,  
1401 Gekeler Lane, La Grande, OR 97850*

We studied habitat selection by neonatal (2–10 days old) black-tailed deer (*Odocoileus hemionus columbianus*) on Big Flat, Trinity Co., California, during June–August, 1992–1994. Even deer 2–3 days old frequently followed their mothers and occurred in social groups with other adult deer. Neonates used south-facing slopes with gentle terrain and high variability in overstory and concealment cover more often than expected from availability of those habitat variables. Young deer also selected sites with more herbaceous vegetation but avoided areas with more browse. Forage was more digestible at sites with neonates than at random sites, but no difference occurred in nitrogen content of forage between those sites. Variables identified as important components of habitat for young deer more likely were related to the thermal environment of the neonate and nutritional demands of lactating females than to risk of predation. Alternatively, variation in concealment cover may have been related to predation risk, resulting in a positive relationship between forage availability and risk predation. Minimizing the predation:forage ratio was not a viable model for explaining habitat selection in neonates.

**Key words:** *Odocoileus hemionus columbianus*, black-tailed deer, habitat selection, neonates, climate, forage, predation, hider-follower behavior, California

Changes in the behavior of an animal in relation to availability and quality of resources has been a central focus of behavioral ecology (Pulliam, 1989). If selection of habitat by an animal reflects a strategy that enhances survivorship and successful reproduction, models that explain distributions of animals across the landscape can be linked to dynamics of their populations (Pulliam and Danielson, 1991; Rosenzweig, 1981). Numerous models attempt to explain foraging ecology and distribution of species (Stephens and Krebs, 1986). Although procurement of essential resources is likely a driving force in selection of habitat, animals also may be confronted with risk of predation. Balancing the need to acquire re-

sources with the hazard of predation has been the topic of many studies (Bellman and Krasne, 1983; Formanowicz and Brodie, 1988; Fraser and Huntingford, 1986; Lima et al., 1985; Milinski and Heller, 1978; Sih, 1980, 1982; Werner et al., 1983). Our understanding of foraging ecology and habitat selection among ungulates, in particular, has benefited from melding concepts underlying foraging efficiency with constraints of predation (Berger, 1978, 1991; Bleich et al., 1997; Eastland et al., 1989; Edwards, 1983; Ferguson et al., 1988; Kohlmann et al., 1996; Molvar and Bowyer, 1994; Nicholson et al., 1997).

One solution offered to explain how animals deal with conflicting needs to forage

efficiently and avoid predation is selection of habitats (or patches) that minimize the ratio of predation risk to available forage (Pulliam, 1989). Conversely, such animals would tend to avoid other habitats in which predation risk was higher and value of food lower. Experimental evidence from Gilliam and Fraser (1987) suggests that this model will explain habitat selection under some conditions. In landscapes where there is an inverse linear relation between risk of predation and quality and quantity of forage, animals would be distributed mostly in the habitat (or patch) with low predation and high forage. If, however, animals are displaced from this optimal habitat because of intraspecific competition or dominance interactions with superior individuals, subordinates would be expected to distribute themselves along the inverse line into sub-optimal habitats until predation became too severe or forage too limiting for them to persist (*sensu* Fretwell, 1972). This solution does not require tradeoffs between predation risk and forage because these variables are related inversely.

If risk of predation and quality and abundance of forage are related positively, however, the predation : forage ratio is identical for all points along this line and offers no understanding of why the animal selects a particular habitat. Under these circumstances, the animal must balance risk of predation with the need for forage—the correct solution involves a tradeoff between these variables. Dominance hierarchies or competition would result in subordinates being displaced into zones of greater risk of predation or lower availability of forage along this line.

Departures from linearity in these relationships will complicate outcomes but do not obviate the point that we wish to make: tests of the role that predation risk and forage play in determining habitat selection require knowledge of how these variables are interrelated and distributed across the landscape. The correct prediction (i.e., minimize the predation : forage ratio, or tradeoff pre-

dition against forage) will depend on the direction of the relationship between forage and predation risk. Moreover, recognizing that direction may be critical in reconciling why some experimental (Werner et al., 1983) and field studies (Morgan, 1988) do not yield concordant results. We know of no empirical study that adequately addresses this problem.

