PREDATION BEHAVIOUR OF VANCOUVER ISLAND COUGAR (*Puma concolor vancouverensis*) AND ITS RELATION TO MICRO- AND MACROSCALE HABITAT

by

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B.Sc., The University of British Columbia, 1996

A THESIS SUBMITTED IN PARTIAL Fulfillment OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Faculty of Agricultural Sciences)

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April 2003

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ABSTRACT

Little is known of the relationship between cougar (*Puma concolor*) predation and habitat. I investigated cougar predation on North Vancouver Island to determine species, sex, age and condition of prey and microsite and macrohabitat characteristics of feeding sites. Nine radio-collared female cougar were relocated using radiotelemetry from October 1997 to May 1998. Sixty-five feeding sites were located through a combination of intensive triangulation, DGPS and use of a trained Labrador retriever. Columbian black-tailed deer (*Odocoileus hemionus columbianus*) comprised the majority of prey in addition to a raccoon (*Procyon lotor*) and grouse (*Dendragapus obscurus or Bonasa umbellus*). Three Roosevelt elk (*Cervus elaphus roosevelti*) were also found killed by male cougar radio-collared as part of another study. Sex and age of deer killed by cougar appeared to correspond to historical estimates for my study area, although estimates were not available during my study. Deer condition appeared to follow common ungulate fat reserve trends during the course of predation sampling, indicating deer condition was not a factor in their capture. An average annual kill rate of 22.6 deer per female cougar was estimated, although observed interference competition from black bears out of hibernation may increase this rate. Feeding sites were found in areas of dense horizontal cover, presumably associated with cougar hunting style, and/or corresponding to microhabitat use by deer during winter. Feeding sites were closer to roads, at lower elevations and in proximity to young and old growth forests, more than expected. These sites correspond well to studies of deer macrohabitat use.
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ACKNOWLEDGEMENTS

I thank Karen Goh for her dedication to the telemetry through all those rainy days. And to my black lab, Roan, for whom I would never have found most feeding sites. Dr. David Shackleton deserves special thanks for providing me with this opportunity, as well as his support and patience throughout my studies.

The Ministry of Environment, Lands and Parks was integral to my study in terms of cougar capture, equipment, logistical support, and advice. Specifically: G. Brunham, M. DeLaronde, T. Hamilton, D. Janz, M. McAdie, H. Robinson, and H. Schwantje. My thanks to the late K. Atkinson, who helped instigated the study. Several individuals volunteered on the project and I am indebted to their help: S. Foster, T. O’Hare, D. Klinka, C. Wainwright and K. Wickert. Though soaked to the core, they kept going. My special thanks to the houndsmen of Campbell River for their time and dedication. They provided me a special schooling no classroom could give.

My research was supported by Forest Renewal British Columbia, British Columbia Ministry of Environment, Lands, and Parks (MoELP), MacMillan Bloedel Limited, Western Forest Products Limited, Mountain Equipment Co-op, and the University of British Columbia.
INTRODUCTION

For the last 25 years, cougar ecology studies have been largely conducted through radio-telemetry (Hemker et al. 1984; Logan et al. 1986; Neal et al. 1987; Ross and Jalkotzy 1992; Seidensticker et al. 1973). These studies have produced data on cougar survival, home range size, and density across continental western North America. Collectively, the resulting characterization is a versatile predator capable of existing in a wide variety of ecosystems even in the presence of human habitation. But can we say anything further from these studies? Home range size and density differ considerably between areas, but why this is so is unknown. This is where radio-telemetry as traditionally practiced is probably limited—it can indicate that animal home range sizes in California differ from those in Utah, but not why. Radio-telemetry studies have therefore most likely reached their utility in terms of broad patterns of cougar biology. The next logical step is to address the ecological factors underlying these patterns.

In a general context, we can ask why predators utilize particular habitats? The difference potentially lies in the ability to procure prey. For instance, lynx (*Felis lynx*) tend to chase snowshoe hares (*Lepus americanus*) more frequently in sparse vegetation, and less so when ambushing from dense vegetation (Murray et al. 1995), but have higher kill success ambushing than stalking. Coyotes (*Canis latrans*) on the other hand are reportedly more successful in dense versus sparse vegetation, but employ the same hunting strategy in both cover types (Murray et al. 1995). Differences in vegetative cover are correlated to differences in the hunting strategies of lynx and in the success of coyotes. Similarly, ecological factors influence predation success in other species. Huggard (1993) demonstrated that snow depth led to a significant increase in grey wolf (*Canis lupus*) predation of elk (*Cervus elaphus*), and prey age class selection also changed with increasing snow depth. The effects of snow have also been demonstrated in wolf/white-tailed deer (*Odocoileus virginianus*) interactions, where wolves had decreased predation success in shallow snow (Fuller 1991). Considering that snow depth will vary with habitat (e.g., due to
degree of canopy closure, Meidinger and Pojar 1991), habitat probably plays a crucial role in determining success of predators using forested habitats and may, as in the case of lynx, affect the hunting strategy.

Cougar predation of ungulates is reasonably well documented (Iriarte et al. 1990), but its relationship to habitat is not addressed. Here I attempt to address this aspect of cougar ecology by investigating variables that potentially influence cougar predation success. First, I investigate prey selection by cougar, examining issues of sex, age, and condition of prey as well as kill rate to establish baseline estimates for my study area. Second, while differences in predation habitat have been hypothesized for many areas (Franklin et al. 1999; Gagliuso 1991) it has not been proven. A previous study on Vancouver Island (Hahn 2001) found evidence that cougar were feeding in areas of denser cover. Hence I investigate the use of cover in killing or feeding in an attempt to address why cougars use particular habitats. My research objectives are to:

- examine prey species, age and sex,
- establish baseline kill rate estimates,
- investigate the relationship between cougar feeding and vegetative cover, and
- investigate feeding site selection at the landscape level.
METHODS

