Responses by Steller's Jays to Forest Fragmentation on Southwest Vancouver Island and Potential Impacts on Marbled Murrelets

by

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We accept this thesis as conforming
to the required standard

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ABSTRACT

Steller's Jays (*Cyanocitta stelleri*) eat eggs and chicks of the threatened Marbled Murrelet (*Brachyramphus marmoratus*). Clearcut logging, in addition to reducing murrelet nesting habitat, may increase the risk of predation at murrelet nests by drawing jays to recently fragmented landscapes. To assess this risk, I investigated responses by Steller's Jays to man-made edges and clearcut habitat on southwest Vancouver Island in 1996-97.

At three study sites, standard point counts were conducted in old-growth stands bordering artificial (clearcuts and logging roads) and natural (river) edges. Counts indicated that there were significantly more jays in stands adjacent to clearcuts (post-breeding season counts averaged, 1.12 ± 0.23 SE jays per station) than in stands located either by roads (0.69 ± 0.13) or rivers (0.67 ± 0.14). In addition, jay abundance was significantly higher at stand edges (breeding season counts averaged 0.56 ± 0.11 SE and post-breeding counts averaged 1.17 ± 0.16 jays per station) than within stand cores (0.26 ± 0.07 SE and 0.50 ± 0.08 jays per station, respectively) for all stand locations combined. Counts conducted in the middle of clearcuts indicated that there was no significant difference between the number of jays at the centre and edges of clearcuts.

Radio-telemetry and single-point observations of jays that used clearcuts (referred to as cutblock jays, n = 6) and those that did not (referred to as forest-interior jays, n = 5) indicated that there was no difference between groups (mean ± SD) in home-range size (24.6 ± 19.6 ha and 19.0 ± 20.9 ha respectively), total size of core area (3.4 ± 2.8 ha and 1.45 ± 1.31 ha, respectively) and the number of cores used (2.5 ± 0.5 cores per bird for each group). Compositional analysis revealed that edge habitat (50 m on either side of abrupt forest edges) was selected for at the home-range scale (when compared to an area 20 times that of the home range; both groups analysed), and was selected for within jay home ranges (only cutblock jays analysed).

Patterns of micro-habitat use were similar between groups as well. For cutblock jays, the mean percentage (± SD) of observations (all behaviours) at ground, shrub, subcanopy and canopy strata were 8.8 ± 9.3%, 25.4 ±12.6%, 37.7 ± 19.5% and 27.9 ± 19.2% respectively. For forest-interior jays they were 26.8 ± 21.4%, 22.2 ± 16.4%, 22.2 ± 8.1% and 28.8 ± 13.8% respectively. Chi-square analysis of observations of randomly-selected (nontagged) jays categorized as either cutblock birds (in clearcuts or within 75m of a clearcut/forest edge, n = 30) or forest-interior birds (≥ 200 m from the nearest clearcut/forest edge, n = 24) indicated that the relative frequencies of observations of all four strata were the same. Observations of jays foraging indicated that clearcut jays foraged at the canopy level nearly 10 (tagged jays) and four (randomly-selected jays) times more than forest-interior jays, but this was partly due to the ease of viewing the canopy from cutblocks than from within the forest.

I propose that forest fragmentation does not alter a jay's response to its environment: spatial requirements, and macro and micro-habitat use were similar between jays that used new open habitat and those that did not. However, fragmentation does lead to a greater number of jays at edges and in stands bordering anthropogenic disturbance. These results suggest that the creation of edges either causes a shift in the distribution of jays across the landscape (moving from undisturbed to disturbed habitats) or attracts jays and causes an overall increase in jay populations in areas managed for timber harvesting. My data were insufficient to resolve these alternatives, but in either case murrelet nests in fragmented landscapes are exposed to more edge habitat and may therefore still be at greater risk to predation by jays. This risk can be minimized by reducing edge habitat through adjustments to harvesting schedules and the spatial distribution of cutblocks, leave-areas and roads.

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To Derek and Everest

GENERAL INTRODUCTION

Timber harvesting and other anthropogenic activities, such as road building, are resulting in the rapid conversion of extensive forest tracts into fragmented patches. One outcome of this large-scale change is a substantial increase in the amount of edge per unit area of habitat (Temple and Cary 1988, Weins 1994). Historically, this was viewed as a positive process because the juxtaposition of two different habitats resulted in increased abundance and diversity of species, particularly game animals (Leopold 1933, Forman 1997). However, there has been a growing awareness of the potentially adverse effects of increased edge area on community structure, population processes, and inter- and intra-species relationships (Harris and Silva-Lopez 1992, Merriam and Wegner 1992, Simberloff 1994). One important relationship that can be altered is avian predator-prey interactions (Yahner 1988, Martin and Clobert 1996).

Although food supply and suitable habitat are widely accepted as the main limiting factors in bird populations, predation has the potential to affect bird numbers significantly (Newton 1993, Martin 1995, Robinson *et al.* 1995). Predation of eggs, chicks, and adults, if additional to other causes of mortality, can limit recruitment into the breeding population and may reduce or halt population growth (Andrén and Angelstam 1988, Newton 1993, Hartman *et al.* 1997). In unaltered systems, predator-prey relationships generally maintain an equilibrium because losses to predators are compensatory to other causes of mortality (Newton 1993), but what happens if this balance is shifted, as is usually the case in landscapes altered by humans? Often, "new" habitats are colonized by common, opportunistic predators (Harris and Silva-Lopez 1992, Villard and Taylor 1994) that may augment the levels of predation (Whitcomb *et al.* 1981, Wilcove *et al.* 1986). The extent to which this shift is manifested depends on the numbers and behaviour of both the prey and the predator (Andrén *et al.* 1985, Small and Hunter 1988, Newton 1993, Picman and Schriml 1994).

Several members of the Corvidae (ravens, crows, and jays) are predators at nests (Angelstam 1986, Bayne *et al.* 1997, Neimuth and Boyce 1997, Hannon and Cotterill 1998), and respond opportunistically to areas of human activity and disturbance (Gates and Gysel 1978, Yahner *et al.* 1993, Andrén 1995). Many corvid species are more abundant at forest edges than in fields and forests (Whitcomb *et al.* 1981, Wilcove 1985, Neimuth and Boyce 1997) or have densities that are positively related to the proportion of agricultural lands and fragmented forests available (Yahner and Scott 1988, Andrén 1992, Schieck *et al.* 1995). Recognition of the threat posed by corvids has recently led to concern in the Pacific Northwest over the potential impact of Steller's Jays (*Cyanocitta stelleri*) on the breeding success of a unique tree-nesting seabird, the Marbled Murrelet (*Brachyramphus marmoratus*) (Nelson and Hamer 1995a, Ralph *et al.* 1995).

The Steller's Jay is a conspicuous crested jay of coniferous forests found in southeastern Alaska, British Columbia west of the Rockies, through the western States, and south into Nicaragua (Greene *et al.* 1998). In British Columbia, it is abundant in the Lower Mainland and on Vancouver Island. Breeding Bird Surveys in BC and California indicate that Steller's Jay numbers are increasing (Marzluff *et al.* 1994, Campbell *et al.* 1997).

Although Steller's Jays have a varied diet consisting of fruits, berries, insects and invertebrates, they are "notorious" nest robbers and of occasionally taking small adult birds (Bent 1946, Engels and Sexton 1994). Anecdotal observations of predatory acts by jays include: killing and consuming adult Pymgy Nuthatches (*Sitta pygmaea*) and Gray-headed Juncos (*Junco caniceps*) (Carothers and Sharber 1972); taking Varied Thrush nestlings (*Ixoreus naevius*) (pers. obs. this study); and robbing nests of Northern Orioles (*Icterus galbula*) (Iron and Pittaway 1995) and Black-headed Grosbeaks (*Pheucticus melanocephalus*) (Hill 1988). Recently, nest monitoring studies and nest predation experiments have revealed that Steller's Jays are one of the major nest predators of Marbled Murrelets (Naslund *et al.* 1995, Nelson and Hamer 1995a, Manley 1999, Luginbuhl *et al.* in press).

The Marbled Murrelet is a small diving seabird in the family Alcidae. It forages in nearshore coastal waters throughout its range, which extends from Alaska to central California (Ralph *et al.* 1995). This species is a prime example of a sensitive forest nesting bird, because in most of its range it depends on old seral-stage stands for breeding (Nelson and Hamer 1995b). Its nests are usually situated on large mossy limbs high in the canopy of old-growth conifers (Nelson and Hamer 1995b, Manley 1999). Loss of this nesting habitat through timber harvesting is believed to be largely responsible for current population declines (Ralph *et al.* 1995). For this reason, the species has been listed as threatened or endangered in British Columbia, Washington, Oregon and California (Rodway *et al.* 1992, Nelson 1997).

New information suggests that murrelet populations may be at further risk because clutch failure due to predation is high. In a recent study in British Columbia, 67% of observed nests failed, and of these, 86% were attributed to predation (Manley 1999). Predation of breeding adults is particularly detrimental to the maintenance or growth of seabird populations (Gaston and Masselink 1997), but because Marbled Murrelets lay only one egg and usually attempt only a single clutch per breeding season, egg and chick survival are crucial for recruitment (Desanto and Nelson 1995, Nelson and Hamer 1995a). Increased rates of nest predation could significantly impact recruitment and potentially reduce overall population numbers (Nelson and Hamer 1995b). As forests become fragmented and stands become isolated, a greater percentage of the forest will be adjacent to edge habitat and non-forested areas (Temple and Cary 1988). This change in landscape structure is likely to alter historical predator-prey interactions (Newton 1993, Nelson and Hamer 1995b). Therefore, any conservation measures applied to murrelets should take into account the behaviour and habitat use of their predators.

The Steller's Jay has seldom been studied; hence we know very little about its ecology or how it uses modified forest landscapes (Greene *et al.* 1998). As a result, we have a limited ability to predict its impact on the nesting success of Marbled Murrelets. To obtain information that would help address this problem, I investigated the extent to which jays respond to forest fragmentation, both numerically and behaviourally, on the southwest coast of Vancouver Island, BC. Using standard bird censusing techniques, I determined jay distribution and abundance relative to forest disturbance (Chapter 1). Using radio-telemetry, I measured home-range size (Chapter 2) and habitat use (Chapter 3) of two groups of jays, those that utilized "new" clearcut habitat and those that did not. I then correlated this information with what we know of murrelet breeding biology and nest characteristics, to evaluate the potential risks that jays pose to murrelets (Chapter 4).

DESCRIPTION OF STUDY AREA

West coast Vancouver Island

Based on British Columbia's ecoregional classification system, the west coast of Vancouver Island lies within the Windward Island Mountains Ecosection of the Western Vancouver Island Ecoregion (Coast and Mountain Ecoprovince) (Demarchi 1996). This entire coastal area falls within the Coastal Western Hemlock (CWH) biogeoclimatic zone, which occurs at low to middle elevations west of the Coast Mountains for the full extent of the province. The CWH zone is characterized by a mean annual temperature of 8 C and a mean annual precipitation of 2 228 mm (range 1 000 to 4 400 mm). Due to this mild moist climate, the zone is the most productive forest region in Canada (Pojar *et al.* 1991).

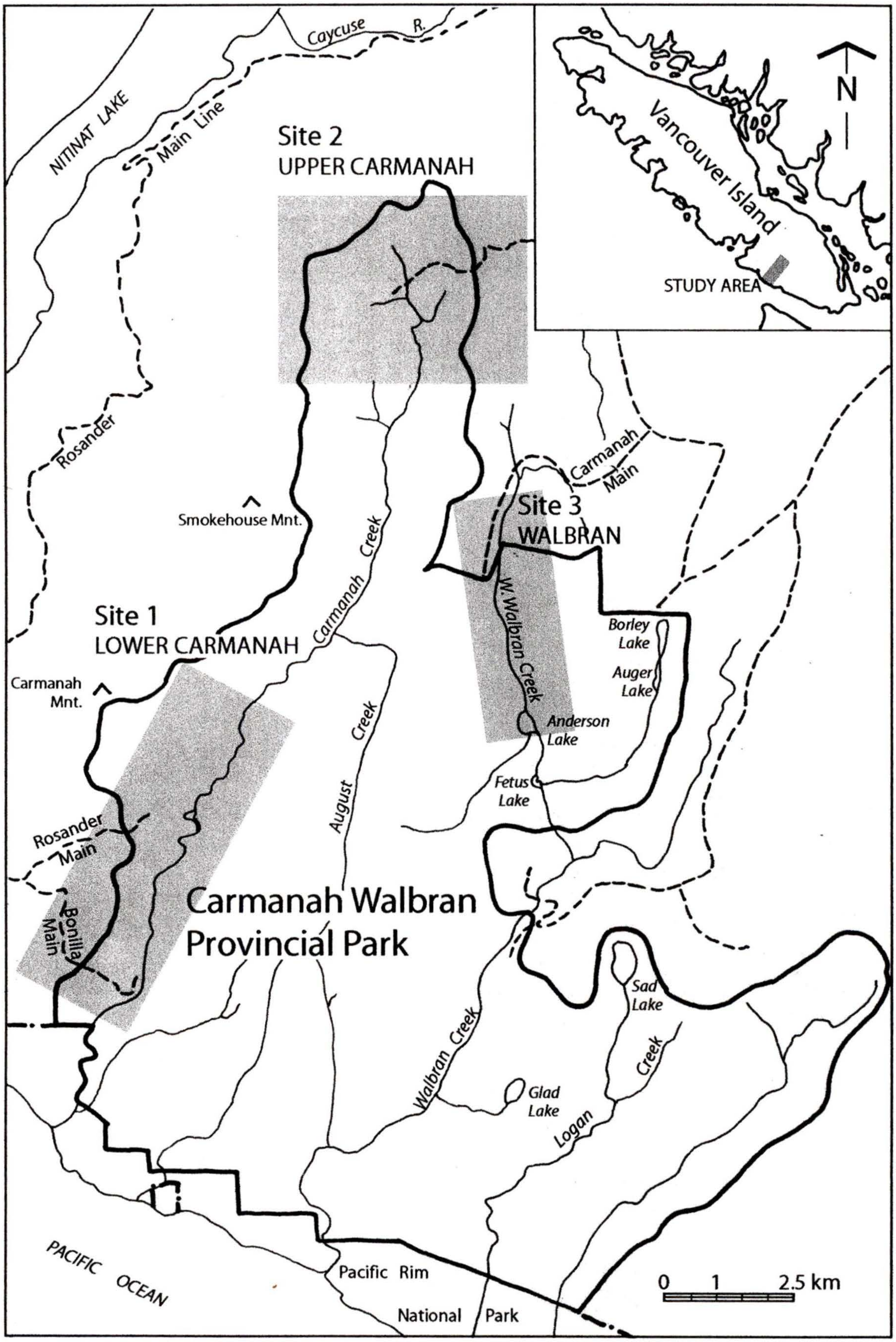
Most of Vancouver Island's remaining old-growth forests (829 000 ha in 1990, down from 1.69 million ha in 1954) are located on the west coast of the island (Young 1991). The dominant trees are western hemlock (*Tsuga heterophylla*), western red-cedar (*Thuja plicata*), and amabalis fir (*Abies amabilis*). Douglas-fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*) are also widespread; the former is more abundant in drier areas, whereas the latter is restricted to floodplains and the coastal fringe (Pojar *et al.* 1991). All five of these tree species commonly attain ages of 300-700 years in productive old seral-stage stands. These ancient temperate-zone rainforests are complex in stand structure, age class, and species composition due to rare fire events and time (Pojar and MacKinnon 1994).

More than 80% of the island's Crown forest lands have been allocated to logging in the form of Tree Farm Licences held by private forest companies and Timber Supply Areas managed by the Ministry of Forests (Pedersen 1995). Approximately 13% of Vancouver Island's 3.2 million ha is currently protected in parks and reserves, of which 6.6% encompasses old-growth forests (Riddell *et al.* 1997).

Carmanah and Walbran Watersheds

The study area was located in two adjacent watersheds, the Carmanah and

Figure 1. Carmanah-Walbran Provincial Park and locations of the three study sites.


Caycuse R.
NITINAT LAKE
Main Line
Site 2
UPPER CARMANAH
Vancouver Island
N
STUDY AREA
Rosander
Smokehouse Mnt.
Carmanah Main
Site 3
WALBRAN
Carmanah Creek
Site 1
LOWER CARMANAH
Carmanah Mnt.
W. Walbran Creek
Borley Lake
Auger Lake
Anderson Lake
August Creek
Fetus Lake
Rosander Main
Bonilla Main
Carmanah Walbran Provincial Park
Sad Lake
Walbran Creek
Logan Creek
Glad Lake
PACIFIC OCEAN
Pacific Rim National Park
0 1 2.5 km

Walbran valleys (48° 40'N, 124° 40' W; Fig. 1). These valleys are significant in that they are the last intact watersheds of considerable size (greater than 5 000 ha) on the southern west coast of Vancouver Island. They lie 100 km north-west of Victoria, BC, within the Port Alberni Forest District (Vancouver Forest Region) and between the communities of Bamfield and Port Renfrew.

The Carmanah watershed is 6 700 ha in size. In 1988 and 1989, timber harvesting occurred adjacent to the north-west boundary of the watershed and near its headwaters. In 1990, in response to public concern, 3 600 ha in the lower half of the valley were protected in Carmanah Provincial Park (BC Parks 1993). The Walbran watershed to the south, encompasses 13 000 ha. Nearly half of this valley (the east fork of Walbran Creek and the headwaters of the west fork) was logged during the late 1980s (Moore 1991). In 1995, the upper half of the Carmanah watershed, along with the remaining contiguous forested areas of the Walbran watershed, were incorporated into the park. In addition, two other smaller valleys (Logan Creek and Cullite Creek) were included. The park was renamed Carmanah Walbran Provincial Park, and now encompasses 16 450 ha (Leavers 1996; Fig. 1). Timber harvesting continues along its perimeter.

Both watersheds are located almost entirely in the CWH - submontane very wet maritime (CWHvm1) biogeoclimatic variant (Green and Klinka 1994). The lower sections of each creek extend into the CWH - southern very wet hypermaritime (CWHvh1) variant along the outer coast, and at elevations greater than 600 m the CWH - montane very wet maritime (CWHvm2) variant is found. CWHvm1 is characterized by wet, humid climates. Mean (± SD) annual precipitation is 2 787 ± 680 mm. Mean precipitation from April to September is 752 ± 200 mm. The temperature rarely dips below freezing and for five months of the year the mean temperature is greater than 10 C (Pojar *et al.* 1991).

Carmanah and Walbran Creeks flow south-west and drain into the Pacific Ocean. They exhibit a pool and riffle structure throughout their length, where erosion occurs on the outer convex side of turns and deposition takes place along the inner concave sides. The forest canopy is open over both creeks. These characteristics are typical of 3rd and 4th order streams (Forman 1997).

In the Carmanah and Walbran valleys, Sitka spruce trees dominate the riparian areas and floodplains. A majority of the veteran spruce are over 70 m tall, with a diameter at breast height of 1.5-3.0 m (Leavers 1996). Red alder (*Alnus rubra*) is common along the creeks and forms large patches where the creek has changed course. Various mixtures of western hemlock, western red-cedar and amabilis fir occur on the valley slopes. In both areas the understorey has a well developed shrub layer. Red huckleberry (*Vaccinium parvifolium*), stink current (*Ribes bracteosum*), salmonberry (*Rubus spectabilis*) and red elderberry (*Sambucus racemosa*) are prevalent in the valley bottoms whereas *Vaccinium* spp. and salal (*Gaultheria shallon*) dominate the slopes.

The moss layer is also well developed in both areas and usually includes step moss (*Hylocomium splendens*) and lanky moss (*Rhytidiadelphus loreus*). The herb layer is diverse in the riparian area. Sword fern (*Polystichum munitum*) is the dominant species but lady fern (*Athyrium filix-femina*), false lily-of-the-valley (*Maianthemum dilatatum*) and foamflower (*Tiarella trifoliata*) are among many easily found species. On slopes the herb layer is poorly developed. Deer fern (*Blechnum spicant*) is common and bunchberry (*Cornus canadensis*) is often present. Skunk cabbage (*Lysichiton americanum*) is usually associated with depressions and seepage sites in both the valley bottom and slopes. Open boggy areas that form in depressions on slopes in the lower reaches of each watershed (grading into CWHvh1) are also common. Generally they consist of shore pine (*Pinus contorta contorta*), *Sphagnum* spp., bog laurel (*Kalmia microphylla occidentalis*) and deer cabbage (*Fauria crista-galli*).

A wide variety of mammals (11 species; pers. obs. this study), reptiles, and amphibians (10 species; Cochran and Thoms 1996), and birds (58 species; pers. obs. this study) inhabit the Carmanah-Walbran watersheds. Ongoing research on Marbled Murrelets, which was initiated in 1989, indicates that these watersheds provide prime murrelet nesting habitat and that the murrelet population in these valleys is significant to the provincial population (Burger 1995a,b). Protection of murrelet nesting habitat is a wildlife management objective of the Park (Leavers 1996).

CHAPTER 1. STELLER'S JAY ABUNDANCE AND DISTRIBUTION RELATIVE TO ANTHROPOGENIC DISTURBANCE

INTRODUCTION

The number of predators in an area can influence predation rates on a particular prey species (Newton 1993). Predation rates of eggs and chicks in real and artificial nests has been augmented where predators are abundant (Gibbs 1991, Andrén 1992, Angelstam 1992, Engels and Sexton 1994, Leimgruber *et al.* 1994, Neimuth and Boyce 1997). This may happen regardless of the abundance of the prey, because the greater the number of predators, the more likely it is that predation will take place (Newton 1993). This density-independent relationship occurs because an overall increase in the number of predators can lead to greater contact with the prey source and increased rates of incidental predation (Andrén 1995).

Rarely are predator densities even across landscapes. Often, physical or environmental features concentrate predators in time and space (Martin 1987, Andrén 1992). In areas subject to anthropogenic disturbance such as farmlands and managed forests, resulting edges have attracted predators (Wilcove 1985, Angelstam 1986, Sargent *et al.* 1998). Many avian predators such as corvids, exhibit an edge effect; that is, they occur in greater densities at or near forest edges than in adjacent forests or fields (Whitcomb *et al.* 1981, Kroodsma 1984, Neimuth and Boyce 1997, Sargent *et al.* 1998, Sieving and Willson 1998).

The Blue Jay (*Cyanocitta cristata*), a congener of the Steller's Jay, is associated with edges (Kroodsma 1984, Wilcove 1985, Danielson *et al.* 1997, Neimuth and Boyce, 1997, Sargent *et al.* 1998), and it is likely that the abundance of Steller's Jay is edge-related as well. However, few studies have quantified this association (Marzluff and Restani 1999). Given that Steller's Jays are documented nest predators (Manley 1999, Luginbuhl *et al.*, in press) and that their numbers are increasing (Campbell *et al.* 1997), it is important that we determine their abundance and distribution in relation to forest edges created through anthropogenic activities. This will give us, in part, the information necessary to predict and mitigate possible associated edge effects such as nest predation of sensitive forest nesting birds, including the Marbled Murrelet.

To that end, I measured the abundance and distribution of Steller's Jays in stands bordering artificial edges (altered by two prevalent forestry activities, road building and clearcut logging), and in stands associated with natural edges (riparian areas within a park). I also examined jay abundance relative to clearcuts. Four questions were posed for investigation:

1. Is overall jay abundance greater in stands associated with disturbance?
2. Is jay abundance greater at the edge than within the stand?
3. Does edge-type (artificial or natural) influence jay abundance?
4. How does jay abundance within clearcuts compare with abundance at the clearcut-forest edge?

METHODS

Point-count protocol

I used point-counts (Ralph *et al.* 1993) to determine the relative abundance of jays. To allow greater flexibility in analysis, two point-count methods were combined. I used unlimited-radius plots and simultaneously recorded individuals in fixed-radius plots of 50 m and 100 m (Thompson and Schwalbach 1995). The fixed radii allowed me to establish bird-habitat relationships and reduced biases due to visual and auditory obstruction of bird detections due to vegetative cover (Scoullar 1980, Petit *et al.* 1995, Wolf *et al.* 1995). The 100 m and unlimited radius plots ensured that most jays within an area were counted because passerines with large home ranges such as the Steller's Jay are easily missed within small plots (Thompson and Schwalbach 1995, Tarvin *et al.* 1998)

Counts were conducted only during favourable weather conditions (minimal wind and precipitation), to increase the detection of bird vocalizations and reduce count variation (Ralph *et al.* 1993). Counts lasted 10 minutes. This sampling period was a compromise among count efficiency (greatest percentage of birds detected, number of stations that can be visited), detectability of birds that were inconspicuous or vocalized infrequently (Buskirk and McDonald 1995, Dawson *et al.* 1995), and the cumulative effect of sampling errors in counts greater than 10 minutes (Smith *et al.* 1998).

Sampling design

A stratified sampling approach was used in the layout of point-count stations at three widely separated study sites: upper and lower Carmanah Creek and the west fork of Walbran Creek (Figs. 2 and 3). At each site, three different stand-types were chosen based on location: two types associated with man-made or artificial edges bordering clearcuts and logging roads; and one type associated with a natural edge along rivers. In this study, "stand" refers to a section of homogeneous old-growth forest, which in terms of forestry activities would be managed as a unit (Province of British Columbia 1995a). Based on a scale by Logan *et al.* (1985), each of the three edge-types at all study sites had moderate to high edge-contrast ratings.

In each stand, I placed two parallel transect lines (Fig. 3). One transect sampled the stand's edge/ecotone habitat while the other sampled the stand's core habitat (forest habitat >100 m from any forest edge; Temple 1986). In total 18 transects were established. Along each transect, point-count stations were placed at 250 m intervals. At this distance the point-count radius was 125 m, which is the average maximum distance at which most bird calls are detected (Ralph *et al.* 1993). Twelve transects were 1 km in length and had 4 stations. Six transects were 1.25 km long and had 5 stations. The parallel transects were positioned approximately 250 m apart as well, to allow for the 125 m point-count radius, and to place the transect within the stand at an adequate distance from the edge. This minimized possible biotic edge effects, which usually are concentrated within 50 m of the forest edge (Paton 1994, Kremsater and Bunnell 1999).

The placement of stations at the junction of two distinct habitats is not recommended because habitat associations cannot be discerned (Scoullar 1980, Ralph *et al.* 1993). However, because I was specifically interested in jay activity at this junction (not absolute densities), it was necessary to place stations there, and it can be argued that the edge zone (on both sides of the stand edge) represents a unique habitat in itself. In addition, point-count stations located greater than 100 m from the forest edge may fail to

Figure 2. The stratified sampling design used to examine Steller's Jay abundance and distribution in Carmanah and Walbran watersheds, 1996 and 1997.