Parturition and subsequent maternal care of neonates in mammals represent a huge investment—energy demands during lactation are extraordinarily high during that period (Oftedal, 1985, 1992; Sadleir, 1980; White and Luick, 1984). Moreover, nutritional demands to meet those needs occur in a relatively limited period for ungulates living in Arctic and temperate environments (Bowyer, 1991; Rachlow and Bowyer, 1991, 1994). Female cervids in poor physical condition tend to give birth to small, weak young that often suffer high rates of mortality (Clutton-Brock et al., 1987; Julander et al., 1961; Reimers et al., 1983; Sams et al., 1996; Thorne et al., 1976). Milk yield in ruminants declines with forage quality (Loudon, 1985), and undernourished females may fail to provide adequate maternal care of neonates (Langenau and Lerg, 1976; Rachlow and Bowyer, 1994). Moreover, climatic extremes hold the potential to directly affect young (Parker and Wong, 1987; Parker et al., 1984).

Many of the life-history characteristics of ungulates are thought to be shaped by risk of predation (Berger, 1978, 1991; Festa-Bianchet, 1988; Hirth, 1977; Molvar and Bowyer, 1994), and predators are capable of regulating populations of ungulates under certain conditions (Dale et al., 1994; Van Ballenberghe, 1987; Van Ballenberghe and Ballard, 1994). For *Odocoileus*, neonates are especially vulnerable to predators (Bowyer, 1987; Kie and White, 1985).

We tested relative effects of predation risk, climate, and forage on habitat selection by neonatal black-tailed deer (*O. hemionus columbianus*) and determined if these cervids made tradeoffs between predation risk

and forage, or minimized the predation: forage ratio. We chose young deer to test our ideas about habitat selection for several reasons. Selection of habitat is likely to depend upon a dynamic set of conditions that include the "state" of the individual, its environment, and perhaps its past and potential future states (Mangel and Clark, 1986). We address the need for dynamic "state variables" by measuring habitat selection in a narrow window in which needs for food and avoiding predation are relatively fixed near maxima in this large herbivore.

#### METHODS

*Study area.*—We conducted research on black-tailed deer on Big Flat near the headwaters of Coffee Creek (41°05'N, 122°56'W) in Trinity Co., California. Average elevation was 1,600 m; the area was characterized by moist meadows dominated by perennial grasses, sedges, and forbs intermixed with stands of corn lily (*Veratrum californicum*). Coffee Creek transected much of the study site, and riparian vegetation included willow (*Salix*), alder (*Alnus*), and scattered herbaceous plants. Gravel tailings from former mining for gold occurred along Coffee Creek at the southern end of the study area; the northern end of the area was bounded by the South Fork of the Salmon River. Meadows were adjacent to stands of conifers typified by Douglas fir (*Pseudotsuga menziesii*) and Ponderosa pine (*Pinus ponderosa*) with an understory of scrub oak (*Quercus*), gooseberry (*Ribes roezlii*), and manzanita (*Arctostaphylos*). Montane shrubs, including those associated with conifers, and mountain whitehorn (*Ceanothus cordulatus*) occurred on steep slopes above the conifers (Bowyer et al., 1996).

Most annual precipitation (ca. 95 cm) in these mountains fell as winter snow. Snow had melted at Big Flat by early May during our study, creating small ponds in low-lying meadows; surrounding peaks of the Salmon-Trinity Alps were snow covered until late July. Summer rains were infrequent and associated with brief thunderstorms. Daytime temperatures in summer often were  $\geq 28^{\circ}\text{C}$ .

Black-tailed deer migrated to Big Flat in late April and remained until September, when they began to move to winter ranges at lower elevations (Boroski et al., 1996; Bowyer et al., 1996;

Loft et al., 1984). Most deer gave birth in late June and early July, although a few young were born in late July (Bowyer et al., 1996).

We observed coyotes (*Canis latrans*), bobcats (*Lynx rufus*), black bears (*Ursus americanus*), and sign of mountain lions (*Felis concolor*) on Big Flat. Domestic dogs also roamed meadows used by deer. Domestic herbivores, including horses and cattle, were pastured on areas adjacent to Big Flat.

*Sampling of deer.*—We used several techniques to determine locations of neonatal deer. We observed deer each morning and evening by driving for ca. 2 h along a 9-km road that traversed our study area. We systematically searched areas adjacent to the road with binoculars for 4 days each week from June through August 1992–1994. Additionally, we opportunistically gathered data on neonates during other field activities (e.g., vegetation sampling).