Study Area

The study area covers about 2500 km² centered around the Adam and Eve River drainages on northeast Vancouver Island, British Columbia, Canada (Figure 1). The latitudes and longitudes bounding the area are: NE corner, 50°27.718'N, 179°58.374'W; SE corner, 50°15.905'N, 168°4.047'W; NW corner, 50°21.869'N, 162°28.148'W; and SW corner, 50°15.789'N, 156°21.735'W. Elevations range from sea level to ca. 1800 m on Mt. Cain. The area is actively logged and is comprised of a mosaic of forest age-stand classes, ranging from

Figure 1. Landsat TM overview of forest age mosaic. Light red (light grey in black and white) indicates recent clearcuts while darker green (dark grey in black and white) indicates old growth forest. Cougar feeding sites are shown in white.
new clearcuts to old growth. Two forested biogeoclimatic zones (Meidinger and Pojar 1991) dominate the area and are described below. The Alpine Tundra Zone is present at high elevations.

The Coastal Western Hemlock (CWH) zone occurs from low (sea level) to middle (900 m) elevations and is characterized by a cool mesothermal climate with cool summers and mild winters. Major tree species include western hemlock (*Tsuga heterophylla*), followed by western redcedar (*Thuja plicata*), douglas fir (*pseudotsuga menziesii*), amabilis fir (*Abies amabilis*), shore (lodgepole) pine (*Pinus contorta*), and red alder (*Alnus rubra*). The CWH zone is, on average, the rainiest zone in British Columbia with a mean annual precipitation of 2228 mm, although it ranges from 1000 to 4400 mm. Between 15% and 50% of the total precipitation falls as snow depending on latitude. Mean annual temperatures range from −6.6°C in the coldest months to 10.5°C in the warmest, but the mean monthly temperature is above 10°C for 4 to 6 months of the year.

The Mountain Hemlock zone occurs between about 900 m and 1800 m elevation, and is characterized by short, cool summers and long, cool, wet winters. Major tree species include mountain hemlock (*Tsuga mertensiana*), amabilis fir, and yellow-cedar (*Chamaecyparis nootkatensis*). Precipitation probably ranges from 1700 to 5000 mm per annum, 20 to 70% of which falls as snow, but this has not been fully quantified. Mean annual temperature ranges from 0 to 5°C. The monthly mean temperature is above 10°C for 1 to 3 months of the year, but below 0°C for 1 to 5 months, having an impact on the short growing season for vegetation.

Cougar hunting is permitted in the study area, but harvest levels vary from year to year. It typically occurs between the start and end of snowfall, although in the 1996/97-year it was extended to June. In the 1995/96-year, 5 males and 3 females were killed by hunters in the management unit that encompasses the study area and 75-km south, to Campbell River. During the study, cougar hunters working with the researchers did not kill radiocollared cougar.
Capture and Radiotelemetry

Cougar were captured from December 1996 until February 1998, using procedures modified slightly from Hornocker (1970). In general, logging roads were driven throughout the winter by the researchers, field assistants and by local houndsmen. When cougar tracks were found, Walker or Bluetick hounds were brought to the track. If the scent was sufficiently fresh, the dogs were released and followed the scent trail until the cougar was treed.

Cougar were immobilized with a mixture of Ketamine and Medetomidine according to body weight. Cougar too high in the tree or with an unsafe landing space were not immobilized. Once immobilized, a researcher climbed the tree, attached a rope to the animal and lowered it to the ground. Cougar were then ear-tagged with unique numbers in both ears and radio-collared (Telonics, Mesa, Arizona, USA) with a unique frequency in the 150-151 MHz range. A reversal agent, Atipamezole, was administered and the cougar was observed until it left the area.

Radiotelemetry related to feeding site sampling was conducted from October 1997 to the end of May 1998. We attempted to relocate cougar on consecutive days, with an average relocation rate of 4 per week. Between 3 and 6 bearings were obtained for each location using a Lotek SRX-400 receiver (Lotek Inc., Newmark, Ontario, Canada). An Ashtech Reliance RT (Ashtech, Santa Clara, California, USA) global positioning system (GPS) was used to reference all location data, including tower locations when telemetry was conducted. Locations were differentially corrected in realtime using a Canadian Coast Guard Beacon located at Port Hardy, a 120 km straightline distance from the study site. GPS locations were taken with a minimum of 5 satellites, PDOP < 6 and HRMS/VRMS < 10, resulting in a maximum error of 2-5 m. The Andrews-M or Maximum Likelihood estimate (Lenth 1981a, b) was calculated for each location using LOAS software (Ecological Software Solutions, Sacramento, California, USA). A series of 95 tests of collars in unknown locations were used to determine observer angular standard deviation for calculating location error estimates. When cougar could not be located from the
ground, a Cessna 172 was used for aerial locations. Two antennae were oriented perpendicular to the plane. One test collar was placed in a GPS location unknown to the observer for each flight, and at varying distances to recognizable landmarks (e.g., roads, streams, forest edges) to assess observer error. Error estimates were averaged across repeated flights.

**Feeding Sites**

A cougar was assumed to be at a potential feeding site when it remained in the same approximate location for 2 consecutive days, allowing for telemetry error. It should be noted that my study was biased towards prey that required a minimum of 2 days to consume. If the cougar was still at the feeding site, the researcher walked-in using radiotelemetry to get as close to the cougar as possible. Typically at approximately 20-50 m from the feeding site, the cougar would move ca. 100 m away and remain close by or circle the researcher. During this time the researcher had a trained black Labrador Retriever dog search for and bring the researcher to the feeding site. If the prey species was an ungulate, the carcass was sexed and the bones from a rear leg were removed for femoral marrow fat estimation (Neiland 1970). The teeth from the lower mandible were removed for aging (Gilbert 1966), conducted by Matson's Lab (Matson's Laboratory, Milltown, MT). The researcher then left the area and the cougar returned to finish feeding. If the cougar was not at the feeding site, the researcher used GPS to find the estimated radio-telemetry location and the dog was used to refine the search for the feeding site. Fifty-two feeding sites were found while the cougar was still at the feeding site and the remaining 13 sites were found at the estimated location via GPS.