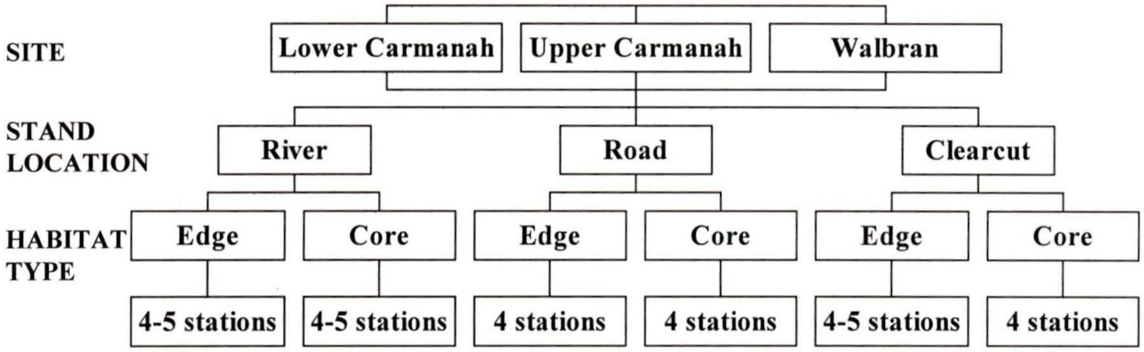
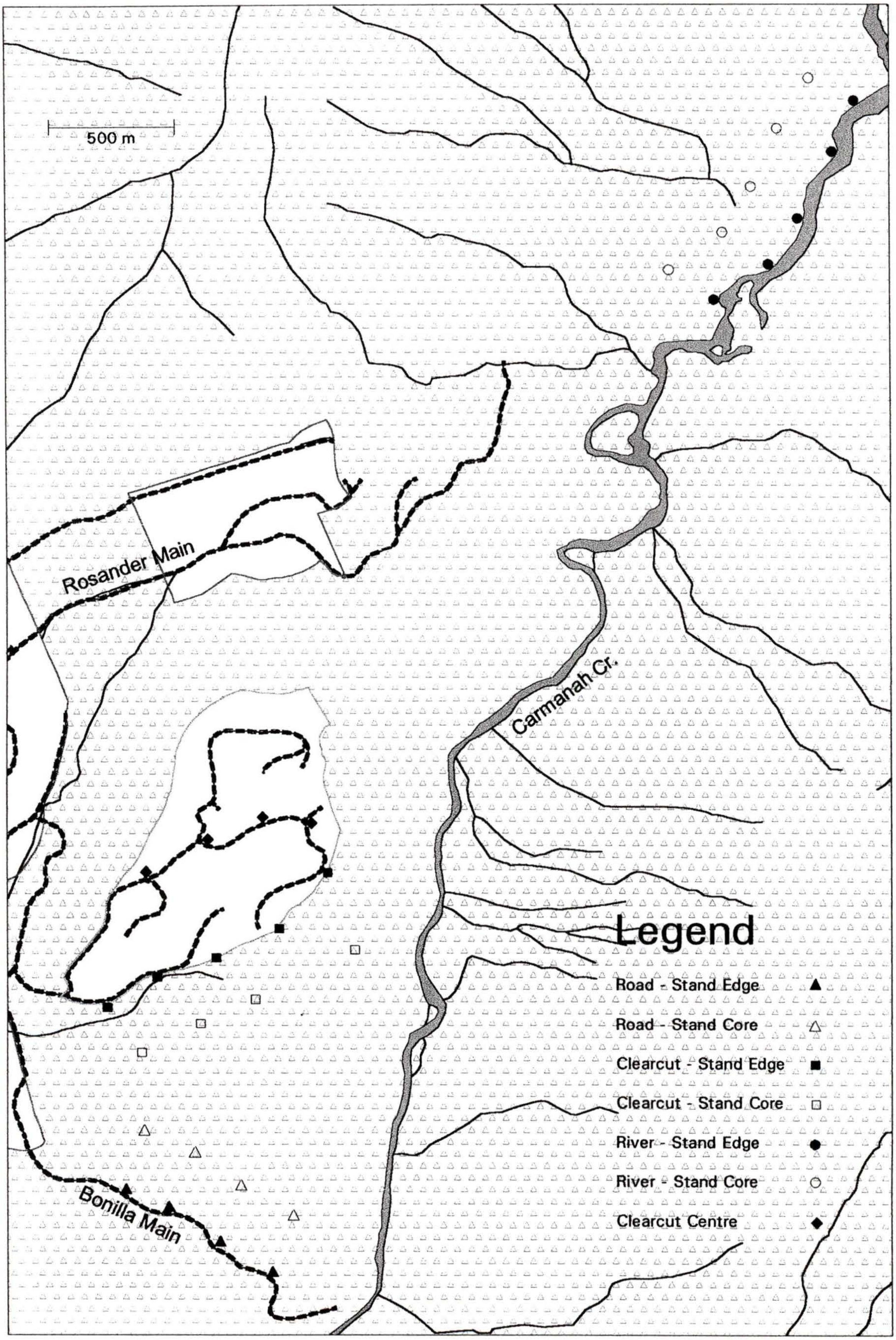

SITE
Lower Carmanah
Upper Carmanah
Walbran
STAND LOCATION
River
Road
Clearcut
HABITAT TYPE
Edge
Core
Edge
Core
Edge
Core
4-5 stations
4-5 stations
4 stations
4 stations
4-5 stations
4 stations

Figure 3. Layout of point-count stations at Site 1, lower Carmanah, used to assess the abundance and distribution of Steller's Jays at the edge and in the core of stands located adjacent to man-made edges (clearcut and road) and natural edges (river). This layout was replicated in upper Carmanah and West Walbran and used in both 1996 and 1997.


500 m
Rosander Main
Carmanah Cr.
Bonilla Main
Legend
Road - Stand Edge ▲
Road - Stand Core △
Clearcut - Stand Edge ■
Clearcut - Stand Core □
River - Stand Edge ●
River - Stand Core ○
Clearcut Centre ◆

detect the true numbers of many bird species at or near edges (Rosenberg and Raphael 1986).

To measure jay abundance within clearcut habitat, an additional transect (with 4-5 point-count stations) was positioned along a spur road in the centre of logged areas in each of the three study sites (Fig. 3). Each station was at least 125 m from the nearest forest edge. Counts from these transects were then compared to corresponding clearcut-edge transects at each site.

I surveyed the parallel transects as a circuit (8-10 stations). Due to difficult terrain, a circuit generally took four hours to complete with counts commencing at the first station of the circuit at sunrise. I surveyed the transects at two-week intervals. A different station was chosen as the starting point of the circuit for each survey to reduce time-of-day bias between edge and core stations (Lynch 1995). In total, four surveys were conducted per transect in 1996 (4 two-week intervals) between July 1 and August 31, and seven surveys per transect in 1997 (7 two-week intervals) between May 16 to August 31. This period included both breeding and post-breeding activities (Campbell *et al.* 1997, pers. obs. this study).

To examine possible visual or vocal detection biases of jays within stands and at stand edges, I classified each jay detection (during all regularly conducted point-counts) as visual, vocal or visual + vocal (when a jay was vocally detected and then observed) and compared detections among these classifications. I further explored possible visibility bias of jay detections at edge stations of stands bordering clearcuts in a separate test, in which I paired each edge station with a temporary station positioned in the stand (in total 13 paired stations), at a perpendicular distance of 10-15 m. This distance included sufficient trees and under-growth to eliminate any visual advantage of being at the clearcut/stand edge. Simultaneous counts were then conducted by two observers at the paired stations. The experiment was done in 1997 and repeated in 1998.

Statistical analyses

The independence of point-count stations along each transect was questioned after I observed jays move between stations on a few occasions. Therefore, I calculated the average number of jays detected per station along each transect for each survey. As a result the transect became the sample unit, not the point-count station. This had the added advantage of balancing the study design (transects had either four or five stations).

I examined seasonal variations in jay abundance by pooling surveys of each transect (edge and core) for each two-week interval. From this information and published data for southern Vancouver Island (Campbell *et al.* 1997), I divided the sample period into breeding (16 May through 30 June) and post-breeding (15 July through 31 August) periods. The July 1-15 surveys were omitted from either sample period because they represented a time of breeding overlap (nesting and fledged birds) for jays. Data were averaged for each period.

I applied factorial analysis of variance models to each data set using S-PLUS 4.5 for Windows (Mathsoft, Inc.1998), to simultaneously investigate whether there was a difference in the number of jays: in stands bordering artificial and natural edges (location factor); at stand edges and cores (habitat factor); and whether there was an interaction between these two factors. Therefore, the main effects of habitat, location, and the interaction habitat by location, were specifically included in the ANOVA models for both the breeding and post-breeding data sets. The effect of site (upper Carmanah, lower Carmanah and Walbran) also was included in each of the models. The effect of year was added to the post-breeding model as well. All other possible interactions were tested for each data set but eliminated from the model if effects were nonsignificant. I used fixed-factor ANOVA because the levels of each factor were specifically chosen (Underwood 1997, Zar 1996). Year was considered a fixed-factor because the seral stage of the clearcuts was dependent on the age of the regenerating stand.

I also used a factorial analysis of variance model to test the effect of clearcut habitat on jay abundance. Four surveys, at the centres and edges of clearcuts respectively, were conducted between July 1 and August 31 in 1996 and 1997. I averaged counts across surveys and made no distinction between breeding and post-breeding periods. I included the main effects of site and year in the model and eliminated interaction terms when tests indicated they were nonsignificant.

I used the breeding and post-breeding 1997 point-count data sets to compare the three jay detection categories; visual, vocal and visual + vocal. I tallied the number of jays in each detection category across all counts at each station and study site to obtain a category percentage within habitat, location and time period. Because jays counted in the visual + vocal category would theoretically be detected even if they had only been heard, I added these numbers to the vocal detection category to obtain a better estimate of total auditory detections.

For the edge visibility experiment, I used a paired sample Student's t-test to determine whether there was a difference in the number of jays detected at stations at the clearcut/forest edge and at adjacent stations 10 m into the forest. Data were pooled for all three study sites and both years. Pooling of data was acceptable because stations used strictly to test the effects of visibility were independent of each other (Zar 1996).

I used a rejection level of $\alpha = 0.05$ throughout.

RESULTS

The number of jay detections were insufficient at the 50-m radius for most analyses, and at the unlimited radius, detections often encompassed an area too large to make habitat associations. The 100-m radius plot provided between 65 and 75% of mean detections in both years. Therefore, data analyses were based on detections for the 100-m radius plot only (Fig. 4).

Seasonal variation

Mean detections were lower from mid May through mid-July than from mid-July through August (Fig. 5). In 1996, detection rates also increased through the latter half of the field season but occurred two weeks in advance of the increase seen in 1997, suggesting that fledging dates varied between years. This information lends support to the division of the surveys into breeding and post-breeding periods and the elimination of the Jul 1-15 surveys from the seasonal dichotomy.

Figure 4. Mean proportion (± SE) of the number of jays detected within radii of 50 m and 100 m of the point-count station as compared to the total number of jays detected at the unlimited radius (100% of detections). Data included all surveys (four in 1996 and seven in 1997) at each of the 75 stations (edge and core).

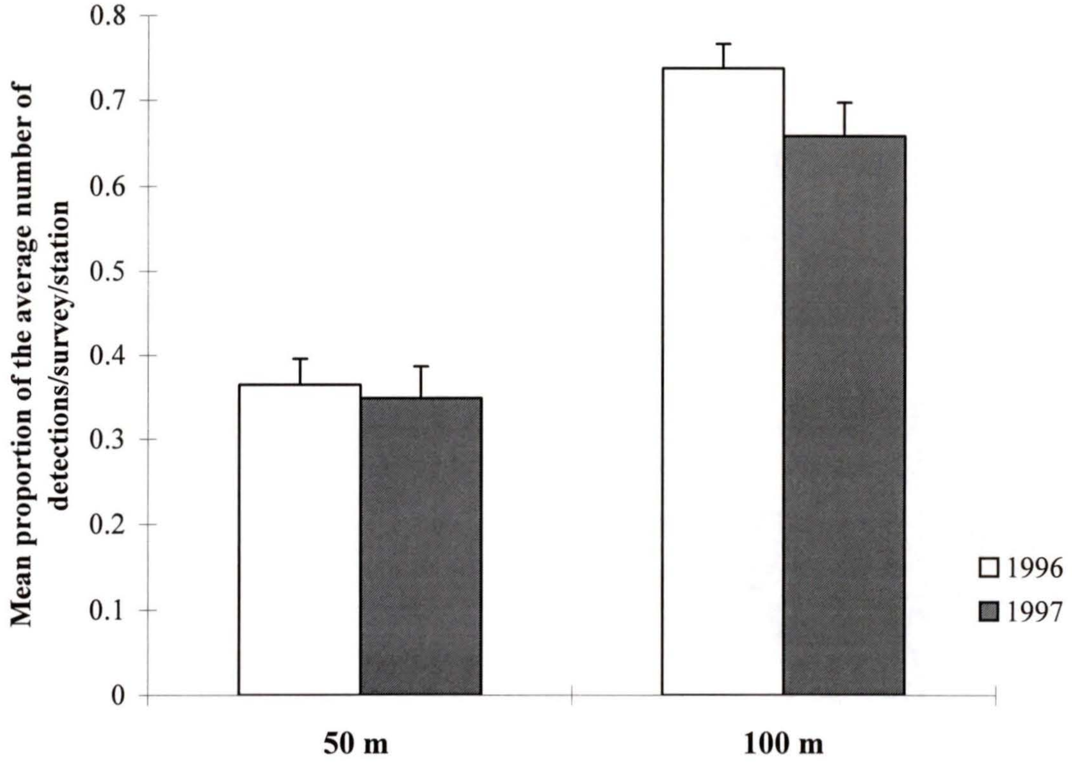
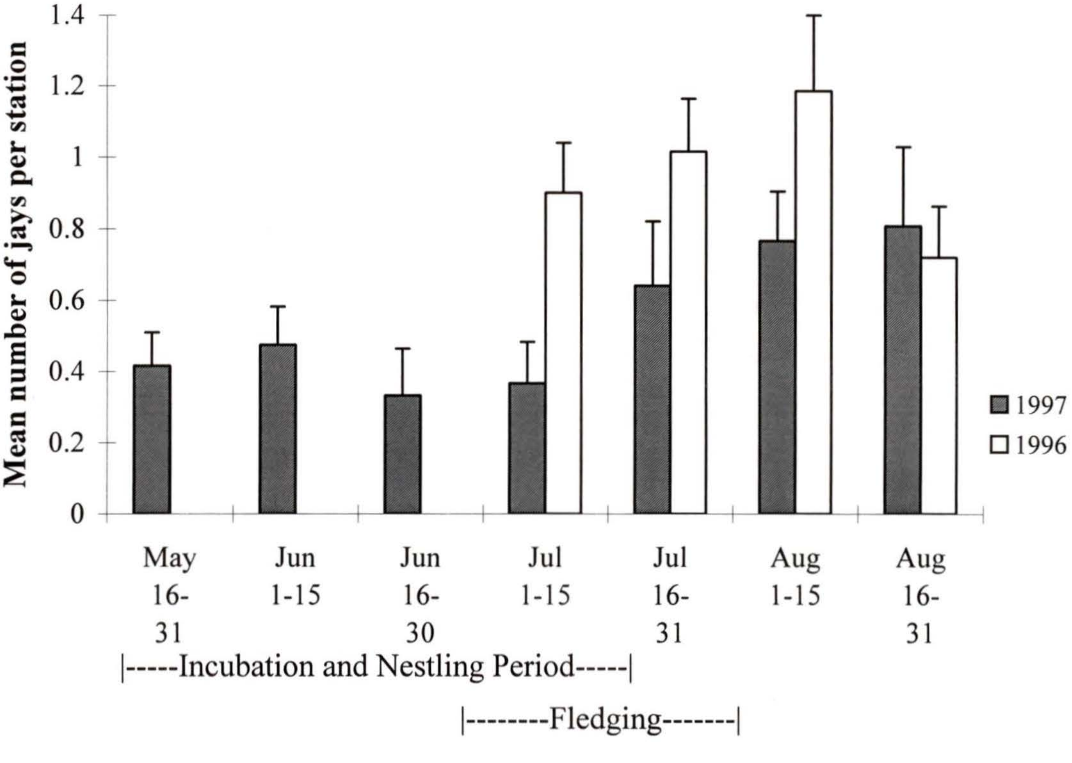

Mean proportion of the average number of detections/survey/station
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
50 m
100 m
□ 1996
■ 1997

Figure 5. The mean number of Steller's Jays detected per station per survey (± SE, n = 18 transects, both edge and core, surveyed every two weeks), increased during the latter half of the summer indicating the addition of fledged jays into the population. Note that there were only four surveys conducted per transect in 1996. The expected breeding chronology for the Steller's Jay on the west coast of Vancouver Island is indicated by the dashed lines (Campbell *et al.*1997, pers. obs. this study).


Mean number of jays per station
1.4
1.2
1
0.8
0.6
0.4
0.2
0
May 16-31
Jun 1-15
Jun 16-30
Jul 1-15
Jul 16-31
Aug 1-15
Aug 16-31
|-----Incubation and Nestling Period-----|
|--------Fledging-------|
■ 1997
□ 1996

Jay abundance relative to habitat and location

Overall, the greatest number of jays was detected in stands bordering roads and clearcuts (Fig. 6). During the breeding period, 0.50 ± 0.17 SE, 0.41 ± 0.10, and 0.31 ± 0.12 jays were detected per station at road, clearcut, and river locations, respectively (n = 6 based on the mean #jays/station/survey for each edge and core transect in each location at 3 study sites). During the post-breeding period, 0.69 ± 0.13 SE, 1.12 ± 0.23 and 0.67 ± 0.14 jays were detected per station at road, clearcut, and river locations, respectively (n = 12 for each location because 1996 data were included). When I examined the effect of location (road, clearcut and river), jay abundance was significantly different for the post-breeding period (ANOVA, $F_{[2,27]} = 3.79$, $P = 0.038$), but not for the breeding period (ANOVA, $F_{[2,10]} = 0.72$, $P = 0.512$) (Table 1). Data per cell were insufficient to detect any significant differences in post-hoc comparisons of the location factor.

Mean jay abundance (detections/station) was consistently greater at the stand edge than at the core regardless of the stand's location for both breeding and post-breeding periods (ANOVA, $F_{[1,10]} = 6.05$, $P = 0.034$ and $F_{[1,27]} = 17.15$, $P < 0.001$, respectively) (Table 1). During the breeding period the mean number of jays at edges of stands adjacent to roads, clearcuts and rivers was 4.9, 1.7 and 1.1 times higher respectively than at stations in the stand core, and during the post-breeding period jay abundance was 2.5, 3.0 and 1.5 times higher, respectively (Fig. 6).

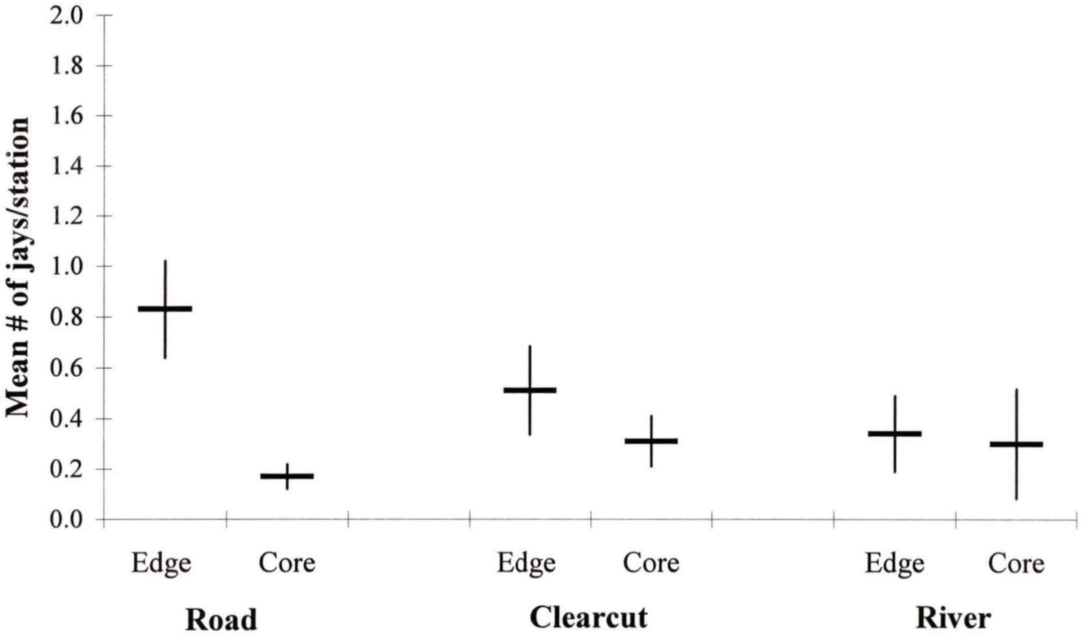
There was a strong, but not statistically significant trend for differences in jay detections when I examined the interaction of location by habitat during the post-breeding period ($F_{[2,27]} = 2.79$, $P = 0.079$; Fig. 6, Table 1). There was no significant effect of the remaining two factors in the model, year (post-breeding analysis only) and sites. With regard to the number of jays in clearcuts, jay abundance was not significantly different between clearcut edge and clearcut centres, nor was it significantly different among sites (Table 1).

Detection biases

When I compared detection categories between periods, there were 7% more

Figure 6. Mean number of jays (± SE) detected per 10-minute point count at edge and core stations for each stand-type investigated during a) breeding (1997 data only, n = 3) and b) post-breeding (1996 and 1997 data combined, n = 6) periods.

a) Breeding



b) Post-breeding

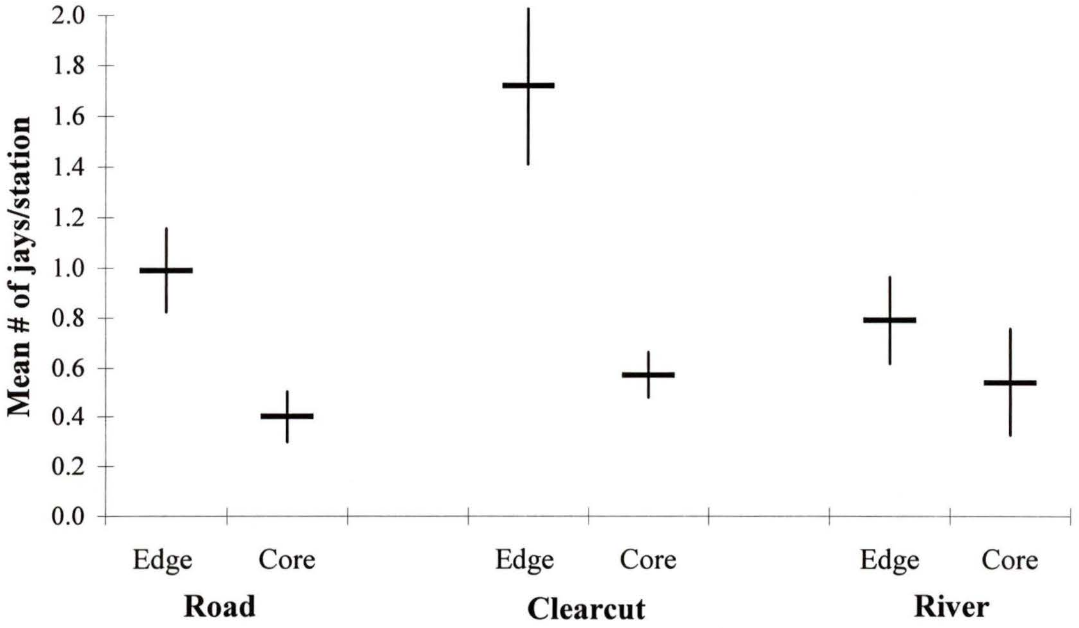


Table 1. ANOVA results for main effects tested in the models used to examine jay abundance and distribution relative to habitat (stand edge and core), stand location (clearcut, road, river) and the interaction of habitat and location using surveys separated into breeding and post-breeding periods. ANOVA results are also given for the main effect, habitat, in the clearcut model. The habitat factor refers to a comparison of jay abundance at the centres and edges of clearcuts. The effects of study site and year, also included in each of the three models, are shown for reference, although no significant effects were found.

Model	**Breeding**				**Post-breeding**				**Clearcut**			
Effects	**Df**	**SS**	**F**	**P**	**Df**	**SS**	**F**	**P**	**Df**	**SS**	**F**	**P**
Habitat	1	0.41	6.05	0.03*	1	3.91	17.15	0.00*	1	0.00	0.02	0.90
Location	2	0.09	0.72	0.51	2	1.73	3.79	0.04*	n/a	n/a	n/a	n/a
Habitat x location	2	0.32	2.35	0.15	2	1.27	2.79	0.08	n/a	n/a	n/a	n/a
Site	2	0.22	1.61	0.29	2	0.11	0.23	0.79	2	1.14	2.57	0.15
Year	1	n/a	n/a	n/a	1	0.34	1.49	0.23	1	0.77	3.43	0.11
Residuals	10	0.70			27	6.16			7	1.56		

n/a - not applicable to model

* $P < 0.05$

visual detections (including simultaneous visual + vocal detections) made at the stand edge during the post-breeding period than the breeding period (based on means of each category across stand-type; Table 2). In the stand core, the trend was similar. The addition of juveniles into the population likely accounts for this difference because overall numbers of jays detected at stations increased during the post-breeding period (Fig. 5). The opposite trend was noted for vocal detections. During the breeding period a greater percentage of detections were vocal at both edge and core habitat (14.5 and 9.5% greater respectively). There were no striking differences among detection categories when compared between stand locations; however, there were noticeable differences among detection categories when compared between edge and core habitats. Means for the entire season indicate that 15.2% of detections were visual at the stand edge whereas only 2.1% of detections were visual at the stand core. Percentage of vocal detections showed an opposite trend. There were 29.0% more vocal detections in the stand core than at edges. However, when values were corrected for total possible auditory detections (vocal + {visual +vocal}), percent auditory detections became more similar between the two habitats (84.8% at the stand edge, 97.9% at the core) (Table 2).

Similar numbers of jays were detected in counts conducted at the paired stations used in the edge-visibility experiment. There was no significant difference between jay detection frequencies at the stand/clearcut edge (mean ± SD; 1.5 ± 2.6 jays/count) and 10-15 m into the stand (1.4 ± 1.9 jays/count; paired t-test, $t = 0.50$, df = 25, $P = 0.31$).

DISCUSSION

Is overall jay abundance greater in stands associated with disturbance?

During the post-breeding period, jay abundance was greater in stands associated with human disturbance such as clearcuts than in stands bordering natural openings such as rivers. This was in keeping with observations obtained in a number of other studies. Rodway and Regehr (2001) documented Steller's Jays more frequently at murrelet survey stations located in fragmented forests than at stations in unfragmented forests of

Table 2. Percentage of detections of jays (at the 100-m radius) that were visual, vocal or both visual and vocal at edge and core stations within each stand location and seasonal period investigated. Theoretically, a jay that was heard and seen (A) could have been detected by auditory means alone (B). Therefore, these detections were combined to form a new category which included all possible auditory detections.

Stand Location	**Stand edge**				**Stand core**			
	Visual	**Vocal B**	**Vis + Voc A**	**A + B**	**Visual**	**Vocal B**	**Vis + Voc A**	**A + B**
Breeding								
Road	6.5	61.3	32.3	93.6	0.0	100.0	0.0	100.0
Clearcut	9.5	85.7	4.8	90.5	0.0	100.0	0.0	100.0
River	14.3	71.4	14.3	85.7	0.0	92.3	7.7	100.0
Mean (n = 9)*	10.1	72.8	17.1	89.9	0.0	97.4	2.6	100.0
Post-breeding								
Road	13.3	51.1	35.6	86.7	0.00	100.0	0.0	100.0
Clearcut	21.3	58.7	20.0	78.7	10.00	70.0	20.0	90.0
River	17.4	65.2	17.4	82.6	0.00	93.8	6.3	100.0
Mean (n = 9)*	17.4	58.3	24.3	82.7	3.3	87.9	8.8	96.7
Entire season								
Road	10.5	55.3	34.2	89.5	0.0	100.0	0.0	100.0
Clearcut	18.8	64.6	16.7	81.3	6.3	81.3	12.5	93.8
River	16.2	67.6	16.2	83.8	0.0	93.1	6.9	100.0
Mean (n = 18)*	15.2	62.5	22.4	84.8	2.1	91.5	6.5	97.9

* The number of transects used to calculate each mean.

Clayoquot Sound. A re-analysis of bird-habitat relationships in managed forests of the west Cascades of Oregon (Hansen *et al.* 1995) revealed that the relative abundance of Steller's Jays was positively related to the degree of stand treatment (old-growth clearcut, natural mature, closed-canopy plantation, and retention). On the Olympic Peninsula, Marzluff *et al.* (2000) studied avian predators in relation to stand structure, human activity and forest fragmentation. They found that the average maximum number of Steller's Jays detected in a 10-minute point count was greater in stands located in fragmented areas than in stands in contiguous forests. This applied to all three levels of stand structure investigated: mature even-aged stands, simple structure; mature uneven-aged stands, complex structure; old-growth stands, very complex structure. However, they did not provide statistical tests.

What is it about stands bordering human disturbance that would attracts jays? Perhaps it is the proximity, size and foraging potential of the open habitat adjacent to these stands. In temperate rain-forests managed for forestry activities, stands in the early stages of forest succession, although structurally simple, are highly productive (Morgan *et al.* 1985). Due to its adaptable nature, the Steller's Jay is likely to discover the foraging potential of these sites (Greene *et al.* 1998). Two studies support this idea. Scoullar (1980) found that jays used grass-forb and pole-sapling stages significantly more than other successional stages at the UBC Research Forest east of Vancouver, and Sadoway (1988) reported that Steller's Jays were often the earliest inhabitants of recently logged areas on Vancouver Island.

Timber harvesting took place in upper and lower Carmanah and in the west Walbran in 1989 and 1990 (Moore 1991); hence the regenerating clearcuts and leave strips along logging roads were at a productive, early seral-stage beneficial to jays (Morgan *et al.* 1985, Sadoway 1988). There was evidence of natural disturbance such as flooding, erosion and blow-down along each of the river sections in the study. Where the rivers had changed course, large patches of alder were present. However, these disturbances and hence the formation of productive early seral-stage patches, were at a relatively small scale in comparison to the disturbance created through road construction and timber harvesting (Oakley *et al.* 1985). Therefore, the rivers in my study (including their gravel bars, log-jams and riparian zones) did not provide as much highly productive foraging area to jays and this may explain the observed differences in relative densities of jays among stand-types.