We attempted to capture neonates that we judged to be 2–10 days old. This assessment was based initially on size, behavior, and pelage of young and confirmed for animals we captured by measuring and weighing them and examining their hooves and umbilicus (Haugen and Speake, 1958; Jackson et al., 1972; White et al., 1972). We did not sample habitat or attempt to capture or otherwise disturb deer that we believed to be <48-h-old to avoid interfering with bonding between mother and young. We captured neonates by walking quickly or running toward the animal. Very young deer undergo an alarm bradycardia when disturbed (Jacobsen, 1979), causing them to remain motionless or only flee short distances. We captured neonates with our hands and restrained them only long enough ( $\leq 5$  min) to affix break-away collars with radio transmitters and obtain morphometrics. All neonates were reunited with their mothers, which typically remained nearby while we gathered data on their young. Despite concerns expressed by Livezey (1990), human scent on neonates from their capture had no effect on their reuniting with their mothers, as Jackson et al. (1972) also noted for white-tailed deer (*O. virginianus*). One neonate, however, may have died as a result of our activities. That individual was found dead 2 days after its capture, but a necropsy performed by a veterinarian from the California Department of Fish and Game failed to reveal cause of death. All aspects of this research were approved by an independent Institutional Animal Care and Use

Committee at the University of Alaska Fairbanks.

All sites where we captured neonates, and some of those in which young deer escaped, were marked with flagging and their locations determined later with a global positioning system (GPS). Only the location for one neonate was used where we observed or captured twins or triplets. Likewise, we discarded one location where a young deer was first observed and later captured  $\leq 200$  m from the same site. We used only locations in which the neonate was undisturbed prior to our attempt to capture it.

*Sampling of neonatal and random sites.*—We confined our sampling to 1 km on either side of the 9-km road to minimize the likelihood of random samples occurring where we were unable to observe and capture neonates. Locations of random samples were determined using a gridded map and obtaining Cartesian coordinates from a random numbers table. We discarded three random sites that were farther from the road than neonatal sites used in our analysis, or that had greater concealment cover than where we located neonates. At each random and neonatal site we determined the location with GPS that was accurate to 2–5 m; we eliminated any site for which that level of resolution could not be achieved. Concealment cover was measured with a cover pole (Griffith and Youtie, 1988) that was 1.2 m in height and divided into 20-cm segments. Percent cover was determined by recording the proportion of those segments that were covered ( $\geq 50\%$ ) by vegetation or topographic features when the pole was observed from the four cardinal directions at a distance of 10 m. We calculated an index to risk of predation by taking the inverse of concealment cover. Gravimetric soil moisture was determined by sampling with a 2-cm diameter soil core to a depth of 10 cm. We noted predominant substrate at the site (e.g., pine needles, bare ground, lichen, moss). We sampled overstory cover with a spherical densiometer (Lemmon, 1957) that was read facing the four cardinal directions from the center of the site (e.g., GPS location where the neonate was first observed, or the center of a random site). We also used a wind gauge to measure maximum wind speed over a 1-min interval at each location.

We estimated forage abundance by sampling along a 50-m transect that was oriented randomly and centered on each GPS location. Percent

cover of shrubs and trees used as forage by deer (browse) was sampled using the line-intercept method (Bonham, 1989; Canfield, 1941). We recorded cumulative crown cover by species for shrubs and trees within the reach of deer ( $\leq 2$  m in height) along the 50-m transect. We collected current annual growth of browse eaten by deer, keeping different species separate for nutritional analyses. We sampled herbaceous plants at 1-m points along the transect (50 total points/transect) recording first “hits” at each point for classes of herbaceous vegetation (i.e., grass, sedge, forb) and later converted those data to percent cover by vegetation class. We clipped herbaceous plants to ground level in four plots along the transect that were pooled into a 0.25-m<sup>2</sup> sample of mixed herbaceous plants. The four subplots were collected in opposite directions along the transect at locations 5 m and 20 m from the center of the transect. We obtained an index to the predation:forage ratio by dividing predation risk by percent cover of herbaceous species.

