

Risk Factors and Mortality of Black-Tailed Deer in a Managed Forest Landscape

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Abstract

We investigated the influence of habitat use on the risk of death of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Heceta Island in Southeast Alaska, USA. A mosaic of even and uneven-aged forests covered much of the island and provided a model setting in which to assess relationships between habitat use and mortality of deer. We radiocollared and monitored 51 adult females, 11 adult males, and 19 young of the year. We compared risk of death with habitat composition, habitat distribution, topography, distances to features such as roads, and functional habitat characteristics such as seasonal forage biomass within 50-, 500-, and 1,000-m circular buffers around relocations of deer. Those buffers encompassed habitats used at scales of radio-relocations, home ranges, and landscapes. We addressed hypotheses that related habitat composition and distribution to risk of death from malnutrition, predation, and hunting. Predation by wolves (*Canis lupus*) and malnutrition were the principal causes of death of adult females and young, whereas hunters killed most adult males. Habitat factors at scales of 500 and 1,000 m had the greatest effect on mortality of adult females and young, whereas habitat characteristics in the immediate vicinity of radio relocations had the greatest effect on mortality of adult males. Malnutrition was positively associated with use of forage-poor habitats such as pole-stage, second-growth forest. Use of precommercially thinned second growth increased risk of death for young deer. Use of level terrain was the most influential factor with respect to predation and increased risk of death at all scales. Use of open habitats, such as muskegs and young clearcuts, also increased risk of death. Use of shrub-sapling-stage clearcuts in landscapes accessible by roads increased risk of death from hunting. We showed that use of specific habitats and the landscape context of those habitats were important factors influencing mortality of deer. We also demonstrated the importance of comparing habitat use with measures of fitness rather than simply with availability when evaluating habitat suitability for deer. Our results should be useful to wildlife researchers investigating contributions of habitat to fitness and population dynamics of ungulates, and to wildlife managers attempting to manipulate habitats to benefit deer populations. (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1403-1415; 2006)

Key words

black-tailed deer, Cox proportional hazards, forest management, habitat use, mortality, Odocoileus hemionus, risk ratios.

Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) are the most abundant and widely distributed ungulates in temperate rainforests of Southeast Alaska, USA (MacDonald and Cook 1996). Although much is known about habitat use (Wallmo and Schoen 1980, Schoen and Kirchhoff 1990, Yeo and Peek 1992, Doerr et al. 2005) and foraging ecology (Hanley and Rogers 1989, Parker et al. 1999) of those deer, researchers have not conducted studies to examine relationships between habitat use and risk factors such as malnutrition, predation, and hunting that affect survivorship, nor have they examined those relationships at multiple scales and among sex and age classes. McNay and Voller (1995) estimated survivorship and cause-specific sources of mortality of female Columbia black-tailed deer (*O. b. columbianus*) on Vancouver Island, Canada, and Klein and Olson (1960) described sources of mortality of Sitka black-tailed deer in Southeast Alaska. Nonetheless, neither of those studies related habitat use to mortality. In addition, there have been few studies published concerning effects of large-scale industrial activity, such as timber harvest, on risk factors for deer.

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Researchers believe causes of death related to severe winter weather to be the primary sources of mortality of deer in Southeast Alaska (Klein and Olson 1960, Klein 1965, Wallmo and Schoen 1980), particularly where snow depth exceeds 50 cm (Hanley and Rogers 1989). In those areas, deer strongly select productive old-growth forest on southern exposures below 250 m elevation in winter (Wallmo and Schoen 1980, Schoen et al. 1988, Schoen and Kirchhoff 1990). Timber harvest has increased fragmentation of forest habitat, creating many small, remnant stands of old-growth forest within a matrix of younger second-growth forest. Fragmentation may reduce the value of forests as winter habitat by forcing deer to remain in small patches of timber isolated by snow (McNay 1995). Over-browsing of forage may occur in those stands because deer may have difficulty moving between patches, effectively reducing carrying capacity (*K*) in winter. Thus, landscape context likely influences availability of forage, and possibly mortality of deer (Kie et al. 2005).

In areas of lower snow accumulation, the importance of productive old-growth habitat for survivorship of deer may be more ambiguous. In the absence of snow, fat accumulated from foraging on high-quality summer and autumn ranges may enable cervids to survive, regardless of the quality of winter habitat (Kie et al. 2003, Stewart et al. 2005).

Nevertheless, forage biomass available to deer in older (≥ 29 yr), even-aged seral stands created by clearcutting is significantly lower than that in old-growth forests or younger (< 29 yr) seral stands during all seasons (Wallmo and Schoen 1980, Alaback 1982, Farmer 2002). Presumably, as the proportion of older seral stands increases on the landscape, forage for deer will decline, resulting in lower populations regardless of winter weather (Wallmo and Schoen 1980, Rose 1982, Schoen and Kirchhoff 1990, Person et al. 1996).

Predation by wolves (*Canis lupus ligoni*), black bears (*Ursus americanus*), and brown bears (*U. arctos*) is a significant source of mortality of deer in Southeast Alaska. Wolves usually take advantage of habitats that enable them to stalk and chase prey over short distances (Mech 1970, Kunkel and Pletscher 2001). These canids also prefer hunting in flat or gentle terrain (Kunkel and Pletscher 2001), indicating that topography may be an important factor influencing risk of predation for deer. Wolves may detect deer occupying landscapes dominated by open habitats, such as new clearcuts or muskeg heaths, more easily and deer may have less contiguously distributed cover available to escape predation. Further, weather, habitat quality, and landscape characteristics may interact to affect the vulnerability of deer to predation.

Hunting is also a major source of mortality for black-tailed deer, particularly for adult and yearling males. About 9,000 recreational and subsistence hunters in Southeast Alaska (Straugh and Rice 2002) harvest approximately 12,000 deer annually. Open habitats, such as young or new clearcuts, and landscapes that enable hunters to detect deer likely increase risk of mortality from hunting. In addition, roads built during logging may facilitate hunter access to deer (Trombulak and Frissell 2000, U.S. Forest Service 2003).

We examined relations between habitat use by radio-collared Sitka black-tailed deer of different age classes and sexes, and risk factors that affected mortality. We evaluated habitat use at multiple scales that enabled us to relate local habitat characteristics and broader landscape-level features to risks of death from predation, malnutrition, and hunting. In addition, we addressed the following specific hypotheses related to risk of death: 1) habitat characteristics across multiple scales will influence risk of death from all sources of mortality; specifically, habitat variables related to distribution and arrangement of habitats and topography will significantly affect risk of death; 2) availability of forage has a relationship with risk of death from causes related to malnutrition; thus, greater use by deer of habitats with depauperate understory vegetation will increase risk of death from malnutrition, particularly during winters with deep snow; 3) deer use of brushy habitats offering thicker contiguous escape cover will reduce risk of predation by wolves and we predict use by deer of open habitats will increase risk of death from predation; and 4) risk of death from hunting has a relationship with open habitats and roads; deer more closely associated with road corridors will have higher risk of death from hunting. We addressed all 4

hypotheses for adult and yearling females. We could address only our hypotheses concerning effects of scale and hunting for adult and yearling males, and only those concerning effects of scale, malnutrition, and predation for young.

