

# Behavioural limits to movement: The effect on habitat choices for Columbian black-tailed deer

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## Abstract

We used radio telemetry to compare movements, habitat use, and survival of 122 Columbian black-tailed deer (*Odocoileus hemionus columbianus*) on 4 study areas on Vancouver Island, British Columbia, Canada. Seventy-four of the deer remained alive long enough to classify their movement behaviours; 2 deer dispersed, 28 were migratory, and 44 remained resident. All deer used young seral stages year-round but older forests >250 yrs were chosen during periods of inclement winter weather, especially by those deer that migrated. Residents lived mostly at lower elevations and used younger forests. Deer that migrated lived at higher elevations during summer. All deer showed loyalty to geographic locations and to movement behaviours during changes in winter weather, even after removal of their traditional winter habitat. We concluded that selection of habitat during inclement winter weather was controlled by local topography and climate on the natal range. Natal ranges established at high elevations necessarily led to annual migrations but also afforded higher survival rates, apparently because most mortality occurred during late spring at lower elevations.

## Introduction

Initial research in habitat with high snow-fall suggested that old-growth forests were beneficial to black-tailed deer (Wallmo and Schoen 1980, Bunnell and Jones 1984, Bunnell 1985). Potential conflict between forest harvesting and maintenance of black-tailed deer populations was exposed resulting in several research programs. Black-tailed deer show movement patterns that initial analyses suggested were related to broad habitat features (Bunnell 1990). For management to be effective these patterns needed to be documented well enough that responses to habitat alteration could be predicted under various conditions. This paper integrates results of several studies to document how behavioral features of black-tailed deer limit selection of habitats and their responses to habitat alterations.

## Methods

We studied deer at 4 locations on Vancouver Island, British Columbia, Canada. The Nimpkish River valley area (50°08' N, 126°30' W) has a southern aspect, while the main valley ranges in elevation from 200-1820 m asl. The Nanaimo River (49°02' N, 124°12' W) and the Chemainus River (48°56' N, 124°05' W) are located to the southeast and had considerable southern exposure. These watersheds range in elevation from 300-1540 m. The Caycuse River (48°48' N, 124°30' W) located to the southwest flows west but had many subdrainages flowing south or north, and ranged least in elevation, from 300-1250 m.

The dominant ecosystem at lower elevations is Coastal Western Hemlock (CWH) and, at higher elevations, Mountain



Hemlock (MH) (Meidinger and Pojar 1991). These ecosystems were represented at each study site, but the Caycuse River valley had only a small amount of MH. Extensive harvest of trees had occurred at each site, and the resulting mosaic of forest seral-age classes varied among sites. Generally, Chemainus River had the least amount of old-growth (>250 yrs) forests (6%) and the most area in second-growth (6-120 yrs) forests (82%). The Caycuse and Nimpkish River sites were similar; each had about 40% old-growth, and 30% second-growth. Nanaimo River had about 30% old-growth and 50% second-growth. All sites had 10-20% in "unforested" young habitat (0-5 yrs).

Climate on Vancouver Island is characterized by temperate, wet weather; no month has a mean temperature below 0°C and the mean temperature of the warmest month is 17°C. Usually there are 291 frost-free days, an average of 820 mm of snow, and a mean precipitation of 2140 mm each year (Meidinger and Pojar 1991).

#### Deer locations

Radio-collared deer were located by triangulation (White and Garrott 1991) once per week and once within each quarter of a day. Deer locations were estimated using the maximum likelihood estimator (Lenth 1981).

#### Definitions and analytical procedures

"Natal" areas were defined as ranges occupied during the natal period (late-May throughout June) (Cowan 1956). We assumed that the natal area was close to the real location of birth (Hamlin and Mackie 1989). Spatially separate "alternate" ranges occupied at any other time of the year were identified by migrations between them and the natal range. Migration and dispersal differed, in that migration had predictable returns (Sinclair 1984) while dispersals did not (Bunnell and Harestad 1983). Migratory deer were called "obligate" if they were consistent annually and "facultative" if migrations occurred irregularly.