We sampled neonatal sites within 12–24 h of capturing or observing a young deer. Random sites were sampled each week throughout the period that we sampled neonates. We tried to sample about the same number of neonatal and random sites each week; sampling neonatal sites quickly, however, often resulted in random sites being sampled later in a particular week than sites with young deer.

*Analyses of forage quality.*—We placed herbaceous vegetation from the 0.25 m<sup>2</sup> of subplots and current annual growth (including leaves) clipped from woody plants in labeled plastic bags and froze them. Vegetation samples were weighed later to the nearest 0.01 g and transferred to paper bags where they were dried at 50°C to a constant weight. Percent moisture of vegetation was calculated after they were reweighed; samples were ground in a Wiley mill so they would pass a 1-mm mesh screen. Forage quality was estimated with *in vitro* dry matter digestibility (IVDMD), with rumen liquor of caribou (*Rangifer tarandus*) as the inoculum, and from percent nitrogen in vegetative samples (Van Soest, 1982); both were determined by Forage Quality Laboratory of the Institute of Arctic Biology at the University of Alaska Fairbanks.

*Analyses of data from the Geographic Information System.*—We used the ARC/INFO (En-

vironmental Systems Research Institute, Redlands, CA) Geographic Information System (GIS) to derive several variables to analyze for both neonatal and random sites. We digitized maps of habitat types or vegetation associations (meadow, riparian, open conifer, conifer, montane shrub—Bowyer et al., 1996) drawn from aerial photographs that were truthed from the ground as well as from observations made from a small fixed-winged aircraft. We used the grids module of ARC/INFO, with a cell size of 80 m, to determine aspect and steepness of slope. We calculated terrain ruggedness by multiplying the *SD* of slope times the angular deviation of aspect (Nicholson et al., 1977). We determined distances to water and the road for each location using the GIS. We also calculated the “viewshed,” which was the distance a deer (1.2 m in height) might view to a maximum distance of 300 m based on topography. Thus, we measured habitat selection across two scales: immediately around the site (50 m) and at a macroscale (300 m).

*Statistical analyses.*—We used step-wise logistic regression (Agresti, 1990) with an  $\alpha$ -to-enter of 0.15 and an  $\alpha$ -to-remove of 0.16 to determine which variables separated neonatal sites (coded 1) from random sites (coded 0). Because a neonate may have been present at a random site other than when we sampled it, that analysis provided a conservative measure of habitat selection. We controlled for multicollinearity by eliminating one of any pair of variables with  $r \geq |0.45|$ . We determined that the fit of the logistic regression was apt using the Hosmer-Lemeshow test for goodness-of-fit (Agresti, 1990). We used the log-odds ratio to determine importance of individual variables to the ability of the model to separate neonatal from random sites (i.e., habitat selection). Deer selected habitat when use was greater than availability and avoided it when use was less than availability.

Because forage species were not available at some sites that we sampled (or there was an insufficient amount for chemical analyses), measurements of forage quality could not be included in the logistic-regression model, which required no missing data. Consequently, those data were analyzed separately using a multivariate analysis of variance (MANOVA—Johnson and Wichern, 1982); data were arcsine-square root transformed to meet the assumption of that analysis. We treated different species of browse as separate samples, even if they came from the

same site, which had the effect of inflating sample size for statistical comparisons involving browse. Thus, we reduced  $\alpha$  to 0.01 to help correct for overestimating sample size in tests that involved nutritional quality of forage. An  $\alpha = 0.05$  was adopted for all other tests.

## RESULTS

Thirty-six of 40 young black-tailed deer were located at the heel of their mothers or were bedded nearby ( $\leq 10$  m), including deer that were judged to be only 2–3 days old. Those neonates often accompanied adult females into large open meadows or open stands of conifers where adults foraged and bedded in social groups—females with even very young offspring usually were not secluded from other adults. When older neonates (6–10 days old) that we captured gave alarm squeals, several adult females often approached and remained nearby until we released those young deer.

Our analysis of habitat selection by neonatal deer initially was subdivided into categories that contained variables related to geography, topography, climate, risk of predation, and forage availability (Table 1). Because year failed to enter our logistic-regression model ( $P > 0.15$ ), all 3 years were pooled to increase sample size.

