

# MORTALITY CAUSES AND SURVIVAL ESTIMATES FOR ADULT FEMALE COLUMBIAN BLACK-TAILED DEER

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**Abstract:** Declines in black-tailed deer (*Odocoileus hemionus columbianus*) populations and in hunter harvests of deer on Vancouver Island have been contrary to management objectives since the late 1970s. Because predators were presumed the major cause of declines, arguments for retention of winter habitat were difficult to support and managers were asked to reduce deer mortality before addressing habitat concerns. Changes in population management were instigated even though estimates of deer survival rates were lacking and little was known about mortality causes. We documented mortality causes and estimated average monthly survival ( $\hat{S}$ ) for 105 radio-collared black-tailed deer at 4 sites on Vancouver Island, British Columbia, from February 1982 through June 1991. Predation accounted for 61% of all deaths ( $n = 54$ ) and occurred mostly during February–June. Average annual survival was 74% ( $\hat{S} = 97.5\%$ ,  $SE = 0.3\%$ ). We used logistic regression to model monthly cause-specific mortality ( $M_i$ ) and  $\hat{S}$  using 5 independent variables: study area, seasonal movement behavior of deer, monthly elevation used by deer, month of year, and mean monthly snow depth. The model that best (Akaike's Information Criterion [AIC] = 624.02; Chatfield 1992) explained  $M_i$  and  $\hat{S}$  was based on seasonal movement behavior. Resident deer remaining at low elevations were more ( $P = 0.024$ ) prone to predation. We recommend that retention of old, intact forests at low elevations is basic to rebuilding deer populations on Vancouver Island.

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Interactions among wolves (*Canis lupus*), black-tailed deer, and deer hunters dominate the predator-ungulate system on Vancouver Island (Janz and Hatter 1986). Declines of deer resulting from predation (50–70% from 1976–82) and declines in hunter harvests have been contrary to management objectives. Because predators were presumed the major cause of the declines (Jones and Mason 1983), the argument for retention of winter habitat (Bunnell 1985) was difficult to make to those wishing to use the land for other purposes (Janz and Hatter 1986). Managers were forced to reduce deer mortality before addressing habitat concerns. Consequently, attention has been focused on population modeling (Hatter and Janz 1994) to foster management initiatives that help restore deer populations. Specific management has been to reduce bag limits for deer hunters on Vancouver Island and to provisionally instigate limited control of wolves in some areas (Janz and Hatter 1986).

Population management requires information on factors that cause population changes, principally survival and reproductive rates (Caughley 1976). Although reproductive rates for black-tailed deer were documented (Taber

1953, Cowan 1956, Golley 1957, Thomas 1970, Thomas and Cowan 1975, Thomas 1983), survival rate estimates were not. Survival is usually measured indirectly in surveys of recruitment and gross population changes (Harestad and Jones 1981, Janz 1989; see Hatter 1988 for an exception), and mortality studies have focused on single, rather than all, mortality causes (Klein and Olson 1960, Smith 1968, Hebert et al. 1982, Jones and Mason 1983, van Ballenberghe and Hanley 1984).

Typically, winter weather has been advanced as a factor influencing survival, having direct and indirect effects. Snow covers forage and impedes locomotion (Harestad et al. 1982), creating a direct effect on individual energy balances and, hence, survival. Shifts in use of habitat resulting from snow can modify survival rates indirectly due to consequent shifts in predator efficiency and/or prey vulnerability (Mech 1977, Messier and Barrette 1985, Nelson and Mech 1991). Without specific information on the range of mortality causes, mortality and survival rates, and environmental and behavioral factors affecting survival, changes in population management will be ad hoc.

We investigated survival rates and mortality



causes for adult female black-tailed deer at 4 areas on Vancouver Island. Mortality data came from deer that were radiocollared for another study (McNay and Doyle 1990) and were used to (1) document causes of mortality, (2) estimate average monthly cause-specific mortality ( $M_i$ ), (3) estimate average monthly survival ( $\hat{S}$ ), and (4) assess the relative effect of 5 variables on  $M_i$  and  $\hat{S}$  (study area, seasonal movement behavior of deer, monthly elevation used by deer, month of year, and mean monthly snow depth).