Habitats were: old (>250 yrs), mature (61-120 yrs), pole-sapling (15-60 yrs), young (6-14 yrs), unforested (0-5 yrs), and non-merchantable-forest (rock, water, subalpine, and alpine). If a deer was recorded using old growth at any time, it was classified as an old-growth deer, otherwise it was a second-growth deer.

All distances and directions were measured as straight lines from the last recorded location to the current location. Departure and arrival dates from one range to another, or from one location to another, were taken to be the half-way point between the date last observed to the date of the current observation.

#### Winter range removal

Candidate forest stands of typical winter habitat (e.g., Bunnell 1985, Nyberg et al. 1986) were selected for harvest at Chemainus and Nimpkish Rivers (see McNay et al. submitted). We also were able to opportunistically collect data from a third site at Nanaimo River that was partially harvested after our deer were collared.

Analyses treated only data for winter and spring (Dec 16-June 15), the period when deer most often inhabited winter range. The collared deer were followed at least one winter prior to, and subsequent to, logging of winter habitat.

#### Survival estimates

Deer were aged at the time of collaring and followed until death when the cause of mortality was determined (see McNay and Voller submitted). We used program SURVIVE (White and Garrott 1991:225) to estimate annual survival and the influence of 4 independent categorical factors on survival: study site, year, habitat selection group (old- or second-growth), and movement behaviour (migratory or resident). We also used CATMOD (SAS Institute Inc., Cary, North Carolina, USA) to incorporate refinements to the survival interval (from annual to



monthly intervals), and the movement behaviour (obligate and facultative).

## Results and discussion

We collared 122 deer at 4 study areas (115 females and 7 males) and monitored them for 76,693 deer-days. The majority of deer were collared as adults at Nanaimo River. Forty-eight deer with <3 mo data were omitted from analyses. We collected 8624 weekly locations on the remaining 74 deer (Table 1).

### Movements

The only dispersals were by 2 female deer collared as juveniles at the Nimpkish River site. They left the collaring site together in late June and spent the following summer 7 km east. During fall, they travelled another 18 km east and one was killed by a vehicle. The remaining disperser returned, at the end of October, and settled at the same location used the previous summer.

Migration ( $n = 202$ ) occurred at all sites to alternate ranges by October 20 ( $\bar{z} = 24.33$ ;  $n = 38$ ;  $P < 0.05$ ) for obligate migratory deer, and December 10 ( $\bar{z} = 20.19$ ;  $n = 56$ ;  $P < 0.05$ ) for facultative deer. Return migrations to natal ranges generally occurred before the birth of fawns by May 26 ( $\bar{z} = 35.43$ ;  $n = 45$ ;  $P < 0.05$ ) for obligate migratory deer, and about February 21 ( $\bar{z} = 10.01$ ;  $n = 63$ ;  $P > 0.05$ ) for facultative deer. Obligate deer

travelled to alternate ranges annually, usually before snowfall began (2 of 38 moves in snow) and returned after melt (0 of 45 returns in snow). Facultative deer usually departed only after snowpacks had accumulated on natal ranges (42 of 56 in snow) and returned before snow ablation had completed (16 of 63 in snow). If no snow fell, facultative deer usually did not leave their natal range. Obligate deer spent more than half of each year ( $\bar{x} = 209$  d;  $n = 34$ ;  $SE = 8.77$ ) away from the natal range, while facultative deer spent less than a quarter of each year on alternate ranges ( $\bar{x} = 66$  d;  $n = 33$ ;  $SE = 10.05$ ). Obligate migrators showed no consistent directional tendencies in movement; facultative migrators always followed the direction of the valley.

Facultative deer appeared reluctant to leave the natal area and did so only if snowfall modified their habitat. These deer had established their natal areas at mid- to high elevations (Fig. 1) where snowpacks were ephemeral. Obligate migrators established their natal ranges at higher elevations (Fig. 1) and appeared to move in anticipation of inclement winter weather. Nanaimo River was the most variable study site with low elevation habitats that were snow free in some years, and mountainous subalpine habitats that received some snow every year. There, our sample of deer consisted of 23 residents, 7 facultatives, and 10 obligates. Studies from other locations support the

Table 1. The sex, age classes, and number of relocations made for a sample of radio-collared, black-tailed deer at four study sites on Vancouver Island, British Columbia. Superscripted values are the number of deer that lived long enough to classify into movement-behaviour groups.