Based on the opportunistic jay observations that Burger *et al.* (1997) obtained during murrelet studies in the Carmanah and Walbran valleys from 1992 to 1996, a location effect should have been detected in the breeding period data set as well. They found that the percent occurrence and relative abundance of jays was significantly higher at murrelet survey stations located near roads and clearcuts than at stations located at creek sites in undisturbed forests. These surveys were carried out between May 1 and August 7 each year, which includes the Steller's Jay breeding period (Fig. 5), and therefore demonstrate that stand location was an important influence on jay distribution at this time as well.

The absence of a location effect during the breeding period may be due to factors affecting the "effect size" (the size of the difference between the null hypothesis and the specified alternative hypothesis; Underwood 1997), the sample size and the power of the test. In counts conducted during the breeding period, the mean abundance of jays detected per station was up to 50% less than during the post-breeding period (Fig. 5). This reduction in relative densities was likely due to two factors: 1) that the population was comprised only of adults at this time (Brown 1963) and, 2) that breeding birds vocalized less and moved secretively to and from the nest (Brown 1964, Hope 1980). Both factors could cause an overall reduction in jay detections, which in turn could affect the effect size in the data set (Underwood 1997). In addition, only one year of data was available for breeding period analysis; therefore, this data set had half the sample size of that used in the post-breeding analysis. Within-year sample size could not have been increased with additional study sites/replicates because this was not logistically possible. As I was not able to specify the exact alternative hypothesis prior to commencing the study, the power of the test could not be pre-determined (Underwood 1997).

Is jay abundance greater at the edge than within the stand?

Jays in the Carmanah and Walbran valleys were not distributed evenly across stands. In general, they were more abundant at the edge than within the stand regardless of the stand's location adjacent to man-made or natural openings. Several forest bird studies claim similar results. Rodway and Regehr (2001) found that Steller's Jays were more abundant at natural edges in Clayoquot Sound, west coast Vancouver Island. They recorded jays with 4% greater frequency at survey stations located at ocean edges and on stream channels, compared with stations in the forest interior. At Mt. Pinos, California, Hile (1993) found that Steller's Jay densities were greatest at the Pinyon Scrub/Jeffrey Pine forest ecotone. Sieving and Willson (1998) and Bryant (1994), while studying nest predation in southeastern Alaska and northeast Vancouver Island, respectively, found that the abundance of Steller's Jays was greater at forest borders than forest cores. These studies, along with my findings on the southwest coast of Vancouver Island, suggest that jays aggregate at edges throughout fragmented and contiguous forests of the Pacific Northwest.

There is often a disproportionate use of riparian zones and forest ecotones by wildlife (Thomas *et al.* 1979a and b, Kessler and Kogut 1985). The influence of microclimatic factors such as light intensity, wind speed, air temperature and humidity that are altered at abrupt edges (Forman 1997, Matlack 1994, Saunders *et al.* 1991) leads to increased vegetation biomass, diversity, and structure (Logan *et al.* 1985, Oakley *et al.* 1985). Jays could be attracted to these highly productive edges because they offer an abundant and varied supply of food (Hansson 1983, Nilsson 1992, Andrén 1995, Marzluff and Restani 1999). I frequently observed jays "fly-catching" from mature and old-growth trees or picking berries from shrubs at river, road and clearcut stand edges. Jays also may be attracted to the juxtaposition of two habitats (Scoullar 1980, Hansson 1994, Andrén 1995, Kremsater and Bunnell 1999). Jays specifically used mature and old-growth stands for caching food and nesting, but frequently foraged on substrates associated with edges such as road shoulders, shrubs, saplings, deciduous trees and logs along creek beds and in clearcuts.

Does edge-type (artificial or natural) influence jay abundance?

My data indicate that there is a possible trend for greater jay abundance at artificial edges than natural edges after juvenile jays have fledged (ANOVA, interaction habitat x location, $F_{[2,27]} = 2.79$, $P = 0.079$). When relative abundance between edge and stand core was compared for all three locations, it was evident that the difference among levels of the habitat factor was not constant at all levels of the location factor (Fig. 6). As with the absence of a location effect during the breeding period (discussed above) the sample size and thus power of the test were likely insufficient to detect possible differences. On the other hand, if we accept that there was no interaction between these factors then it can be said that the effect of habitat and location were additive and in this manner edge-type would still influence jay abundance.

Why would abundance of jays be greater at artificial edges? Either adult jays are being drawn from the forest interior to clearcut and road edges where they establish new territories and home ranges, or new jays are moving into the valleys from neighbouring populations. In addition, abundance at edges during the post-breeding period may in part be due to juvenile jays aggregating at edges after fledging (pers. obs. this study). If edges are better jay habitat and can support greater numbers, then perhaps more juveniles would remain and establish territories in these habitats, thereby causing a net increase in jay densities in Carmanah-Walbran.

Jay abundance within clearcuts

Numbers of jays were similar in the centre and at the edge of clearcuts during the latter half of the summer. My telemetry work (Chapters 2 and 3), and a comprehensive study by Scoullar (1980) on the habitat needs of forest birds of the west coast, indicate that perhaps these findings are not unusual. Data analysis of radio-tagged jays from the same study area indicates that some jays spent nearly 80% of their time in the middle of clearcuts (Chapter 3). This finding is consistent with Scoullar (1980) who frequently observed jays foraging in clearcuts. However, in western Oregon, Luginbuhl (pers. comm.) found that jay numbers may be greater at clearcut edges than at the centre of clearcuts depending on when surveys are conducted (three sampling periods corresponding to the availability of different berry crops; month x distance interaction; $\lambda_{(8, 6)} = 0.02$, $P = 0.06$). Regardless of whether there are greater numbers of jays at the centre or at the edges of clearcuts, this information suggests early seral-stage stands are used by jays and may be attractive foraging areas at certain times of the year. I observed jays eating various berry crops as they ripened, commencing with salmonberry, then red huckleberry, and later in the summer, red elderberry. During the latter half of the summer, skunk cabbage was also an important food readily available at moist sites throughout clearcuts (Chapter 3).

Detection biases

Detection biases were negligible at the edge and in the stand core. Although a greater percentage of detections were visual at edge stations, when auditory methods of detecting a bird were compared, the difference between the two habitats diminished. Scoullar's (1980) experiments revealed that there was little difference in the ability of bird songs, including those of the Steller's Jay to travel through air or forest canopy up to a distance of 100 m. Steller's Jays are gregarious, vocal birds with upwards of 15 different calls and songs (Brown 1964, Hope 1980), hence, most birds would be detected vocally and with equal ability at edge or in core habitat up to the 100-m point-count radius. In addition, the difference in detectability between the two habitats may be due to a true difference in jay density, as was discovered by Tarvin *et al.* (1998) in their evaluation of density estimates of Blue Jays. Lastly, when testing edge-visibility biases I found no detection advantages of standing at the edge as opposed to 10-15 m into the stand because most jays were detected either visually and vocally, or through vocal means alone. The above information, coupled with the lengthy count time used and the numerous surveys of each transect, ensures that birds that were present were likely to be detected (Petit *et al.* 1995, Luginbuhl *et al.* in press), and suggests that the differences in relative abundance of jays between the two habitats is real.

Summary

Steller's Jays were not distributed evenly across forest stands in Carmanah-Walbran. They were more abundant at the edge than within a stand. In addition, jays were more abundant at stands bordering artificial edges than at stands adjacent to natural edges. These results indicate that the creation of edges benefits Steller's Jays in some manner, possibly by providing better food and cover resources.

An aggregation of jays at edges can be produced by two processes. First, jays may shift their distribution locally from undisturbed to disturbed habitats. This would result in no net change in overall density, but a decrease in the numbers of jays in the forest interior. Second, there may be an influx of jays from adjacent watersheds to artificial edges. In this case there would be an overall increase in jay numbers because there would be higher densities at edges while densities in the forest interior would remain the same. With either process, Marbled Murrelet nests near edges would be at greater risk of predation by jays, but the risk in the forest interior would differ. It would decline in the first case but remain constant in the second case. However, because fragmentation leads to a greater proportion of edge per unit area of habitat, it would cause an overall increase in the risk of predation at murrelet nests.

CHAPTER 2. SPATIAL USE BY STELLER'S JAYS IN EARLY SERAL STAGE STANDS AND OLD-GROWTH FORESTS

INTRODUCTION

Of equal importance to the number and distribution of predators in evaluating the risk of predation to birds that are prey species is the predator's behaviour (Newton 1993). An important component of a predator's behaviour which warrants examination is its patterns of spatial use (Samuel and Fuller 1994). Area requirements of individuals (both size and shape) affect territory size and hence population density (Ralph *et al.* 1993, Samuel and Fuller 1994). As seen in Chapter 1, Steller's Jay populations are not evenly distributed across landscapes managed for timber harvesting. To further explain jay distribution in the Carmanah and Walbran watersheds and thus gain a better understanding of the Steller's Jay as predators during the Marbled Murrelet breeding season, I examined spatial patterns of individual jays.

Timber harvesting can create large open tracts of land and increases edge habitat. These changes may influence how a jay perceives and uses its surroundings and in turn alter its foraging strategies and predatory behaviour. Therefore, I determined and compared the size and shape of home ranges used by two groups of jays: those associated with early seral stage stands or clearcuts (hereafter referred to as cutblock jays); and those associated with relatively undisturbed old-growth forests >100 m from clearcut edges (hereafter referred to as forest-interior jays). I addressed the following questions:

1) Which home-range estimator best describes patterns of spatial use by Steller's Jays?
2) What is the home-range area of jays in the Carmanah watershed?
3) Is there a difference in size and shape of home ranges used by cutblock and forest-interior jays?
4) Does timber harvesting affect overall patterns of space use by Steller's Jays?

METHODS

I used radio-telemetry to obtain location information necessary to calculate home-range statistics on jays in 1996 and 1997. I considered less invasive methods such as observing individually marked jays or mark-recapture techniques as suggested by Harris *et al.* (1990) and Samuel and Fuller (1994). However, I determined through reconnaissance work that both methods were logistically not feasible due to the sample size required, the difficulty in recapturing jays, and my inability to follow jays or identify leg bands in dense vegetation. In addition, telemetry was the best method to obtain information on behaviours and habitat use (discussed in Chapter 3) because it allows for the study of animals that are difficult to detect and avoids observer bias towards conspicuous individuals or obvious behaviours (Williams 1990).

Capture and radio-tagging

Jays were trapped for radio-tagging using a variety of methods including mist nets, noose carpets (1-m^2 section of ½ in. wire mesh covered with slip knots made of 10 lb. test monofilament "chameleon" fishing line) and circular walk-in traps (made of chicken wire). Traps were baited with peanuts and placed in the two habitats of interest, old-growth forest and clearcut. In the forest habitat, traps were placed in openings created by the river and park access roads, and in forest core areas (a minimum distance of 250 m from any forest openings). I attempted to trap jays in both interior old-growth habitat and clearcut habitat in each of the three study sites (Chapter 1, Fig. 1).

In accordance with University of Victoria animal care protocols, I observed traps continuously when set to prevent injury or escape of jays. Captured jays were placed in bags and weighed using a 300-g Pesola spring scale. Wing chord and culmen measurements were taken using a wing ruler and Vernier callipers, respectively. The condition of the brood patch along with any other distinguishing features were noted, following Ralph *et al.* (1993). All trapped birds were banded with standard metal bands (size 3) on the right leg and a combination of two coloured plastic leg bands (one on each leg). This enabled observers to identify birds individually, by study site, and by habitat (forest-interior or cutblock).

I attached transmitters to after-hatch-year birds (hereafter referred to as adults) only. Hatch-year birds (hereafter referred to as juveniles), although readily trapped by July, had different foraging movements than adults, travelled in large groups, lacked territories, and began to disperse from the study area by mid-August (pers. obs. this study). These differences would likely produce unstable and biased home-range estimates.

The transmitters used in this study had a whip-type transmitting antenna, 20 cm in length, which is a better signal radiator than other types (Samuel and Fuller 1994). An inspection of the radio on retrapped individuals during the 1996 field season (n = 3) revealed that jays were able to bend and sever the antenna and in one case, remove the antenna altogether. I had the manufacturer double antenna strength on radio-tags used in 1997, and monitored antenna presence periodically through the remainder of each field season by assessing signal parameters when the bird was in close range or by direct observation. Tagged jays were unable to detach their antennas in 1997.

Transmitters were attached using a harness method because glue-on, suture, or tail mount techniques were insufficient for the purposes of this study (Houston and Greenwood 1993, Johnson *et al.* 1991). The "Y" configuration of the harness, suggested by Buehler *et al.* (1995), was modified to a square design so that the harness rested on either side of the sternum. The harness was made of 1/8" Teflon® ribbon. To prevent jays from dislodging the transmitter, it was placed on the back between the wings, with the antenna running down the length of the body. This position provided the added benefit of not interfering with wing and tail movement or the jay's centre of gravity.

The added weight and decreased aerodynamics caused by carrying a transmitter, translates into an increase in overall energy expenditure for a bird used in a telemetry study (Samuel and Fuller 1994, White and Garrott 1990). To reduce energy costs, transmitter and harness were limited to a combined weight of less than 5 g, approximately 3% of the jay's body weight. Potential drag was reduced by positioning the transmitter and harness under the feathers before securing the transmitter. The radio was further preened in place by the jay itself after release.

Data collection

All telemetry was conducted on foot during daylight hours. Observers used a portable receiver (Wildlife Materials model TRX-2000s) in conjunction with a hand-held collapsible three-element yagi antenna. Antennas of this type offer good directionality (Samuel and Fuller 1994).

To obtain locations on tagged jays, observers used homing techniques as described by Samuel and Fuller (1994), rather than triangulation, because they eliminated many sources of error (Harris *et al.* 1990) and because the telemetry portion of my study had a dual purpose (estimates of home-range as well as an examination of behaviour and habitat use, Chapter 3). Signal strength and directionality varied greatly with a jay's position relative to the ground and jays often changed location quickly, making it difficult for even the seasoned tracker to obtain reliable bearings. While tracking, the objective was to obtain visual contact (maintaining sufficient distance so as not to disturb the bird) and collect data on habitat use. If it was not possible to obtain a visual contact, tracking continued until the animal was "boxed-in" or the observer was confident of the bird's location to within an area approximately 20 m x 20 m. This was considered an acceptable and biologically relevant scale, given the jay's active nature (White and Garrott 1990).

Continuous radio-tracking of fast-moving species is generally not feasible (Harris *et al.* 1990). Therefore, I used a discontinuous sampling regime modelled after Andersen and Rongstad (1989). I relocated tagged jays in bursts (1-5 locations/day over 3-4 days) separated by long inter-burst periods (10-13 days) throughout late spring and summer months (May-September, roughly corresponding to the murrelet's breeding period). Although this design somewhat compromises independence between locations, Andersen and Rongstad (1989) found that such a design produced only a minor bias in range estimates. In addition, such a design is able to provide behavioural information often missed when only sampling once a day (Harris *et al.* 1990). To reduce auto-correlation problems, locations were taken at random times throughout the day, and only locations separated by 30 minutes and/or 75 m were used for range analysis. I attempted to obtain

25 locations per jay. This was the number of locations Marzluff *et al.* (1999) found adequately sampled home ranges of Steller's Jays on the Olympic Peninsula, Washington.

If a jay could not be located during a tracking burst, I made frequent attempts over several weeks to obtain a signal from various high points throughout Carmanah and adjacent valleys and during routine tracking of other birds. If after one month, a signal could not be detected, I concluded that the radio had failed or that the bird had left the study area, but I periodically monitored signals of missing birds for the remainder of each field season.

Data analysis

Global positioning devices do not work well in densely-forested narrow valleys. Therefore, observers described each location relative to obvious landmarks and plotted them on aerial photos and detailed 1:5000 base maps. Locations lacking an easy landmark were flagged and chained out at the end of the field season. A Universal Transverse Mercator (a metric measurement coordinate system) grid was placed over maps of the study area to obtain coordinates of each location for home-range analyses (White and Garrott 1990).

As recommended by Harris *et al.* (1990) and Samuel and Fuller (1994), I measured home-range area using two estimates: a non-statistical technique, minimum convex polygon (MCP); and a probabilistic technique, fixed-kernel density estimator. The 100% MCP estimate (based on 100% of locations for each animal) does not attempt to predict the animal's location between fixes and hence makes no assumptions regarding the "shape" of the area utilized (Harris et al. 1990, Worton 1987). It is the most widely used home-range estimate and often the most comparable across studies, because different home-range programs calculate 100% polygons in the same manner (Harris *et al.* 1990, Gallerani-Lawson and Rodgers 1997). In addition, because the polygon or range boundary encompasses all the fixes it is less affected by auto-correlation of location points (Harris *et al.* 1990).

MCPs were constructed with the program Ranges V (Kenward and Hodder 1996). Incremental area analysis, in which range area is re-calculated after the addition (one at a time) of each consecutive location in the sample, was used to determine asymptotes of home-range areas to assess stability of the range estimate. Because polygon estimates are often correlated with the number of locations used (Boulanger and White 1990), I used scatter plots and regression analysis to examine the relationship between jay home-range area and sampling effort (Zar 1996).

Of the many new probabilistic models which attempt to describe an animal's utilization distribution, I chose a kernel density estimator because it is non-parametric in nature; that is, it makes no assumption with regard to the shape of the utilization distribution (Worton 1989, Harris *et al.* 1990, Seaman and Powell 1996). It can estimate the density of a distribution at any point because a kernel or probability density is placed over each observation in the sample (Seaman and Powell 1996). This was important because I suspected that utilization distributions for jays would be non-normal or have multiple peaks (more than one centre of activity; Kenward and Hodder 1996, Seaman and Powell 1996). In addition, kernel estimators yield stable area estimates with fewer fixes (15-20) than MCP and, unlike harmonic mean methods, are not biased by grid size (Worton 1995, Kenward and Hodder 1996).

Based on recommendations by Worton (1995), Seaman and Powell (1996), and Seaman *et al.* (1998), I used least squared cross validation to determine the optimal kernel width (also known as the bandwidth or smoothing parameter). Fixed kernels "fix" or use the same bandwidth across the plane and cross validation is the most objective approach to date for selecting the smoothing parameter that minimizes the difference between the estimated and true density (Seaman and Powell 1996). I did not use adaptive kernel methods, in which the bandwidth is adjusted so that less smoothing occurs in areas of high use and more smoothing occurs in areas of low use, because they "ballooned" the utilization distribution in areas of low density (or the tails of the distribution).

To convert the utilization distribution density estimate into an estimate of home-range size, the study site was divided into a grid. I used a grid resolution of 100 units (which equals 100 x 100 grid intersections). The probability associated with each grid cell (based on the volume in the cell) was then calculated and a contour was drawn around the smallest number of cells with the specified probability (in this study 99%).

This produced a probability volume-contour, which directly related the utilization distribution to the area it represents (Hovey 1998). Bootstrap resampling of each location data set (n = 1000), was used to assess bias of kernel home-range estimates (Lanyon 1987), which Worton (1995) calculates as the "mean value of the estimator minus the value of the quantity being estimated." For all kernel analyses, I used the program "The Home-ranger version 1.1" (Hovey 1998).

For statistical techniques, it is assumed that location points obtained from a tagged animal represent a random sample. Hence, it is important that locations be independent (Cresswell and Smith 1992, Worton 1987, Van Winkle 1975). This is often a difficult assumption to meet when repeatedly relocating the same animal (Anderson and Rongstad 1989, Garrott and White 1990). Therefore, I measured auto-correlation within the set of locations for each jay, using Schoener's (1981) t^2/r^2 ratio (where t^2 is the mean squared distance between successive locations and r^2 is an estimate of the mean squared distance to the geometric center of the locations) and the corresponding test statistic developed by Swihart and Slade (1985). Critical values for $\alpha = 0.25$ were used to lessen the probability of type II errors because the objective was to find a sampling interval that would lead to acceptance of H_0: independence between successive locations (Swihart and Slade 1985).

I assessed home-range shape with two measurements, range span and eccentricity. Range span was a measurement of the longest linear distance between two locations. Eccentricity was the ratio derived from the range span and the measurement of the widest axis perpendicular to the span.

Using a paired sample Student's t-test, I tested differences between kernel and MCP estimates. I used a Wilcoxon rank sum test (Zar 1996) to test for differences in home-range estimates, range span, and eccentricity between forest-interior and cutblock jays (both MCP and kernel). I used a rejection level of $\alpha = 0.05$. For analyses and map production, home-range outlines (100% MCP and 99% fixed kernel) were imported into the drafting software program AutoCAD 2000 (Autodesk Inc. 2000), along with modified (confidential polygon data removed) forest cover maps provided by BC Forest Service.

RESULTS

Capture and radio-tagging

Trapping attempts commenced in late April of 1996 and 1997 and continued through early June due to the difficulty in capturing an adequate number of jays from each study site. An additional trapping attempt was made in July of both years after losing some tagged jays. Throughout the trapping period, I repeatedly attempted to trap jays at six different trapping stations located in forest core habitat (> 100 m from any type of edge) but was unable to catch a single jay. I was also unsuccessful at catching jays at study site 3, the West Walbran; therefore, only two study sites were represented.

In 1996, 69.5 trap hours and 28 trapping attempts were needed to capture 15 jays (Table 3). In 1997, 50.5 trap hours and 25 trapping attempts resulted in the capture of 12 jays. The noose carpet proved to be the most successful method in both years, and resulted in the capture of 67% of the jays. Measurements of wing chord, culmen and body mass overlapped between adults and juveniles (Table 4).

I radio-tagged 18 adult jays (10 in 1996, 8 in 1997). I assumed that these jays represented a random sample of the population because I was unable to distinguish sexes (males and females have identical plumage) or age beyond after-hatch-year status (adult plumage is attained in the jay's first fall). The wide range in weights, culmen and wing chord measurements (Table 4) lends validity to this assumption. There was no evidence of a bimodal distribution in any of the measurements.

Data collection

Only 5 of 10 jays radio-tagged in 1996 were successfully tracked. A number of jays could not be tracked because of signal failure due to a reduction in radio antenna length. I also suspect that two jays left the area, possibly because they were only first-year birds that were not part of the resident adult breeding population (in their second year).

Of the eight jays fitted with transmitters in 1997, I was able to obtain a sufficient number of locations for home-range analysis for only five. One jay (J-519) was tracked for only 2 ½ weeks before leaving the study area. I was unable to track two radio-tagged

Table 3. Trapping and radio-tagging summary.

	Jay age		Trapping method			Total
Year	**Adult**	**Juvenile**	**Carpet**	**Walk-in**	**Mist-net**	**caught**
1996	12	3	13	0	2	15
1997	11	1	5	7	0	12
Total	23	4	18	7	2	27

Table 4. Summary of measurements of captured jays.

		Wing chord (mm)		Culmen (mm)		Mass (g)	
Age	**n**	**Mean ±SD**	**Range**	**Mean ±SD**	**Range**	**Mean ±SD**	**Range**
Adult	23	147 ± 4.4	137 - 155	29.7 ± 1.6	26.7 - 33.1	142 ± 9.9	127 - 164
Juvenile	4	150 ± 5.3	146 - 158	27.9 ± 2.7	24.0 - 30.0	149 ± 7.9	141 - 158
Both	27	148 ± 4.6	137 - 158	29.4 ± 1.8	24.0 - 33.1	143 ± 9.8	127 - 164

jays: I suspect that one of these birds also left the study area, and I found that the other bird had been killed and "hidden" in a cliff-side burrow. Jay "loss" in both years resulted in an unequal sample size of tagged jays across cutblock and forest-interior groups (Table 5).

The majority of locations in 1996 (87%, n = 159) and all 166 locations in 1997 were obtained during June, July and August. On average, I obtained 31.7 home-range locations per bird (excluding J-519) over a mean period of 11.3 weeks (Table 5). Generally, jays were located twice on any given tracking day. The majority of these locations were visuals (mean across jays, 72%). I used triangulation on only four occasions on four different birds. All other locations were acquired by homing or boxing in the individual. Particulars for J-519 were included in Table 5 for reference but, because I was unable to obtain enough locations on this bird for valid home-range analysis (see next section), these values were excluded from the means.

Home-range size

Minimum convex polygon

Plots produced from incremental area analysis indicated that home-range area for adequately sampled jays (jays with > 25 locations each) stabilized (reached an asymptote) at approximately 26 locations (Fig. 7a). Individual increment plots were produced for jays 606, 250, 128 because they were not adequately sampled (< 25 locations). Plots indicated that the home-range area of jays 606 and 250 stabilized with 23 and 20 locations respectively (Fig. 7b). Based on this information, all of the above jays were included in home-range analyses and comparisons. An increment plot of J-128's home-range did not reach an obvious asymptote, therefore, an area estimate for this jay was questionable. However, given that on average 80% of this jay's home-range was described in 18 locations (Fig 7b), I included it in further analyses. J-519's home-range did not reach an asymptote with only eight locations. For this reason the home-range estimate for this jay was not reliable and not used in analyses.

There was no correlation between home-range area and the number of weeks

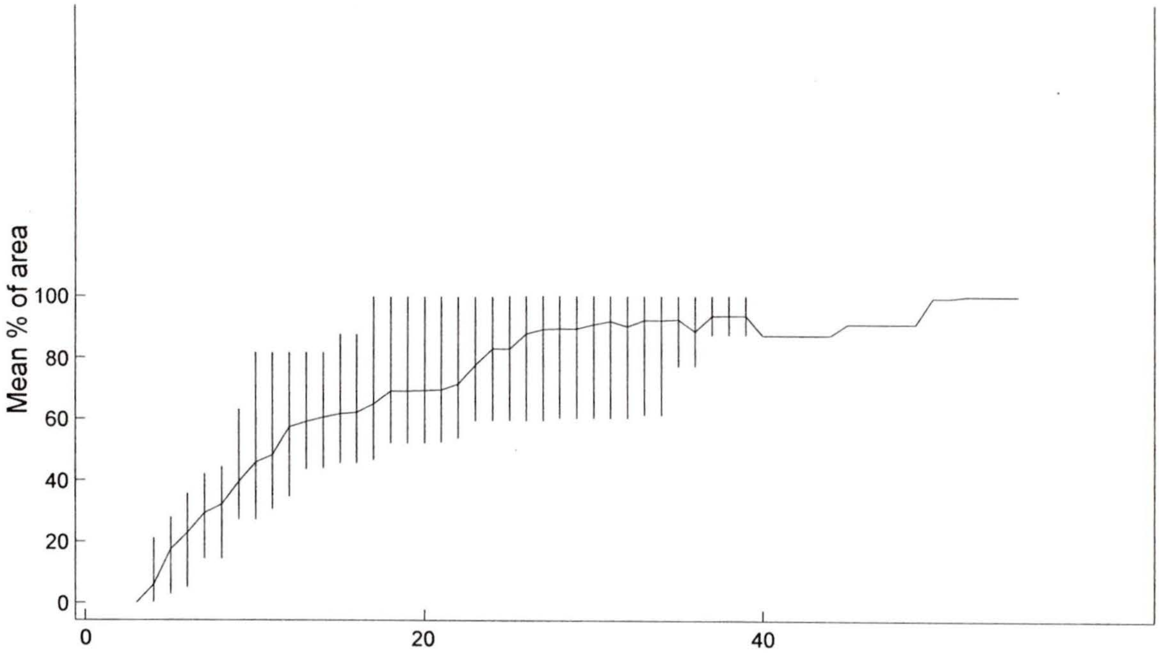
Table 5. Summary of tracking effort for each radio-tagged jay, including number of weeks tracked, number of locations obtained for each jay, percentage of locations that were confirmed by visual observation, and mean number of relocations per day.