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## STUDY AREAS

The study took place at 4 locations on Vancouver Island: Nanaimo (49°02'N, 124°12'W), Chemainus (48°56'N, 124°05'W), Nimpkish (50°08'N, 126°30'W), and Caycuse (48°48'N, 124°30'W) River valleys. Nanaimo and Chemainus rivers were neighboring systems 43 km northeast of Caycuse River and 202 km southeast of Nimpkish River. Study areas were 200–300 km<sup>2</sup> with valley bottoms located at 200 m above sea level (asl). Peaks ranged from 1,249 m asl at Caycuse to 1,821 m asl at Nimpkish. The Chemainus, Nanaimo, and Nimpkish rivers were relatively open, flat-bottomed valleys (U-shaped), while Caycuse River had steeper slopes and least flat area at low elevations (a V-shaped valley).

All study areas were extensively logged by clear-cutting resulting in habitats ranging from recently deforested (0–5 yr old) to old (>250 yr old) forests. Arrangement of habitats was typical of coastal logging with valley bottoms in young (6–60 yr old) forests, most mid-slopes deforest-

ed, and higher elevations and headwaters in old forests. Generally, Chemainus River had the least old (about 6%) and most young (about 82%) forests. Caycuse and Nimpkish sites had similar amounts of old (40%) and young (30%) forests. Nanaimo River had about 30% old forest and about 50% young forest. Each study site was 10–20% deforested.

Wolves, mountain lions (*Felis concolor*), and humans preyed on adult deer on Vancouver Island (Jones and Mason 1983, Janz 1989). Some wolves were removed from all study areas as part of ongoing predator management, although the greatest effort occurred at Nanaimo (35 removed since 1982) and Nimpkish (44 wolves removed from 1987 to 1991) rivers. Local trappers sporadically removed wolves at Caycuse (1 wolf removed in 1985 and 2 in 1986). We removed 1 cougar from Nanaimo River in 1988. All areas were open to buck deer and cougar hunting during their respective seasons. In addition, there was a limited entry hunt for antlerless deer at Nanaimo River during 4 weekends each November.

Vancouver Island was temperate and wet; no month had a mean temperature <0°C, and mean temperature of the warmest month was 17°C. Usually there were 291 frost-free days, an average 820 mm of snow, and a mean precipitation of 2,140 mm each year (Meidinger and Pojar 1991).

## METHODS

We fitted deer with radio transmitters containing mortality sensors from 1982 to 1988 at Nanaimo River, in 1989–90 at Nimpkish and Caycuse rivers, and in 1989 at Chemainus River. In 1988–90, we captured most deer during winter in Clover traps (Clover 1956) and manually restrained them while fitting radio collars. During 1982–87, and when trapping was unsuccessful, we immobilized deer with powdered anectine delivered in darts shot from a CAPCHUR gun. We monitored radio-collared deer  $\geq 1$  time/week for 4 years after capture or until death, provided we could maintain radio contact. Deer dying  $\leq 12$  days after capture ( $n = 3$ ) were excluded from analyses because we could not positively rule out capture myopathy (Harthoon 1977).

We established age classes of deer by tooth wear and replacement at the time of collaring (Robinette et al. 1957). This technique was sufficient to classify deer as fawns (<1 yr old),



yearlings (between 1 and 2 yr old), or adults (>2 yr old). We assigned all subadults common birthdates of 15 June, to determine when they reached adult status.

### Mortality Causes

Upon monitoring mortality signals, usually 1–4 days after death, we sought deer and determined likely mortality cause. Death was by 1 of 6 causes: predation by wolves or cougars, human related (legal hunting and poaching), malnutrition, accident, or unknown. We identified predation, legal hunting, and poaching by condition of the corpse (Roy and Dorrance 1976). We classified fresh kills with neck or head injuries, clean incisions at the gut, and partially buried remains as predation by cougars. Kills with considerable mid- and hind-section injury and comparatively more scattered, unburied remains were classified as predation by wolves. When there was only a small amount of carcass remaining and no definite evidence of other mortality causes, we considered wolf predation as the likely cause of death. We determined nutritional status from examination of bone marrow (Cheatum 1949). Red, gelatinous, bone marrow suggested malnutrition was the predisposing cause of mortality.