Study Area

We conducted our research on Heceta Island ($55^{\circ}45'$ N, $133^{\circ}45'$ W) in the Tongass National Forest of Southeast Alaska. Southeast Alaska contains $> 2,000$ islands comprising the Alexander Archipelago (Fig. 1). Heceta Island is approximately 180 km^2 and is located on the southwestern edge of the archipelago. Elevations on Heceta Island range from 0–915 m. There usually was little winter snow accumulation below 150-m elevation during our study; however, a moderately severe winter occurred in 1998–1999. During that winter, snow accumulations reached 67 cm at

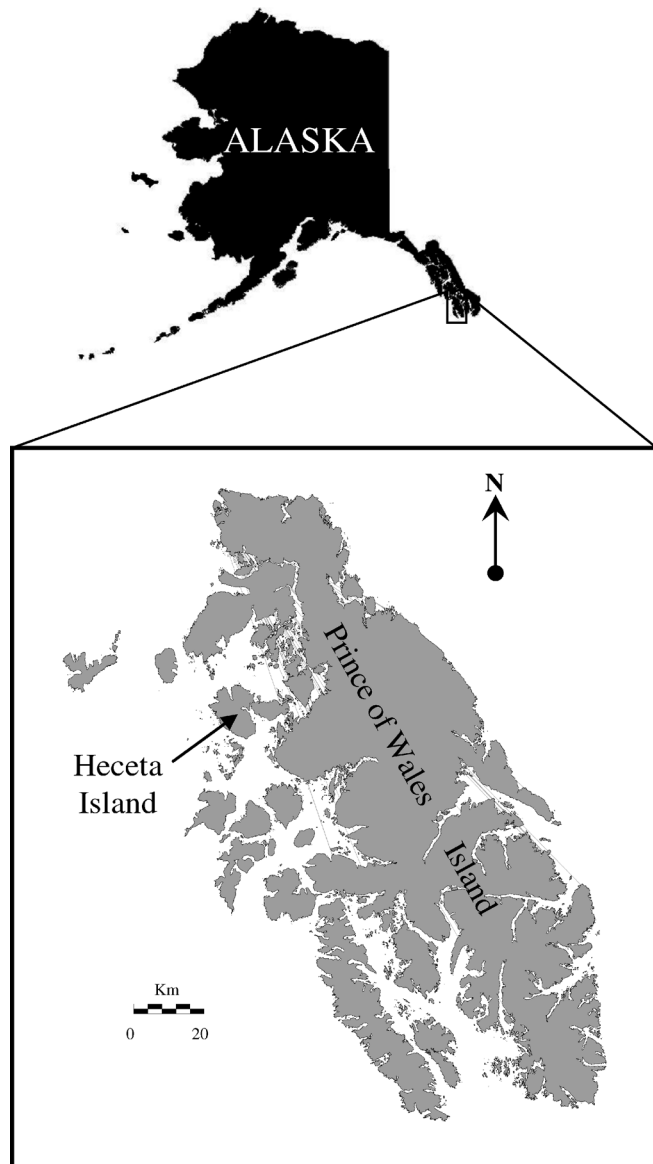


Figure 1. Map of Southeast Alaska, USA, showing the study area on Heceta Island where we investigated relationships between habitat characteristics and mortality of Sitka black-tailed deer, 1997–2000.

sea level by February, with depths exceeding 150 cm at higher elevations.

Heceta Island supports productive coniferous forest typical of coastal temperate rainforests of the Pacific Northwest (Harris and Farr 1974, Alaback 1982). Those forests generally have well-developed understories composed of herbaceous forbs and shrubs (Alaback 1982). Industrial-scale logging began on Heceta Island in 1955 and peaked in the 1980s. Prior to 1955, small stands of timber were partially harvested or clearcut along some shorelines. Large-scale harvesting began at low elevation close to shorelines and gradually expanded to higher elevations inland. Consequently, older logged stands were closer to sea level and the youngest cuts were at slightly higher elevations. Clearcut timber harvesting was the dominant regime of forest management. By the beginning of our study in 1996, 33% of the total area, or 42% of productive forestlands, on Heceta Island had been logged (U.S. Forest Service 1996). Of second-growth forest identified by the United States Forest Service on the island, 75% was in young seral forest (<29 yr postlogging), and 25% was in older seral forest (≥ 29 yr postlogging) during our study. An estimated 83% of the island was accessible by road (U.S. Forest Service 1996). Hunters and logging crews used roads seasonally to drive all-terrain vehicles and trucks. A logging camp of 10–20 people operated on the island from April to November during our study.

Wolves were the only significant predator of deer on the island. We occasionally observed black bears, but their numbers were low. Density of deer was >11 animals/km² (Kirchhoff 1998, Farmer 2002), which was moderately high for the region. Deer-hunting seasons on Heceta Island began 1 August and closed 31 December, with a bag limit of 4 adult male deer. A shorter antlerless deer season began 15 October and ended 31 December but was restricted to federally qualified subsistence hunters.

Methods

We captured deer using tranquilizer darts, drop-nets, and net guns from September 1996–November 1999. We chemically immobilized deer that we darted with a 5:1 combination of xylazine HCl and ketamine HCl. We handled all other deer without chemical restraint. We placed radiotelemetry collars (Mod 500, Telonics, Inc., Mesa, Arizona) on deer classified as adults (≥ 24 months old), yearlings (12–24 months old), or young (<12 months old). We fitted young <4 months old with breakaway telemetry collars (Mod 200 Telonics, Inc., Mesa, Arizona) designed to drop off as deer attained adult size, permitting us to monitor them for 12–20 months postcapture. State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee approved all animal immobilization and handling procedures, which conformed to guidelines specified by the American Society of Mammalogists (Animal Care and Use Committee 1998).

We relocated deer from the air and ground, and determined locations of deer obtained from the ground

from at least 2 azimuths. We recorded radio-locations obtained from fixed-winged aircraft on low-level aerial photographs. We overlaid locations on geographically referenced orthophotographs (1:15,840 scale) and assigned Universal Transverse Mercator (UTM) coordinates to each location. We assessed accuracy and precision of radio-telemetry locations by periodically testing observers with radiocollars at locations unknown to them ($n = 12$, for aerial locations and $n = 52$ for ground-based locations). Mean errors for aerial and ground-based telemetry locations were 57 m (SE = 19 m) and 55 m (SE = 15 m), respectively. We used a 24-hour randomized schedule for ground-based telemetry, with one relocation/animal/week from March 1997 to June 2000. We chose that sampling interval to minimize autocorrelation in relocation data. We located study animals from the air once per month if we could not locate them from the road system. We obtained 4,232 telemetry relocations. We recorded 40% of radio-locations during night and 60% during daylight. We calculated 95% and 50% adaptive kernel home ranges for deer with ≥ 30 relocations (Worton 1989) using CALHOME (Kie et al. 1996).