Logistic regression identified six variables that significantly ( $P < 0.001$ ) discriminated between random sites and those with young deer: sin slope, terrain ruggedness, *CV* overstory cover, *CV* concealment cover, cover of browse, and cover of herbs (Table 1). The model correctly classified 89.7% of 94 randomly located or neonatal sites. Neonates avoided north-facing slopes (i.e., selected south-facing ones), avoided rugged terrain, selected for high variability in overstory and concealment cover, selected sites with herbs (grasses, sedges, and forbs), and avoided sites with browse (Fig. 1). Neonates selected gentle south-facing slopes with herbaceous vegetation and variable overstory (a tree) and concealment cover (e.g., a tree trunk).

We tested for differences in forage qual-

TABLE 1.—Summary statistics for habitat characteristics of random and neonatal sites of black-tailed deer, Big Flat, Trinity Co., California, June–August, 1992–1994.

Habitat variables	Neonatal sites ( <i>n</i> = 40)		Random sites ( <i>n</i> = 54)	
	$\bar{X}$	<i>SD</i>	$\bar{X}$	<i>SD</i>
<b>Geographical</b>				
Distance to streams (m)	300	241	268	264
Distance to forest (m)	44	62	88	116
Distance to roads (m)	109	101	167	124
<b>Topographical</b>				
Sin aspect <sup>a</sup>	0.10	0.85	0.22	0.84
Cos aspect <sup>b</sup>	−0.05	0.53	−0.03	0.52
Slope (%)	12.4	8.9	13.9	7.2
Terrain ruggedness <sup>c</sup>	3,918	2,918	4,585	3,370
Elevation (m)	1,523	34	1,527	52
<b>Climatic</b>				
Julian date	186	9	190	11
Wind speed (km/h)	2.8	3.2	2.7	4.1
Soil moisture (%)	23.2	41.2	25.9	39.3
Overstory cover (%)	35.5	21.8	49.0	23.7
CV overstory cover (%)	78.6	64.3	36.4	36.0
<b>Predation</b>				
Concealment cover (%)	35.4	17.7	34.7	22.0
CV concealment cover (%)	108.8	64.3	104.2	66.2
Visibility (m) <sup>d</sup>	251	97	234	108
<b>Forage</b>				
Browse (%)	3.6	6.2	9.9	13.2
Herbs (%)	43.3	22.7	24.0	22.5

<sup>a</sup> N-S aspects

<sup>b</sup> E-W aspects

<sup>c</sup> *SD* slope times angular deviation of aspect (Nicholson et al., 1997)

<sup>d</sup> Viewshed analysis from ARC/INFO; distance over which a deer (1.2 m in height) might see to a maximum distance of 300 m based on topographic relief.

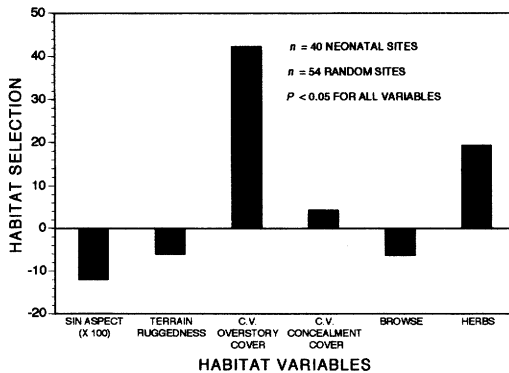


FIG. 1.—Selection (used minus available) of habitats by neonatal black-tailed deer on Big Flat, Trinity Co., California during June–July, 1992–1994. Variables were selected by a logistic regression that classified 89.7% of neonatal and random sites correctly.

ity at random sites and ones with neonates using MANOVA (Table 2), with nitrogen content and IVDMD as dependent variables and site (random, neonate) and forage class (browse, herbs) as main effects. The overall test was significant ( $F = 5.18$ ,  $d.f. = 2,128$ ,  $P = 0.007$ ), and differences were primarily because neonates occurred at sites with more digestible forage and herbaceous vegetation was more digestible than browse (Table 2). That outcome was consistent with neonates selecting sites with more herbaceous vegetation (Table 1, Fig. 1).

The relationship between predation risk and forage in this environment was difficult to access. No correlation ( $P = 0.66$ ) existed between cover of herbaceous species (an index to forage) and concealment cover (an index to risk of predation). Moreover, con-

TABLE 2.—Differences between quality of forage (nitrogen content and *in vitro* dry matter digestibility—IVDMD) for black-tailed deer at neonatal and random sites, and between browse and herbs on Big Flat, Trinity Co., California, during June–July, 1992–1994. P-values between rows indicate *a posteriori* tests following a significant overall test with MANOVA ( $P = 0.0007$ ).