### Mortality and Survival Rate Estimation

We used logistic regression (SAS Inst. Inc. 1985) to compute maximum likelihood estimates for monthly  $M_i$  and  $\hat{S}_i$ , while simultaneously assessing the effects of 5 variables. Four of the independent variables were categorical: (1) study area had 4 levels (Caycuse, Chemainus, Nanaimo, and Nimpkish), (2) seasonal movement behavior of deer had 3 levels (migratory, resident, or unknown), (3) monthly elevations used had 3 levels (<600 m asl, >600 m asl, and unknown), and (4) month had 12 levels corresponding to each month of the year. The fifth variable was mean monthly snow depth measured daily at the closest airport to each study area (Atmos. Environ. Serv., Environ. Can., Vancouver, B.C.). We censored deer with failed radios ( $n = 3$ ), or that lost collars prematurely ( $n = 1$ ), from analyses in the month during which they could no longer be monitored. We conducted tests among individual survival estimates, or between estimates of  $M_i$ , using the CONTRAST statement in PROC CATMOD (SAS Inst. Inc. 1985).

Our philosophy for choosing the model that

most closely mimicked the observed data followed White and Garrott (1990:222). We posed different hierarchical subsets of the main factors as models. In the most general model, all factors contributed to  $M_i$  and  $\hat{S}_i$  levels of the dependent variable. We compared this model (the null hypothesis) with simpler nested models, or subsets, of the main factors (alternative hypotheses) using likelihood-ratio tests (White and Bartmann 1983). We continued iterative testing of nested models until the null hypothesis was rejected, thereby revealing which alternative model was most economical and consistent with observed rates. Choice of the best model was corroborated on the basis of the AIC (Chatfield 1992:197), a statistic used to assess parsimony of model construction.

### RESULTS

We captured and monitored 95 adult female deer throughout 1982–91. During the same period, we caught 12 female yearlings and 12 female fawns, of which 9 yearlings and 1 fawn aged into the adult cohort and were added to our sample. Although we caught deer in each month, most captures (71%) occurred from January through March reflecting our greater effort and increased capture success during these months. Collectively, 105 deer yielded 2,182 deer-months of data.

#### Estimates of Cause-specific Mortality

We recorded 54 mortalities and 4 collar failures, most of which (64%) occurred either from April through June or during November (Fig. 1). Average monthly mortality due to predators was 1.5%, with predation by cougars being the most important cause of mortality (Table 1). Predation by cougars was greater ( $P = 0.012$ ) in Caycuse and Chemainus than in Nanaimo or Nimpkish rivers (Table 1). Predation by wolves was similar to that by cougars; however, we found no difference in predation by wolves among study areas ( $P > 0.614$ ). Human-related mortality was 0.4% monthly, or half the mortality caused by either cougars or wolves.

Generally, monthly change in  $M$  was most evident in the leading causes of mortality (Table 2). Peaks in  $M$  occurred in February and from April through July due to wolves, from March through May due to cougars, and in November due to humans.



Fig. 1. Monthly mortality by cause recorded for radio-collared, adult female black-tailed deer on Vancouver Island, British Columbia, 1982-91. Values above histograms indicate the total sample size in number of deer-months.

Some migratory deer, however, survived at rates more comparable with resident deer once elevation was considered. Although  $\hat{S}$  for mi-

<sup>a</sup> Maximum likelihood estimates of monthly mortality (%) were computed using logistic regression (CATMOD; SAS Inst. Inc. 1985). Estimates with the same or no letter among areas, or among causes for totals, are not different ( $P > 0.10$ ).



Table 2. Mortality (%  $M^a$ ) by month of year for 3 leading causes of mortality for radio-collared, adult female black-tailed deer on Vancouver Island, British Columbia, 1982–91.

Month	Deer months	Mortality cause								
		Cougar			Wolf			Human		
		$n^b$	$M$	SE	$n$	$M$	SE	$n$	$M$	SE
Jan	160	1	0.6	0.5	1	0.6	0.5	0		
Feb	175	1	0.6	0.4	2	1.1	0.7	0		
Mar	192	3	1.6	0.8	1	0.5	0.5	1	0.5	0.4
Apr	221	5	2.3	1.0	2	0.9	0.5	2	0.9	0.5
May	211	4	1.9	0.9	3	1.4	0.8	0		
Jun	208	1	0.5	0.5	2	1.0	0.7	1	0.5	0.5
Jul	170	1	0.6	0.4	2	1.2	0.7	0		
Aug	171	0			0			0		
Sep	169	0			0			1	0.6	0.4
Oct	170	0			1	0.6	0.6	0		
Nov	171	1	0.6	0.6	0			4	2.3	1.2
Dec	164	1	0.6	0.6	1	0.6	0.6	0		

<sup>a</sup> Max. likelihood estimates of monthly mortality (%) were computed using logistic regression (CATMOD; SAS Inst. Inc. 1985).