Survival Analysis

We monitored deer every 48 hours to detect mortality signals, which we usually investigated on the day of detection. We determined cause of death and location of each carcass. Nutritional status at time of death was most often estimated by examination of femoral bone marrow (Cheatum 1949), unless the carcass was sufficiently intact to perform a necropsy. Unfortunately, in many instances examining bone marrow only enabled us to detect malnutrition if deer were in advanced stages of nutritional stress (Klein and Olson 1960).

To minimize the possibility of including capture-related mortalities in our survival estimates, we only used data from deer that survived >2 weeks postcapture. Three deer died within that period after capture and we did not include them in our analyses. We estimated survivorship in weeks for young, yearlings, and adults with staggered-entry Kaplan-Meier survivorship functions (Efron 1988, Pollock et al. 1989). We used log-rank tests to compare survivorship functions among age and sex strata (Pollock et al. 1989). If survivorship curves for 2 strata did not differ significantly ($P > 0.10$), we pooled data from those strata for subsequent analyses. We calculated rates of mortality by cause of death for all strata.

Habitat Correlates of Survivorship

We placed circular buffers with radii of 50, 500, and 1,000 m around each radio-location. Fifty-meter buffers encompassed habitats within an area equal to the average error surrounding radio-locations, 500-m buffers encompassed habitats within an area slightly larger than the average home range of an adult female deer, and 1,000-m buffers encompassed areas 4 times the size of an average deer home range. We divided variables considered as potential predictors of death into 5 groups: 1) habitat composition, 2)

Table 1. Grouped variables^a evaluated with Cox proportional hazards models to assess their potential influence on risk of death for radiocollared deer on Heceta Island, Alaska, USA, 1997–2000.

Variable group		Description
Habitat composition		
Vegetation class ^b		proportion of buffer composed of a particular vegetation class
Habitat distribution		
Diversity		$\Sigma[p_i \times \ln(p_i)]$, where p_i = proportion of 7×7 -pixel kernel in vegetation class i summed over kernel and then averaged over buffer
Fragmentation		$(n-1)/(c-1)$, where n = number of vegetation classes in 7×7 -pixel kernel and $c = 49$; result is averaged over buffer
Edge density		(total perimeter of all vegetation classes – perimeter of buffer)/area of buffer
Road density		km of road in buffer/area of buffer
Patch size (by vegetation class)		area of largest patch of particular vegetation class intersecting buffer
Distance Measures		
Riparian distance		average distance (m) from any point within buffer to lakes or streams
Road distance		average distance (m) from any point within buffer to roads
Developed land		average distance (m) from any point within buffer to clearcuts or other developed lands
Topographic features		
Northerly aspect		proportion of buffer facing 315–45°
Southerly aspect		proportion of buffer facing 135–225°
Easterly aspect		proportion of buffer facing 45–135°
Westerly aspect		proportion of buffer facing 225–315°
Flat terrain		proportion of buffer with no aspect
Slope		average degrees of slope within buffer
Elevation		average elevation (m) within buffer
Functional characteristics		
Visibility distance		average visibility distance (m) within buffer
Summer forage biomass		total biomass (kg/ha) of forage within buffer after spring green-up and before autumn senescence
Winter forage biomass		total biomass (kg/ha) of forage within buffer after autumn senescence and before spring green-up

^a Variables were summed or averaged within 50-m, 500-m, and 1,000-m circular buffers around each radio relocation. Values of each variable tabulated within buffers were then averaged over all buffers for all radio-locations for each deer and for each buffer scale. We analyzed variable groups separately.

^b See Table 2.

habitat distribution, 3) distance measures, 4) topographic features, and 5) functional characteristics (Table 1). We averaged variables in each group over all radio-locations for individual deer at each buffer scale; thus, sample size was the number of deer, not radio-locations. The habitat composition group consisted of variables that represented the proportions of buffers in each of 11 discrete vegetation classes (Farmer 2002) and roads (Table 2). Habitat distribution included variables representing distribution of vegetation classes, such as patch size, diversity, fragmentation, and density of edge within and adjacent to buffers. Distance measures were linear distances from prominent habitat features such as roads, lakes, and streams. Topographic variables measured physical characteristics of the area such as aspect, slope, and elevation within buffers. Functional variables reduced vegetative characteristics of habitats to biomass of forage for deer and visibility distance.

We obtained estimates of summer forage biomass from 394 vegetation plots of 0.2 ha located along 70 randomly located transects sampled during summer 1997 and 1998 (Farmer 2002). During an initial pilot study, we ocularly estimated percent cover of *Vaccinium* shrubs, evergreen forbs, and deciduous forbs in 27 plots that included vegetation classes with understory biomass ranging from low to high, and then we clipped all new annual growth from those plants. We regressed estimates of percent cover against dry weight of clipped vegetation to derive equations

that predicted dry-weight biomass from percent cover for *Vaccinium* shrubs (dry wt = 0.69 [percent cover], $r^2 = 0.95$, $P < 0.001$), deciduous forbs (dry wt = 0.12 [percent cover] + 0.003 [percent cover]², $r^2 = 0.99$, $P < 0.001$), and evergreen forbs (dry wt = 1.08 [percent cover], $r^2 = 0.93$, $P < 0.001$). We then used those regression equations to estimate forage biomass from estimates of percent cover for the plots located along transects (Farmer 2002). We likely underestimated forage because we did not account for biomass removed by deer before we sampled the plots. We estimated forage biomass in winter by subtracting the biomass of leaves on woody shrubs and all deciduous forbs from estimates of forage biomass in summer. Thus, those values did not account for snow cover. Visibility distance was the maximum distance at which a 2-m-tall range pole was visible from the center of each plot (Farmer 2002). We calculated average values of forage biomass and visibility distances for all plots in each vegetation class, and used those values to estimate total forage biomass and average visibility distance within radio-location buffers.

We derived digital habitat and topographic maps used in our analyses from United States Forest Service Geographic Information System (GIS) coverages for the Tongass National Forest and digital elevation models from the United States Geological Survey. We conducted geographic analyses using IDRISI Kilimanjaro raster GIS software

Table 2. Descriptions of vegetation classes used in Cox proportional hazards analyses to assess their potential influence on risk of death for radiocollared deer on Heceta Island, Alaska, USA, 1997–2000.