Study Site	Adults		Yearling		Fawn		Total		Number of locations*
	M	F	M	F	M	F	M	F	
Caycuse	0	20 <sup>(10)</sup>	1	1	5 <sup>(2)</sup>	2 <sup>(1)</sup>	6 <sup>(2)</sup>	23 <sup>(11)</sup>	1582
Chemainus	0	14 <sup>(7)</sup>	0	2	0	4 <sup>(1)</sup>	0	20 <sup>(8)</sup>	784
Nanaimo	1 <sup>(1)</sup>	42 <sup>(32)</sup>	0	10 <sup>(7)</sup>	0	5	1 <sup>(1)</sup>	57 <sup>(39)</sup>	860
Nimpkish	0	12 <sup>(10)</sup>	0	2 <sup>(2)</sup>	0	1 <sup>(1)</sup>	0	15 <sup>(13)</sup>	5398

\* - for superscripted deer only.



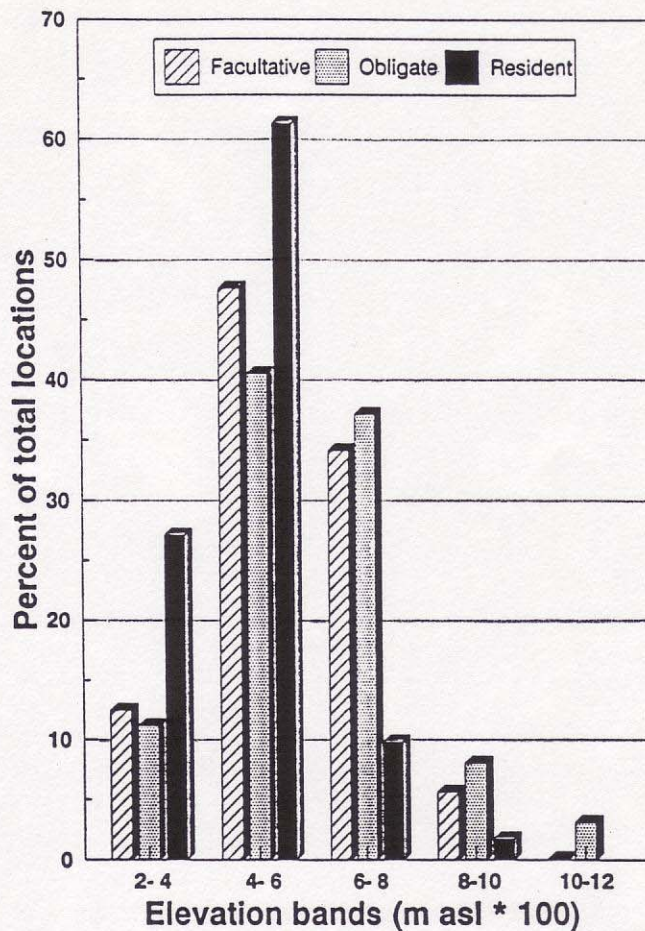


Figure 1. Percent of total locations recorded at different elevation bands (m asl) for radio-collared, black-tailed deer of three different movement-behaviour types.

notion that migration is site dependent (Kufeld et al. 1989; Brown 1992) and is usually initiated by specific, weather-related phenomenon (McCullough 1964, Loft et al. 1989), snow depth (Gilbert et al. 1970), or the condition of seasonal forage (Garrott et al. 1987). We concluded that local topography and climate at the natal range provided a continuum in the need to use alternate ranges. Where inclement winter weather can be expected in most years deer migrate annually to alternate ranges, but at lower elevations, deer leave the natal area only when necessary. At lowest elevations, deer are resident because inclement winter weather occurs infrequently and no topographic opportunity exists for escape.

Similar to other studies (Bunnell and Harestad 1983; Garrott et al. 1987; Hamlin and Mackie 1989), dispersal was observed

infrequently. We concluded that adoption of a natal range was strongly dependent on the maternal natal range, similar to studies by Hirth (1977) and Hamlin and Mackie (1989). Fidelity to the natal area did not vary among periods ( $\bar{x} = 327$  m;  $n = 93$ ;  $SE = 30.49$ ), nor was there any effect due to migratory behaviour ( $P > .05$ ), similar to Garrott et al. (1987).