Annual kill rate was calculated strictly on the locations I could verify as feeding sites for each cougar during my observation periods. The minimum annual kill rate for each female cougar was calculated as:

\[
\text{Minimum annual kill rate} = 365 \times \frac{\text{number of kills}}{\text{number of days located}}
\]
This was averaged for all the females. I assumed feeding sites \((n = 4)\) from one dependent juvenile collared male represented those of his uncollared mother and included them in my calculations.

**Microsite**

After the cougar had left the feeding site for a minimum of 2 days I returned to the site to conduct vegetation and structural sampling. A 11.29 m radius circular plot (400 m²) was centered on the feeding site for all vegetation sampling; this is considered a prudent plot size to represent a coastal forest ecosystem (K. Klinka, pers. comm. UBC, Vancouver 1995). I estimated visually: percent cover and height of the overstory canopy and shrub layers as well as 2 indices of horizontal cover. The first index, intended to represent cougar visibility, used a 2.5 cm by 1 m pole of alternating 10 cm black or white sections placed at the plot center. I then estimated the percent visibility of the pole at 3 and 10 m from the plot center while crouching, as well as the distance at which the pole could not be discerned at each of the 4 cardinal directions. The second index, intended to estimate vegetation in the shrub layer, used a 30 cm x 2.5 m canvas coverboard divided into 10 alternating sections of fluorescent orange or white. This was placed at the plot center and I estimated, while crouching, the percent visibility for each section of the coverboard at 3 and 10 m from the plot center, on the 4 cardinal directions. These measurements were repeated at a second plot located 100 m in a random direction from the feeding site to represent an available habitat. I recorded the location of both plots with the GPS receiver.

I developed a Resource Selection Function (RSF; Manly *et al.* 1993) using logistic regression models to test for selection by cougar. I created models based on sampling time cost and expected biological significance for the variables measured. The model chi-square \((G_M)\), analogous to the regression sum of squares (Menard 1995), was used to evaluate the model.
significance and to test for differences between models. Selection coefficients of the RSF were examined to indicate weighting of variables relative to each other and direction of selection (negative/positive). I tested coefficient significance by obtaining the P-value of the ratio of the selection coefficient to its standard error from the standard normal distribution using $\alpha=0.05$ (Manly et al. 1993). Coefficient significance does not reflect overall model goodness-of-fit, merely the relative contribution of the variable coefficient to selection for that model. All proportions were arcsine square root transformed prior to analyses to normalize the data.

**Macrosite**

To examine macroscale selection for feeding sites, I used ArcInfo (Environmental Systems Research Institute, Redlands, California, USA) export coverages provided by MacMillan Bloedel Ltd. (MB), Western Forest Products Ltd. (WFP) and the Ministry of Environment, Lands and Parks, B.C (MELP). MB and WFP forest cover data were combined into one coverage. A Triangular-irregular network (TIN) was derived from Terrain Resource Inventory Map (TRIM) Digital Elevation Models (DEM) using Arcview software with the 3D and Spatial Analyst extensions (Environmental Systems Research Institute, Redlands, California, USA). Forest age categories (Oliver 1992) were reclassified according to expected use by black-tailed deer (Table 1) as decided by local biologists (D. Janz pers. comm. MELP, Nanaimo 1999; A. MacKinnon pers. comm. B.C. Ministry of Forests (MOF), Victoria 1999; D. Meidinger pers. comm. MOF, Victoria 1999; F. Nuszdorfer pers. comm. MOF, Nanaimo 1999; B. Nyberg pers. comm. MOF, Victoria 1999). Thus, cougar feeding site habitat use was evaluated in terms of their expected primary prey (A. Hahn, unpubl. data). The resulting coverages were queried in Arcview for forest age, distance to roads, distance to streams, and distance to forest edge. Using a custom Arcview script, I queried the coverages for the habitat type of the nearest adjoining forest, as well as slope, aspect and elevation. Random points were generated using an Arcview
script (Cederholm 1999). Although the variance of each variable remained approximately constant after 2000 points, 10,000 points were used to provide an accurate assessment of available habitat and because the computational power was available.

Table 1. Forest age classes as determined by local biologists. Forest age categories were evaluated on characteristics thought useful to deer.

<table>
<thead>
<tr>
<th>Forest Age Classes</th>
<th>Benefit to Deer</th>
<th>Age (years)</th>
<th>Percentages Within the Study Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand Initiation I</td>
<td>Security (via high predator visibility) High Food</td>
<td>0-5</td>
<td>3.7</td>
</tr>
<tr>
<td>Stand Initiation II</td>
<td>Security (low visibility), high food</td>
<td>6-15</td>
<td>9.3</td>
</tr>
<tr>
<td>Young</td>
<td>Security (low visibility), some food</td>
<td>16-30</td>
<td>12.2</td>
</tr>
<tr>
<td>Stem Exclusion</td>
<td>Thermal</td>
<td>31-60</td>
<td>6.4</td>
</tr>
<tr>
<td>Understory Reinitiation</td>
<td>Some thermal, some food</td>
<td>61-90</td>
<td>2.6</td>
</tr>
<tr>
<td>Mature Phase I</td>
<td>Food, thermal</td>
<td>91-170</td>
<td>1.2</td>
</tr>
<tr>
<td>Mature Phase II</td>
<td>Food, thermal</td>
<td>171-250</td>
<td>8.6</td>
</tr>
<tr>
<td>Old Growth</td>
<td>Food, thermal, security (low visibility)</td>
<td>250+</td>
<td>53.6</td>
</tr>
<tr>
<td>Other (including Alpine and Rock)</td>
<td>N/A</td>
<td>N/A</td>
<td>2.4</td>
</tr>
</tbody>
</table>