Vegetation class	Description
Muskeg	Predominantly heath or bog-like muskegs with sparse distribution of conifers; offered limited forage in summer and winter.
Riparian	Fresh-water lake or stream including thin strip of terrestrial habitats along stream banks and lake shores; terrestrial habitats varied from open fens and marshes to uneven aged hemlock–spruce forest with well-developed understories; forested stream banks and shorelines provided abundant forage in all seasons.
Open-canopy old-growth forest	Primarily uneven-aged hemlock–cedar forest <58.3 m ³ /ha gross timber volume; well-developed understory offered abundant forage during snow-free months.
Coarse-canopy old-growth forest	Primarily uneven-aged hemlock–spruce forest ≥58 m ³ /ha gross timber volume; well-developed understory provided abundant forage in all seasons.
Closed-canopy old-growth forest	Relatively small stands of hemlock–spruce forest ≥58 m ³ /ha gross timber volume situated on productive alluvial soils associated with some riparian zones; relatively closed canopy resulted in lower forage biomass than coarse-canopy old growth; provided moderate density of forage in all seasons.
Clearcuts ≤8 yr	Even-aged clearcuts ≤8 yr postlogging at mid-point (1998) of our study; canopy was completely removed, conifer regeneration was at seedling stage; moderate biomass of shrubs and forbs, abundant slash; provided moderate level of forage during snow-free months.
Clearcuts 9–18 yr	Young shrub-sapling-stage clearcuts 9–18 yr postlogging at mid-point of our study; open canopy, conifer regeneration was at sapling stage, abundant shrub and forb biomass during snow-free months; highest abundance of summer forage compared to other habitats.
Clearcuts 19–28 yr	Older shrub-sapling-stage clearcuts 19–28 yr postlogging; conifer regeneration was at large sapling stage; canopy was beginning to close over, reducing amount of light reaching forest floor; shrub and forb biomass was patchily distributed; moderate abundance of forage provided during snow-free periods.
Clearcuts 29–38 yr	Pole-stage clearcuts 28–38 yr postlogging; conifer regeneration 15–55 cm diameter at breast height (dbh), dense forest canopy prevented light from reaching forest floor; depauperate understory biomass offered little forage during all seasons.
Thinned clearcuts 28–30 yr	Even-aged clearcuts 29–30 yr postlogging that were precommercially thinned at 15–20 yr; even-aged conifer regeneration was at pole stage but canopy was patchy, allowing light to reach forest floor; abundant shrubs and forbs provided forage during snow-free months. Large amounts of woody slash from thinning covered forest floor. Piles of slash were often 1–2 m high.
Clearcuts >38 yr	Young-sawtimber seral forest >38 yr postlogging; conifer regeneration >25 cm dbh; dense canopy precluded light resulting in depauperate understory biomass; little forage available during all seasons.
Road corridor	Unpaved roadways and adjacent habitats within 20-m road right of way. Twenty-meter width was determined by the minimum cell resolution of raster Geographic Information System layers.

(Clark Labs, Worcester, Massachusetts). The raster cell resolution was 20 m.

We used Cox proportional hazards regression (Cox 1972, Hosmer and Lemeshow 1989, Lee 1992, Riggs and Pollock 1992, SPSS 2004) to test for associations between habitat variables in each group and mortality of deer. We derived separate models for each variable group. We interpreted sign and magnitude of regression coefficients as indicative of relationships between the predictor variables and hazard functions, or risks. We also included variables representing year and season of capture to address potential effects of our staggered-entry design on proportional-hazards models (Riggs and Pollock 1992). We initially employed Akaike's Information Criterion (Burnham and Anderson 1998, 2004) to select variables included in each model; however, the best subset models usually included covariates that were correlated strongly, making inference about model coefficients difficult. Alternatively, we selected covariates using forward and backward stepping (SPSS 2004), and screened them for multicollinearity.

Proportional-hazards regression requires that hazard functions of each sample group or strata included in the same analysis be proportional (Cox 1972, Hosmer and Lemeshow 1989, Lee 1992). We tested that assumption for deer

stratified by age and sex by comparing hazard functions for each stratum. We analyzed strata in which hazard functions were not parallel separately. We also tested time-dependent effects of covariates on the assumption of proportional hazards for deer in a stratum by calculating Schoenfeld residuals for each covariate and plotting them against survival time (Hess 1995). We assumed proportionality of hazards if residuals were randomly scattered around zero.

We analyzed each group of variables separately to enable us to compare the relative influences of different variable groups on risk of death. We addressed within-group correlations by testing for correlations between covariates. For each comparison with a correlation <−0.5 or >0.5, we included the covariate with the strongest correlation with death in further analyses and eliminated the other collinear variables. Further, we examined coefficients during stepwise selection for changes when ≥1 variables entered the model. If we suspected multicollinearity, we examined correlations between coefficients and tested univariate models for each covariate pair with strongly correlated coefficients ($r < -0.5$ or $r > 0.5$). If that procedure did not resolve the problem, we excluded covariates least relevant to our hypotheses.

We retained variables in proportional hazards models that had *P* values for their coefficients ≤0.10 and calculated risk

Table 3. Annual survivorship (l_x) and cause-specific rates of mortality for radiocollared black-tailed deer on Heceta Island, Alaska, USA, 1997–2000.

	N	l_x	SE	Cause of death			
				Predation	Malnutrition	Hunting	Other
All deer	81	0.69	0.05	0.09	0.10	0.10	0.02
Ad/yr M	11	0.55	0.15	0.09	0.00	0.28	0.08
Ad/yr F	51	0.80	0.06	0.09	0.05	0.06	0.00
Young	19	0.51	0.12	0.10	0.31	0.04	0.04

ratios for those variables. We chose $\alpha = 0.1$ because some variables showed large effect sizes, or risk ratios, but were not significant ($P > 0.05$) at the 95% level. Consequently, we accepted a 10% level of risk because we believed that it was sufficient to indicate biological importance of covariates (Johnson 1999, Jones and Tukey 2000). A risk ratio estimates change in relative risk of death for an incremental change in magnitude of a predictor variable (Riggs and Pollock 1992); hence, that value represents the independent contribution to risk of death made by a covariate, regardless of the dimensions of the variable. Researchers can estimate risk ratios for categorical variables or continuous covariates (Riggs and Pollock 1992). We compared relative risks among variables by calculating risk ratios for a 10% increase in each covariate. We considered a variable to be a significant predictor of death if the 90% confidence interval for the ratio did not include 1. In general, risk ratios >2.0 or <0.5 indicated large effects of covariates on risk of death (Riggs and Pollock 1992).

Because risk ratios represented the independent contribution of each covariate to risk of death, we were able to derive a measure, relative influence (RI), which summed the effect sizes of all covariates in a model. We defined RI as the absolute value of the sum of log-transformed risk ratios for a model representing a variable group or for all models within a particular buffer scale. We then used RI to qualitatively compare effect sizes of variable groups and buffer scales on risk of death within each sex and age group.

Results

We captured and successfully monitored 49 adult and yearling females, 11 adult and yearling males, and 19 young of the year between October 1996 and June 2000. We captured 3 young as neonates and the remainder during midsummer or early autumn. Mean 95% adaptive kernel home ranges for adult and yearling females were 78.2 ha (SE = 12.7, $n = 41$) and mean 50% home ranges were 9.2 ha (SE = 0.9, $n = 41$). For adult and yearling males, mean 95% adaptive kernel home ranges were 110.0 ha (SE = 24.9, $n = 11$) and mean 50% home ranges were 16.1 ha (SE = 2.6, $n = 11$). We did not estimate home ranges of young because few had >30 relocations before they died or became yearlings. Only one deer migrated seasonally. All other deer maintained the same home ranges throughout the year.