#### Habitat use

Although the use of young and pole-sapling forests was generally 65-75% at all sites but Caycuse, site-dependent patterns were evident (Fig. 2). Use of young and pole-sapling forests at Caycuse was 34%, with 42% occurring in unforested habitats. Use of unforested habitats elsewhere ranged from 7% to 15%, and use of old-growth forests was 7-14%.



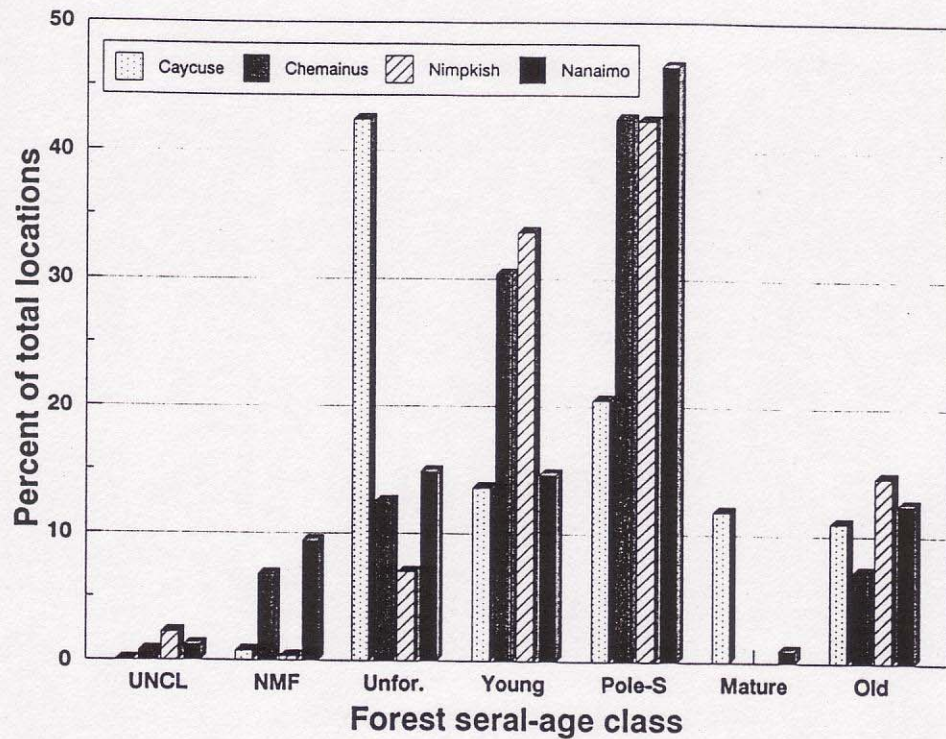


Figure 2. Habitats chosen by radio-collared black-tailed deer at four study sites on Vancouver Island, British Columbia (UNCL = unclassified but open; NMF = non-merchantable forest, including rock, water, subalpine, and alpine; Unfor = 0-5 years post logging; Young = 6 to 14 year old stands; Pole-S = pole-sapling stage, 15-60 years old; Mature = 61 to 120 years old; Old = old-growth, >250 years old).

Habitat use differed ( $P < 0.05$ ) between natal and alternate ranges primarily in a switch of seral age classes (Fig. 3). Natal ranges were characterized by less use of unforested habitats (16% vs 25%) and younger habitats (20% vs 30%) and greater use of older (mature and old-growth) forests (25% vs 45%). All 12 obligate migratory deer and 10 of the 16 facultative deer used old-growth on alternate ranges. Resident deer did not have as much access to old-growth and 25 of 44 used it. Six facultative deer had no access to old-growth. Twenty-eight deer were clover-trapped in old-growth and 11 were trapped in second-growth. Over half of the deer trapped in old-growth were migratory, and all but one of the deer trapped in second-growth were resident.

We concluded that old-growth forests were preferred habitat when inclement winter weather occurred. Summer habitats were composed primarily of young and unforested habitat combinations. Resident

deer used primarily young second-growth habitats year-round, and only where remnant stands of old-growth occurred did they use them. These findings are similar to those of Yeo and Peek (1992) in south-east Alaska.