		Weeks	Number of	Percentage	Locations/tracking day	
Jay	**Year**	**tracked**	**locations**	**visuals**	**Mean**	**SD**
Forest-interior						
220	1996	20.0	55	91	1.8	1.23
007	1996	18.6	31	100	1.8	1.18
159	1997	6.0	27	85	2.3	1.28
069	1996	10.3	34	79	3.1	1.30
(519)	1997	(2.4)	(8)	(63)	(1.3)	(0.52)
Cutblock						
459	1997	12.3	34	59	1.5	0.86
398	1997	12.3	35	49	1.7	1.01
606	1997	6.0	23	48	1.5	0.64
008	1997	11.7	39	64	2.3	1.76
250	1996	8.0	20	70	2.5	1.69
128	1996	8.0	19	74	2.1	0.78
Mean*		11.3	31.7	71.9	2.1	1.2

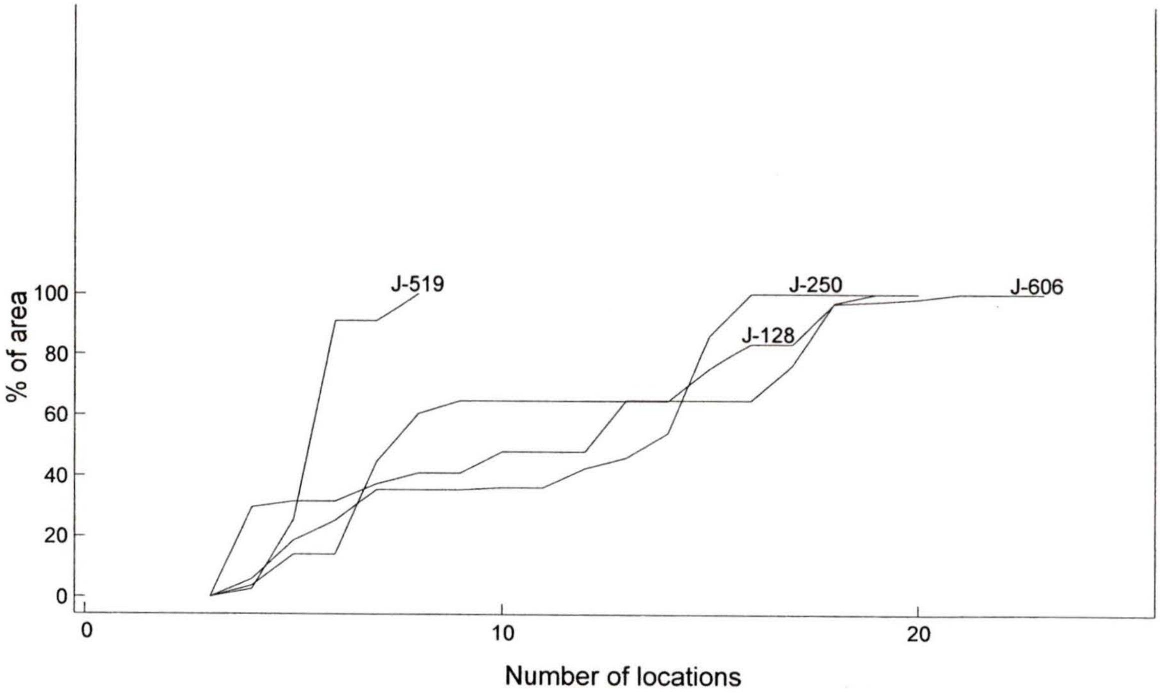
*Jay 519 not included in the calculation of means due to an insufficient number of locations.

Figure 7. a) Multi-range incremental area plot of tagged-jays (based on 100% MCP) that were located > 25 times, showing that home range estimates stabilized at 26 locations. The solid line represents the mean percentage of the home-range sampled by successive locations (n = 7 jays). The vertical lines represent the spread of values about the mean. b) Individual incremental area plots for jays with ≤ 25 locations, indicating that area estimates were stable for J-250 and J-606 with < 20 locations. J-128 appeared to follow a similar trend.

a). Multi-range plot (includes jays 220, 007, 159, 069, 459, 398, and 008)



b). Individual plots.



tracked (Fig. 8a; $r^2 = 0.056$, $P = 0.484$) or sampling effort (number of locations) and range area (Fig. 8b; $r^2 = 0.0002$, $P = 0.968$).

MCP home-range estimates varied greatly across all jays (range 9.0 - 61.0 ha) and within forest-interior and cutblock groups (Table 6), hence no significant difference between groups was found (Wilcoxon rank sum test, W = 18, n = 4, m = 6, $P = 0.476$).. Mean home-range size (mean ± SD) for forest-interior birds was 19.0 ± 20.9 ha (n = 4), and for cutblock birds was 24.6 ± 19.6 ha (n = 6).

Fixed kernel density estimator

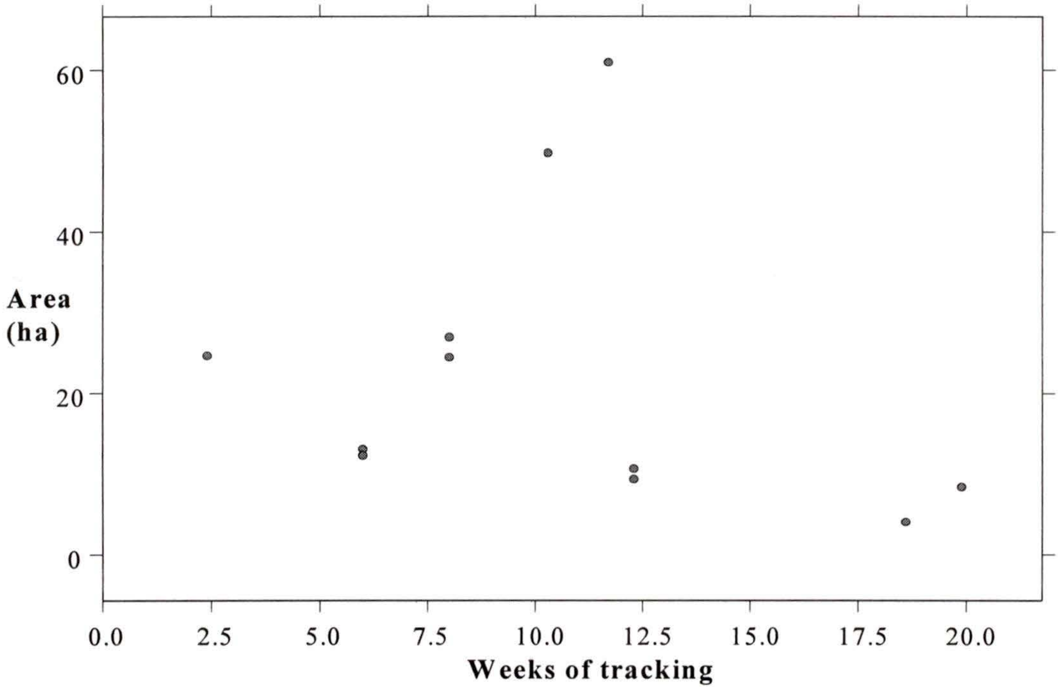
Only three sets of location data (jays 159, 398 and 128) were statistically independent ($t^2r^2{}_{\mathrm{obs}} > t^2r^2{}_{\mathrm{crit}}$; Table 7). Four other location data sets "approached" independence, so I modified the original data sets for each jay by eliminating locations made less than 60 minutes after the previous location. I then recalculated Schoener ratios and test statistics to determine if the modified data sets were statistically independent. Two additional data sets (jays 220 and 606) achieved independence. However, because statistical independence did not significantly change home-range estimates (mean of differences = 2.1 ha, paired t-test, $t = 2.25$, df = 9, $P = 0.051$) but substantially reduced the home range of J-128 whose location data set was statistically independent prior to being modified (Table 7), I proceeded with fixed kernel analysis of the original data sets only.

Bootstrap resampling revealed a negative bias in all fixed kernel home-range estimates, likely because cross-validation procedures still produced an overestimate of the smoothing parameter. Therefore, a post-hoc adjustment was applied to the smoothing parameter. Post-hoc adjustments of 0.25- 0.30 x the smoothing parameter were the best compromise for obtaining consistent range boundaries using an iterative approach and relatively unbiased estimates with increased precision (Fig. 9).

As with MCP estimates, fixed kernel estimates also varied within and between forest-interior and cutblock groups (Table 6) but not to the same extent (between 13.0 and 56.0 ha). In general, fixed kernel estimates were larger than MCP estimates. However, the group and grand means were quite similar between both estimators and there was no

Figure 8. Scatter plot showing no correlation between 100% MCP home-range estimates (ha) for tagged jays with a) time span of tracking effort (weeks) and b) sampling effort (number of locations).

(a).


Area
(ha)
0
20
40
60
0.0
2.5
5.0
7.5
10.0
12.5
15.0
17.5
20.0
Weeks of tracking

(b).

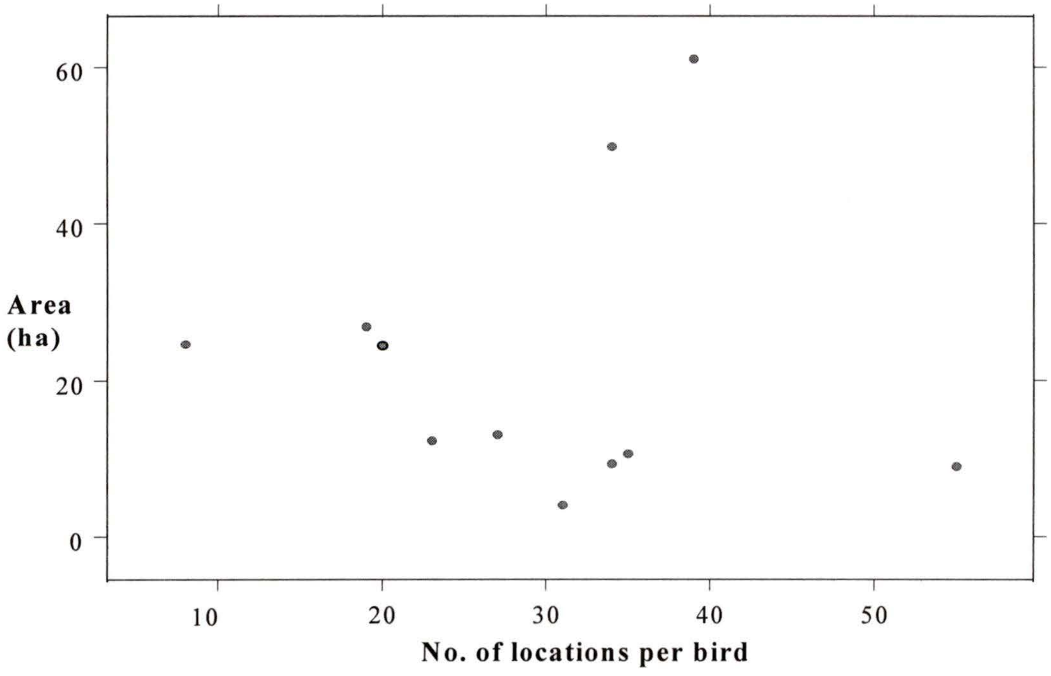

Area
(ha)
0
20
40
60
10
20
30
40
50
No. of locations per bird

Table 6. Home-range estimates (100% MCP and 99% fixed kernel), range span, and eccentricity ratios (based on MCP home-ranges) for tagged jays in Carmanah, May-September, 1996 and 1997.

Jay*	**MCP**			**Kernel**
	ha	**Span (m)**	**Eccentricity ratio**	**ha**
Forest-interior				
220	9.0	620	2.67	18.7
007	4.1	512	3.87	13.0
159	13.1	1057	6.10	20.0
069	49.8	1245	2.02	27.3
Mean	19.0	858.5	3.67	19.8
SD	20.9	349.2	1.80	5.9
Cutblock				
459	9.4	525	1.79	17.1
398	10.7	509	1.44	19.5
606	12.4	632	2.24	20.8
008	61.0	1770	3.04	56.0
250	24.5	815	1.70	45.3
128	30.0	790	1.46	26.3
Mean	24.6	840.2	1.95	30.8
SD	19.6	473.3	0.61	16.0
Grand mean	22.4	847.5	2.63	26.4
SD	19.2	406.4	1.44	13.7

* See Table 5 for number of locations/jay.

Table 7. Schoener ratios (t^2/r^2 observed and critical values*) and the corresponding change in sample size (▲n) and fixed kernel estimates (▲ha) for the original data sets (locations = 30 minutes apart) and modified data sets (locations = 60 minutes apart) for each tagged jay.

	Original		**Modified**			
Jay	t^2/r^2 *obs*	t^2/r^2 *crit*	t^2/r^2 *obs*	t^2/r^2 *crit*	**▲n**	**▲ha**
Forest-interior						
220	1.69	1.84	1.92*	1.82	-7	-1.4
007	1.11	1.77	1.57	1.72	-9	-0.9
159	2.21*	1.75	2.30*	1.74	-1	-0.1
069	1.52	1.81	1.67	1.77	-11	-1.3
Cutblock						
459	1.80	1.82	1.79	1.80	-4	+0.2
398	2.13*	1.83	2.02*	1.81	-7	-1.4
606	1.67	1.76	1.84*	1.75	-4	+0.2
008	1.08	1.80	1.17	1.78	-8	-1.8
250	1.05	1.76	0.98	1.72	-5	-9.2
128	2.07*	1.76	2.04*	1.73	-3	-5.1

---

* Test statistics were based on equations presented in Swihart and Slade (1985); observed values greater than critical values indicate independence at α=0.25. A large α was used to lessen the probability of type II errors.

significant difference between kernel and MCP estimates (paired t-test, $t = 1.08$, df = 9, $P = 0.308$). In addition, like MCP estimates, home-range area derived from fixed kernel estimates was not significantly different for forest-interior and cutblock jays (Wilcoxon rank sum test, W = 17, n = 4, m = 6, $P = 0.352$).

Home-range shape

In general, MCP and kernel estimators represented home-range shape in different ways. MCP produced polygons with many edges and often enclosed large areas with no locations (e.g., 008, J069, J128). Fixed kernel contours did not include areas lacking locations and thus the home-ranges for these same jays were disjointed with polygons representing separate nodes of activity (Fig. 10a-j).

Home-range span varied greatly within and between jay groups but there was no significant difference between forest-interior and cutblock jays (Table 8, W =23, n = 4, m = 6, $P = 0.910$). Eccentricity ratios were greater for forest-interior birds than cutblock birds, indicating that they had more elongated home ranges, but again the difference was not significant (W = 31, n = 4, m = 6, $P = 0.067$).

DISCUSSION

Biological considerations and potential bias

Banding and tagging effects

I was not directly concerned with demographic parameters in this study. However, the effects of banding and tagging on breeding behaviour and overall survival could indirectly affect other aspects of behaviour, particularly feeding behaviour and movement patterns.

Leg bands may affect visual "communication" between conspecifics of some species. However, studies have demonstrated that species lacking bright plumage or sexual dimorphism suffer no significant behavioural changes as a result of banding with either metal or coloured plastic leg bands (Zann 1994, Calvo and Furness 1992). In addition, it has been shown that plastic bands have UV reflectance similar to background

Figure 9. Mean (✳) plus minimum and maximum (vertical bars) fixed kernel home-range bootstrap estimates based on 1000 replicates. Results indicate that fixed kernel estimates derived from the actual locations obtained for each jay (o) were slightly biased.

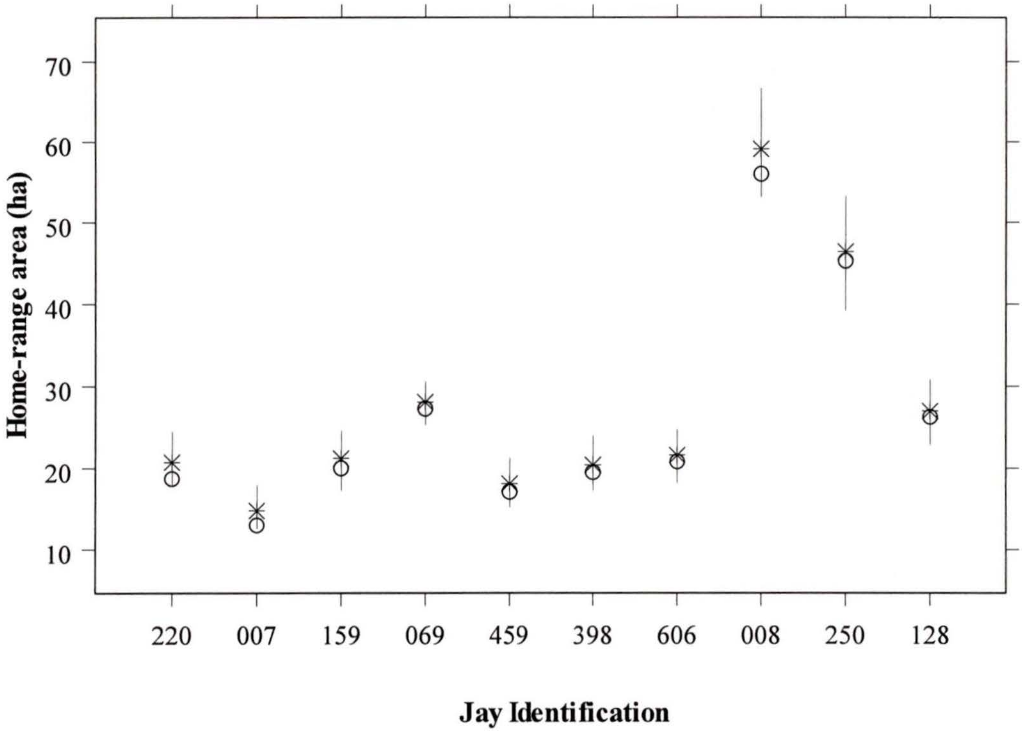
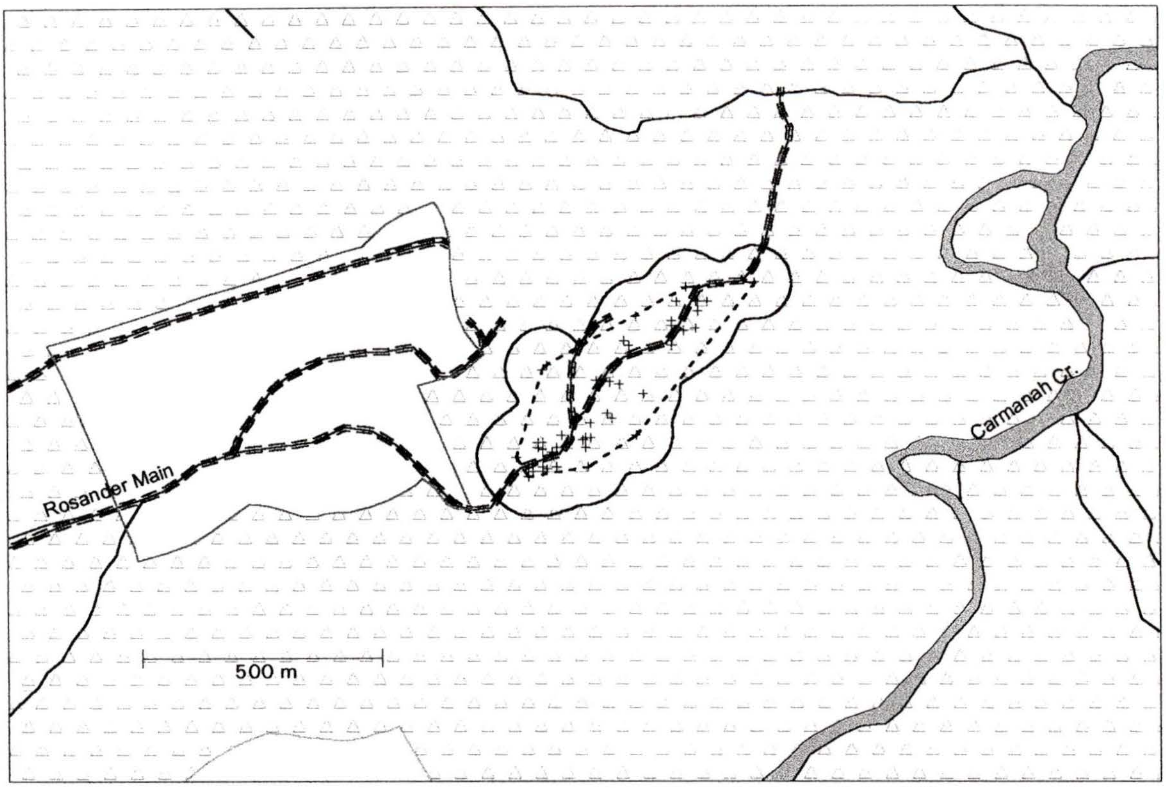
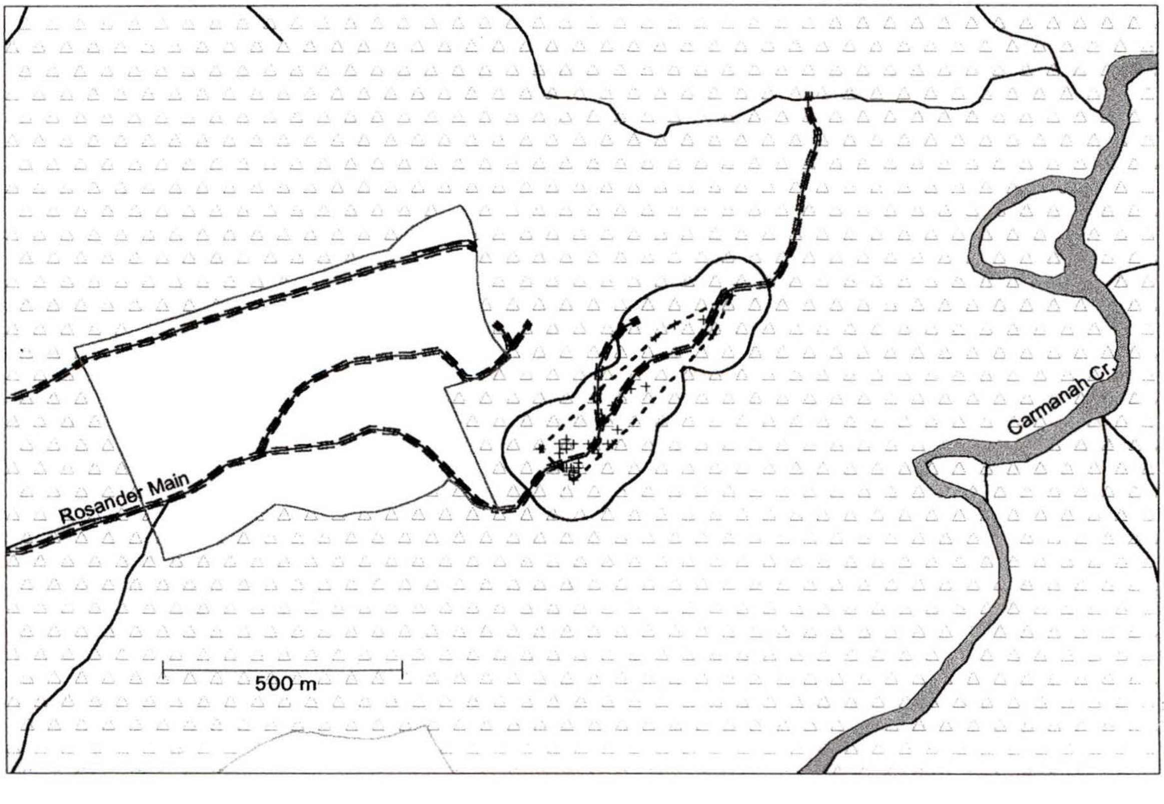

Home-range area (ha)
10
20
30
40
50
60
70
220
007
159
069
459
398
606
008
250
128
Jay Identification

Figure 10. Home-range outlines derived from 100% MCP (dashed line) and 99% fixed kernel volume contours (curved line) for each tagged jay (a-j).

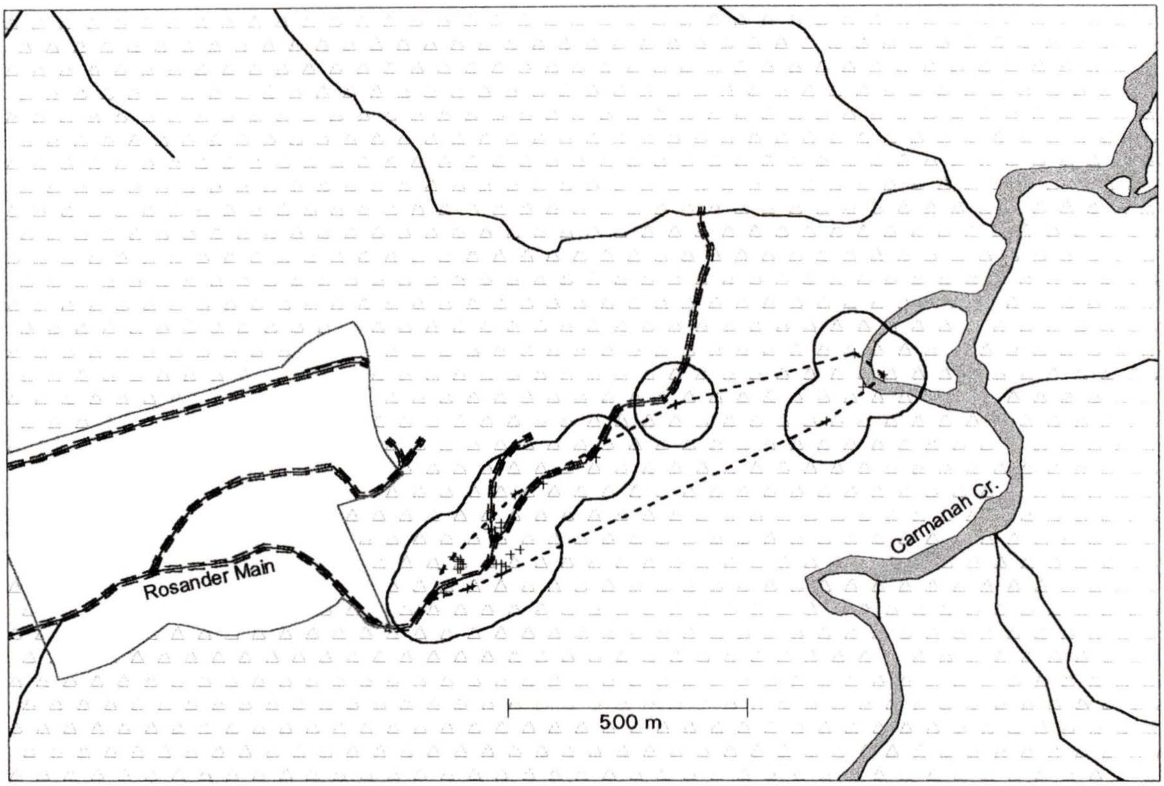
a). J-220, forest-interior jay in lower Carmanah.



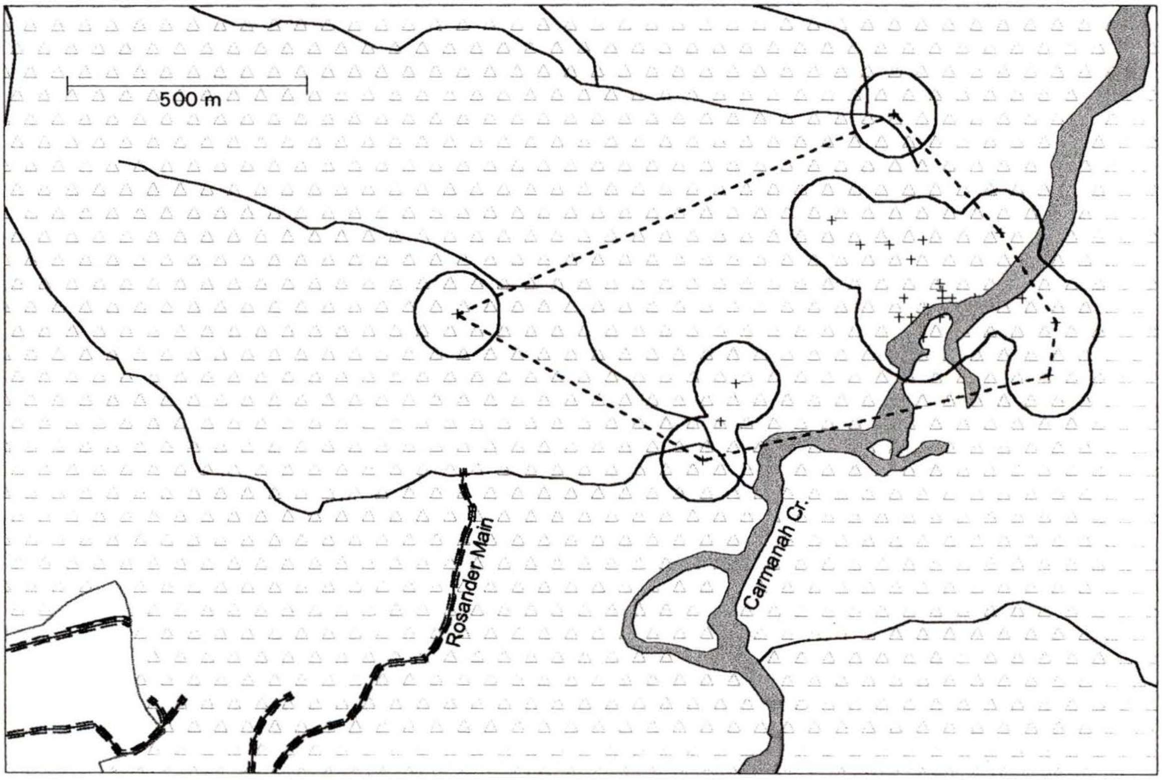
b). J-007, forest-interior jay in lower Carmanah.