Survival Analysis

Thirty-nine deer died during the study, of which 20 were adult or yearling females, 7 were adult or yearling males, and

12 were young. We could not test for proportionality of hazard functions between adult and yearling males or male and female young because of small sample sizes and correspondingly low power to detect differences. Consequently, we assumed proportionality and combined adult and yearlings together for analyses, although we acknowledge that they may differ in some life-history requirements. For similar reasons, we combined male and female young together. The hazard function for yearling females was similar to adults (log-rank test, $\chi^2 = 0.18$, $P = 0.67$); therefore, they also were pooled for further analyses.

Annual survivorship of deer was 69% (SE = 5.4%), with young of the year having the highest mortality and adult and yearling females the lowest (Table 3). Mean survival times in weeks from date of capture were 114.9 (SE = 8.1) for adult and yearling females, 84.1 (SE = 17.6) for adult and yearling males, and 51.3 (SE = 8.6) for young. Fifty percent of all young died within 1 year of capture. Predation by wolves accounted for most deaths of adult and yearling females, hunting was the primary source of mortality for adult and yearling males, and causes related to malnutrition killed the most young (Table 3). In 3 instances, predation was the proximate cause of death of deer that were determined to be severely malnourished. Hazard functions for adult and yearling females, adult and yearling males, and young were not proportional; therefore, we treated each group separately during Cox regression analyses. Variables representing year and season of capture did not enter any of the proportional hazards models ($P > 0.15$); therefore, we assumed that our staggered-entry design did not confound analyses of risk of death.

Mortality of Adult and Yearling Females

We monitored 51 adult and yearling females, including 2 female young that survived their first year and became yearlings. We stratified our sample of adult and yearling females into 3 groups representing mortality by predation, malnutrition, and hunting. Overall, topographic features such as proportion of flat terrain and slope exerted the strongest influence on mortality of adult and yearling females at all scales (RI = 11.0). Variables related to habitat composition (RI = 5.5) and distribution (RI = 3.7) were the next most important correlates of risk of death, followed by functional characteristics of vegetative classes (RI = 2.6), and finally distance measures (RI = 2.0). Variables that were significant predictors of death at the 500-m scale exerted the greatest influence on risk of death of adult and yearling females (RI = 11.4), followed by features tabulated within

Table 4. Cox proportional hazards regression analyses for adult and yearling female black-tailed deer on Heceta Island, Alaska, USA, 1997–2000. We present results for predation as source of mortality at 3 spatial scales. Covariates shown are from separate models for variable groups representing habitat composition (a), habitat distribution (b), distance measures (c), topographic features (d), and functional characteristics (e).

Covariate	Model chi-square	Model P	β^a	P	RR ^b	90% CI
50-m scale						
Muskeg (a)	5.374	0.068	2.636	0.065	1.302	1.028–1.648
North aspect (d)	30.001	0.005	0.335	0.014	1.709	1.194–2.447
Slope (d)	23.596	0.002	–0.745	0.004	0.064	0.013–0.314
500-m scale						
Muskeg (a)	3.165	0.075	7.990	0.023	1.515	1.121–2.047
Open-canopy forest (a)	5.587	0.061	–16.543	0.083	0.570	0.334–0.973
Patch-size clearcut ≤ 8 yr (b)	3.952	0.047	0.047	0.071	1.218	1.017–1.459
North aspect (d)	4.763	0.029	0.005	0.007	1.759	1.212–2.555
Flat terrain (d)	13.563	0.001	0.041	0.007	4.948	1.885–12.991
1,000-m scale						
Clearcut ≤ 8 yr (a)	4.999	0.025	13.141	0.044	1.335	1.053–1.693
Edge density (b)	7.068	0.008	0.040	0.015	5.155	1.746–15.217
North aspect (d)	6.193	0.013	0.002	0.005	2.155	1.144–4.062
Flat terrain (d)	17.142	<0.000	0.012	0.018	4.759	1.628–13.908

^a Regression coefficients indicate strength and direction of relations between hazard functions and habitat variables. All regression coefficients significant at $\alpha = 0.10$ are reported.

^b We standardized risk ratios (RR) and 90% confidence intervals (CI) for a 10% increase in covariates.

1,000-m buffers (RI = 9.7). Habitat features within 50-m buffers had the smallest effect (RI = 8.7).

Predation.—Wolves killed 10 adult and yearling females. Eight of those were killed during winter and spring, and 5 during the moderately severe winter of 1998–1999. We did not include 3 adult females that were severely malnourished when killed by wolves in our analyses of risk of predation, but we did include them in our analysis of risk of death from malnutrition. Flat terrain, slope, and northerly aspect exerted the most consistent influence on risk of death from predation at all scales (Table 4). A 10% increase in slope reduced risk 93% at the 50-m scale. In contrast, a 10% increase in proportion of flat terrain within 500-m and 1,000-m buffers increased risk 395% and 376%, respectively. In addition, at the 1,000-m scale, density of edge was strongly associated with risk of predation, increasing that risk 416%. Use or patch size of muskegs and clearcuts ≤ 8 years old, which are open habitats, increased risk of death.

Use of open-canopy old-growth forest, a habitat with dense understory vegetation, reduced risk of death at the 500-m scale.

Malnutrition.—Wolves killed 3 adult or yearling females that were severely malnourished at time of death. All of those deaths occurred during spring 1999 following a moderately severe winter. Slope was the most influential variable reducing risk of death from malnutrition (Table 5), which was significant at the 50-m and 500-m scales. At the 1,000-m scale, biomass of winter forage strongly reduced risk of malnutrition. Use of habitats that offered little forage year-round (clearcuts 29–38 yr old) or during winter (clearcuts 19–28 yr old) consistently increased risk of death from malnutrition at all scales. Indeed, at the 1,000-m scale, use of clearcuts 19–28 years old increased risk of death 341%. The strong positive relation between risk of death and visibility distance was another indication that habitats offering little forage increased risk of death because visibility

Table 5. Cox proportional hazards regression analyses for adult and yearling female black-tailed deer on Heceta Island, Alaska, USA, 1997–2000. We present results for malnutrition as source of mortality at 3 spatial scales. Covariates shown are from separate models for variable groups representing habitat composition (a), habitat distribution (b), distance measures (c), topographic features (d), and functional characteristics (e).

Covariate	Model chi-square	Model P	β^a	P	RR ^b	90% CI
50-m scale						
Clearcut 29–38 yr (a)	5.079	0.024	4.261	0.054	1.531	1.064–2.205
Slope (d)	3.688	0.055	–0.450	0.089	0.186	0.036–0.953
500-m scale						
Clearcut 29–38 yr (a)	3.864	0.049	5.387	0.085	1.714	1.023–2.872
Patch-size clearcut 19–28 yr (b)	9.062	0.003	0.012	0.030	1.783	1.107–2.874
Slope (d)	5.024	0.025	–0.544	0.054	0.235	0.068–0.811
Visibility distance (e)	5.968	0.015	0.850	0.056	9.840	1.365–70.926
1,000-m scale						
Clearcut 19–28 yr (a)	13.202	<0.000	22.244	0.012	4.409	1.655–11.744
Patch-size clearcut 19–28 yr (b)	5.751	0.016	0.011	0.051	1.699	1.054–2.738
Winter forage biomass (e)	3.447	0.063	–0.079	0.084	0.476	0.234–0.971

^a Regression coefficients indicate strength and direction of relations between hazard functions and habitat variables. All regression coefficients significant at $\alpha = 0.10$ are reported.