#### Response to removal of winter habitat

Regardless of behaviour type, deer showed little tendency ( $P > 0.05$ ) to leave home range after old-growth was harvested (Fig. 4a). Only old-growth resident deer enlarged their home ranges in the post-treatment period (Fig. 4b). Similar results were obtained by Gasaway et al. (1989) who studied the response of moose to habitat improvements. Others found no detrimental tendency for deer (Hood and Inglis 1974) to move away from habitat disturbances. We found no significant response by deer to the harvest of the three winter ranges, although data collected through more severe winter weather may prove different. Nevertheless, we expect changes in habitat selection, if



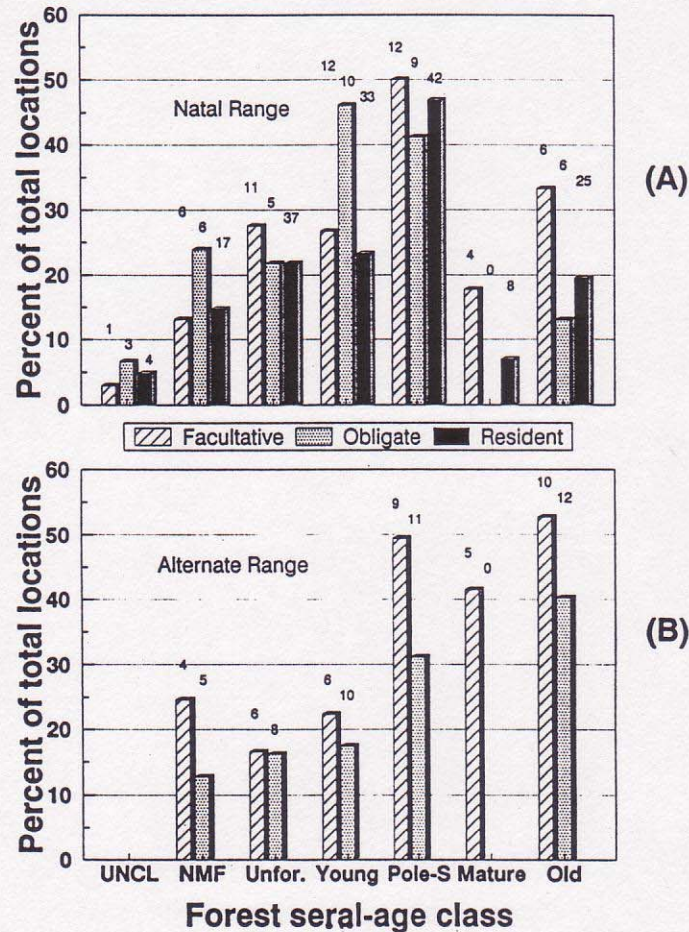


Figure 3. Habitats chosen by radio-collared black-tailed deer of three different movement-behaviour types, on a) natal ranges and b) alternate, winter ranges. Forest seral-age classes as in Figure 2.

they do occur, would take place over several years.

#### Survival estimates

We recorded 78 mortalities (73 females, 5 males), most between Feb and June. Predation and malnutrition were the most frequent causes, primarily in spring (McNay and Voller submitted). We did not detect habitat or annual effects on survival ( $P > 0.05$ ), but survival varied with movement behaviour and month ( $P < 0.05$ ). Obligate migratory deer generally had high annual

survival rates ( $\bar{x} = 97\%$ ;  $n = 402$  deer months;  $SE = 0.5\%$ ), while facultative and resident deer had two periods of significantly lower survival rates: Mar-May ( $\bar{x} = 75\%$ ;  $n = 519$  deer months;  $SE = 2\%$ ) and Nov ( $\bar{x} = 66\%$ ;  $n = 156$  deer months;  $SE = 2\%$ ).