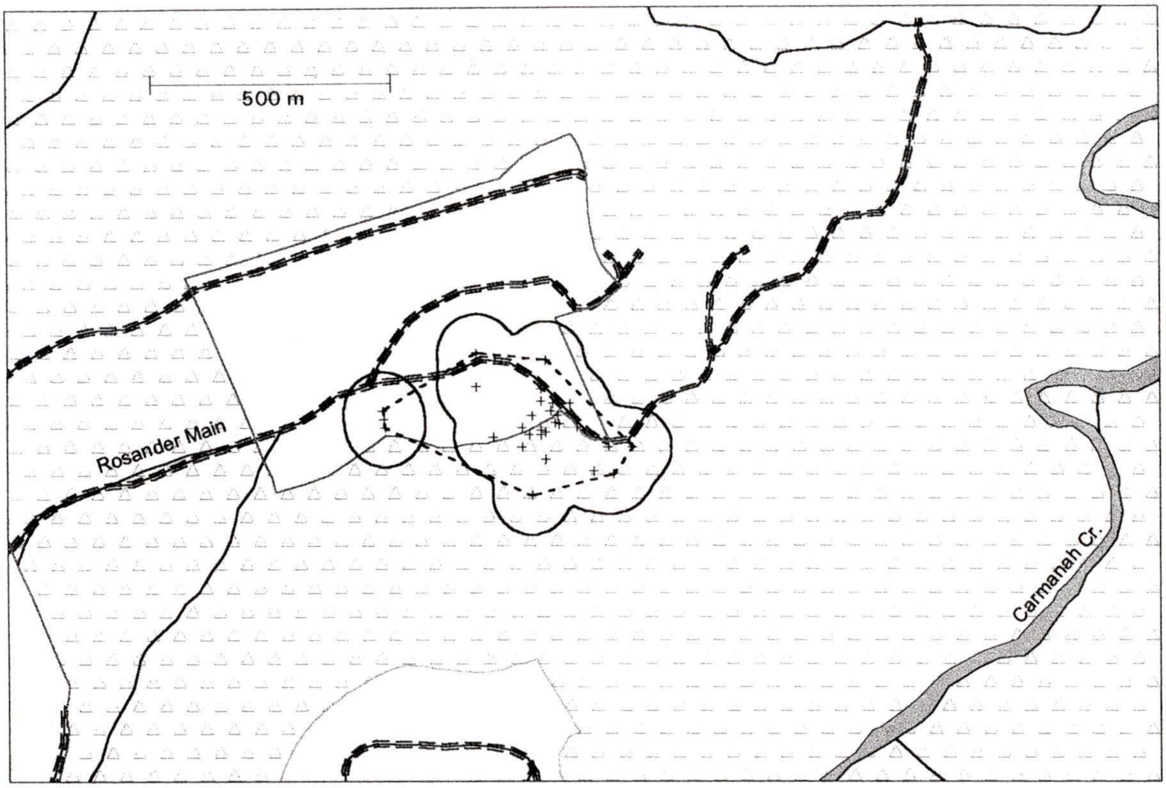
c). J-159, forest-interior jay in lower Carmanah.



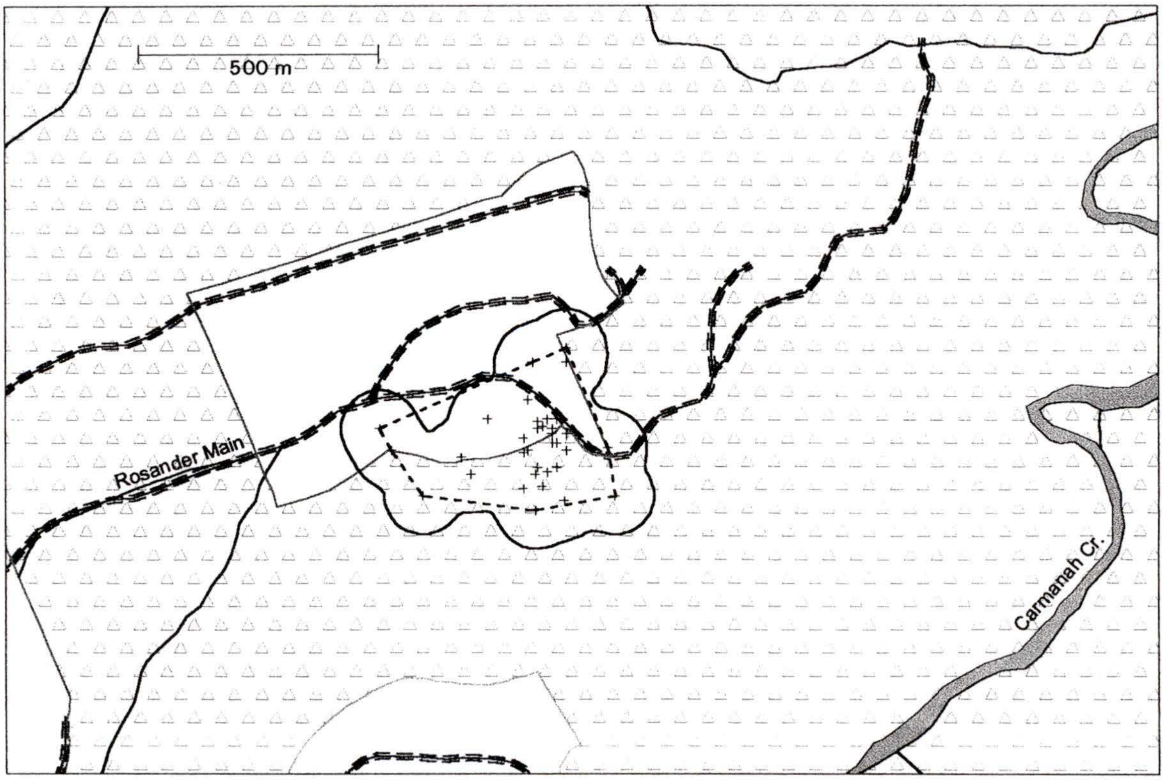
d). J-069, forest-interior jay in lower Carmanah.



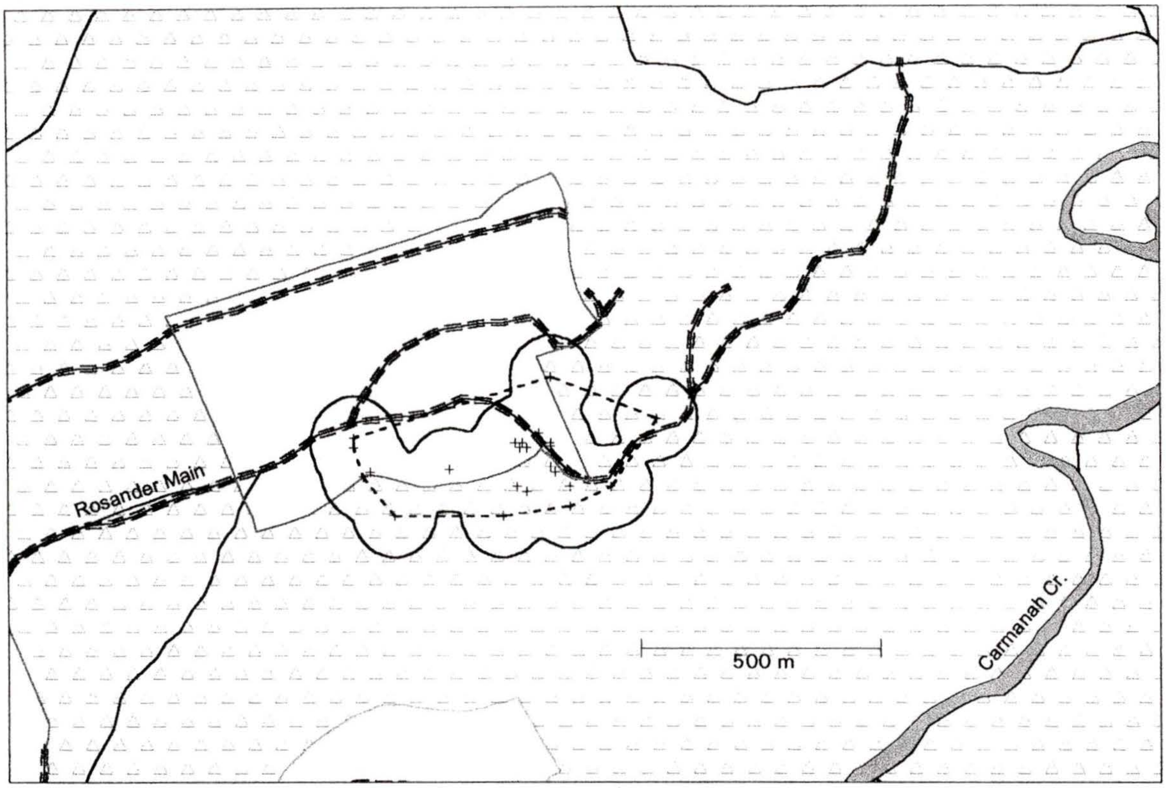
e). J-459, cutblock jay in lower Carmanah.



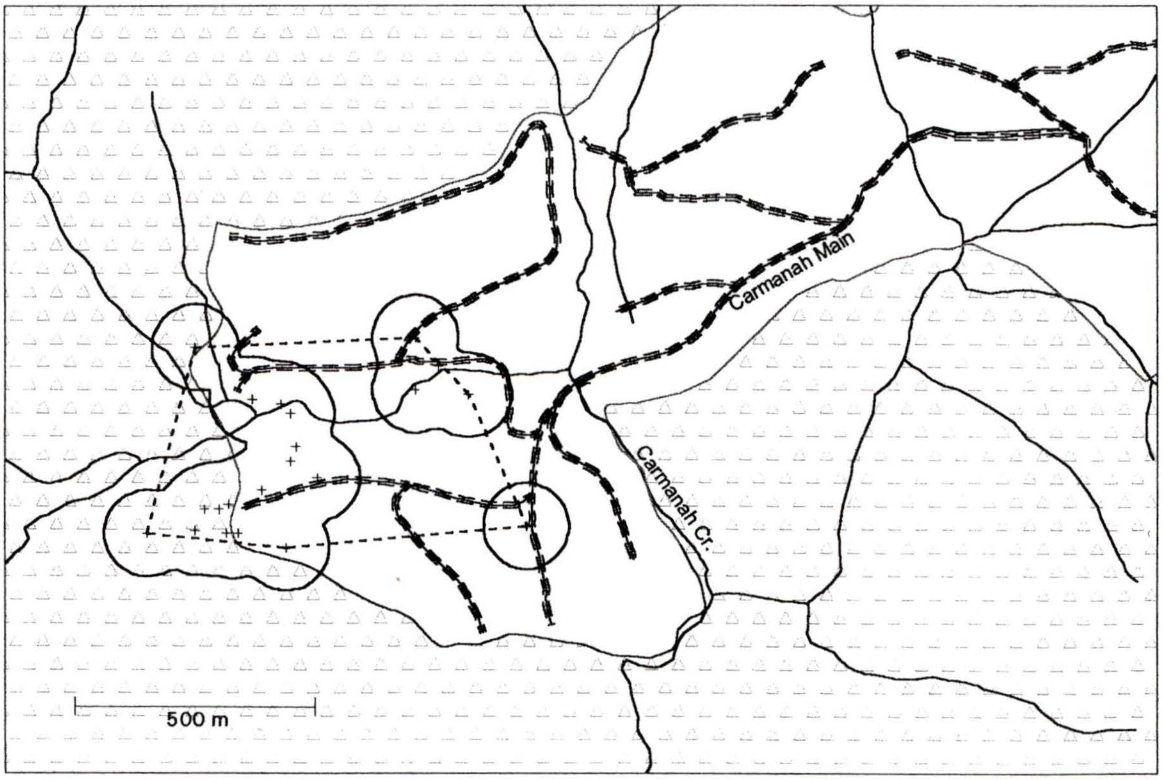
f). J-398, cutblock jay in lower Carmanah.



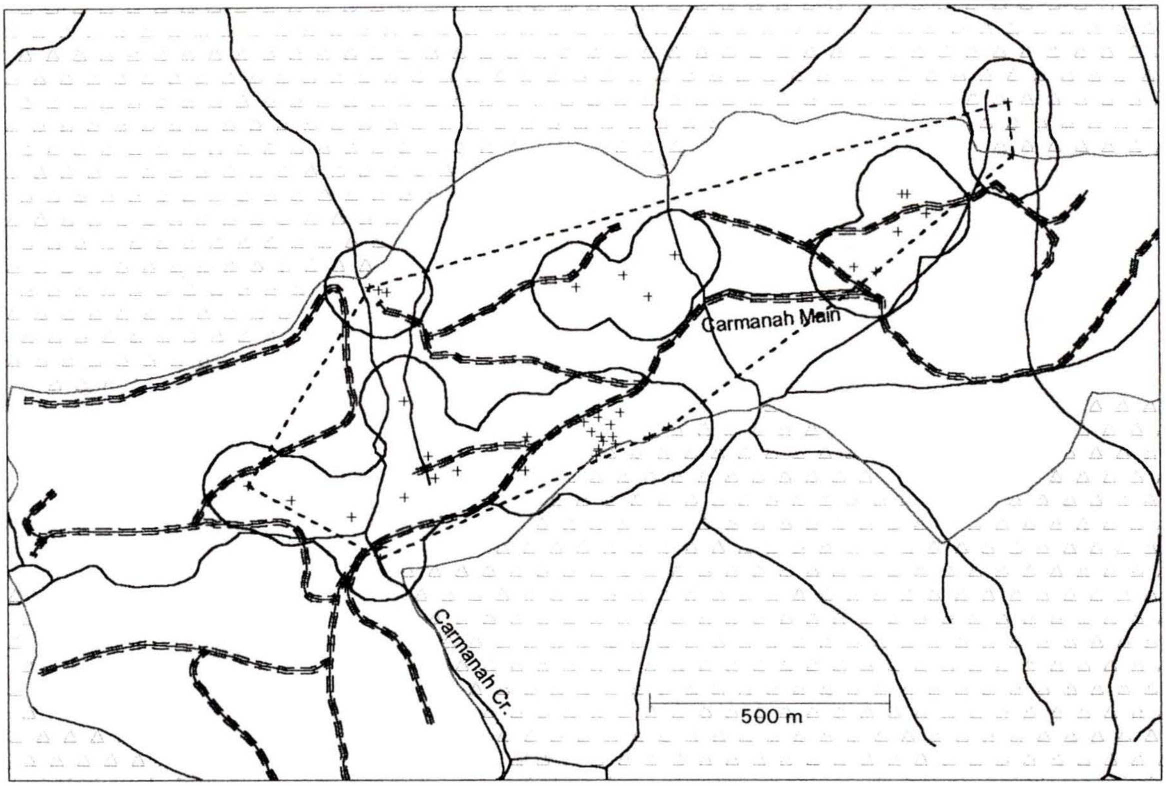
g). J-606, cutblock jay in lower Carmanah.



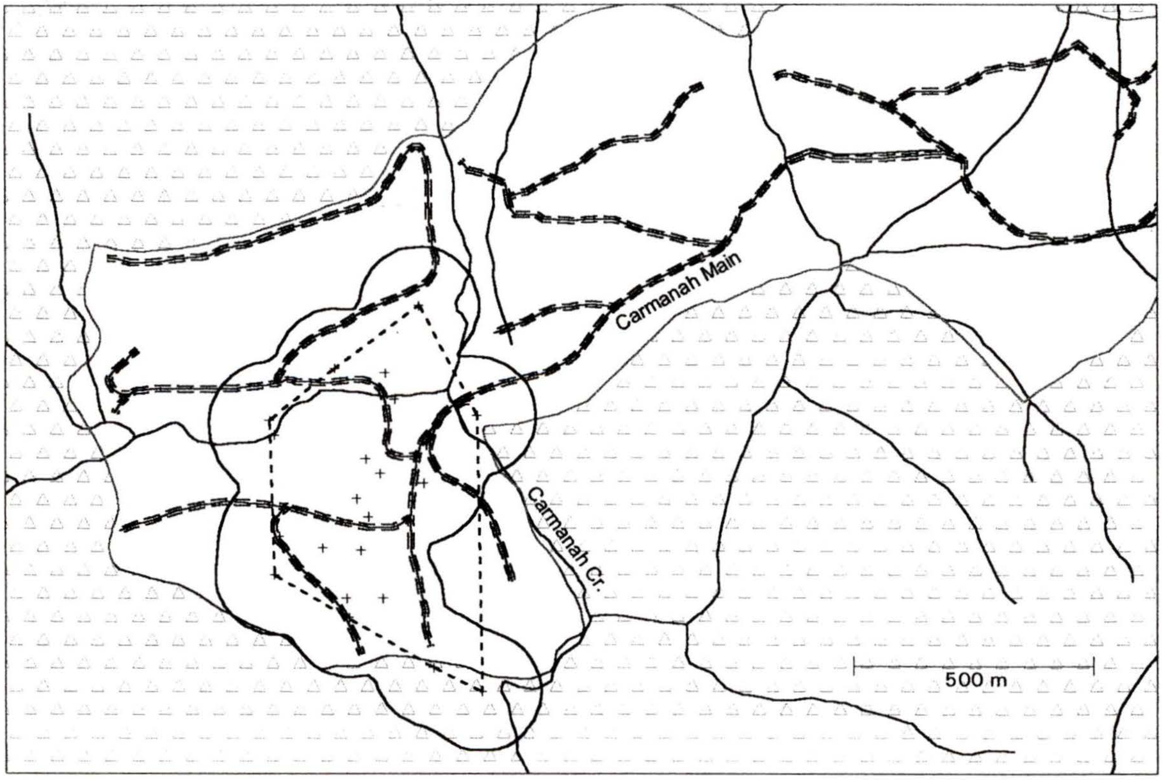
h). J-128, cutblock jay in upper Carmanah.



i). J-008, cutblock jay in upper Carmanah.



j). J-250 cutblock jay in upper Carmanah.



levels common in the avian visible spectrum and should not interfere with intraspecific signaling (McGraw *et al.* 1999). Although the jays in this study were initially preoccupied with the bands, pecking and pulling at them, they resumed normal activities within 24-48 hours and there is no evidence to suggest that the bands caused further behavioural problems.

Radio-tags did not appear to affect pair bonds or breeding success. Tagged jays initially spent an abnormal amount of time preening both the harness and transmitter, but, as with the leg bands, this behaviour usually subsided within a day. All tagged jays that were mated, maintained their pair bonds after handling. Although I did not observe jays at the nest, E. Neatherlin (pers. comm.) reported that 80% (n = 30) of similarly tagged jays in his study successfully reared young (based on observations of fledged individuals being fed by tagged adults). For these reasons, I assumed that behavioural changes caused by bands and radio-tags were minimal, or if present, were consistent for forest-interior and cutblock jays.

Although the weight and drag of transmitters were very small, there remained some concern with regard to foraging behaviour and movement patterns. Some studies reported decreased travelling distances for tagged woodland birds (Hooge 1991, Powell *et al.* 1998), or the possibility of decreased bill loads and increased foraging bouts (Pennycuick *et al.* 1989). I could not detect any overt difference in foraging behaviour or movement patterns between tagged and untagged jays, and I observed tagged jays readily carrying large food items and feeding offspring. In addition, jay movements are characterized by short distance flights between trees and by hopping from limb to limb up trees. Pennycuick *et al.* (1989) found that these type of behaviours reduce the effects of added mass. Overall, the extra weight and drag represented a relatively minor burden and did not result in any observable behavioural differences that would affect home-range size.

Effect of jay age

A bird's age may also affect home-range estimates because young birds tend not to have established territories (Ralph *et al.* 1993). While trapping, I was unable to distinguish age beyond after-hatch-year status and likely tagged a few individuals that were just entering their second year (i.e. born the previous summer) and were not part of the resident breeding population. Had I been able to track these birds, I might have obtained upward biased range estimates. Instead, it is likely that the majority of tagged jays that left the study area were these young birds, leaving only resident breeding adults in my sample of tagged birds.

Telemetry conducted in October of 1996 supports the idea that the tagged jays were resident adults. None of the jays that had been tracked through the summer that year had left the study area or their territory by the fall, although point count results (Chapter 1) indicated that the overall jay population was decreasing by mid August. In addition, I observed two individuals marked in 1996 using the same home ranges in 1997. These observations agree with those of Brown (1963) who reported that adult Steller's Jays of Tilden Regional Park, California, were relatively sedentary and that all but one pair of banded adults remained in the study area throughout the year. This information suggests that the jays tracked in this study were all resident adults entering at least their third year, and thus home-range estimates for these birds should be reliable and comparable.

Which home-range estimate best describes Steller's Jay patterns of spatial use?

MCP and kernel estimators provided useful representations of Steller's Jay home-ranges in Carmanah Valley. Both methods defined the area of jay activity and provided fairly consistent results across jays. However, each method had limitations and the estimates derived need to be viewed with that in mind.

MCP estimator

If one describes an animal's home-range with Burt's (1943) original definition: "that area traversed by the individual in its normal activities of food gathering, mating and caring for young," then the 100% MCP method provided a reliable representation and estimate of home-range area for jays. Many argue that MCP methods over-estimate range area because the polygon encloses areas never traversed by the animal (Worton 1987, Harris *et al.* 1990). In my study, several polygons did enclose large areas where the bird was never observed. However, given jay behaviour, one cannot rule out the possibility that jays could be using that area. Jays are active, vagile birds, which could easily traverse all areas encompassed by the polygon within minutes.

The polygons constructed with MCP range analysis may actually under-represent the true home-range. Polygons generally failed to encompass areas within forests where jays regularly cached food items, due to the difficulty that observers experienced in obtaining a location or fix on this behaviour. Jays often returned from caching to forage again within three minutes, and unless an observer was already standing in the forest to witness this event, or it took place near the forest edge, it went unobserved. For this reason, caching locations were under-represented in the location sample, yet they comprise an important component of a jay's home-range. These biases offset one another somewhat and therefore the 100% MCP estimate is a useful measure of home-range area.

Another criticism of MCP methods is the influence of sample size (number of locations) on range size (Worton 1987). I found that the size of most jay ranges levelled off with 26 locations and with as few as 19 locations, which suggests that the estimates were relatively stable and hence comparable. In addition, like Marzluff *et al.* (1999), I found no correlation between home-range area and sampling effort (Fig. 8), which indicates that a possible bias in this regard was minimal.

Fixed kernel estimator

It is necessary to use a more explicit definition of home-range when using statistical estimators, one that includes frequency distributions, probabilities and specified proportions of the utilization distribution to describe home-range (Seaman and Powell 1996, Worton 1989). Although the fixed kernel estimator represented home-range areas differently from MCP estimators, they accurately represented the areas where tagged animals were likely to be found. Kernel ranges were made of small disjointed units, or contours of equal probability. The benefit of this approach was that areas, in which locations were likely to have been missed, were included in the range estimate by virtue of their proximity to a centre of activity. Hence, caching sites would have been included in the range. Kernel analysis was also better able to reflect the jay's uneven use of their home-ranges because areas of intense activity were represented in the utilization distribution and thus the contours of probability which define the area.

However, exploratory analysis revealed flaws in kernel estimators, which may limit the comparability of range estimates within and between studies. Using simulated data sets, Seaman and Powell (1996) found that kernel results varied greatly with varying bandwidths (smoothing parameters), but that fixed kernel estimators coupled with least squared cross validation provided range estimates with the least bias. However, when trying to find the best estimator, like Worton (1995), I found that kernel range estimates were heavily influenced by the choice of post-hoc adjustment and that it was difficult to obtain an unbiased range estimate. This would indicate that a post-hoc adjustment that works well for one data set may not work well for another, which makes comparisons between studies difficult.

Range bias and the difficulty in defining the optimal smoothing parameter may also, in part, be a result of autocorrelation within the sets of location data. Creswell and Smith (1992) investigated the effects of dependent data on methods of range analysis and found kernel estimators to be particularly sensitive to levels of autocorrelation. At high levels of autocorrelation it was difficult to find an optimal smoothing parameter and range estimates became progressively smaller in relation to MCP estimates of the same range. This suggests that successive locations for J008 and J069 were somewhat inter-dependent because MCP estimates were larger for these two birds (Table 6). This would also explain the minor bias in range estimates that was found for all jays when compared to bootstrap estimates (Fig 10).

Anderson and Rongstad (1989) and Reynolds and Laundre (1990) showed that the time interval between locations required to achieve statistical independence sacrificed behavioural information. They surmised that the animal's mobility ultimately influenced the degree of autocorrelation between successive relocations, and found that similar range estimates could be obtained from data sets considered biologically independent but statistically dependent. Given jay behaviour and mobility, and the fact that range estimates were not significantly different between the 30 and 60 minute data sets, location data from my study could be classified as biologically independent.

What are the area requirements for jays in Carmanah watershed?

Both estimators yielded similar mean home-range estimates for jays in Carmanah (100% MCP: 22.4 ha; 99% fixed kernel: 26.4 ha). These estimates are three times smaller than mean estimates obtained by E. Neatherlin (pers.comm.) for Steller's Jays on the Olympic Peninsula (100% MCP, mean ± SE = 79.8 ±15.87 ha, n = 32), but well within the range of estimates he obtained (5-429 ha). Both studies suggest that it is difficult to describe Steller's Jay home-range area requirements with mean estimates.

Variations among birds were consistent with both methods, indicating that area requirements were individualistic. Jays 007 and 220, for example, almost exclusively used the area in the park that received the most visitor traffic and were often seen foraging in campsites. This behaviour might explain the relatively small area used by these birds. However, it is difficult to make generalizations with regard to area requirements of the other tagged birds.

Perhaps individual area requirements were not as different as MCP estimates indicated. Kernel estimates varied less because jays with large range spans (J069, J008, J250) had discontinuous areas of activity. This suggests that the area requirements of individuals were not different, but that areas of use or centres of activity were more widely spaced, possibly because the number and quality of foraging patches within a jay's home-range varied.

Is there a difference between groups in the size and shape of home-ranges?

I found no significant difference between home-range areas for forest-interior and cutblock jays. This may be due to the influence of the unusually large MCP home-range estimates for J-069 (a forest-interior jay) and J-008 (a cutblock jay); both examples of large unused areas enclosed by the polygon. This variance made it difficult to discern a true difference between groups. However, mean kernel estimates were not affected in this way and yielded no difference between groups either. Given that home-range size was so variable among such a small sample of jays, it would be unlikely that larger sample sizes would fair any better at detecting a difference between groups.

Forest-interior jays may establish home-ranges that are more elongated in shape than cutblock jays (Table 6, Fig. 10). Although the difference in eccentricity ratios was not significant between groups, three of four forest-interior jays had distinctly long narrow ranges positioned along an access road that bisected old-growth forest. The position of these ranges was likely influenced by the use of these roads by park visitors. As the main point of access to the park trail system, this road was regularly traversed by back-packers and day-hikers. Food scraps are an inevitable by-product of this traffic and on a number of occasions I observed two of the interior-forest jays foraging beneath picnic tables. These observations suggest that behaviour of jays, and in turn their pattern of spatial use, may be influenced by human activities.

Does timber harvesting affect overall patterns of spatial use by individual jays?

There is insufficient evidence to indicate that timber harvesting affects spatial requirements of jays. The creation of new open habitat did not produce distinctly larger or smaller home-ranges than those in the forest-interior, nor did it significantly affect how those ranges were aligned relative to edges. Marzluff *et al.* (1999) found that jays of the Olympic Peninsula ($n = 32$) tended to have larger ranges far from humans, in fragmented landscapes and in old-growth forests, but they found no significant differences in these variables (P-values > 0.1). Perhaps new habitats, such as clearcuts, represent new opportunities, not loss, and are thus used in the same manner as old-growth habitats. These data attest to the adaptable nature of jays and confirm their status as habitat generalists.

CHAPTER 3. HABITAT USE AND BEHAVIOUR OF STELLER'S JAYS IN EARLY SERAL STAGE STANDS AND OLD-GROWTH FORESTS

INTRODUCTION

The frequency of predation events is often dependent not only on the density of predators, but on their habitat use and behaviour as well. In general, the number of habitats used by a predator species will determine whether predation rates are dependent or independent of the predator's population size. In addition, if habitat use is edge related, then edge shape, length and abruptness, as well as specific edge-use by the predator, will further affect predation rates in these areas (Andren 1992, 1995). On the other hand, the variety of prey species consumed by the predator dictates whether predation rates will be dependent or independent of a particular prey population (Newton 1993).

Studies specifically designed to investigate the behaviour and habitat use of nest predators are rare (Marzluff and Restani 1999). Lack of information regarding habitat use and behaviour of nest predators, and ways in which both of these components might change when the landscape is altered, can lead to erroneous conclusions regarding the predator's potential impact on its prey. Therefore, it is important to understand as much of the predator's ecology as possible, in both altered and unaltered settings, before implementing management plans for either the prey or predator species. To that end, I compared the habitat use, selection, and behaviour of the two jay groups established in Chapter 3 (cutblock and forest-interior jays) to determine how Steller's Jays use their environment and how this use is influenced by timber harvesting.