^b We standardized risk ratios (RR) and 90% confidence intervals (CI) for a 10% increase in covariates.

Table 6. Cox proportional hazards regression analysis for adult and yearling female black-tailed deer on Heceta Island, Alaska, USA, 1997–2000. We present results for hunting as source of mortality at 3 spatial scales. Covariates shown are from separate models for variable groups representing habitat composition (a), habitat distribution (b), distance measures (c), topographic features (d), and functional characteristics (e).

Covariate	Model chi-square	Model P	β^a	P	RR ^b	90% CI
50-m scale						
Flat terrain (d)	8.578	0.003	1.691	0.012	9.010	2.127–38.164
Visibility distance (e)	5.228	0.022	0.273	0.043	2.293	1.165–4.514
500-m scale						
Clearcut 19–28 yr (a)	7.660	0.006	9.218	0.034	2.251	1.195–4.238
Patch-size riparian (b)	12.749	<0.000	0.049	0.012	1.509	1.144–1.991
Distance from roads (c)	3.349	0.067	0.009	0.094	7.645	1.185–49.328
Flat terrain (d)	6.244	0.012	0.032	0.023	3.483	1.415–8.575
1,000-m scale						
Clearcut 19–28 yrs (a)	7.674	0.006	10.478	0.033	2.012	1.172–3.452
Patch-size clearcut 19–28 yr (b)	4.262	0.039	0.008	0.069	1.470	1.070–2.021
Flat terrain (d)	5.190	0.023	0.012	0.050	4.759	1.314–17.236

^a Regression coefficients indicate strength and direction of relations between hazard functions and habitat variables. All regression coefficients significant at $\alpha = 0.10$ are reported.

^b We standardized risk ratios (RR) and 90% confidence intervals (CI) for a 10% increase in covariates.

distance was correlated with clearcuts 19–28 years old ($r = 0.51$, $P = 0.002$). Effects of slope and visibility distance also likely reflected effects of predation, which was the proximate cause of death for malnourished adult and yearling females in our sample.

Hunting.—Hunters illegally killed 4 adult and yearling females. Hunters did not harvest any deer during the special antlerless season. Use of flat terrain was the most influential variable; strongly increasing risk of death from hunting at all scales (Table 6). A 10% increase in flat terrain within buffers increased risk of death 801%, 248%, and 376% for 50-m, 500-m, and 1,000-m scales, respectively. Surprisingly, distance from roads increased risk of death at the 500-m scale. At 500-m and 1,000-m scales, use of 19–28-year-old clearcuts strongly increased risk of death. Likewise, patch size of riparian habitat and clearcuts 19–28 years old

increased risk of death from hunting at 500-m and 1,000-m scales, respectively.

Mortality of Adult and Yearling Males

Of 11 adult and yearling males monitored during the study, hunters killed 5, wolves killed 1, and 1 died from a cause unrelated to hunting, predation, or malnutrition. Our sample of adult and yearling males was too small to stratify mortality by source. Nonetheless, our results largely identified habitat variables related to death from hunting (Table 7). Topography exerted the greatest influence on risk of death (RI = 6.6), followed by habitat composition within buffers (RI = 3.3), distance measures (RI = 1.9), functional characteristics (RI = 1.3), and finally habitat distribution (RI = 1.2). In contrast to adult and yearling females, habitat features at the 50-m scale had the greatest effect on risk of death for adult and yearling males (RI = 8.8), followed by

Table 7. Cox proportional hazards regression analysis for adult and yearling male black-tailed deer on Heceta Island, Alaska, USA, 1997–2000. Results are presented for all sources of mortality combined at 3 spatial scales. Covariates shown are from separate models for variable groups representing habitat composition (a), habitat distribution (b), distance measures (c), topographic features (d), and functional characteristics (e).

Covariate	Model chi-square	Model P	β^a	P	RR ^b	90% CI
50-m scale						
Clearcut 9–18 yr (a)	3.585	0.058	2.656	0.068	1.304	1.026–1.658
Road corridor (c)	6.602	0.037	21.426	0.093	8.522	1.038–69.931
Patch-size clearcut 9–18 yr (b)	5.564	0.018	0.024	0.064	1.712	1.059–2.768
Flat terrain (d)	4.791	0.029	−4.545	0.040	0.003	0.000–0.313
500-m scale						
Clearcut 9–18 yr (a)	5.183	0.023	4.333	0.045	1.420	1.064–1.895
Patch-size clearcut 9–18 yr (b)	5.473	0.019	0.024	0.040	1.712	1.140–2.571
Distance from developed land (c)	3.895	0.048	−0.013	0.098	0.158	0.024–1.029
Summer forage biomass (e)	4.185	0.041	0.018	0.055	1.818	1.051–3.144
1,000-m scale						
Clearcut 9–18 yr (a)	6.253	0.012	9.230	0.028	1.692	1.139–2.514
Patch-size clearcut 29–38 yr (b)	5.706	0.017	−0.002	0.040	0.829	0.711–0.968
Distance from developed land (c)	3.722	0.054	−0.011	0.087	0.217	0.044–1.079
Elevation (d)	3.365	0.067	0.017	0.086	2.149	1.023–4.515
Summer forage biomass (e)	6.964	0.008	0.027	0.025	2.118	1.222–3.673

^a Regression coefficients indicate strength and direction of relations between hazard functions and habitat variables. All regression coefficients significant at $\alpha = 0.10$ are reported.

^b We standardized risk ratios (RR) and 90% confidence intervals (CI) for a 10% increase in covariates.

Table 8. Cox proportional hazards regression analysis for male and female young black-tailed deer on Heceta Island, Alaska, USA, 1997–2000. Results are presented for all sources of mortality combined at 3 spatial scales. Covariates shown are from separate models for variable groups representing habitat composition (a), habitat distribution (b), distance measures (c), topographic features (d), and functional characteristics (e).