<sup>b</sup> No. of deer killed by the specific mortality cause.

gratory deer at low elevations was not different ( $P = 0.991$ ) from  $\hat{S}$  for resident deer at high elevations (Table 4), a comparison of the opposite (migratory deer at high elevations vs. resident deer at low elevations) was significant ( $P = 0.015$ ). Survival did not differ between elevations for resident ( $P = 0.142$ ) or for migratory ( $P = 0.184$ ) deer.

In August, September, and December–March, deer  $\hat{S}$  rarely dropped below 99%, or 89% annually (Table 4). Survival for resident deer at low elevations from April through July, by comparison, was rarely >97% (73% annu.). By comparison,  $\hat{S}$  for migratory deer at low elevations was <97% only during April (Table 4).

Except in November, survival in most winter months remained high (Table 4) and, consequently, we could demonstrate only a weak relationship between  $\hat{S}$  and mean monthly snow depth ( $P = 0.098$ ). Mean monthly snow depth during the study was 11 cm ( $n = 106$ ,  $SD = 18$  cm) and ranged 0–66 cm.

## DISCUSSION

### Causes of Mortality

There have been no previously published estimates of cause-specific mortality rates reported for black-tailed deer. Our estimate of predation by wolves (0.7% mon.) was half the 17% annual mortality reported by Nelson and Mech (1986) for predation on adult, female white-tailed deer (*O. virginianus*) by wolves but greater than that reported for predation on adult

female mule deer (*O. h. hemionus*) by coyotes (*Canis latrans*) (Hamlin and Mackie 1989). The rate in our study is likely, in part, a reflection of ongoing removal of wolves (Janzen 1989). Still, wolves and cougars were primary causes of mortality for our radio-collared deer (Table 1) and, together, created a mortality rate similar to that reported by Nelson and Mech (1986). Klein and Olson (1960) reported starvation as the most frequent cause of mortality for sitka black-tailed deer (*O. h. sitkensis*), but most mortality reported in their study came from areas having more severe winter weather than we had in our study. In the absence of severe winter weather and relatively heavy predation by wolves, cougars, and humans (78% of all deaths), it is not surprising that malnutrition was rarely observed.

Cougars established activity centers, especially from March through May, and killed deer in isolated stands of old-growth forests, most of which were reserved as winter habitat for deer (Janzen 1989). Predation by cougars has been considered unimportant (Janzen and Hatter 1986), but our data indicate they can have strong local effects that are intense in late winter months. Predation by cougars may have increased during the mid- to late 1980s concomitant with removal of some wolves, if predation was compensatory. However, Hamlin and Mackie (1989) considered compensatory mortality unlikely in the adult, female segment of a mule deer population ( $\bar{x}$  annu. mortality was only 6.2%). Alternatively, we may simply notice predation by cougars more now because kills occur in winter



ranges that, through time and continued forest harvesting, have become more isolated in space.

Wolves, by comparison, generally appeared to be less site specific and less seasonal in their kills even though most kills occurred during winter and spring. A notable lack of mortality by any cause existed in summer. Both predators likely concentrate on fawns rather than adults as prey during summer (Scott and Shackleton 1980, Hatter 1988).

### Factors Affecting Survival

Estimates of survival, excluding deer of unknown behavior, ranged from 73% annually for resident deer at low elevations to 95% annually for migratory deer at high elevations. Survival rates for adult female deer from studies on mule and white-tailed deer are similar to our findings: 78% for white-tailed deer in Montana (Dusek et al. 1989), 79% for white-tailed deer in Minnesota (Nelson and Mech 1986), 57.0–97.8% for mule deer in Montana (Hamlin and Mackie 1989), and 76–100% for mule deer in Colorado (White and Bartmann 1983, White et al. 1987, Bartmann et al. 1992).