Selection of habitats, when components are used disproportionately to their availability, is hierarchical in nature (Manly *et al.* 1993, Jones 2001). The broadest scale of selection is a species' geographic range and the narrowest scale might be the food items chosen from within a foraging patch. Selection criteria used at each spatial scale are likely to vary, particularly if selection at one level is dependent on selection that has occurred at a higher level (Johnson 1980, McClean *et al.* 1998). To incorporate this concept, I investigated habitat use at various macro-habitat (partial landscape, stand, patch) and micro-habitat (within tree or shrub) scales (Pribil and Picman 1997). Jay behaviour was examined only at the micro-habitat level. Five objectives were addressed:

Macro-habitat

1. Determine the selection of jay home-ranges relative to the habitat composition available in the surrounding area.
2. Determine the selection of habitats within home-ranges of jays, relative to the habitats available in the home-range.
3. Examine the habitat composition, location, and size of areas intensively used by jays (hereafter referred to as core areas) within their home-range.

Micro-habitat

4. Describe the use of forest strata (ground to canopy) by tagged and untagged jays, and the common behaviours associated with each stratum.
5. Examine substrate use and food items taken.

METHODS

Macro-habitat scales

Selection of home-range

For the purpose of determining which habitats were important in the selection of home-ranges by jays, three habitat types were recognized (based on point count results, Chapter 1): edge, clearcut and forest (stand core in Chapter 1). I defined "edge" habitat as a 100 m wide strip, centred (50 m on either side) on any abrupt forest edge (artificial or natural). "Clearcut" habitat comprised early seral stage stands, generally < 10 years old, that were greater than 50 m from a clearcut edge. All forested areas (old-growth) greater than 50 m from artificial or natural edges were considered "forest" habitat. The 100 m edge habitat or zone was based on two arguments. Although abiotic edge effects can extend hundreds of metres into the forest, there is general agreement that biotic edge effects (such as nest predation and parasitism) are concentrated within the first 50 m (Hansson 1983, Paton 1994, Kremsater and Bunnell 1999). Opportunistic observations made during this study at clearcut edges indicated that the first 50 m beyond the forest were extensively used by passerine species and suggests that biotic edge effects may extend out from the forest as well.

Using these three habitat types, I calculated the proportions of each habitat comprising home ranges of individual jays determined in Chapter 2 (used habitat) and of areas surrounding each range (available habitat, described below). Only home ranges derived from 100% MCP analysis were used (Kenward and Hodder 1996). J-519 was omitted from any analyses or calculations based on its home-range area (see Chapter 2) but was included in any calculations for which only radio-locations were required.

Habitat availability was determined on an individual basis for each jay and was based on a circular area, 20 times that of the jay's home-range, centred on the mid-point of the longest axis within the range. This method yielded an area of availability that was relative to each individual, would be easily accessible to the individual, and included enough surrounding habitat for comparison purposes with the home range (Jones 2001).

I used compositional analysis to compare used habitat to available habitat, to determine which habitat types were important (being selected) at the home-range scale. Compositional analysis, which is frequently used in avian habitat selection studies (Linkhart *et al.* 1998, Mazur *et al*. 1998, Tella *et al.* 1998, Hall *et al.*1999, Miller *et al.* 1999, Smith *et al.* 1999), allows for the simultaneous examination of all habitat types (important when determining selection) and comparison between scales (Aebischer *et al.* 1993, Manly *et al.* 1993). It also has the advantage of using the individual bird, rather than detection locations, as the sample unit which is the appropriate experimental unit if making inferences to the population (Otis and White 1999). It thereby accounts for within-animal and between-animal variation needed in hypothesis testing (Aebischer and Robertson 1992). In addition, compositional analysis is able to normalize and eliminate dependence between proportions caused by the "unit sum constraint" (Aebischer *et al.* 1993).

For compositional analysis, the proportions of each habitat type within used and available habitat for each jay, which each sum to one, were converted to independent values by first forming ratios. I used the proportion of forest habitat as the denominator to calculate these ratios (Aebischer and Roberston 1992). For habitat types that were available but not utilized (use was so low that it was not detected), a value of 0.001 was substituted for use (Aebischer *et al.* 1993). These values were then transformed using natural log transformation of ratios, i.e., "log-ratio" transformation (Aebischer and Robertson 1992). The pairwise differences of log-ratios (used - available) were then evaluated for each jay, and means (±SE) calculated across jays.

Using Wilk's Lambda (Λ) test statistic, a multivariate analogue of the t-test, I tested for non-random use of each habitat type (the null hypothesis that the average across all jays of each log-ratio difference equalled zero). Once non-random use of habitat types was established, a matrix of log-ratio differences of all possible pairs of habitat types (element) was produced for each jay, and the mean (±SE) calculated across all jays for each element in the matrix. Habitats were ranked by summing the sign (+ or -) of each element in each row of the matrix. If the log-ratio mean (±SE) of an element was significantly different from 0 based on a simple *t*-test (comparison of the mean with 0) with 2 degrees of freedom, then it indicated that not only was habitat use ranked but that their was a significant difference in the relative use of habitat types. All compositional analyses were performed with the software package "Resource Selection for Windows" (Leban 1999, unpublished freeware).

Selection within home-ranges

I assessed habitat selection within home-ranges of cutblock jays (defined, Chapter 3) because they, unlike forest-interior jays, had access to all 3 habitat types. Simplifying habitat categories to accommodate forest-interior jays in analysis (edge and non-edge categories for example) would not adequately explain habitat selection by cutblock jays (Thomas and Taylor, 1990).

I used compositional analysis (as described above) to assess habitat selection at this scale as well, but the proportion of habitat used was based on radio-locations, and compared with the habitat composition within the home-range. Otis and White (1999) and Aebischer *et al.* (1993) argue that it is acceptable to use location data in this manner because location points (if collected in an unbiased manner, thereby producing a stable estimate of range size) represent a subsample of an animal's habitat use or "trajectory through space and time." Also, because the animal is the sample unit in the statistical test used in compositional analysis, the subsample of locations for each animal does not inflate the effect being tested.

Core areas within jay home-ranges

To visually represent core areas of use within home-ranges of jays, I used hierarchical incremental cluster analysis. I used the "nearest neighbour rule" to govern the addition of each radio-location into the clusters (Ranges V software; Kenward and Hodder 1996). A cluster technique was used because it is non-statistical (not based on estimation of fix density distributions like kernel analysis) and hence is not hampered by autocorrelation of locations. I suspected that jays would have more than one core, and this technique is adept at identifying separate areas of intense use (Wray *et al.* 1992, Kenward and Hodder 1996).

The proportion of locations included in core areas was determined separately for each jay. Home-range analysis (Chapter 3) indicated that spatial use by jays varied among individuals; therefore I assumed core use would vary as well. For each jay, I constructed utilization plots (graph of area plotted against percentage of locations) and used the inflexion point at which the slope of the line markedly changed (represented a large increase in area) to define the core (Harris *et al.* 1990).

Core polygons produced in Ranges V were imported into the drafting program Autocad 2000, to measure each habitat type described above and the distance of cores from nearest forest edge. Wilcoxon rank sum test (Zar 1996) was used to test for differences between groups (forest-interior and cutblock jays) in mean core size, number of cores, distance of cores from edge, and proportion of edge habitat. Edge composition of cores (all tagged jays) was compared to that of the home range using Student's paired t-test.

Micro-habitat scales

I examined jay behaviour and habitat use relative to vertical forest structure using single-point observations (observations of the animal's activities at first contact only) of radio-tracked jays and jays encountered opportunistically (hereafter referred to as randomly selected jays). J-519 was included in all micro-habitat analyses although excluded from home-range and core estimates. For tagged jays, observation sample points were separated by at least five minutes, which was ample time for a jay to move to a different micro-habitat. Often I saw jays travel 100-300 m in one minute or less.

Observations of randomly selected jays were either of birds well into the forest interior (≥ 200 m from the nearest clearcut edge, but could be near other edges such as roads or rivers) or near clearcuts (in clearcuts or within the adjacent stand <75 m from a clearcut edge). Based on this division of observations (there were no observations of birds between 75 and 200 m), randomly selected jays were designated as either forest-interior or cutblock jays for comparative purposes with tagged jays. If a group of non-tagged jays were observed, information was collected on only one individual (Bell *et al.* 1990).

The single-point method provided a number of advantages over other common observation techniques. A pilot study conducted in 1996 revealed that focal observation techniques (extended uninterrupted observation of an individual) could not be used, because dense foliage in old-growth and early seral stage stands precluded any continuous tracking or observations of constantly moving jays. For the same reason, sequential observation techniques (data recorded at set intervals or for a certain number of desired behaviours; Recher and Gebski 1990) could not be used. In addition, the single-point method produced less bias than the other methods toward locations where birds were conspicuous (Hejl *et al.* 1990).

During observations of either tagged or randomly selected jays, I recorded the following information for each sighting: estimated height (m) of jay above the ground; its position relative to vertical forest structure (e.g., ground, lower 1/3 of canopy); and canopy height (m). I recorded the jay's behaviour using one of four categories: travel (all forms of directed movement such as flying, hopping or walking); perch (stationary activities while perched such as preening, resting, and scanning); interaction (any behaviour directed toward a conspecific such as those related to mating and parental care or behaviours directed toward other species); and forage (all aspects of searching, gathering and handling food). General substrate use, which in this study refers to the plant species or object (such as logs and stumps) on which the jay was perched, along with the substrate's height, was documented. During foraging observations, I tried to identify the food items taken, without disturbing the bird. I recorded the date, time, location, and habitat (edge, clearcut and forest) for each observation. The frequency of human activity, predominantly car traffic, camping, picnicking or hiking was rated as low (> 1 week interval between encounters with car or foot traffic), moderate (car or foot traffic encountered weekly), or high (car or foot traffic encountered daily).

I used four forest strata categories for analyses: canopy (>15 m), subcanopy (2.5 - 15 m), shrub (0.5 - 2.5 m) and ground (< 0.5 m). These measurements were approximations based on plant structure rather than height alone because as canopy heights varied, so did canopy and subcanopy designations. I summarized data sets from tagged and randomly selected jays separately because they could not be pooled. Repeated observations of tagged individuals, statistically, could not be considered independent and would have introduced inappropriate sample variance (Hejl *et al.* 1990, Noon and Block 1990). Because the number of observations varied among tagged jays, I separated individuals throughout data summary (except for food items consumed) and used proportion of strata use, behaviours, and substrate use of each tagged jay to calculate group means. I applied contingency tables and Chi-square analysis (Zar 1996) to the data set of randomly selected jays to examine the relative frequencies of strata use between cutblock and forest-interior jays.

I used a rejection level of $\alpha = 0.05$ throughout.

RESULTS

Macro-habitat use

Home-range versus surrounding area

Edge was an important habitat feature which distinguished home-ranges of all tagged jays (forest-interior and cutblock) from the surrounding area. The only habitat shared by all tagged jays at the home-range scale was edge (Table 8). The mean

Table 8. The proportion of each habitat type used within each jay's home-range (100% MCP) and that available based on a circular area surrounding each range (20 x home-range area).

	Home-range**			**Surrounding area**			
Jay group	**Edge**	**Clearcut**	**Forest**	**Edge**	**Clearcut**	**Forest**	**(ha)**
Forest-interior*							
220	0.74	0.00	0.26	0.21	0.07	0.73	180
007	0.95	0.00	0.05	0.26	0.05	0.69	81
159	0.32	0.00	0.68	0.24	0.03	0.73	262
069	0.18	0.00	0.82	0.10	0.004	0.89	995
Mean	0.55	0.00	0.45	0.20	0.04	0.76	
SD	0.36	0.00	0.36	0.07	0.03	0.09	
Cutblock							
459	0.51	0.33	0.16	0.24	0.18	0.58	187
398	0.53	0.27	0.20	0.22	0.18	0.60	214
606	0.62	0.26	0.12	0.20	0.14	0.66	247
008	0.06	0.93	0.00	0.06	0.12	0.82	1220
250	0.07	0.93	0.00	0.12	0.25	0.63	490
128	0.14	0.78	0.08	0.08	0.18	0.74	439
Mean	0.32	0.58	0.10	0.15	0.18	0.67	
SD	0.26	0.33	0.08	0.08	0.05	0.09	

*J-519 omitted because estimates of range area were unreliable (see chapter 2).

** Home-range areas can be found in Table 6, Chapter 2.

proportion of edge habitat across all home ranges (0.41 ± 0.30 SD) was over double that in the designated surrounding area (0.17 ± 0.07 SD) and significantly different (paired t-test, $t = 2.26$, df = 9, $P = 0.013$). The proportion of edge habitat within home-ranges of forest-interior and cutblock jays did not differ: likely a function of small sample size (Wilcoxon rank sum test; W = 30, n = 4, m = 6, $P = 0.257$). Jay 519 was not included in these analyses because I was unable to calculate a reliable home-range area for this jay, and hence it was not logical to calculate proportions of habitat types within such a range.

The overall comparison of habitat use from jay home-ranges (both cutblock and forest-interior jays) compared with habitat available around the home-range yielded Lambda (Λ) = 0.25, $X^2 2 = 13.93$, $P < 0.001$. Therefore, jays did not establish their home-ranges randomly in the valley. The relative use of habitat types was ranked: edge > clearcut > forest, with clear differences among the three habitat types. Relative use of forest habitat was significantly less than clearcut habitat, and relative use of edge habitat was significantly more than clearcut habitat (Table 9).

Use and selection of habitats within home-ranges

The use of forest, edge and clearcut habitat varied among jays, but several patterns were evident (Fig. 11). Edge was the only habitat used by all tagged jays. The mean proportion of locations in edge habitat for forest-interior jays and for cutblock jays was 85.2 ± 13.4% SD (n = 5, J-519 included because proportions were based on the number of locations) and 54.9 ± 29.2% (n = 6), respectively. Forest habitat was used by 80 % of forest-interior jays and 83% of cutblock jays with a mean proportion of locations of 14.8 ± 13.4% and 7.5 ± 5.3%, respectively. Clearcut habitat (> 50 m into the cutblock) was used by 83% of cutblock jays and the mean proportion of locations in clearcut habitat for this group was 37.6 ± 33.0%. All but one tagged jay (J- 007) utilized two habitat types, and 67% of cutblock jays used all three habitat types available to them.

Both cutblock and forest-interior jays were most often found within 50 m of forest edges (Fig. 12). Both groups showed a distinct drop in the number of locations beyond the first 50 m into the clearcut/gap and into the forest core, but cutblock jays were not as tightly aligned with the edge as forest-interior birds. Cutblock jays spread out from the

Table 9. Matrix of means and standard errors of each element averaged over all 10 tagged jays. An element refers to the pairwise difference of log-ratios of used (MCP home-range) minus available habitat (a circular area 20 times that of the home-range). Habitats were ranked by summing the "+" signs of each element in each row of the matrix.

	Habitat				
Habitat	**Edge**	**Clearcut**	**Forest**	**(+)**	**Rank**
Edge		+2.85 ± 1.53	+3.29 ± 0.94*	2	1
Clearcut	-2.85 ± 1.53		+0.44 ± 2.12	1	2
Forest	-3.29 ± 0.94*	-0.44 ± 2.12		0	3

* Indicates significant deviation from random on a simple *t*-test (comparison of the mean with 0, df = 2, $P < 0.05$).

Figure 11. Proportion of locations in edge, clearcut and forest habitat types for each tagged jay in Carmanah Valley, 1996 and 1997. See Table 5, Chapter 2 for the number of locations for each jay. J-519 was included because proportions were based on number of locations not area.

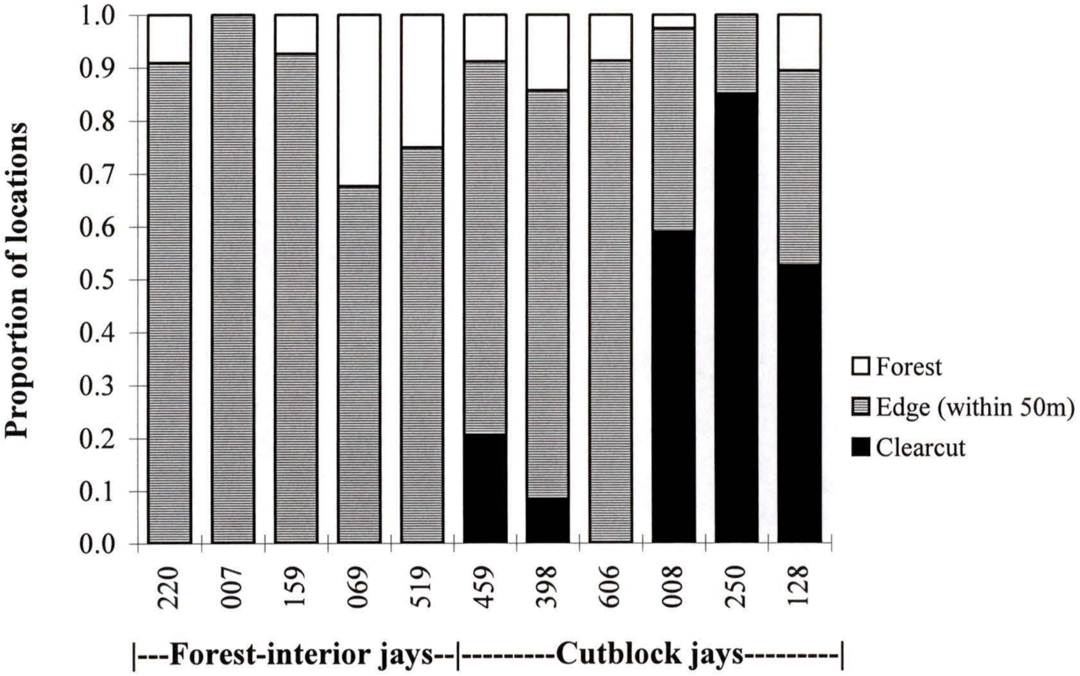
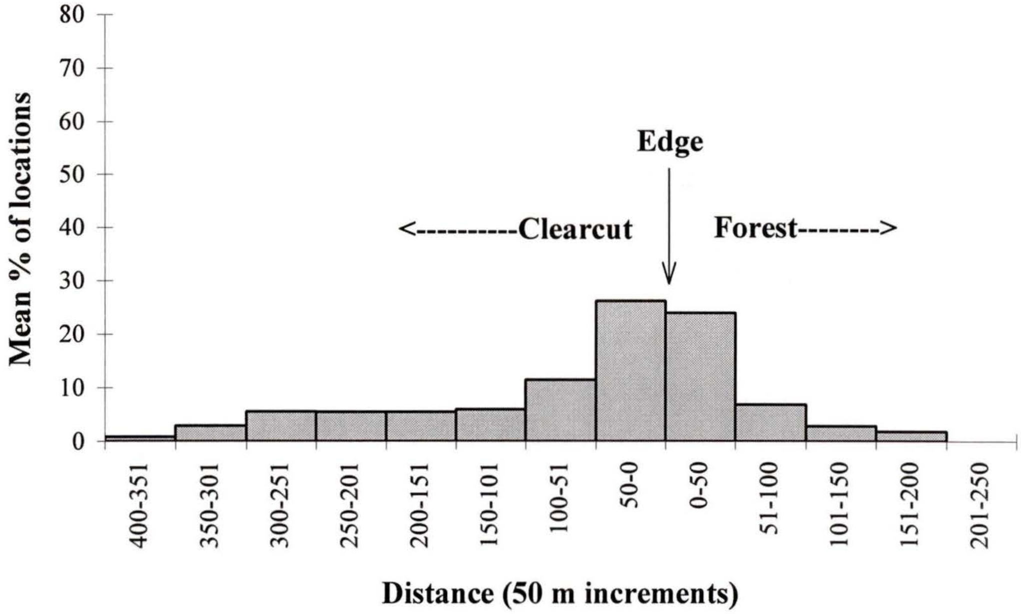
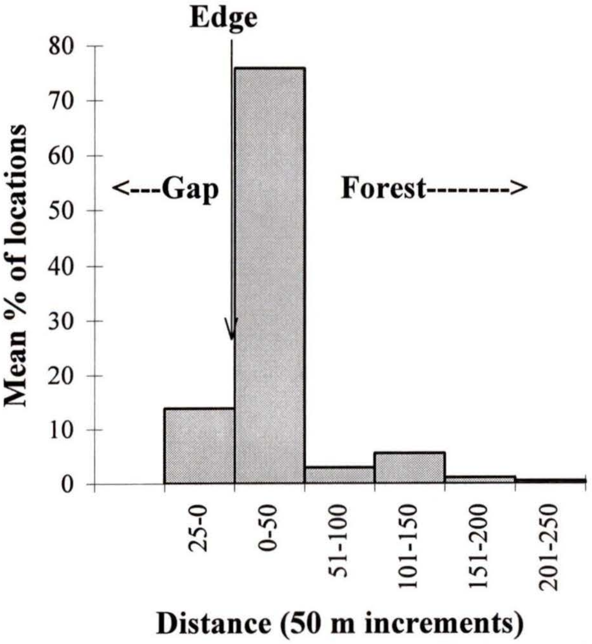

Proportion of locations
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
220
007
159
069
519
459
398
606
008
250
128
|---Forest-interior jays--|---------Cutblock jays---------|
☐ Forest
▤ Edge (within 50m)
■ Clearcut

Figure 12. Mean percent of locations of a) cutblock jays (n = 6) and b) forest-interior jays (n = 5) at 50 m increments from the forest edge. See Table 5, Chapter 2, for the number of locations for each bird. Because forest-interior jays do not go into the clearcuts, a direct comparison of the percentage of locations at each distance could not be made. Also note that the first increment into the gap for forest-interior jays was only 25 m.

a) Cutblock jays



b) Forest-interior jays



edge in both directions more frequently. Because the number of 50-m intervals varied between cutblock and forest-interior birds they were not directly comparable. In addition, gap width varied for forest-interior jays, particularly along rivers; therefore, the gap interval was made less than 50 m.

Overall, use of the three habitat types by cutblock jays based on radio-location distribution, differed significantly from the habitat distribution within the MCP home-range ($\Lambda = 0.29$, $P < 0.05$, to $X^2_2 = 7.42$). Among cutblock jays, use of the three habitat types was not random. The ranking matrix indicated that, edge > forest > clearcut, with a significant difference between pairs of ranks (Table 10). Forest-interior jays were excluded from this analysis because clearcut habitat was not available to them at this scale.

Use and composition of core areas within home-ranges

Cumulative home-range area plotted against percentage of locations was used to define core areas of use by each jay. Figure 13 is an example of one such plot and indicates that the core area for J-159 was defined with 75% of the locations. For other jays, core areas were defined with 65-85% of locations (Table 11). Jays had two to four core areas (median 2). The average area of cores was 2.08 ± 1.81 ha. Edge habitat was present in 90% of core areas and the proportion of this habitat within the cores was significantly higher than proportions found in the home-range (paired t-test, $t = 3.25$, df = 9, $P = 0.009$). Forest habitat was present in only 50% of core areas of tagged jays (Table 11, Fig. 14).

Although the mean distance of cores to the nearest forest edge was 36 times less for forest-interior jays than cutblock jays (Table 11), when measurements were compared between groups no significant difference was found (Wilcoxon rank sum with Z correction, $Z = 1.47$, $P = 0.139$). Core area measurements did not significantly differ between groups either (Wilcoxon rank sum, $W = 15$, $n = 4$, $m = 6$, $P = 0.171$). The mean proportion of edge habitat for forest-interior jays was almost double that of cutblock jays, but again measurements were not significantly different between groups ($W = 30$, $n = 4$, $m = 6$, $P = 0.114$).

Table 10. Matrix of means and standard errors of each element averaged over all 6 cutblock jays. In this case, an element refers to the pairwise difference of log-ratios of used (proportion of radio locations in each habitat type) minus available habitat (MCP home-range). Habitats were ranked as in Table 9.

	Habitat				
Habitat	**Edge**	**Clearcut**	**Forest**	(+)	**Rank**
Edge		+2.89 ± 1.55	+0.58 ± 0.19*	2	1
Clearcut	-2.89 ± 1.55		-2.31 ± 1.55	0	3
Forest	-0.58 ± 0.19*	+2.31 ± 1.55		1	2

* Indicates significant deviation from random on a simple *t*-test (comparison of the mean with 0, df = 2, $P < 0.05$).

Figure 13. One example (J-159) of a utilization plot. The cumulative area plotted against percent locations was used to define core areas of use by each jay. The point of inflexion in this example occurred at 75% of the total number of locations and this was designated as the core.

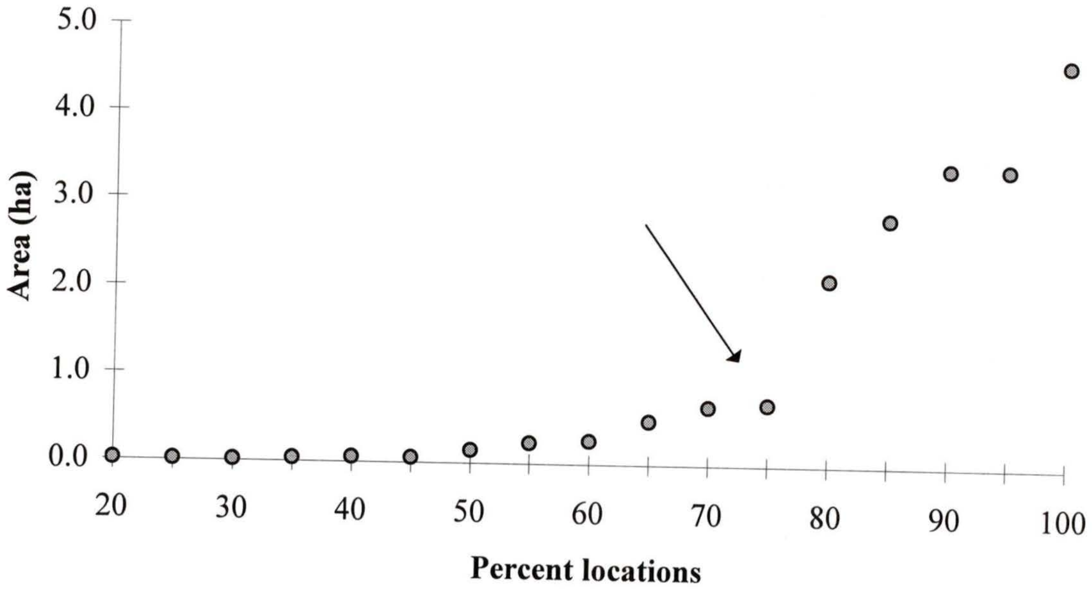
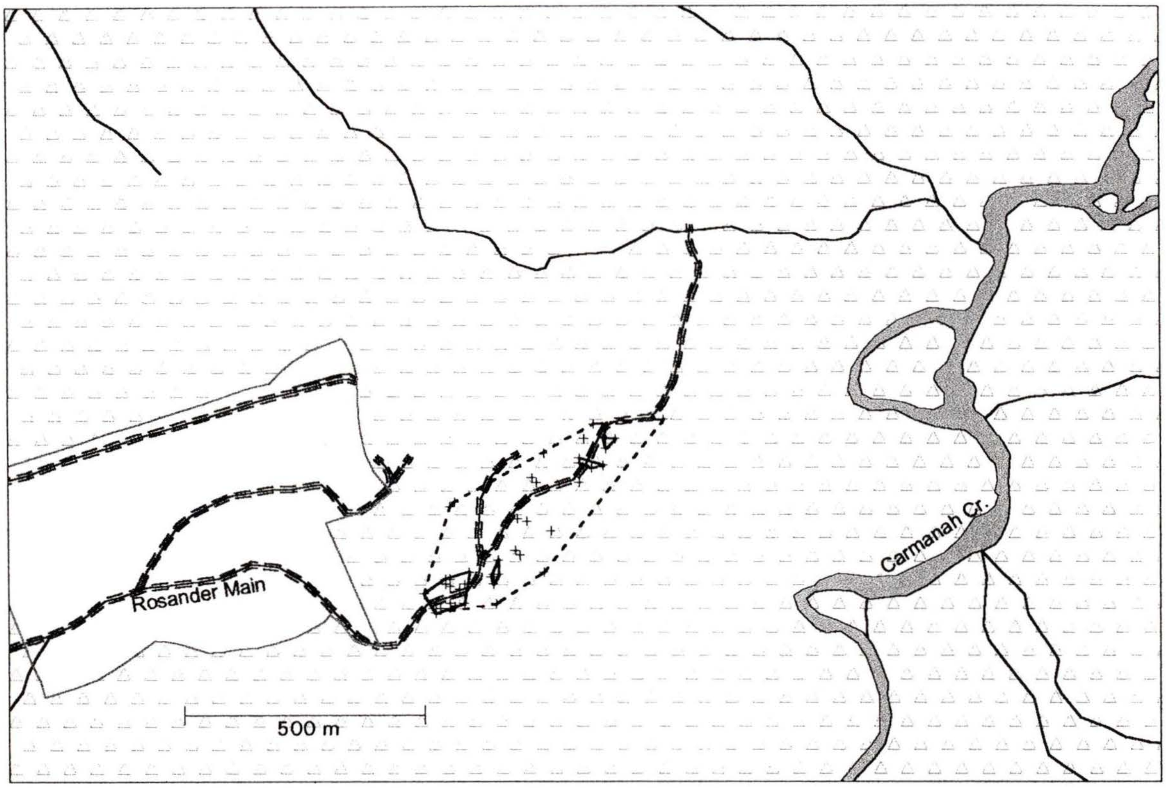

5.0
4.0
3.0
2.0
1.0
0.0
Area (ha)
20
30
40
50
60
70
80
90
100
Percent locations

Table 11. The results of cluster core analysis including the percent locations (determined with utilization plots), the number of cores in each home-range, the average distance of cores to the nearest forest edge, total area of all cores in the home-range and total core area.