Covariate	Model chi-square	Model P	β^a	P	RR ^b	90% CI
50-m scale						
Thinned clearcut 28–30 yr (a)	16.408	<0.000	4.466	0.025	1.563	1.124–2.173
Clearcut 29–38 yr (a)	19.615	<0.000	4.887	0.001	1.630	1.298–2.077
Patch-size clearcut 29–38 yr (b)	18.304	<0.000	0.004	0.001	1.454	1.246–1.697
Summer forage biomass (e)	16.788	<0.000	–0.016	0.001	0.558	0.413–0.754
500-m scale						
Thinned clearcut 28–30 yr (a)	11.382	0.001	4.186	0.029	1.318	1.070–1.624
Clearcut 29–38 yr (a)	14.755	0.001	4.620	0.002	1.587	1.235–2.040
Edge density (b)	5.294	0.021	–0.028	0.017	0.219	0.075–0.641
Patch-size thinned clearcut (b)	9.470	0.009	0.003	0.031	1.324	1.135–1.545
Summer forage biomass (e)	10.555	0.001	–0.013	0.002	0.649	0.522–0.809
1,000-m scale						
Clearcut 29–38 yr (a)	7.886	0.005	4.051	0.010	1.297	1.099–1.531
Diversity (b)	8.278	0.004	–17.423	0.006	0.367	0.201–0.672
Flat terrain (d)	3.107	0.078	–0.007	0.087	0.403	0.171–0.949
Summer forage biomass (e)	7.435	0.006	–0.015	0.008	0.659	0.500–0.868

^a Regression coefficients indicate strength and direction of relations between hazard functions and habitat variables. All regression coefficients significant at $\alpha = 0.10$ are reported.

^b We standardized risk ratios (RR) and 90% confidence intervals (CI) for a 10% increase in covariates.

those tabulated at the 500-m scale (RI = 3.3), and finally those at the 1,000-m scale (RI = 2.2).

Variables most strongly related to death at the 50-m scale were use of roads and level terrain. Ten percent increase in use of roads increased risk of death by 752%. In contrast, a 10% increase in flat terrain within 50-m buffers reduced risk of death from hunting to almost zero. Use of clearcuts 9–18 years old and patch size of habitat also had a positive association with death at the 50-m scale.

Consistent with results at the 50-m scale, patch size and use of clearcuts 9–18 years old at the 500-m scale increased risk by 71% and 42%, respectively, concomitant with a 10% increase in each variable. Forage biomass in summer also had a positive association with death, increasing risk by 82%. Distance from managed land had a negative association with death. The risk ratio showed that a 10% increase in average distance from clearcut logged habitat reduced risk of death for deer by 84%; however, the 90% confidence interval included 1, indicating the relation was not significant at $\alpha = 0.1$.

Results at the 1,000-m scale were similar to those at the 500-m scale. Use of clearcuts 9–18 years old and forage biomass in summer had a positive association with death. Elevation entered our model as a strong positive correlate with death at the landscape scale because young shrub-sapling-stage clearcuts were located in the hillier interior portions of Heceta Island. Patch size of clearcuts 29–38 years old reduced risk of death by 17%, concomitant with a 10% increase in size. Finally, deer that increased average distance from clearcut-logged habitat by 10% reduced risk of death 79%; however, the 90% confidence limits for the risk ratio included 1.

Mortality of Young

We combined all 19 young deer into a single analysis for each scale because sample size was too small to stratify by sex or cause of mortality. Six young died from causes related to

malnutrition, and wolves killed 4; therefore, our Cox regression analyses largely identified factors related to death from malnutrition or predation (Table 8). All young deer that died from malnutrition were females. Unlike adult males and females, variables related to distribution of habitats were the most important predictors of risk of death for young (RI = 3.2). Variables representing habitat composition were the next most important (RI = 1.9), followed by functional variables (1.4), and finally topography (0.9). No distance measures were associated significantly ($P \leq 0.1$) with risk of death of young. Similar to adult and yearling females, habitat features at the 500-m scale were the most influential (RI = 3.0), followed by features tabulated at the 1,000-m scale (RI = 2.6). Habitat features within 50-m buffers were the least influential (RI = 1.9).

The proportion of buffers composed of clearcuts 29–38 years old had the largest positive association with death at all scales. Risk ratios indicated that 10% increases in average proportions of that habitat within 50-m, 500-m, and 1,000-m buffers increased risk of death by 63%, 59%, and 30%, respectively. Clearcuts 29–38 years old were in a pole stage of regeneration with sparse understory vegetation; hence, forage biomass in summer had a negative association with death at all scales. Patch size of that habitat had a positive correlation with death of deer at the 50-m scale. In addition, thinned clearcuts 28–30 years old increased risk of death by 56% at the 50-m scale and by 32% at the 500-m scale concomitant with 10% increases in that habitat within buffers. At the 500-m scale, patch size of thinned clearcuts had a positive association with death. Habitat features with the greatest negative associations with death were edge density at the 500-m scale and habitat diversity at the 1,000-m scale. A 10% increase in either variable reduced risk of death by 78% and 63%, respectively. Use of flat terrain also reduced risk of death for young at the 1,000-m scale.

Discussion

Habitat characteristics exerted strong influences, which differed among sex and age classes, on mortality of black-tailed deer at multiple scales. Overall, for females >1 year old and young of both sexes, habitat variables tabulated at 500-m and 1,000-m scales had the greatest influence on mortality. No variable representing habitat composition at the scale of radio relocations (50-m) had a large effect (risk ratio <0.5 or risk ratio >2.0) on risk of death for those sex and age classes. That result suggests that factors integrated over large scales, rather than use of any particular location or habitat, influenced mortality of adult females and young. Variables related to topography had the greatest influence on risk of death for adult and yearling females, while variables related to habitat distribution were the most influential for young deer. Those results were consistent for all sources of mortality and supported our hypothesis that landscape-scale habitat features would affect mortality. Kie et al. (2002) showed that landscape features integrated across large scales explained most variation in home-range size of female mule deer, concluding that females responded to large-scale features at least as much as to their immediate surroundings. Our results are consistent with Kie et al. (2002) and we extended their conclusions to include mortality of deer.

We hypothesized that use of forage-poor habitats would increase risk of death from causes related to malnutrition, particularly during winters with snow when *K* may be reduced substantially. Associations between 29–38-year-old seral forest and death of adult and yearling females and young deer due to malnutrition supported our hypothesis. Indeed, both composition and patch size of that pole-stage second-growth habitat had an association with higher risk of death from causes related to malnutrition. We did not observe a relation between clearcuts ≥ 39 years old and death from malnutrition; however, forage-poor habitat made up only 1.8% of the study area and was likely too rare for us to detect influence.

The pattern of survivorship that we observed, with young experiencing the highest mortality, was consistent with results for other ungulate populations (Caughley 1966, McCullough 1979, Clutton-Brock et al. 1982, Bartmann et al. 1992, Gaillard et al. 2000). Gaillard et al. (2000) suggested that most changes in population growth of ungulates could be due to variation in recruitment rather than adult survivorship. Consequently, habitat characteristics that affect mortality of young likely have important influences on ungulate population dynamics. Young are particularly sensitive to habitat quality because they require food resources to support both growth and maintenance (Parker et al. 1993, 1999, Bowyer et al. 1998). Snow during winter 1998–1999 increased energetic costs, causing nutritional stress on young deer. Hence, death of young had a positive relationship with use of forage-poor habitats. Risk of death of young had a negative association with average forage biomass in summer at all spatial scales, inferring that range conditions in summer played a significant role in over-

winter survivorship. Indeed, increasing evidence highlights the importance of summer forage for maintaining healthy populations of cervids (Stewart et al. 2005), in addition to forage available in winter.