Survival was related more closely to seasonal movement behavior of deer, or to elevations used by deer, than to study area, month, or average monthly snow depth. Migratory deer exhibited highest  $\hat{S}$ , which is especially relevant considering timing and primary causes of mortality. Predators, the most dominant mortality agent, concentrated on adult female deer from February through July when differences between survival of migratory and resident deer were greatest. Harestad (1979) found that most migratory deer departed winter ranges during March, coincident with the onset of high predation rates. After March, migratory deer were at higher elevations, in steeper terrain, and in habitat with less roads compared with the locations of resident deer (Harestad 1979; Schoen and Kirchhoff 1985; McNay, unpubl. data). We concluded that most migratory deer, either coincidentally or purposefully, reduced risk of mortality due to predators by leaving low elevation winter ranges as soon as they could in spring.

Our findings contrast those of Nelson and Mech (1991) for white-tailed deer in Minnesota. Their data showed that migratory deer suffered greater mortality due to higher risk during fall migrations. Distances covered by white-tailed deer for migration averaged 16 km in Minnesota

Table 3. Akaike's Information Criterion (AIC)<sup>a</sup> and likelihood-ratio tests (LR  $\chi^2$ )<sup>b</sup> between competing models of monthly fate (cause-specific mortality or survival) of radio-collared, adult female black-tailed deer on Vancouver Island, British Columbia, 1982–91. Hierarchical models of 4 categorical variables (A = study area, B = seasonal movement behavior of deer, E = mon. elevations used by deer, and M = month of the yr) are listed from the most general (all factors = A·B·E·M) to the most reduced model (no factors = N).

General	AIC	Reduced	LR $\chi^2$	df	P
A·B·E·M	720.19	A·B·E	71.33	66	0.305
		A·B·M	7.98	12	0.787
		B·E·M	16.73	18	0.542
		A·E·M	16.48	12	0.170
A·B·E	659.52	A·B	7.39	12	0.831
		A·E	15.54	12	0.213
		B·E	17.20	18	0.509
A·B·M	704.17	A·B	70.74	66	0.322
		A·M	73.28	12	0.000
		B·M	16.56	18	0.554
B·E·M	700.92	B·E	71.80	66	0.292
		B·M	7.81	12	0.800
		E·M	15.18	12	0.232
A·E·M	712.67	A·E	70.39	66	0.333
		A·M	64.78	12	0.000
		E·M	15.43	18	0.632
A·B	642.91	A	82.12	12	0.000
		B	17.11	18	0.516
A·E	651.06	A	73.97	12	0.000
		E	16.17	18	0.581
B·E	640.72	B	7.30	12	0.837
		E	14.51	12	0.269
A·M	753.45	A	79.58	66	0.122
		M	22.18	18	0.224
B·M	684.73	B	71.29	66	0.306
		M	78.90	12	0.000
E·M	692.10	E	71.13	66	0.311
		M	71.53	18	0.000
A	701.03	N	24.39	18	0.143
B	624.02	N	89.40	12	0.000
E	631.23	N	82.19	12	0.000
M	739.63	N	81.79	66	0.091

<sup>a</sup> AIC indexes model parsimony (Chatfield 1992) and is calculated as  $(-2 \ln[\text{max. likelihood}] + 2 [\text{no. of independent parameters}])$ .

<sup>b</sup> Likelihood-ratio tests were  $(-2 \ln[\text{max. likelihood reduced model}] - (-2 \ln[\text{max. likelihood general model}]))$ .

but were  $\leq 8$  km for black-tailed deer (Harestad 1979, Schoen and Kirchhoff 1985). Perhaps more important, migration appears to be a more predictable event as a result of regular winter weather in continental regions. In coastal climates with more ephemeral winter weather and insular valleys, migration appears to be shorter and less predictable (Harestad 1979, Schoen and Kirchhoff 1985). In the former scenario, wolves may be more able to exploit the vulnerability of deer during migration.

### MANAGEMENT IMPLICATIONS

Annual survival rates for resident deer at low elevations (73%) were unlikely adequate to sus-



Table 4. Monthly survival (%)<sup>a</sup> for 2 known and 1 unknown seasonal movement behaviors of radio-collared, adult female black-tailed deer at 2 broad elevations in m above sea level (asl) on Vancouver Island, British Columbia, 1982–91.