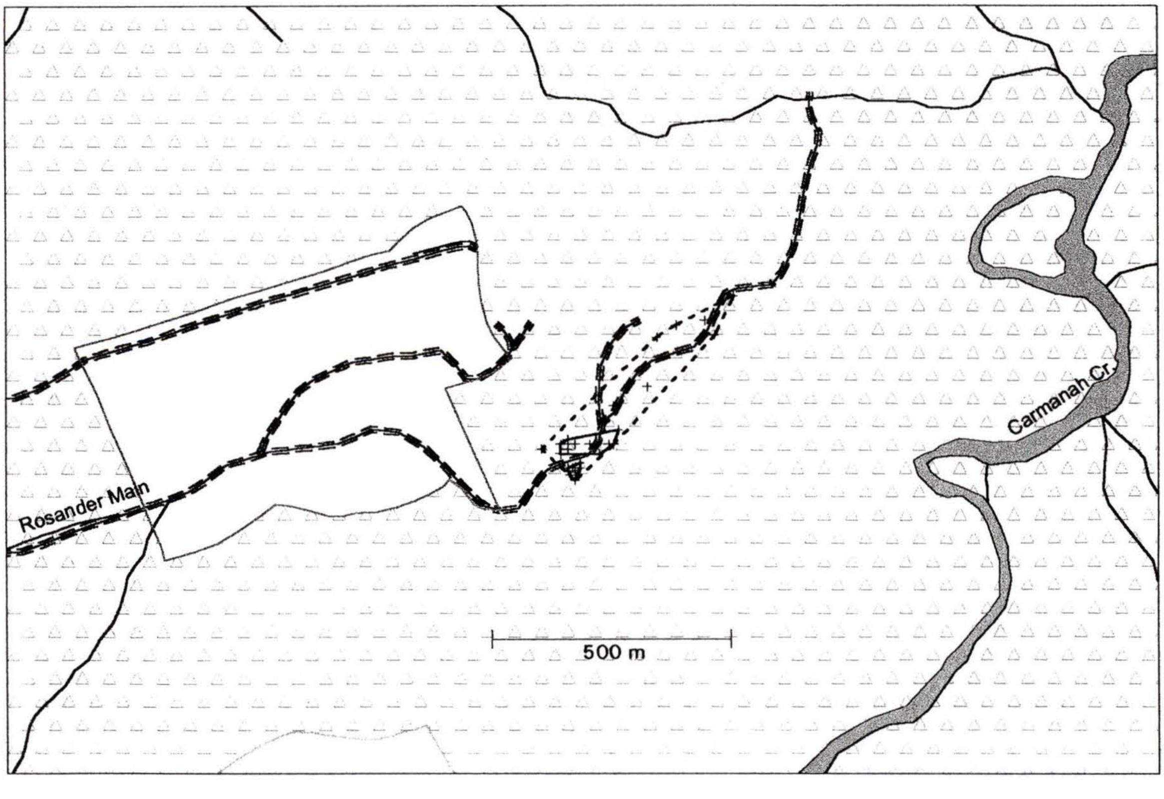
	Summary of cluster analysis				**Proportion of habitat type within the core**		
Jay	**% locations used to define core habitat**	**Number of cores**	**Mean distance to forest edge (m)**	**Total area (ha)**	**Edge**	**Clearcut**	**Forest**
Forest							
220	70	4	5	0.6	1.00	n/a	0.00
007	75	2	0	0.5	1.00	n/a	0.00
159	75	2	0	0.7	1.00	n/a	0.00
069	85	2	0	3.3	0.29	n/a	0.71
Mean	76.3	2.5	1.3	1.5	0.82		0.18
SD	4.8	0.5	2.5	1.3	0.35		0.35
Cutblock							
459	85	2	0	2.2	0.78	0.15	0.07
398	75	2	0	1.8	0.56	0.05	0.39
606	80	3	13	0.9	0.91	0.02	0.07
008	75	4	75	2.8	0.24	0.76	0.00
250	70	2	40	6.5	0.00	1.00	0.00
128	65	2	140	1.7	0.51	0.44	0.04
Mean	75.0	2.5	44.7	3.4	0.50	0.40	0.09
SD	7.1	0.5	54.8	2.8	0.34	0.40	0.15
All jays							
Mean	75.5	2.5	27.3	2.1	0.63	0.40	0.13
SD	6.4	0.9	46.6	1.8	0.36	0.40	0.24

Figure 14. Core areas used by tagged jays (solid line), determined by incremental cluster analysis (nearest neighbour joining rule) and shown within the 100% minimum convex polygon (dashed line).

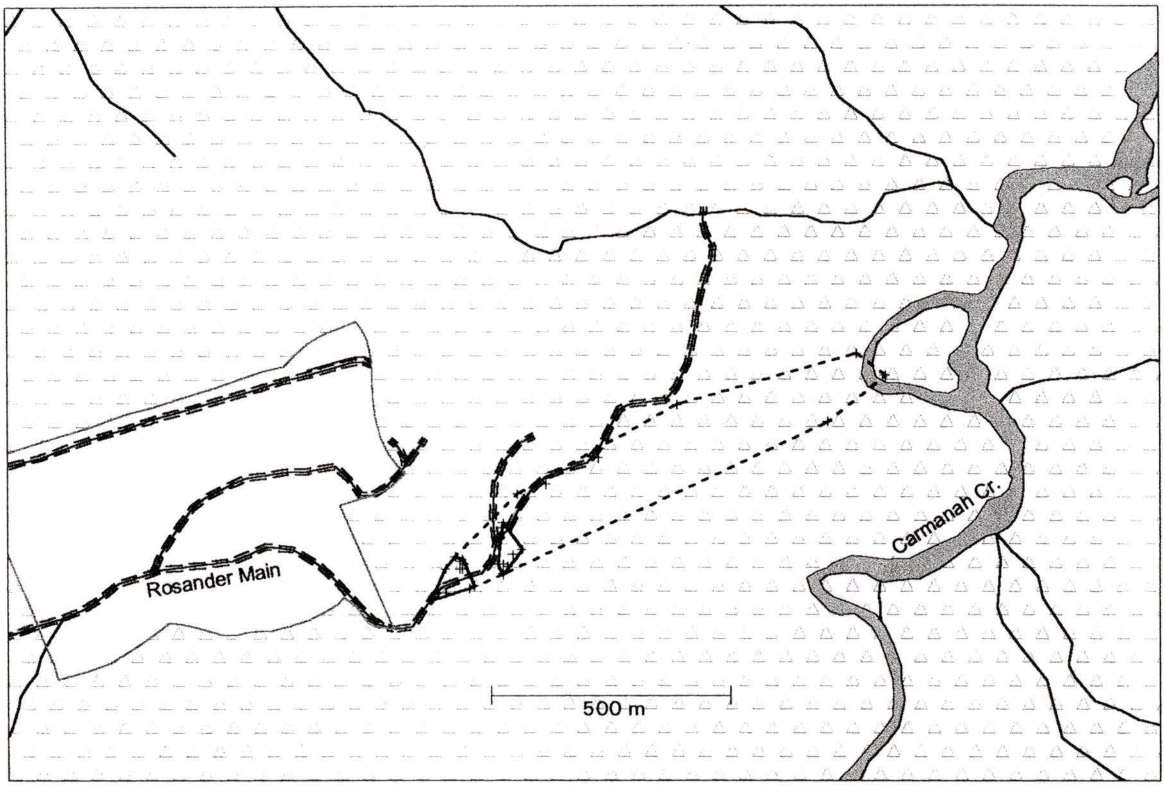
a). J-220, forest-interior jay in lower Carmanah.



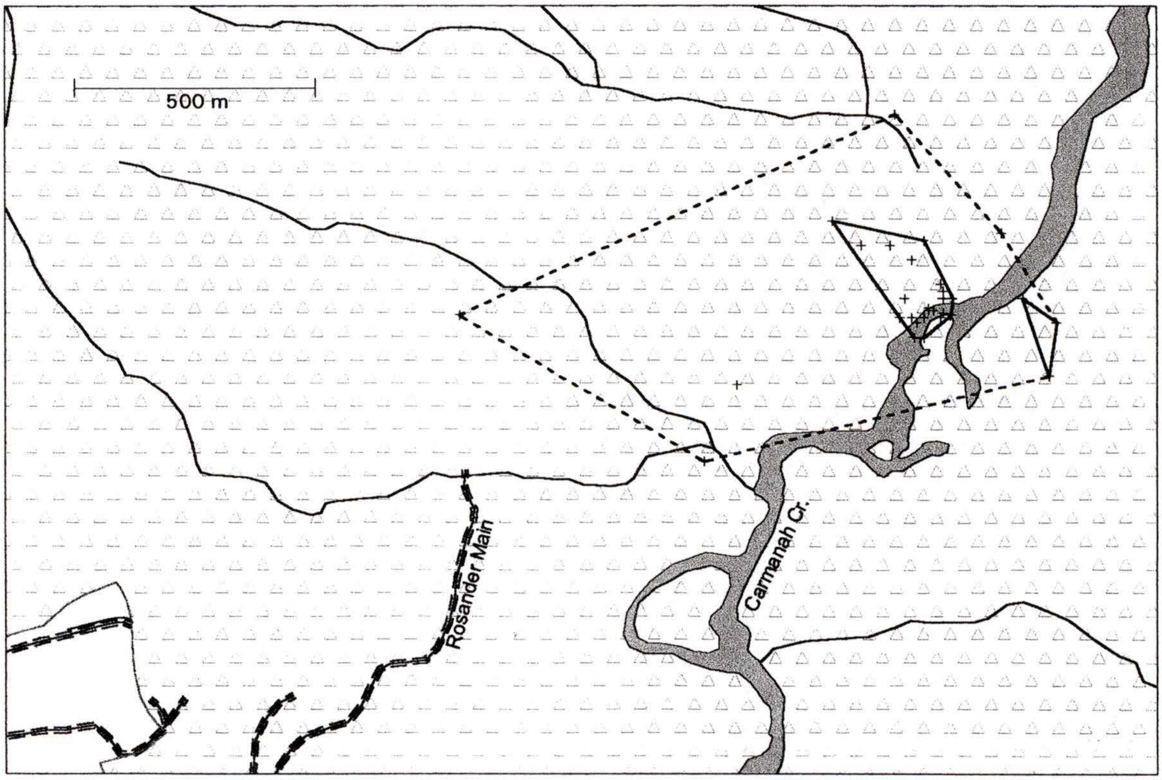
b). J-007, forest-interior jay in lower Carmanah.



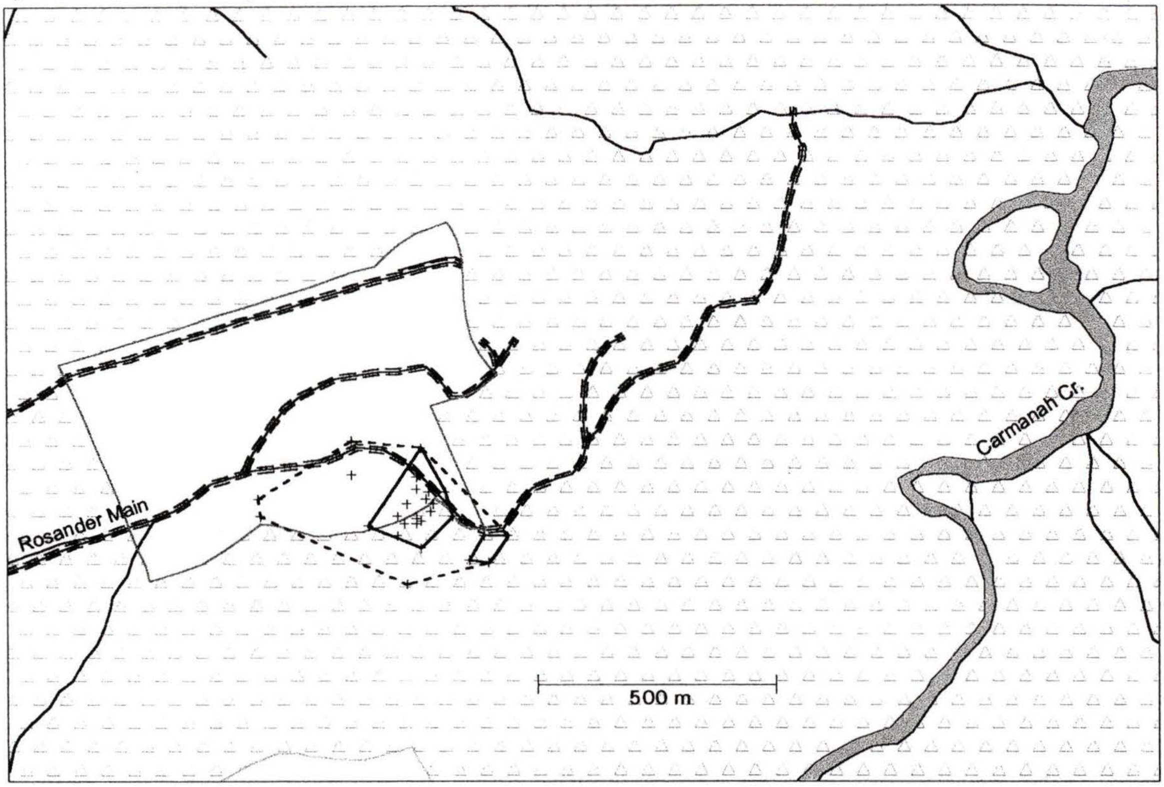
c). J-159, forest-interior jay in lower Carmanah.



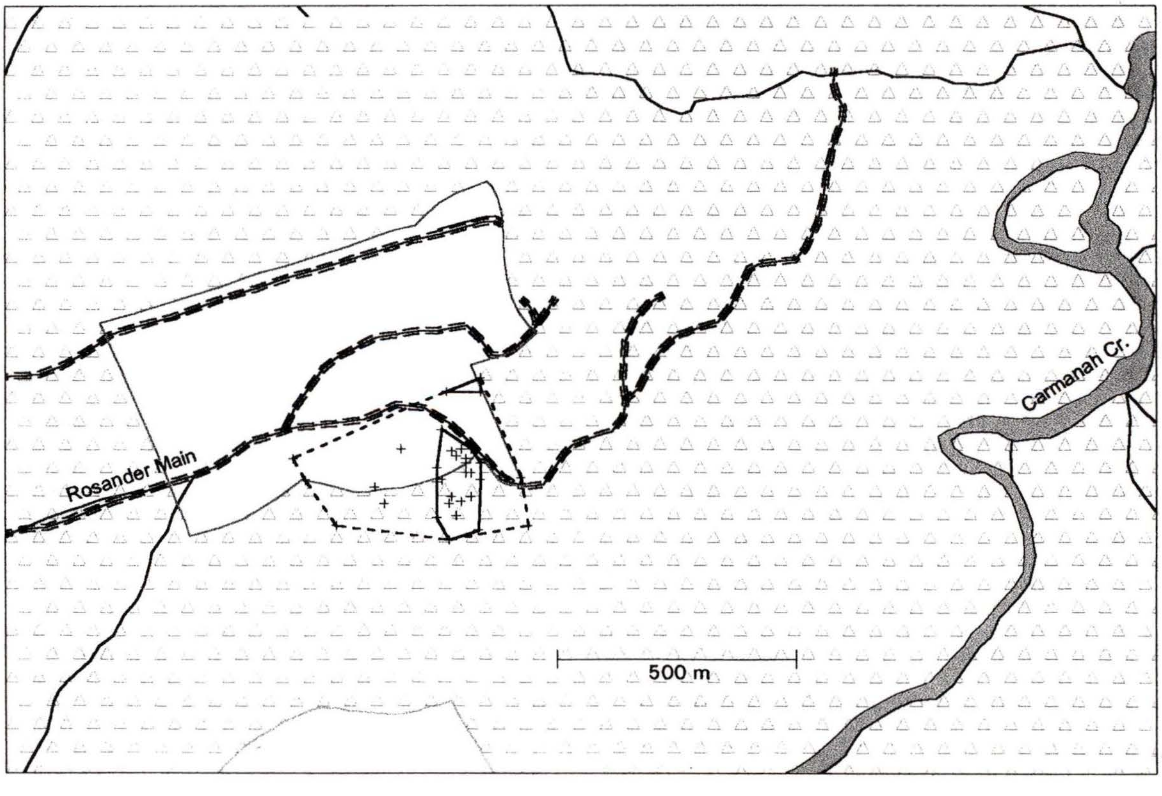
d). J-069, forest-interior jay in lower Carmanah.



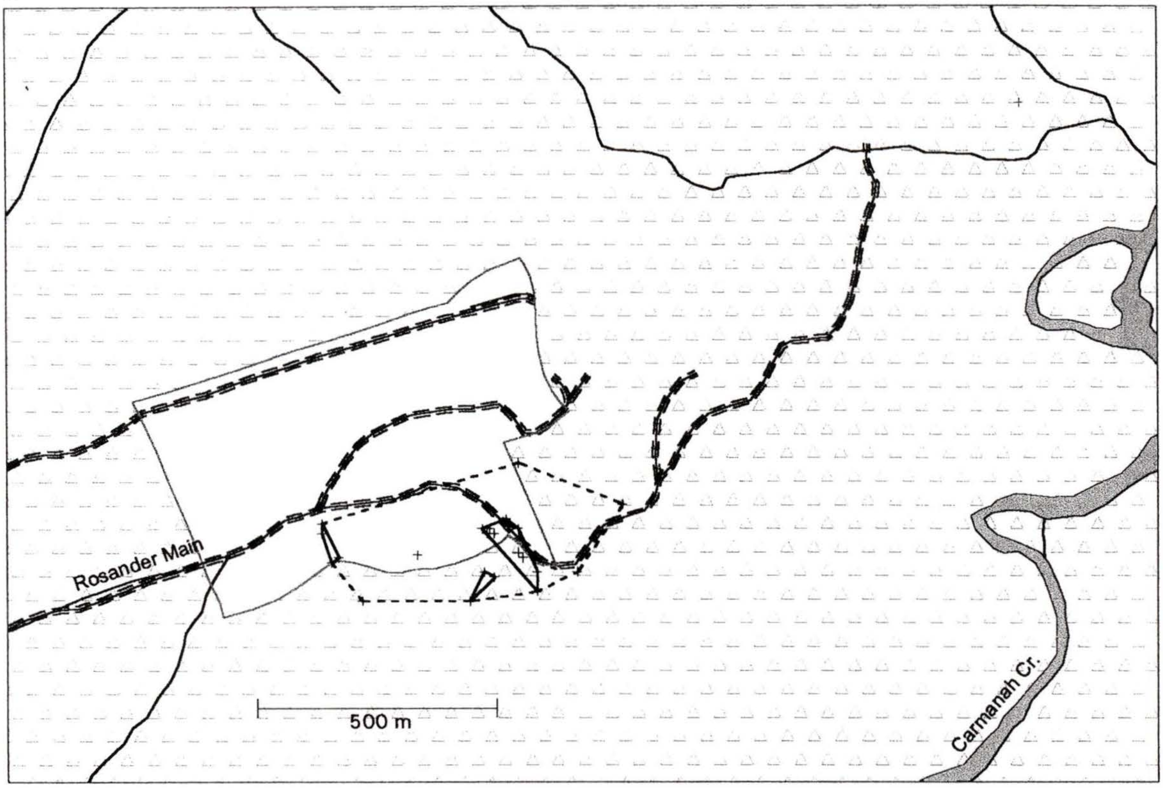
e). J-459, cutblock jay in lower Carmanah.



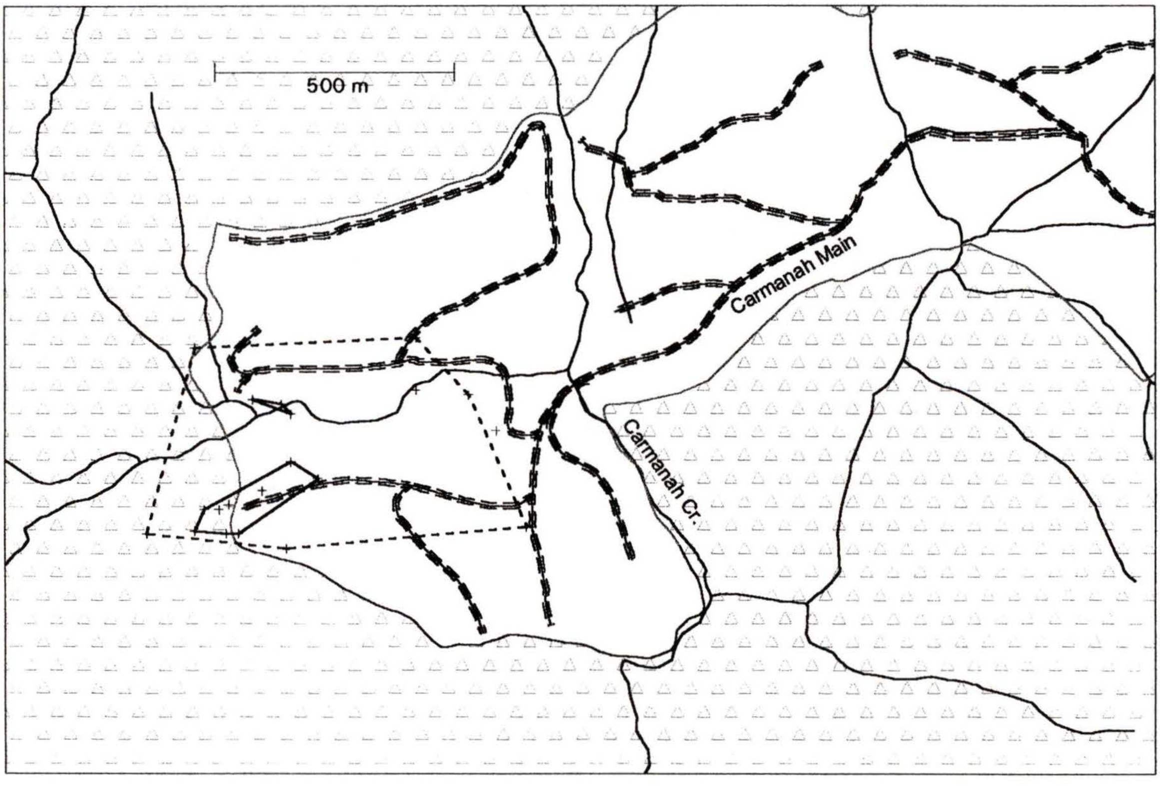
f). J-398, cutblock jay in lower Carmanah.



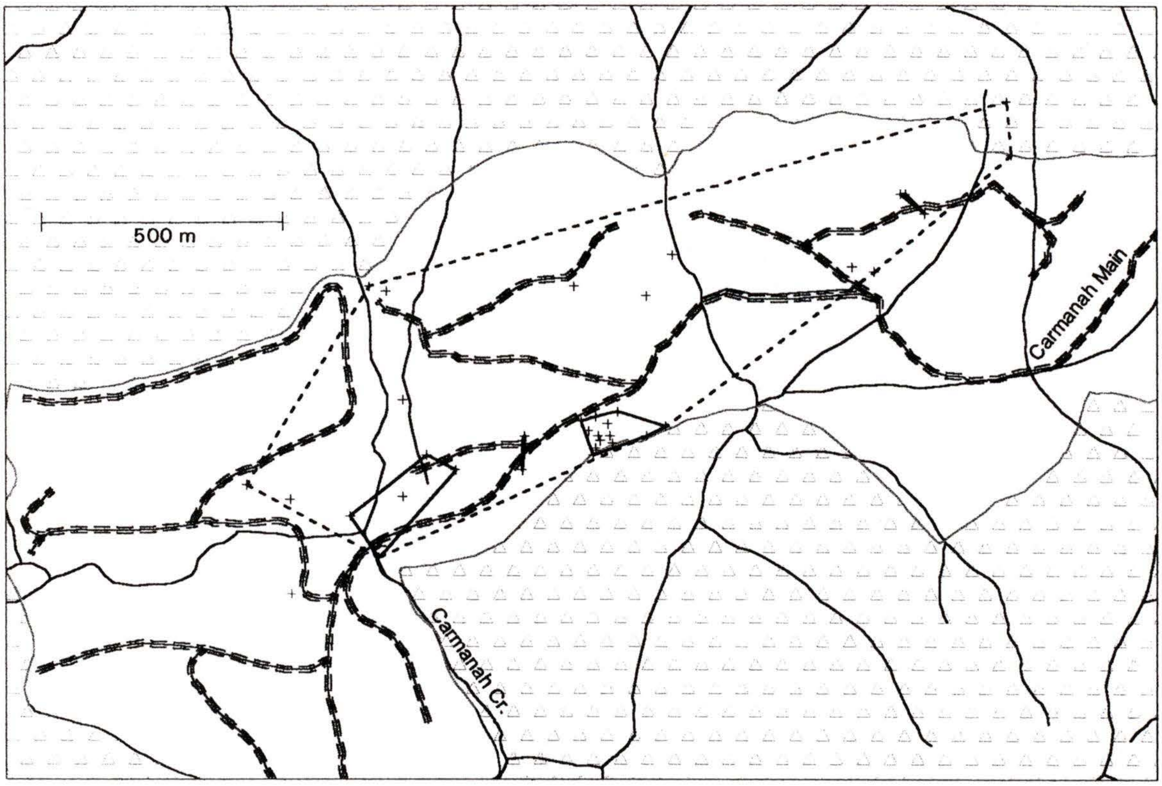
g). J-606, cutblock jay in lower Carmanah.



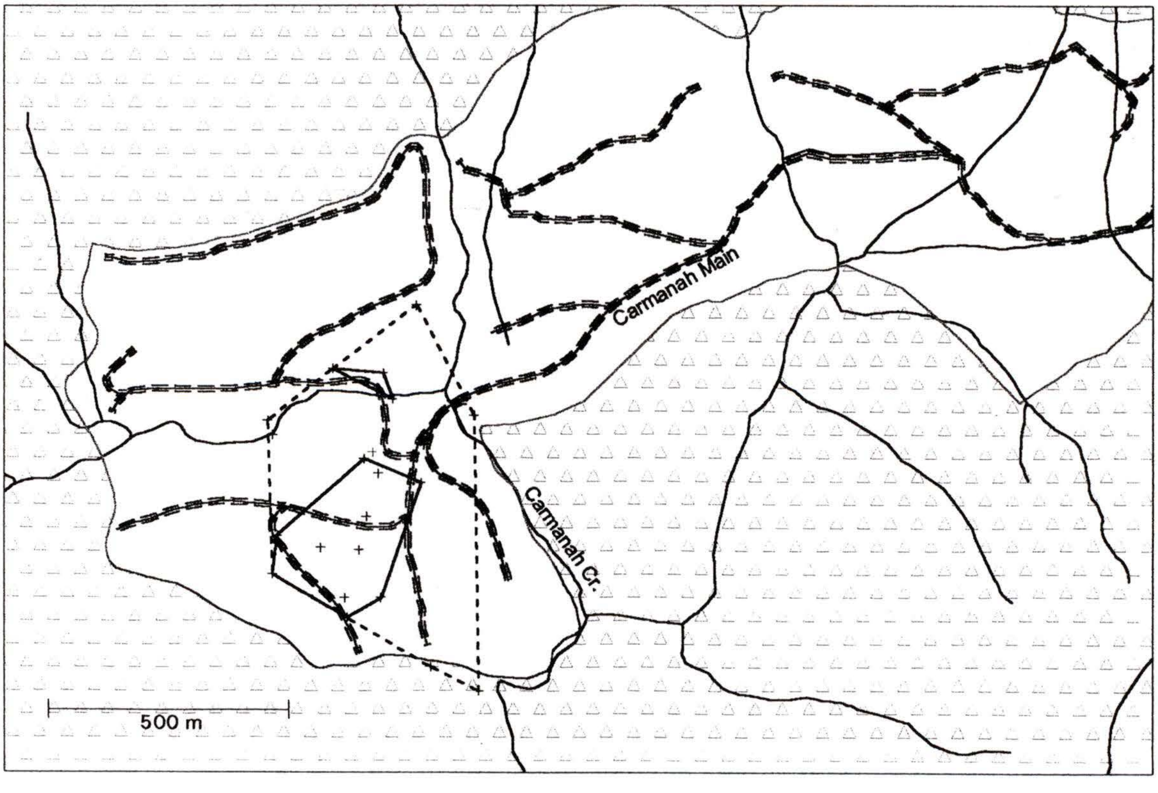
h). J-128, cutblock jay in upper Carmanah.



i). J-008, cutblock jay in upper Carmanah.



j). J-250, cutblock jay in upper Carmanah.