Thinned 28–30-year-old second-growth forest had a positive association with death of young deer, which was surprising considering that habitat generally provided abundant forage. The distribution of understory plants, however, was highly variable compared with other forage-rich habitats. For example, estimates of average forage biomass for vegetation sampling plots located in thinned 28–30-year-old second growth had coefficients of variation for biomass of evergreen forbs and *Vaccinium* shrubs that were 50% and 170% greater than coefficients in open-canopy old-growth forest, a habitat with comparable total forage (Farmer 2002). Further, precommercial thinning on Heceta Island did not chip, burn, or remove cut trees. Therefore, large piles of rotting slash up to 2 m high covered much of the ground and were still present during our study. That slash may have hindered movements of young deer in thinned seral forest, limiting availability of food and increasing risk of death from malnutrition.

We predicted that use of habitats with dense understory vegetation would likely lower risk of predation and that use of open habitats, such as muskegs, would increase risk of predation. Our results supported that hypothesis; however, slope, flat terrain, and northerly aspect were more important factors than use of any particular habitat or vegetation class in the context of influencing risk of predation. Kunkel and Pletscher (2001) reported that wolves selected flat or gently rolling terrain when preying on moose (*Alces alces*). Our data indicated that wolves behaved similarly on Heceta Island. Hillsides and steep terrain may enable deer to detect predators more easily and make pursuit more difficult for wolves. Most deer killed by wolves died during the snowy winter of 1998–1999. Hence, greater accumulation of snow on level terrain and northerly aspects probably contributed to risk of predation. Snow accumulation can impose significant energetic costs on deer that compromise physical condition (Bunnell and Jones 1984, Parker et al. 1984) and increase risk of predation (Fuller 1991, Okarma et al. 1995). Another variable with a strong positive association with predation was density of edge at the 1,000-m scale, which indicated that deer inhabiting landscapes fragmented into small patches of habitats likely were vulnerable to predation by wolves.

In contrast to females and young, habitat features identified at the scale of radio-locations were the most important habitat variables affecting risk of death for males >1 year old. Hunters harvested almost all adult or yearling males that died in our study near roads. Use of road corridors and flat terrain at the scale of radio-locations overwhelmed all other habitat variables affecting mortality of adult and yearling males. That result was probably related to the fact that most adult males were killed by hunters in landscapes dominated by clearcuts 9–18 years old. Understory vegetation was very dense in those shrub-sapling-stage

clearcuts, which was why forage biomass in summer had a positive association with death, but the forest canopy was open and conifer regeneration was only 1–2 m high. Deer standing on slopes near roads were easily visible to hunters, but those located in flat pockets were not. Thus, habitat features within the immediate vicinity of locations used by adult and yearling males had the greatest influence on death. Generally, logged habitats and watersheds increased the risk of male harvesting. An exception to that, however, was that patch size of pole-stage second growth (29–38 yr old) had a negative association with death for adult and yearling males at the 1,000-m scale. Low density of deer in landscapes dominated by pole-stage seral forest (Farmer 2002) likely discouraged hunting in that habitat.

During our study, hunters killed adult and yearling females under very different circumstances from adult males. Hunters took all harvested adult and yearling females illegally. Nonetheless, similar to adult and yearling males, landscapes dominated by clearcuts were associated with higher risk of death for adult and yearling females at all spatial scales. Those clearcut habitats, however, were in a later shrub-sapling successional stage characterized by higher coniferous regeneration and more patchily distributed forage. In contrast to males, use of flat terrain and distance from roads had a positive association with death from hunting. Hunters poaching deer likely behaved furtively and were opportunistic, avoiding areas with frequent human activity. Consequently, those individuals likely selected upland areas that were easily accessible, but further from roads, or flat beaches only accessible by boat, to avoid detection.

With the exception of open-canopy old-growth forest reducing risk of predation, we detected no strongly negative or positive relations between use by deer of old-growth forest and risk of death. Clearcuts and seral forest, however, generally increased risk of death for all sex and age groups of deer, and at all spatial scales, regardless of source of mortality. Consequently, we conclude that even-aged forest management on Heceta Island had significant demographic consequences for deer. Mortality, however, is only one component of population dynamics, and without data concerning reproduction, emigration, and immigration, we urge caution about inferring too much concerning effects of clearcut logging on deer populations. Additional study is necessary to determine if gains in other vital rates, such as reproduction, will offset higher mortality in logged landscapes. Nonetheless, some logged habitats and landscapes contributed to higher mortality of young, indicating that any gains in reproduction may not necessarily result in greater recruitment.

Finally, studies concerning habitat selection by deer have been the primary sources of data concerning habitat quality in Southeast Alaska (Wallmo and Schoen 1980, Rose 1982, Schoen and Kirchhoff 1990, Yeo and Peek 1992, Doerr et al. 2005). Nonetheless, habitat selection alone is insufficient to adequately characterize the contribution of habitats and their distribution to dynamics of animal populations (Van

Horne 1983, Hobbs and Hanley 1990). In Southeast Alaska, clearcut watersheds represent a novel environment to deer accustomed to fine-grained forest habitats, which may explain why even-aged forest management increased risk of death despite evidence of selection by deer of some young seral forest habitats (Yeo and Peek 1992, Doerr et al. 2005). Hence, relating habitat use and risks of mortality at multiple scales is as critical as considering habitat selection when evaluating habitat quality for deer (Caughley 1994).

Management Implications

We suggest that land managers weigh landscape-scale features, such as habitat patch size, habitat diversity, density of edge, and topography, at least as much as habitat composition when planning timber harvest and other development projects in Southeast Alaska and in other forested environments. For example, to reduce risk of predation, managers should avoid fragmentation of large contiguous blocks of old-growth forest habitat on flat or gently rolling terrain at low elevation. Timber harvest that fragments forest habitat would be better on hillsides that offer deer effective escape terrain. Managers should adjust harvest rates of trees within watersheds to avoid the eventual creation of large, dominant patches of seral forest >29 years old. Patch size of precommercially thinned seral forest should be small and interspersed with forage-rich habitats such as open- and coarse-canopy old-growth forest. If extensive thinning of contiguous areas of seral forest occurs, managers should treat slash to speed decomposition of woody debris and to reduce obstacles that limit movements of deer.

Our results highlight the potential conflicts arising from habitat manipulations that may benefit one sex or age class, but be detrimental to another (Stewart et al. 2003). For example, timber harvest on slopes may be preferred with respect to reducing risk of death from predation; however, it likely would increase risk of mortality of adult males from hunting. Moreover, because sexes of deer segregate from one another for much of the year (Bowyer 1984, 2004, Bowyer et al. 1996), it would be naive to assume that single habitat-management prescriptions would universally benefit all deer. Indeed, with respect to sexes, Kie et al. (1999) argued that habitat requirements of male and female deer were sufficiently different to warrant management as separated species.

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