A RSF was created as in the microsite analysis, using a logistic regression model. Models were created according to hypothesized biological importance. Model selection proceeded in a similar fashion to microsite model selection, although the 57 feeding sites were compared to 10,000 available points as opposed to equivalent numbers in the case of the microsite analysis. This did not pose a problem because the power of the logistic regression is based on the number of samples in the smaller category (D. Cram pers. comm., Stanford University, Stanford 1999). Models presented should be evaluated based on model chi-square ($G_M$), simplicity and ability to be applied to other study areas with different habitats.
RESULTS

Predation Characteristics

When cougar were approached at a feeding site, they were never seen although telemetry indicated they remained nearby. Cougars were never observed to be physically aggressive or to overtly defend feeding sites while researchers approached. Aggressive vocalization was heard from a mother with two 3 to 4 month old juveniles. She was captured on a feeding site near a river and remained at the feeding site for 3 additional days. One other female was captured on a feeding site without incident.

Carcass remains usually consisted of broken middle leg bones (radius/tibia), lower leg bones (carpal/metapodial), pelvis, portions of the upper spinal column, skull and the lower mandible. If the middle leg bones were absent, the lower bones were typically broken. A pile of deer hair centered the feeding site, although sometimes there was one major hair pile and several smaller ones within a 5 m radius. The digestive tract (rumen, intestines) was usually located close by (1-5 m) buried under 2-3 cm of forest litter/duff, if available. If duff was not available, the digestive tract was left in the open and at a few sites it wasn’t found and was assumed to have been consumed. Unburied scat was present at most feeding sites and occasionally I found scat buried under one or more duff piles. Towards the end of April 1998, a deer foetus was found buried near the gut pile at 2 separate feeding sites. In only 1 instance was a large amount of flesh (~30%) left on the only large male deer killed in my sample. Deer carcasses at other feeding sites were cleaned of muscle tissue.

A total of 65 feeding sites were found. Sixty black-tailed deer comprised the majority of prey (92%) in addition to 3 Roosevelt elk (Cervus elaphus roosevelti), 1 raccoon (Procyon lotor) and 1 grouse (Dendragapus obscurus or Bonasa umbellus; Figure 2). Most of the sexed adult deer (n = 34, 26 female, 8 male and 5 unknown) were female (76%). Juveniles (<1 year old)
comprised 20 deer kills (33%, 7 female, 9 male and 4 unknown, Figure 3). All deer had less than 80% bone marrow fat concentrations, with 21% having less than 25% fat.

![Chart showing species, sex and age of 65 prey found at cougar feeding sites.]

Figure 2. Species, sex and age of 65 prey found at cougar feeding sites.

The average annual female cougar kill rate was 22.6 ± 1.62 (SE; range=15.53 to 28.63, n=9 cougar) deer. Females with kittens did not have a statistically higher kill rate (mean=23.1, SE=2.85, range=15.5 to 28.8, n=5) than those without kittens (mean=21.4, SE=1.19, range=18.7 to 23.9, n=4; one-tailed t-test, α=0.05, p=0.32). Female cougar remained at feeding sites an average of 4.0 ± 0.39 (SE) days. Females with kittens spent the same number of days at feeding sites as females without (one-tailed t-test, α=0.05, p=0.33).
Figure 3. Frequency of tooth cementum ages of deer found at 56 cougar feeding sites.

Black bears (*Ursus americanus*) were found on 4 feeding sites. In those cases, the cougar remained on a feeding site for 2 days, then moved approximately 200 m away, and either stayed 3 to 4 days before leaving (n=2) or left the area immediately (n=2). Investigation of the feeding site revealed a bear on the kill at 2 feeding sites, and bear scat at 2 others.

**Microsite Characteristics**

Fifty-seven feeding sites and paired random “available” plots were sampled. Feeding sites had on average taller shrub and canopy layers and more canopy cover than random plots (Table 2). Feedings sites also had greater horizontal cover (lower percent visibility) on average. However, confidence intervals overlapped in all but 2 cases.

Nine of the 12 models tested had a significant fit, with model 3 (all variables) having the best fit (Table 3). Univariate models explained considerably less variation than multivariate models. For instance, the black and white pole visibility models (11, 12) measured at 3 m and 10 m from the feeding site were not significant, and the collapsed coverboard model (8) had a
model chi-square ($G_M$) of 6.158. As well, the most economical sampling time model (1) of only shrub and canopy height/cover was not significant. However, the mixed models based on horizontal cover variables (2-6, 8, 9) were significant. Differences between the models were not significantly different, indicating the simpler models using fewer variables could also be used.

Table 2. Average cover variables measured at feeding sites (used) and random sites (available). Fifty-seven sites were sampled in both cases. Where values are presented as percent visibility; lower values indicate more cover. Variables where confidence intervals did not overlap are indicated with an *.