Site or forage category	Nitrogen (%)			IVDMD (%)		
	$\bar{X}$	SE	n	$\bar{X}$	SE	n
Random	1.6	0.06	75	50.1	1.010	75
Neonatal	1.7	0.06	57	55.6	1.10	57
Browse	1.7	0.05	101	50.7	0.90	101
Herbs	1.7	0.07	31	58.3	1.60	31

concealment cover failed to enter our logistic-regression model (Fig. 1). Inverse relationships did occur, however, between mean concealment cover and CV of concealment cover for each location ( $r = -0.59$ ,  $P = 0.001$ ) and herbaceous vegetation and CV of concealment cover for each location ( $r = -0.22$ ,  $P = 0.03$ ). Interpreting mean values for concealment cover was straightforward; increasing cover ostensibly lowered risk of predation by better concealing neonates. If we treated the inverse of mean concealment cover as an index to risk of predation and divided by the proportion of herbaceous vegetation at sites, the overall predation:forage ratio was lower for neonatal (0.07) than random (1.20) sites but did not differ significantly ( $P > 0.05$ ). Understanding how the CV of concealment cover at each site related to risk of predation was more difficult. If we assumed that increasing variation in cover lowered risk of predation, the inverse of that variable divided by the proportion of herbs at sites yielded a predation:forage ratio that was similar ( $P > 0.10$ ) between neonatal (0.02) and random (0.04) sites.

#### DISCUSSION

Several outcomes from this study were unexpected. First, *Odocoileus* is thought to be the quintessential example of an ungulate with young that hide rather than follow the female continuously (Lent, 1974; Walther, 1984). A hider strategy of maternal

care for black-tailed deer in our study likely would have resulted in variables related to predation rather than forage dominating our logistic-regression model. Only one variable potentially related to predation (CV of concealment cover) entered this model (Fig. 1). Moreover, we observed deer 2–3 days old accompanying females that were foraging in meadows with other adult deer. The hider-follower dichotomy did not predict habitat selection by deer in our study, and our observations document that variation in this strategy occurs among populations of *Odocoileus*. Green and Rothstein (1993) likewise expressed concern over the degree to which bison (*Bison bison*), a classical example of a follower, fit the expected pattern. We question the usefulness of the hider-follower concept as an organizing principle for ecological or behavioral research and suggest that more studies of intraspecific variation in this phenomenon are required before it can be applied in a useful manner.

Riparian zones have been identified as critical habitat for parturient black-tailed deer (Loft et al., 1984). Our data indicate, however, that riparian habitat per se may not be the element selected by neonates. For instance, distance to streams (an index to the importance of riparian habitat) was similar for both neonatal and random sites (Table 1) and failed to significantly improve our logistic-regression model. Browse, in-

cluding willows and alders that characterized riparian areas on Big Flat, was avoided by neonates (Fig. 1). We believe that differences between studies relate to the importance of moist meadows to young deer. Loft et al. (1984) combined riparian and wet-meadow habitats, which often co-occurred on their study area. On Big Flat, however, there were extensive areas of riparian habitat, especially along Coffee Creek, that were not closely associated with meadows. Thus, we hypothesize that moist meadows are critical habitat for neonates. Significant selection of sites with more herbaceous species by neonates (Fig. 1) and greater digestibility of these plants (Table 2) support our view. Additional evidence for this idea was provided by Bowyer et al. (1996), who reported that young black-tailed deer used meadow habitat more often than riparian areas through their first summer of life. Bowyer (1984, 1986) documented that young mule deer in southern California selected moist meadows, where availability of free water was more important than on Big Flat where water was ubiquitous.

We proposed to evaluate the role of climate, risk of predation, and forage in habitat selection by neonatal deer. Indeed, the logistic regression included a suite of variables that discriminated neonatal sites from random ones (Fig. 1). Two variables that we categorized as topographical, however, may be related more closely to climate or habitat needs of neonates. First, selection for south-facing slopes likely reflected the influence of climatic variables on neonates. Although daytime temperatures on south-facing slopes could be hot ( $\geq 28^{\circ}\text{C}$ ), mornings were often cool and typified by dew-covered vegetation, especially in meadows. Thus, neonates on south-facing slopes may have been in a more favorable thermal environment, with more sunlight and warmer temperatures, particularly in morning. Second, neonates selected less-rugged terrain (Fig. 1). Meadow and open-conifer habitats in which young deer occurred most often

(Bowyer et al., 1996) were on gentler slopes than the surrounding forest of dense conifers. We suspect that terrain ruggedness is, in part, a surrogate for meadows in our model.