Month	Mon. mode of elevations used by deer											
	< 600 m asl						> 600 m asl					
	Resident			Migratory			Resident			Migratory		
	n <sup>b</sup>	$\hat{S}$	SE	n	$\hat{S}$	SE	n	$\hat{S}$	SE	n	$\hat{S}$	SE
Jan	62	98.4	1.2	35	99.2	0.7	39	99.3	0.6	22	99.6	0.4
Feb	65	97.9	1.3	37	99.0	0.8	44	99.1	0.7	25	99.5	0.4
Mar	74	98.2	1.0	35	99.1	0.6	37	98.7	0.8	34	99.5	0.4
Apr	87	96.6	1.4	36	96.0	2.8	37	97.7	1.2	43	99.2	0.6
May	72	96.4	1.6	50	97.2	1.7	33	98.5	0.9	46	99.1	0.6
Jun	73	97.4	1.3	48	97.9	1.7	25	98.7	0.9	55	99.6	0.3
Jul	60	96.6	1.8	43	98.8	0.9	22	98.4	1.1	42	99.5	0.4
Aug	59	99.0	1.1	45	99.9	0.0	23	99.4	0.8	42	99.9	0.0
Sep	60	99.3	0.7	41	99.9	0.0	21	99.1	1.0	45	99.9	0.0
Oct	72	98.5	1.2	30	97.8	2.4	19	99.7	0.4	47	99.9	0.2
Nov	83	93.5	2.4	22	99.5	0.4	38	93.8	3.7	26	99.7	0.3
Dec	73	98.5	1.1	25	99.2	0.7	37	99.3	0.6	27	99.6	0.4
											$\hat{S}$	SE
											83.0	11.3
											81.2	10.6
											77.5	9.1
											59.2	9.5
											66.9	10.5
											74.5	10.7
											74.1	12.4
											92.8	9.7
											89.0	11.9
											84.2	13.4
											51.3	16.9
											83.8	11.2

<sup>a</sup> Max likelihood estimates of monthly survival (%) were computed using logistic regression (CATMOD; SAS Inst. Inc. 1985).<sup>b</sup> No. of deer killed by the specific mortality cause.

tain their populations. We constructed a simple Leslie matrix (Leslie 1945) to assess recruitment necessary to stabilize such a population. We used age-specific productivity rates reported by Thomas (1983), adult survival rates from this study, and held yearling survival constant at 60% while varying fawn recruitment within reported limits from Janz (1989). At the upper level of reported recruitment (about 25%), all but the low elevation resident population increased. To stabilize that population with 27% adult mortality, it was necessary to have about 30% recruitment from the fawn population, a level rarely observed on Vancouver Island (Janz 1989). Black-tailed deer are not as fecund as other conspecifics (Thomas 1983) and are therefore more sensitive to adult mortality (van Ballenberghe and Hanley 1984). Furthermore, recruitment into the adult population is low in the presence of predation by wolves (Jones and Mason 1983, Hatter 1988, Janz 1989). Although we could not estimate subadult survival in this study, we judged it low. Of the 24 female, radio-collared, subadults, only 1 fawn and 9 yearlings lived to become adults. We concluded that risk of mortality to adults at low elevations likely outweighed potential benefits in habitat quality (Gates 1968) derived from the early seral forests that follow forest-harvesting operations. Road construction undoubtedly provides easy access throughout lower valley elevations for wolves, cougars, and humans and, hence, direct access to deer.

Forest harvesting also creates an isolation of old-growth winter ranges and may directly influence predation by concentrating prey and focusing predators' attention on specific sites, especially during late winter when deer are most vulnerable (Nelson and Mech 1986). Isolation of winter habitat seems particularly important because no migratory deer were caught in young forests during winter. Although migratory deer had high annual survival (95%), we remain suspicious about the vitality of that portion of the population. Their absence in young forests could imply 1, or a combination, of several processes: (1) migratory deer concentrate increasingly in diminishing old-growth areas with eventual reduction of their survival due to deteriorating range condition, (2) mortality of migratory deer in subadult age classes is high, or (3) subadults abandon migratory tactics in favor of resident habitat selection patterns. The implication of losing migratory deer could be a reduction in



population resiliency because the remaining resident deer are subject to comparatively higher mortality.

In apparent contrast to the weakening rationale for retention of old-growth winter habitat for deer because of declining deer populations (Janz and Hatter 1986), we consider our results to indicate that a retention of older, intact forests is basic to rebuilding deer populations. Forest harvesting, hence, road building and spatial isolation of winter habitats, may intensify predation on 1 segment of deer populations (resident deer) and indirectly impede recruitment to the other segment (migratory deer). The result likely contributes to declines in deer populations and an overall loss of population resiliency.

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