<table>
<thead>
<tr>
<th>Cover Variable</th>
<th>Abbreviation</th>
<th>Used</th>
<th>Available</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub height (m)</td>
<td>SH</td>
<td>1.4</td>
<td>1.2</td>
</tr>
<tr>
<td>Shrub % cover</td>
<td>SC</td>
<td>22.1</td>
<td>23.6</td>
</tr>
<tr>
<td>Canopy height (m)</td>
<td>CH</td>
<td>18.8</td>
<td>16.4</td>
</tr>
<tr>
<td>Canopy % cover</td>
<td>CC</td>
<td>30.4</td>
<td>27.8</td>
</tr>
<tr>
<td>Cover board % visibility from top to bottom:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.25-2.50 m</td>
<td>C1</td>
<td>35.4</td>
<td>44.7</td>
</tr>
<tr>
<td>2.00-2.25 m</td>
<td>C2</td>
<td>33.3</td>
<td>44.1</td>
</tr>
<tr>
<td>1.75-2.00 m</td>
<td>C3</td>
<td>28.0</td>
<td>40.4</td>
</tr>
<tr>
<td>1.50-1.75 m</td>
<td>C4</td>
<td>25.6</td>
<td>39.1</td>
</tr>
<tr>
<td>1.25-1.50 m</td>
<td>C5</td>
<td>21.9</td>
<td>33.3</td>
</tr>
<tr>
<td>1.00-1.25 m</td>
<td>C6</td>
<td>19.0</td>
<td>30.0</td>
</tr>
<tr>
<td>0.75-1.00 m</td>
<td>C7*</td>
<td>12.4</td>
<td>24.8</td>
</tr>
<tr>
<td>0.50-0.75 m</td>
<td>C8</td>
<td>10.8</td>
<td>20.9</td>
</tr>
<tr>
<td>0.25-0.50 m</td>
<td>C9</td>
<td>7.2</td>
<td>14.6</td>
</tr>
<tr>
<td>0.00-0.25 m</td>
<td>C10</td>
<td>4.5</td>
<td>7.6</td>
</tr>
<tr>
<td>Black and white pole % visibility</td>
<td>DIS10</td>
<td>9.9</td>
<td>12.7</td>
</tr>
<tr>
<td>at a distance of 10 m</td>
<td>DIS3</td>
<td>51.4</td>
<td>58.5</td>
</tr>
<tr>
<td>Distance to disappearance (m)</td>
<td>DIS*</td>
<td>15.1</td>
<td>9.6</td>
</tr>
<tr>
<td>Collapsed coverboard % visibility:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.25 to 2.50 m</td>
<td>CC1</td>
<td>28.1</td>
<td>40.1</td>
</tr>
<tr>
<td>0 to 1.25 m</td>
<td>CC2</td>
<td>9.4</td>
<td>18.3</td>
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Table 3. Models to determine microsite habitat selection, ordered by their ability to differentiate between feeding sites and random sites (n=57) in descending order. See Table 2 for a description of the variables. Significance was determined at $\alpha=0.05$. $D_0$ describes the null model for the logistic regression, where there is no selection. $G_m$ describes the variation explained by the model, analogous to regression sum of squares. Models marked with an * were found to be significantly different from the null model.

<table>
<thead>
<tr>
<th>Model</th>
<th>Do</th>
<th>Gm</th>
<th>df</th>
<th>R^2</th>
<th>L</th>
<th>Variables (see Table 2)</th>
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<tr>
<td>12</td>
<td>163.5827</td>
<td>0.408</td>
<td>1</td>
<td>0.002494</td>
<td>DIS10</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>163.5827</td>
<td>1.969</td>
<td>1</td>
<td>0.012037</td>
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<td></td>
</tr>
<tr>
<td>1</td>
<td>163.5827</td>
<td>3.043</td>
<td>4</td>
<td>0.018602</td>
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</tr>
<tr>
<td>8*</td>
<td>163.5827</td>
<td>6.158</td>
<td>2</td>
<td>0.037645</td>
<td>CC1, CC2</td>
<td></td>
</tr>
<tr>
<td>10*</td>
<td>163.5827</td>
<td>29.392</td>
<td>1</td>
<td>0.179677</td>
<td>DIS</td>
<td></td>
</tr>
<tr>
<td>7*</td>
<td>163.5827</td>
<td>60.479</td>
<td>3</td>
<td>0.369715</td>
<td>DIS, DIS3, DIS10</td>
<td></td>
</tr>
<tr>
<td>2*</td>
<td>163.5827</td>
<td>62.588</td>
<td>7</td>
<td>0.382608</td>
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<td></td>
</tr>
<tr>
<td>9*</td>
<td>163.5827</td>
<td>66.074</td>
<td>3</td>
<td>0.403918</td>
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</tr>
<tr>
<td>6*</td>
<td>163.5827</td>
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<td>3</td>
<td>0.438897</td>
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<td>5*</td>
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<td>72.205</td>
<td>5</td>
<td>0.441397</td>
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<td>9</td>
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<tr>
<td>3*</td>
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<td>83.050</td>
<td>17</td>
<td>0.507694</td>
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</tbody>
</table>

**Macrosite Characteristics**

Cougar used younger forests between 6 and 30 years old (SI II and Young) more than expected by chance (Figure 4). Most feedings sites (39%) were in old growth forests (Figure 4), although this forest age class was used relatively less than available. More than 54% of feeding sites were within 100 m of the road (Figure 5; mean=157 m, SE=22.7, 2.5-851.5, n=57); none were found more than 900 m away. Distance between streams and feeding sites closely followed distance to streams of random points (Figure 6). Feeding sites tended to be closer to young and old growth forests (Figure 7) and on 10 – 20° slopes (Figure 8). Elevation use was greater than expected by availability in the 0 to 500 m and the 600 to 700 m elevation bands (Figure 9). Feeding sites were not observed above 1100 m.
Figure 4. Feeding site (n=57) forest age class (use) versus 10,000 random points (available).

Figure 5. Feeding site (n=57) distance to nearest road (use) versus 10,000 random points (available).
Figure 6. Feeding site (n=57) distance to nearest stream (use) versus 10,000 random points (available).

Figure 7. Nearest different forest age class from the feeding sites' (n=57). Available different forest age class was determined from 10,000 random points.
Figure 8. Feeding site (n=57) slope class (use) versus 10,000 random points (available).

Figure 9. Feeding site (n=57) elevation class (use) versus 10,000 random points (available).
All models tested yield a significant fit (Table 4). Model chi-square values were not different between the All Variables model (A), the No Degree model (B) and the Road/Elevation only model (C). Road/Elevation provided the simplest model and both distance to roads and elevation were significant beta coefficients. The separate model (D) concerned with nearest different forest type was also significant with a model chi-square of 16.65. Proximity to old growth and young forests were significant beta coefficients in the model.