Selection by neonates for sites with greater variation in overstory cover (Fig. 1) probably is related to their thermal needs. The same south-facing slopes that provided warmer sites in morning often were hot by mid-afternoon. We believe that greater variability in overstory cover on sites with neonates was produced by the canopy of a tree; indeed, trees were scattered widely in and around meadows and would provide high values for overstory cover but not in more than one or two of the four samples recorded at such a site; hence, the greater CV for neonatal sites than random sites (Table 1, Fig. 1). We interpret this outcome to mean that neonates on hot south-facing slopes would have the shade from a tree to help moderate effects of high temperatures during afternoon. Fox and Krausman (1994) also noted the importance of thermal cover to neonatal deer.

The one variable that entered our logistic regression that ostensibly was related to predation was the CV of concealment cover, which was greater for neonatal sites (Fig. 1). We question, however, if that variable was related to predation because mean concealment cover was almost identical for random and neonatal sites (Table 1). Moreover, if such variation in cover was related to sites where approaching predators could be seen more readily, we would have expected visibility (Table 1) to enter our model, but it failed to do so. Consequently, the most likely interpretation for greater variation in concealment cover at sites with neonates related to overstory cover (i.e., the trunk of the tree that increased variability in overstory cover also caused more variation in concealment cover). Thus, we hypothesize that this variable entering the model was an artifact from females with young deer seeking a more favorable thermal environment.

Our analysis did not clearly discriminate between needs of mother and young for habitat components. Both abundance and quality of forage clearly played a role in habitat selection by females with neonates. Sites with neonates had significantly more herbs and less browse than random sites (Fig. 1), which again reflected use of meadows by neonates. Forage at sites with neonates was significantly more digestible than forage at random sites (Table 2), and nitrogen content of forage at neonatal sites also was higher but not significantly so (Table 2). Of course, such young deer were not yet feeding on plants, and outcomes related to forage abundance and quality undoubtedly reflected nutritional needs of adult females. Lactating deer have high nutritional requirements (Oftedal, 1985, 1992; White, 1983; White and Luick, 1984) that obviously affect habitat selection by their young. This outcome was particularly evident in our study because neonates followed their mothers from an early age.

Analysis of concealment cover and herbs indicated that neonates may select sites that reduced the ratio of predation risk:forage. That concealment cover was important to young deer has been suggested by Loft et al. (1984) and Bowyer (1986). Reduction in hiding cover for neonates by heavy cattle grazing is thought to adversely affect deer range (Bowyer and Bleich, 1984; Loft et al., 1987). Nonetheless, mean concealment cover at neonatal and random sites in our study was nearly identical (Table 1) and, thus, did not improve our ability to discriminate between those sites (Fig. 1). We question if it is appropriate to invoke the predation:forage ratio as an explanation for habitat selection when we cannot demonstrate that variables clearly related to predation risk (e.g., mean concealment cover) were important to young deer (Fig. 1).

Variation in concealment cover was inversely to herbaceous cover. Thus, there was a direct relationship between risk of predation and forage—sites with a patchy distribution of cover (lower risk) also had

less forage. Under these conditions, a trade-off between predation risk and forage would be expected, and the predation risk:forage ratio should be similar between sites, which occurred. Consequently, young deer would make tradeoffs between predation risk and nutritional needs of their mothers. We conclude that nutritional needs of lactating mothers and the thermal environment of young deer were primary determinants of habitat selection. Within this matrix of habitat components, young deer also may have attempted to reduce predation risk by locating a patch of cover, especially in open meadows. We cannot clearly discriminate between this hypothesis and one suggesting that variability in concealment cover is an artifact of overstory cover. Clearly, forage quality (Table 2) and abundance (Fig. 1) are important components of habitat for lactating females and their young, and the predation risk:forage ratio will not explain habitat selection adequately in this environment in northern California.

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