We concluded that obligate migratory deer could have been in transit to, or from, their natal ranges during the periods of highest mortality (McNay and Voller submitted). That conclusion contrasts white-tailed deer (*O. virginianus*) in Minnesota, where migratory deer had lower annual



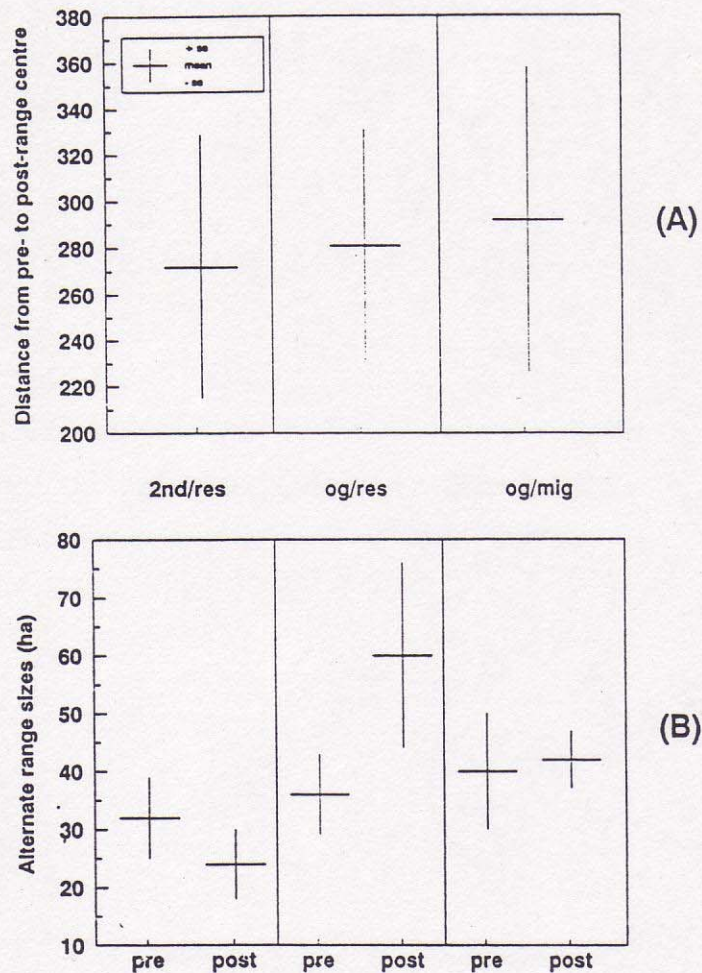


Figure 4. The response of three movement types of black-tailed deer (second-growth residents, old-growth residents, and old-growth migrators) to removal of old-growth, alternate ranges. a) average distance between pre- and post-harvest alternate range centres and b) average alternate range size pre- and post-harvest.

survival compared to residents (Nelson and Mech 1986). Annual survival rates (McNay and Voller submitted) compared favourably with those reported for white-tailed deer in Montana (Dusek et al. 1989) and mule deer (*O. h. hemionus*) in Colorado (White and Bartmann 1983).

### Management implications

We drew three management implications from these findings. First, because individual deer show consistency of movement patterns (resident, facultative, or obligate), their choice and movements did not follow an ideal-free distribution (Fretwell 1972). That is, deer did not demonstrate full knowledge of their surroundings by selecting and filling the best

habitat before occupying less favourable habitat. Response to change in habitat should lag in time, possibly for generations. That delay has serious implications to managers attempting to interpret patterns of deer habitat use, and it is unclear when and what to measure as a response to changes in habitat.

Second, black-tailed deer appeared to do reasonably well in second-growth. However, our findings and those of others (Bunnell and Jones 1984, Bunnell 1985, 1990) showed that deer using old-growth fare better. Our observations suggested that as old-growth is removed there would be fewer and fewer migrators until only one movement tactic, the least successful, is retained. We therefore expect resilience of deer



populations to decline with amounts of old-growth. Deer currently present in second-growth during winter may be only that portion of the initial population displaying resident movement tactics.

Tactics for maintaining wildlife involve stand and landscape level planning. The movement behaviours reported here have implications at the landscape level. Old-growth reserves for winter range, and second-growth treatments to create winter range in managed stands (e.g., Nyberg et al. 1986), should be few but large and on southern aspects at mid-elevations. That approach would accommodate both facultative and obligate migrators and reduce predation. Because resident deer move little and are concentrated at low elevations, reserves and silvicultural treatments to create winter range at those elevations should be spread over many, small areas. Combined, these management actions across the landscape would maintain all three movement behaviours, and resilience within the deer population.

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