Table 4. Models tested for macrosite feeding site selection. See Table 1 for a listing of forest age classes. Significance was determined at \( \alpha = 0.05 \). See Table 3 for a description of \( D_o \) and \( G_m \).

<table>
<thead>
<tr>
<th>Model</th>
<th>( D_o )</th>
<th>( G_m )</th>
<th>df</th>
<th>Significant?</th>
<th>Variables</th>
</tr>
</thead>
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<td></td>
<td></td>
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</tr>
<tr>
<td>A</td>
<td>724.018</td>
<td>50.455</td>
<td>7</td>
<td>Yes</td>
<td>Distance to roads and streams, nearest different forest type, slope, aspect, elevation, forest age</td>
</tr>
<tr>
<td>B</td>
<td>724.018</td>
<td>49.974</td>
<td>5</td>
<td>Yes</td>
<td>Distance to roads and streams, nearest different forest type, elevation, forest age</td>
</tr>
<tr>
<td>C</td>
<td>724.018</td>
<td>49.446</td>
<td>2</td>
<td>Yes</td>
<td>Distance to roads, elevation</td>
</tr>
<tr>
<td><strong>Nearest different forest type</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>705.864</td>
<td>16.65</td>
<td>7</td>
<td>Yes</td>
<td>All forest age classes</td>
</tr>
</tbody>
</table>

**DISCUSSION**

**Behaviour of Cougar**

**Prey**

Female cougar on northern Vancouver Island consumed black-tailed deer as their primary prey. This is consistent with other North American cougar studies where Odocoilid deer comprise \( 68\% \pm 20 \) (SD) of cougar diet (Iriarte et al. 1990). As well, male cougar fed on Roosevelt elk besides black-tailed deer. Cougar were observed feeding on elk in Idaho (Hornocker 1970). My study was likely biased towards large prey species that require at least 2 days to consume. Smaller prey such as beaver (Castor canadensis), were available but might
have been consumed faster than my sampling scheme could detect. However, 20 fawns, 1 raccoon and 1 grouse were at feeding sites, indicating that some small prey were represented in my sampling. Elsewhere, cougar scat and intestinal tract studies have found smaller prey, notably up to 13% porcupines (Erethizon dorsatum) and <5% snowshoe hares, in addition to other small mammals (Maser and Rohweder 1983; Robinette et al. 1959; Spalding and Lesowski 1971; Toweill and Maser 1985). Overwhelmingly though, cougar fed largely on Odocoilid deer in those studies, as in mine.

**Deer Selection**

Vancouver Island cougar consumed primarily adult female deer. Cougar elsewhere are reported to prey on older adult deer (>7 yr; Ackerman et al. 1984; Robinette et al. 1959; Spalding and Lesowski 1971) or males and juveniles (Harveson 1997; Hornocker 1970) more than expected. For the 34 adult sexed deer, the male:female ratio was 0.3:1.0. Population sex ratios of adult deer during my study were not available so I could not determine the degree of prey selection. For my study area, historical summer adult sex ratios obtained during a 1981 and 1982 deer decline was 0.4:1.0 (Hatter 1988). Adjacent to my study area, the sex ratio fluctuated between 50-60% male for 8 of 11 years in the Nimpkish valley (1970-1980; Jones and Mason 1983). Assuming current sex ratios are similar to historical levels, cougar predation of deer was possibly selective for adult females. However in Texas cougar killed mule deer (O. h. hemionus) matching population sex ratios of 0.6:1.0 (Waid 1990). Further investigation with concurrent population sex ratio data is warranted to determine if female deer were selected for by cougar.

Prey selection for juvenile deer was unlikely. Mainland cougar are reported to prey on juveniles equal to population proportions (Harveson 1997; Hornocker 1970). Conversely in Chile, cougar demonstrated selection for guanacos (Lama guanicoe) <12 months of age (Franklin et al. 1999). In my study, juveniles comprised 21% of all deer kill sites. Population
estimates of juveniles were not available during my study. Spring counts of deer for the study area (prefawning) indicate juveniles comprised 21.2% and 22.5% of the deer population during 1980 and 1981 respectively, whereas summer counts (postfawning) varied from 27.4% to 15.1%, respectively (Hatter 1988). Juvenile predation fell within the range of observed historical population levels for the study area, suggesting selection for juveniles was unlikely.

**Prey Health**

Cougar did not appear to be selective for deer condition. Deer marrow fat concentrations ranged mainly from 25% to 75%, with no deer having fat concentrations >80%. Slightly more than 20% of the deer killed by cougar had marrow concentrations <25%, suggesting that deer condition was a predisposing factor in some cougar predation. However, mean monthly marrow fat of prey deer generally decreased through the sampling period (Figure 10). The seasonal trend is similar to those found in other ungulate studies of fat reserves (Anderson et al. 1972; Anderson et al. 1990; Parker et al. 1993) and has been observed elsewhere on Vancouver Island (Jones 1975; Rochelle 1980). Therefore, I believe that the data show cougar were not selecting by deer condition; rather deer predation followed common seasonal population trends for deer condition.
Figure 10. Mean monthly femoral marrow fat from deer carcasses found at feeding sites during the study. Values are based on low monthly sample sizes ranging from 1-10, (mean 5.7).

**Interspecific Competition**

Anecdotal sightings indicate that wolves were present in my study area during at least 2 separate weeks, but I observed no evidence of competition for prey between wolves and cougar. Elsewhere, wolves are known to interfere with cougar, stealing their kills (Kunkel *et al.* 1999) and even hunting and killing cougar (Boyd and Neale 1992; T.K. Ruth unpubl. data cited in Kunkel *et al.* 1999; White and Boyd 1989). During the course of my study there were 2 cougar mortalities, one from unknown causes, but not scavenged, and a second found within 8 hours of death due either to starvation or a parasite as determined by necropsy (Malcolm McAdie DVM, BC Ministry of Environment). Overall, evidence of wolf-cougar interaction was not found despite the presence of both species in my study.

I did find evidence of interspecific competition between cougars and black bears involving bears apparently displacing cougar from feeding sites. However, competition occurred only at the beginning and end of my study, as bears entered into or emerged from hibernation. I did not sample during summer, when competition was probably higher. Black bears, and
coyotes, are reported to take pronghorn (*Antilocapra americana*) kills from cougar (Ockenfels 1994). Interspecific competition for cougar kills may increase the predation rate by cougar, as was observed in a coyote-removal area (Harrison 1988). I believe that further investigation of competitive interactions between cougar and bears is warranted, because competition could increase the deer predation rate by cougar.

**Feeding, Caching and Movements**

Prey carcasses were not covered with substrate (cached). This is contrasted with mainland cougar that are commonly reported as caching prey (Bank and Franklin 1998; Beier *et al.* 1995; Holt 1994; Hornocker 1970; Logan and Irwin 1985) and was also observed further south on Vancouver Island (Hahn, *pers. comm.*, UBC. 2001). Caching is thought to reduce spoilage and/or to hide the prey from scavengers (Franklin *et al.* 1999; Hornocker 1970). In our daytime telemetry, cougar did not leave the feeding site during feeding, except to retrieve kittens after making a kill, and as noted in the case of displacement by black bears. Cougar may reduce scavenger competition by remaining distant from feeding sites when scavengers are present, and remain at the feeding site when scavengers are absent or in hibernation. In my study, I focused on cougar predation behaviour during winter when temperatures were cooler and bears were in hibernation for the majority of my sampling. A study conducted in Idaho during winter found no movements from the feeding site nor displacement by scavengers (Hornocker 1970). This differs from California (Beier *et al.* 1995) where annually cougar remain an average of 400 m from feeding sites during the day. Additionally coyotes were observed to interfere with cougar predation in California (P. Beier, *pers. comms.*, Northern Arizona University, Flagstaff. 2000). Therefore, when present, scavengers may have some effect on cougar movements from feeding sites and cougar behaviour (caching) at the feeding site.
Kill Rate

I estimated that adult female cougar killed on average 22.6 deer annually (SE=1.62, range=15.53-28.63, n=9). This rate falls near the lower end of kill rates reported for cougar. Elsewhere, a higher annual rate was estimated in California (48 large mammals, Beier et al. 1995), Utah (38, Connolly 1949) and Arizona (35-54 deer or young cattle, Shaw 1977). Conversely, cougar were estimated to feed on a less or equal number of deer in Idaho (14-20, Hornocker 1970), and again in Utah during an intensive study of cougar predation (22, Ackerman 1982).

Females with kittens were estimated to kill at a higher rate in Utah (113, Ackerman 1982), and in mainland B.C. on bighorn sheep (Ovis canadensis) and mule deer (ranging from 36.4 to 109.2, Harrison 1988). I did not observe a similar difference. Rather, females with kittens at varying stages of development, killed at the same rate (mean=23.4, SE=2.84, range=15.5-28.6, n=5) as females without kittens (mean=21.67, SE=1.17, range=18.72-23.93, n=4). Sample sizes are small but the means of the 2 groups are similar and standard errors overlap. However, the variation is larger for females with kittens than those without. Both classes of females left little carcass waste behind, even though females without kittens would not have the same feeding requirements as females with kittens. Although not statistically significant given the small sample size, on average, females with kittens spent a longer time (4.2 days) at feeding sites than those without kittens (3.8 days). This does not include the additional time to bring the kittens to the feeding site. Therefore it appears that in winter in my study area cougar kill rate is independent of female cougar reproductive condition (with or without kittens) even considering the additional metabolic costs of transporting and feeding kittens.
Intersexual Prey Partitioning

Differences in prey selection between male and female cougar were evident. Both males in my study were observed feeding on elk whereas females were not. This is not unusual because felids typically take the largest prey they can (Kruuk 1986; Sunquist and Sunquist 1989; Taber et al. 1997). Cougar, a sexually dimorphic species throughout their range (Kurten 1973; Gay and Best 1995), do exhibit this behaviour where prey sources permit. For example, in Alberta, male cougar specialized almost entirely on moose (*Alces alces*) compared to females that preyed largely on the smaller mule deer and elk (Ross and Jalkotzy 1996).

Microsite: Visual Cover

Although there has been frequent speculation in previous cougar studies (Franklin et al. 1999; Gagliuso 1991; Harveson 1997), my study is the first to provide quantitative evidence that cougar feed in areas with greater horizontal cover. These areas have greater vegetative cover 1.25 m above ground, within 10 m of the feeding site. Cover above this height was not selected for. Selection for denser cover at feeding sites could help reduce competition by reducing visibility to scavengers. I observed 4 instances of bears displacing cougar from kills even though the majority of sampling occurred while bears hibernated. This suggests that scavenging may be a factor in cougar feeding site selection.

At only 3 out of 65 feeding sites were drag marks of kills visible, suggesting cougar generally fed on their prey where they killed them. Conversely, cougar in California dragged 17 of 49 kills 28 m on average, to the nearest vegetation (Beier et al. 1995). Although vegetation on Vancouver Island is probably denser and more continuous than in the California study, cougar on Vancouver Island still fed in visually denser areas compared to surrounding habitat. Cougar in Chile were also observed dragging kills to areas of denser cover and caching them (Franklin et al. 1999). Other felids are also reported to drag their kills. For example, lynx moved prey
carcasses an average of 14 m from the kill site, usually to dense vegetation and covered it with available substrate (Jedrzejewski et al. 1993). The use of areas with denser cover is not unique to cougar on Vancouver Island and therefore probably provides some benefit to cougar throughout their range.

Alternatively, cougar predation success may be correlated with the amount of cover. The ability to conceal themselves while ambushing may favour cougar use of denser cover. Cougar are reported to approach prey from downwind, watch, wait and approach as the prey gets closer, until finally ambushing at short distances and delivering a fatal bite (Allen 1950; Bank and Franklin 1998; Branch 1995; Koford 1946). Where cougar are unable to approach close (e.g., < 2 m) because of sparse cover, the attack fails or is not made (Beier et al. 1995; Wilson 1984). Thus, feeding areas of denser visual cover may not only function for hiding prey, but also for successfully ambushing prey. Predation success of other solitary felids has also been strongly correlated with the separation distance - the ability of the felid to get as close as possible before attacking (Branch 1995; Elliot et al. 1977). Denser cover may be needed to even initiate predation attempts.

An obvious third explanation for cougar use of dense visual cover areas is they are reflecting prey use. For example, a study in Alaska using a similar microhabitat methodology to mine, found higher cover in core areas used by Sitka black-tailed deer (O. h. sitkensis) than in non-core areas (Yeo and Peek 1992). Likewise, deer experiencing cougar and wolf predation in Montana preferred more closed habitats in winter (Kunkel et al. 1999). A 5-year study in California found that the distribution of deer killed by cougar could be explained solely by the distribution of the deer population (Pierce et al. 2000). Therefore cougar use of such microhabitats in predation behaviour may also simply be a reflection of prey habitat use.
Not surprisingly, macrohabitat use by predators generally follows that of their prey. For example, in southeastern British Columbia wolves used areas and habitats similar to moose (Seip 1992) and in Italy used habitats in and around livestock prey (Meriggi et al. 1991). Wolves and deer are reported to use coniferous habitats in virtually the same proportions as each other (Fuller 1991). Felids demonstrate similar patterns by generally using significant proportions of their primary prey’s habitat (Rabinowitz 1990). For instance, leopard cats (Felis bengalensis) used habitats with a higher density of small mammal prey proportionately more (Rabinowitz 1990). Lynx used habitats in similar proportion to snowshoe hares through 3 years of study, irrespective of snow class (Murray and Boutin 1994). Cougar feeding site locations on Vancouver Island followed these patterns, following deer habitat use in several key areas, as described below.

Feeding sites were closer to roads than expected (Table 4), suggesting that cougars may have used roads for traveling and/or hunting, and the surrounding habitat for feeding. I observed that 21% of feeding sites were within 25 m of active roads, with one only 2 m away. During winter snow tracking I also found cougars traveled on roads for upwards of 2 km. Use of roads by cougars has also been found in other areas and track counts along roads are sometimes used as a relative index of abundance (Smallwood 1997; van Dyke et al. 1986). However, although cougar predation studies rarely report roads as a significant factor in predation, feeding sites have been found close to old logging roads (Thompson and Stewart 1994). Roads probably provide easy access for predators (wolves, cougar, humans) to deer (McNay and Voller 1995) and presumably, as deer travel down roads, for cougars to ambush them.

Cougar feeding sites were located at lower elevations (<700 m) more than expected. This might be correlated with increased access for predators because the majority of road building has occurred in conjunction with forest harvesting at lower elevations (McNay and Voller 1995). In my study area no statistical collinearity was found between roads and elevation, although roads
are most abundant at lower elevations. However this also correlates with deer habitat use. Most black-tailed deer use lower elevations during winter (Barichello 1975; Schoen and Kirchhoff 1990), generally remaining below the snow pack unless it has a crust that allows travel (Harestad 1979; Schoen and Kirchhoff 1990). Cougar winter habitat use clearly reflects elevation selection, and is a primary factor in habitat selection in our study area (Goh, 2000). Thus, relatively constant access to deer populations at lower elevations results in increased predation success and therefore more feeding sites associated with lower elevations.

Cougar feeding site location and its relation to deer habitat use was also characterized by proximity to forest edges. Feedings sites were located closest to young (27.6%) and old growth (31.0%) forests more than expected from relative availability, and this pattern closely follows deer habitat use on Vancouver Island (Kremsater and Bunnell 1992; Willms 1971) and elsewhere (Chang et al. 1995; Hanley 1983). Deer use areas a short distance from the edge itself, with peak use between 50 m to 200 m from an edge (Chang et al. 1995; Hanley 1983). This pattern is very similar to what I observed for cougar feeding site location - 79% of which occurred within 200 m of forest edges. Perhaps not surprisingly, cougar feeding site selection appears to follow deer habitat use.
CONCLUSIONS

Female Vancouver Island cougar preyed primarily on black-tailed deer, although my study was biased towards larger prey species that took a minimum of 2 days to consume. While most deer were female, prey selection did not appear likely as levels approximated historical population sex ratios. Similarly, juvenile selection fell within the range of historical estimates for this age class. Nor did selection for deer condition appear to affect prey selection because fat levels followed common ungulate seasonal patterns. The estimated kill rate of 22.6 deer annually per adult female cougar is lower than reported in some studies, but is similar to others. Kill rate by adult females appeared to be independent of whether or not they had kittens.

Interspecific competition at the feeding site occurred with black bears at the beginning and end of my study, corresponding to the start and termination of bear hibernation. Bears appeared to displace cougar from feeding sites and then fed on the carcass. This displacement could cause cougar to make more kills and thus increase the predation rate in seasons when bears are most active. Further study of the effects of bears on cougar predation rates is recommended.

Female cougar fed in areas with higher horizontal visual cover. Drag marks were evident at only 3 feeding sites, indicating the cougar fed on deer where they killed them. The use of these higher visual cover areas may reflect an attempt to reduce competitive interactions with bears by reducing visibility of the feeding site. It is equally likely though, that higher cover areas are a reflection of both successful cougar ambushing style and deer microhabitat use in winter.

In the larger landscape, cougar feeding sites were located closer to roads, at lower elevations and in close proximity to young and old growth forests than expected. Feeding sites close to roads suggest that these habitats, or the roads themselves, are associated with increased predation success by cougar. Feeding site selection for lower elevation areas and proximity to young/old growth forests appears to reflect deer winter habitat use.


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