Micro-habitat

Vertical habitat use and associated behaviours

Patterns of micro-habitat use were similar between groups (Fig. 15). For cutblock jays, the mean percentage (± SD) of observations at ground, shrub, subcanopy and canopy strata were 8.8 ± 9.3%, 25.4 ±12.6%, 37.8 ± 19.5% and 27.9 ± 19.2%, respectively. For forest-interior jays they were 26.8 ± 21.4%, 22.2 ± 16.4%, 22.2 ± 8.1% and 28.8 ± 13.8%, respectively. Statistical tests were not performed due to small sample sizes but for randomly selected (nontagged) jays categorized as either cutblock (in clearcuts or within 75m of clearcut/forest edges, n = 30) or forest-interior jays (≥ 200 m from a clearcut-forest edge, n = 24), Chi-square analysis indicated that the relative frequencies of observations of all four levels were the same ($X^2$3 = 4.13, P = 0.25).

Foraging, perching and travelling jays showed variation in their vertical distribution (Fig. 16). Cutblock jays were observed foraging at the canopy level nearly 10 (tagged jays) and 4 (randomly selected jays) times more than forest-interior jays, and cutblock jays utilized all strata more equally than forest-interior jays. Observations of perching and travelling behaviours (tagged jays only) included only 0 - 6% ground level. Sample sizes were insufficient for statistical tests.

Use of specific substrates and food items

Jays used a wide variety of substrates (Table 12). Tree species that received >10% use included western hemlock, western red-cedar and red alder. The use of salmonberry, *Vaccinium* spp. and skunk cabbage was also observed across all groups totalling 2 - 13% of observations. Log substrate received 3 - 11% of observations across all groups. A few substrates were only used by forest-interior jays, including Sitka spruce, salal and stink currant.

Berries, insects and skunk cabbage spikes were important food items (Fig.17). Skunk cabbage was taken approximately twice as often by cutblock jays (tagged or random) than by forest-interior jays. Berries were often eaten by tagged cutblock jays (57%) but not random cutblock jays. Insects were often eaten by both tagged and randomly sampled forest-interior jays (30 - 35% observations respectively). Other food

Figure 15. Proportion of observations per forest stratum for each forest-interior and cutblock jay. Also included are the proportions of pooled observations of randomly selected jays designated as either forest-interior or cutblock birds according to the location of the bird when it was observed (≥ 200 m from the nearest clearcut edge - forest-interior jay, in clearcuts or within forests <75 m from a clearcut edge - cutblock jay). Number of observations per tagged jay and the number of observations of each pooled sample of randomly selected jays is located above each bar.

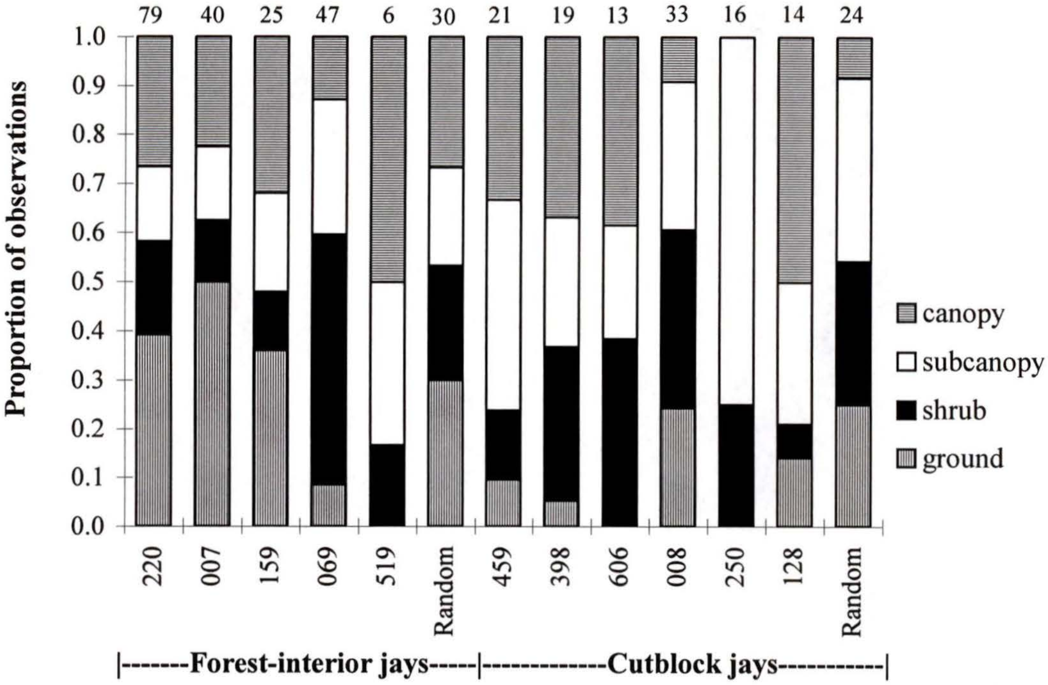

79
40
25
47
6
30
21
19
13
33
16
14
24
Proportion of observations
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
220
007
159
069
519
Random
459
398
606
008
250
128
Random
|-------Forest-interior jays-----|-------------Cutblock jays-----------|
canopy
subcanopy
shrub
ground

Figure 16. Vertical strata use by forest-interior (F) and cutblock (C) jays when foraging (tagged and randomly selected jays), perching and travelling (tagged jays only). For tagged jays, the mean proportion of observations was calculated per category for birds of each group.

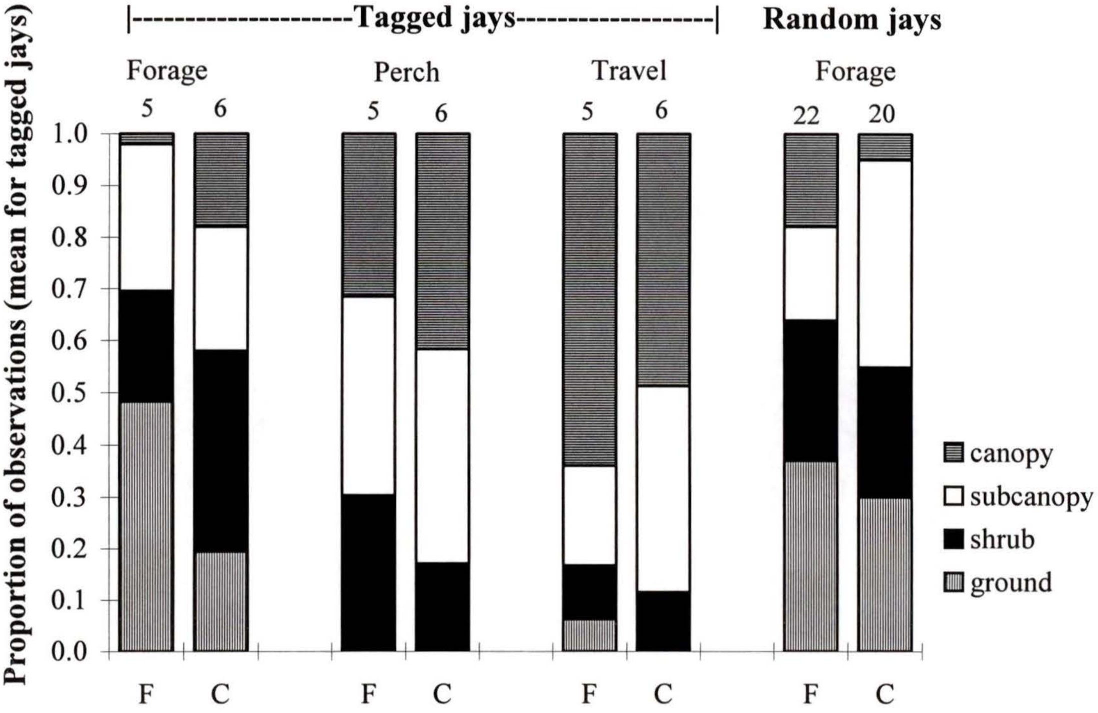
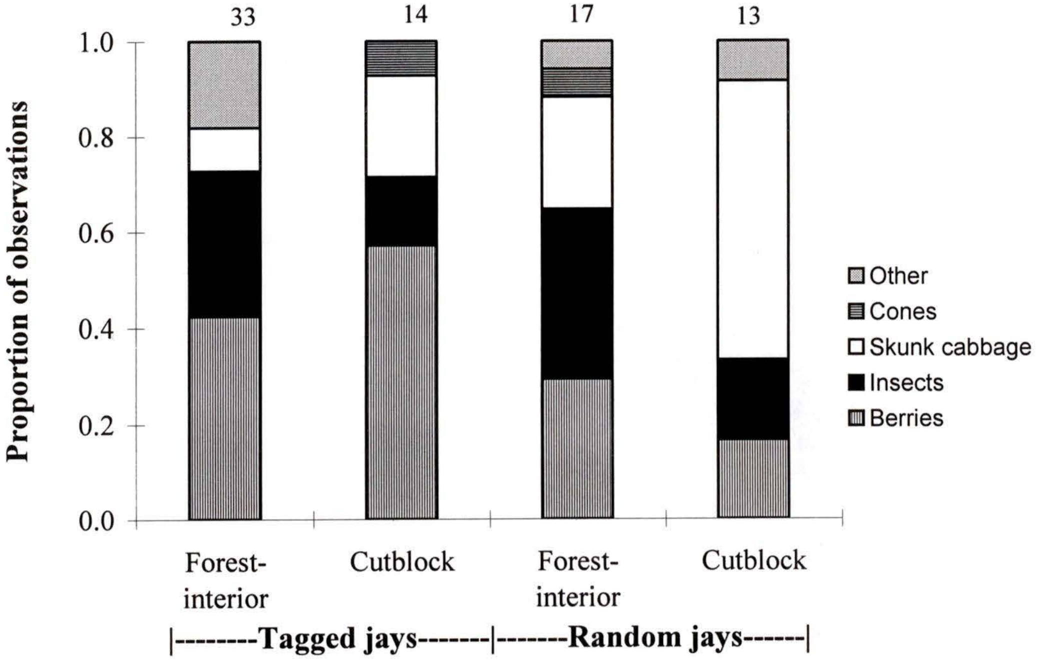

|--------------------Tagged jays-------------------|
Random jays
Forage
Perch
Travel
Forage
5
6
5
6
5
6
22
20
Proportion of observations (mean for tagged jays)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
F
C
F
C
F
C
F
C
canopy
subcanopy
shrub
ground

Table 12. Mean proportion of observations (including all behaviours) of tagged jays and proportion of observations of randomly selected jays on substrates commonly used in Carmanah-Walbran. For tagged jays, the proportional use of each substrate was first calculated for each bird and then averaged for each group (forest-interior jays n = 5, cutblock jays n = 6).

	Tagged jays				**Randomly selected jays**	
	Forest-interior		**Cutblock**		**Forest-interior**	**Cutblock**
Substrate	**Mean**	**SD**	**Mean**	**SD**	**n = 30**	**n = 24**
<u>Trees</u>						
Western hemlock (*Tsuga heterophylla*)	0.14	0.02	0.28	0.21	0.33	0.25
Western redcedar (*Thuja plicata*)	0.18	0.11	0.27	0.20	0.23	0.13
Sitka spruce (*Picea sitchensis*)	0.05	0.07	0.00	0.00	0.00	0.00
Amabilis fir (*Abies amabilis*)	0.01	0.01	0.04	0.09	0.00	0.00
Red alder (*Alnus rubra*)	0.17	0.20	0.13	0.04	0.07	0.13
<u>Shrub</u>						
Salmonberry (*Rubus spectabilis*)	0.02	0.05	0.03	0.05	0.03	0.08
Red elderberry (*Sambucus racemosa*)	0.01	0.02	0.02	0.03	0.00	0.00
Vaccinium spp.	0.03	0.04	0.02	0.03	0.13	0.04
Salal (*Gaultheria shallon*)	0.01	0.02	0.00	0.00	0.00	0.00
Stink currant (*Ribes bracteosum*)	0.00	0.01	0.00	0.00	0.00	0.00
<u>Herb</u>						
Skunk cabbage (*Lysichitum americanum*)	0.07	0.10	0.01	0.02	0.07	0.08
Forb, grass spp.	0.01	0.02	0.04	0.09	0.00	0.00
<u>Decaying wood</u>						
snag/stump	0.01	0.02	0.08	0.07	0.03	0.17
log	0.11	0.14	0.03	0.04	0.07	0.08
<u>Ground</u>						
Bare soil, gravel	0.17	0.17	0.05	0.06	0.03	0.04

Figure 17. Proportion of food items taken by tagged forest-interior and cutblock jays (observations pooled across jays of each group) and randomly selected jays of each group (forest-interior and cutblock). Number of observations from which proportions were calculated is located at the top of each column. Category *other* includes worm, nestling, camp-site debris, moss, gravel, and grass seed. Berries include salmonberry, red huckleberry, Alaskan blueberry, red elderberry, and common snowberry.


33
14
17
13
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of observations
Other
Cones
Skunk cabbage
Insects
Berries
Forest-interior
Cutblock
Forest-interior
Cutblock
|--------Tagged jays-------|-------Random jays------|

items eaten included worms, camp-site refuse, moss in the canopy of Sitka spruce, gravel from parking lots, and grass seeds. Of note, on May 28, 1996, I saw J-220 fly out of the forest from the shrub stratum carrying a ~1 week old Varied Thrush nestling.

DISCUSSION

Macro-habitat use

Edge habitat was an important feature for all tagged jays. Compositional analysis revealed that jays were selecting for edges at the home-range scale (Table 9). Within the home range, habitat use by cutblock jays was not random either (forest-interior birds were not tested). Again jays selected for edge habitat (Table 10). Likewise, the proportion of edge habitat within core areas was significantly greater than that available within the home range, but I did not perform selection analyses using these cores because they did not represent all areas used within the home range. Also of interest at this scale was that forest habitat ranked second for cutblock birds which suggests that the juxtaposition of these structurally different habitats is an important feature for this group.

These results differ from results obtained by Marzluff *et al.* (in prep.) for Steller's Jays of the Olympic Peninsula, Washington. There they found that within the home range, use of edge habitat was dependent on where jays were located relative to human settlement. Jays close to human settlement used edge habitat, which included the forest-settlement interface (e.g., at the edge of town), more than jays far from habitation where edges comprised the forest-clearcut interface. In addition, they found that jays without clearcuts in their home ranges used edge habitat more than those with clearcuts in their home ranges and they suggested that this was due to the limited availability of edge habitat in these ranges. These results may help explain the selection of edge habitat by forest-interior birds in my study. That cutblocks jays of Carmanah selected edge habitat as well may be linked to the lower level of fragmentation, and thus less linear edge, across southwest Vancouver Island as compared to the Olympic Peninsula.

The analysis of habitat selection is based on a number of critical assumptions which can easily affect results and conclusions. It could be argued that the sample of tagged jays were biased toward jays with edges in their home range. All tagged jays were caught near edges, but there was concerted effort to catch jays in forest core habitat as well (see Chapter 2). That I was unsuccessful in doing so reinforces the notion that jays do not spend much time in forest core habitat or that they are less abundant there. It also suggests that it would be unlikely to find a jay that did not have some portion of its range in edge habitat.

When habitat is in blocks, as it was in my study area, the definition of available habitat becomes crucial (Johnson 1980, Porter and Church 1987). I based availability on an area 20 times greater than each jay's home-range (an area which adequately represents spatial use by jays; discussed in Chapter 2). This was an objective approach which took into account the variability of spatial use among jays. Traditional designations of habitat availability based on arbitrary study area boundaries or composite home ranges (McClean *et al.* 1998) pose problems. Either method would have included a disproportionate area of forest habitat and an insufficient area of clearcut habitat. This problem was particularly evident for those birds whose home ranges straddled the watershed/park boundary and encompassed areas managed for timber harvesting. I could have designated a larger area of availability but this would not have changed selection results.

The definition of edge habitat also has important implications with regard to selection analyses. If I had extended edge habitat to 75 or 100 m on either side of the forest edge, selection of this habitat would have been less pronounced or perhaps eliminated. On the other hand, if edge habitat had been defined as <50 m, selection of this habitat would have been more pronounced. Jays were frequently located near edges and there was a distinct drop in locations > 50 m from an edge (Fig. 12). This drop represents a plausible delineation of edge habitat for jays and supports the use of the edge-habitat definition that I used in selection analyses.

The animals' behaviour or the timing of activities are also potential sources of error in the analysis of habitat selection. For example, if locations of tagged animals always corresponded to resting behaviours, or if animals used different habitats for different purposes (i.e., forest for resting, clearcut for foraging), results might not necessarily be representative (Palomares and Delibes 1992, Mysterud and Ims 1998, Jones 2001). However, neither of these problems applied to my study. Jays were tracked at random times during the day to produce an unbiased sample of locations, and except for day and night delineations (active and roosting) jay activities such as foraging, preening, and resting took place at any time of the day and in all habitats (pers. obs. this study).

Of some concern is the lack of independence between some tagged jays. Two forest jays were often seen together (Jays 220 and 007), had overlapping home-ranges and on a few occasions they behaved as if mated (e.g., begging and feeding; Brown 1963). In addition, their home-ranges closely overlapped. If these two jays were indeed a pair, then the assumption of independence between forest jays was violated and I should avoid any extrapolation of results to the population (Alldredge and Ratti 1992). However, because compositional analysis provides relative ranks regardless of significance, and habitat use trends were consistent with other tagged jays, I thought it was plausible to make inferences regarding habitat selection (Aebischer *et al.* 1993).

Cores represented well used foraging patches and they were generally associated with forest edges. They were positioned so that jays had easy access to mature trees used for caching food. Individuals used more than one core area, which was similar to results in Washington (Marzluff *et al.* 1999). The use of multiple cores suggests that jays require more than one foraging patch or used different patches for different purposes. It also suggests that the area encompassed by MCP home-ranges may in part depend on the location and distance between these intensively used areas (Mysterud and Ims 1998). For example (Fig. 14i), the four cores used by J-008 were widely separated, resulting in a large home range. If these core areas had been closer together, perhaps this jay would have had a much smaller home range.

Aside from the obvious difference in the use of clearcuts between forest-interior and cutblock jays (it was not available to forest-interior jays), I found no difference in overall macro-habitat use between the two groups for any of the parameters that were compared. The distance of cores to edge, core area and proportion of edge habitat within cores and in the home-range, were quite different between groups, but statistically were not significant. Either sample size was insufficient to detect a difference or these data reflected what was actually happening in Carmanah. If the latter is true, then these data suggest that forest-interior and cutblock jays used edge habitat, whether artificial or natural, in the same manner. The ranking matrix based on radio-locations of cutblock jays and their home ranges (Table 10) supported this idea as did the plot of mean % radio-locations at 50-m increments (Fig. 12). Although most cutblock jays were readily located in the middle of clearcuts, use of this habitat was less frequent than expected given availability. Despite having access to a third habitat, cutblock jays utilized edge habitat, 50 m on either side of an abrupt clearcut edge, more than expected.

Micro-habitat use

Forest-interior and cutblock jays used multiple forest strata, and the relative use of each stratum was not significantly different between groups (statistically analyzed for randomly selected jays only). The three tagged jays which did not use all four strata types available had likely not been observed enough (only 6-16 single-point observations). Surprisingly, the canopy level was used by cutblock jays as much as by forest-interior jays (except J-250) even though forest habitat was usually limited to only the perimeter of a cutblock jay's home range (Fig. 14). However, these results need to be viewed with some caution. The forest strata were not of equal height. The volume of space increased from layer to layer and would thus cause some bias in observations at the upper layers.

Foraging observations among forest-interior and cutblock jays were most prevalent at the subcanopy stratum and lower, while 70 - 90% of perch and travel behaviours occurred at the canopy and subcanopy levels, and rarely, if at all, at ground level (Fig. 16). Observation bias may have limited the number of foraging observations of both tagged and randomly selected jays in the canopy, but because I was able to distinguish travel and perch behaviours at that level, I assumed that it was small.

Among tagged jays, forest-interior jays foraged at ground level more than cutblock jays. Similarily, Salata (1982) found that Steller's Jays near San Francisco foraged at ground level more frequently when beneath canopy cover than in open habitat. This pattern was not observed with randomly selected forest-interior jays, likely because these jays could not be tracked into the dense underbrush like tagged jays.

In contrast, cutblock jays were often observed foraging in the canopy whereas forest-interior jays were rarely seen foraging at this stratum. Again, the difference was perhaps caused by visibility bias. One had a better view of the canopy when looking at it across an opening such as a clearcut than when standing within the forest looking up. Alternatively, perhaps use of this stratum for foraging was actually different between the two groups. This is possible given that within the home range, forest habitat ranked second in use by cutblock jays. These data suggest that although cutblock jays use forest habitat less than edge habitat, it is important. Perhaps because of microclimatic gradients at clearcut/forest edges (Chen *et al.* 1995) the canopy has a greater abundance of insects, making it an important foraging stratum for cutblock jays.

Jays used a number of substrates (Table 12). Any differences in substrate use between forest-interior and cutblock jays was based on the availability of that substrate. For example, Sitka spruce and stink currant were found only in the valley bottom, to which cutblock jays did not have access. Substrate use likely reflected different behaviours and even specific foraging behaviours not analysed. Redcedar in the clearcut (~ 4 m tall) and in the forest (~ 40 m tall), were often used for perching while Western hemlock and Sitka spruce were frequently used during travelling, flying from tree top to tree top, and caching. Red alder provided sheltered perch sites and evening roost sites but I also often observed jays gleaning insects from alder leaves or "flycatching" from alder branches. Logs were also popular flycatching platforms. All berry-producing shrubs represented potential foraging locations and as each species ripened, jays were often seen picking berries. Both cutblock and forest-interior jays were frequently observed in skunk cabbage patches, taking large pieces of this flower's central spike for caching, or probing into the bare soil beneath its large leaves for insects and worms.

Food items taken by jays reflected substrate use. Items of importance included berries, such as red huckleberry, salmonberry, and red elderberry, and insects (not identified). These items were also commonly eaten by jays in Washington (Marzluff *et al.* 1999). The flower spike of the skunk cabbage plant was an important food item in my study, in Washington (Marzluff *et al.* 1999) and in the Queen Charlotte Islands (Bent 1946).

Summary

Understanding how a predator uses its environment helps determine its impact on prey species. In this chapter, I quantified behaviour and habitat use of Steller's Jays at macro and micro-habitat scales. Analyses of habitat selection indicated that edge habitat was an important feature of home-ranges for both cutblock and forest-interior jays, and that it was used significantly more than clearcut and forest habitat within the home-range of cutblock jays. However, jays were not restricted to any one habitat type available to them and used edge, clearcut and forest habitats. Jays of both groups were not restricted to a specific forest stratum either. They used all four forest strata available.

The Steller's Jay is a habitat generalist or more accurately, a multi-habitat user (Andrén 1992). Of particular concern is the use of canopy and subcanopy strata by jays for caching, perching, travelling and foraging. All these behaviours increase the risk of jays detecting nests of other birds, and particularly nests of the Marbled Murrelet.

Steller's Jays are also prey generalists because they consume a variety of foods (Greene *et al.* 1998). This designation is not surprising given the variety of foods consumed by other corvids and this family's ability to rapidly learn new ways to gather food, recognize new food sources, and adapt to changing environments (Angell 1978, Marzluff *et al.* 1994). Because jays use a number of sources of food, their populations are less directly affected by the availability of any single prey item. In Carmanah-Walbran, a large population of Steller's Jays would increase the risk of predation at nests of the Marbled Murrelet.

CHAPTER 4. MARBLED MURRELET BREEDING HABITS IN RELATION TO STELLER'S JAY ECOLOGY: ASSESSING THE RISK OF PREDATION AT MURRELET NESTS

REVIEW

Murrelet nesting habits

Marbled Murrelets use many strategies to reduce detection of their nests by predators. To blend in better against the forest background, adult murrelets moult their white ventral and scapular feathers in exchange for cryptic plumage prior to the breeding season, and lay well camouflaged eggs. Their chicks use camouflage as well. They have cryptic downy plumage which they retain until the last 8 - 48 hours prior to fledging (Carter and Stein 1995). Travel to and from the nest is infrequent compared with other forest birds, very rapid (> 70 km/h), and usually during low light levels at dawn (up to 120 minutes before sunrise) and dusk (as much as 45 minutes after night fall) (Nelson 1997, Burger 1997). At the nest, vocalizations between adults and chicks are muted. When a predator is near, chicks and adults flatten themselves against their moss nest cup and remain motionless (Nelson and Peck 1995).

For most of their range murrelets place their nests well above the ground in the protective crown of mature conifers to reduce access by mammalian predators (Hamer and Nelson 1995a). Nest have been found as low as 11 m and as high as 54 m above the ground (Burger 2001). The average height of nests located in Carmanah-Walbran was 41 ± 8 m (SD, n = 10; Burger 2001) but these data only include nests found in large trees in the valley bottom. Murrelets also select nest sites with protective cover (Manley 1999), presumably to minimize detection from avian predators (Singer *et al.* 1995). Close proximity of the nest to the tree trunk may also be a protective feature (Singer et al. 1991). Manley and Nelson (1999) reviewed the success of murrelet nests (with known outcomes) from Alaska to California (n = 77) and found that nests within 0.5 m of the tree trunk were more successful than nests > 0.5 m from the trunk.

Marbled Murrelets avoid the potentially intense nest predation pressures experienced by densely populated seabird colonies (Nelson and Hamer 1995a, Gaston and

Masselink 1997, Hartman *et al.* 1997, Blight *et al.* 1999) by nesting in loose aggregations (DeSanto and Nelson 1995). On Vancouver Island, densities of active nests in apparently optimal forest habitat, have been estimated at 0.14 ± 0.14 (SD) nests/ha/year in Clayoquot Sound, (Conroy *et al.* 2001) and 0.15 ± 0.09 nests/ha/year in the Carmanah and Walbran valleys (Burger 2001).

Steller's Jay behaviour

The numerous strategies used by Marbled Murrelets to reduce detection of their nests suggest that murrelets evolved in conjunction with nest predators (Ralph *et al.* 1995). The Steller's Jay was likely one of these predator species. However, the Steller's Jay may be problematic for the murrelet because of its adaptive and "intelligent" nature (Bent 1946), which like many other corvids makes it a potentially effective predator (Angell 1978).

There are many examples of the opportunistic and adaptable nature of Steller's Jays. While trapping jays for telemetry, I observed jays detect, investigate, and utilize a completely foreign food source (peanuts) in less than one day. They learned quickly from a trapping experience, and were rarely re-trapped (although able to procure bait) even when a different trapping method was used. One jay actually learned to shuffle, rather than hop over a noose carpet (see Chapter 2 for description) to the bait, thereby avoiding getting snagged. Jays may have the ability to alter their foraging strategy to include searches of artificial nests used in nest predation experiments. In a recent study in Alaska, Sieving and Willson (1999) surmised that Steller's Jays were using quail eggs (placed in artificial nests) as a food source while rearing their nestlings. They observed a simultaneous and distinct drop in jay activity and predation rates of artificial nests after jays had fledged their young.

More importantly, jays are habitat and prey generalists (Marzluff *et al.* 1994). They were observed in many habitats: clearcuts, bogs, along rivers and roads, and within stands. They used all levels of forest strata: ground, shrub, subcanopy and canopy (Fig. 15, Chapter 3) and were observed on a wide variety of substrates (Table 12). Jays were observed collecting, eating and caching a wide variety of foods, including berries, insects, and the flower spike of the skunk-cabbage (Fig. 17). At the Park campground, jays regularly foraged in the parking lot and under picnic tables on food left by park visitors (pers. obs. this study). I even observed a jay emerging from the underbrush at the forest edge with a Varied Thrush chick in its bill.

The examples above highlight the fact that jays can key in to new opportunities in their environment. Although jays may not seek out murrelet nests, the manner in which they use their environment suggests that incidental contact with murrelet eggs and chicks is likely. In addition, as habitat and prey generalists, Steller's Jays are less directly affected by changes in availability of their prey source and can maintain high numbers by using other food sources (Marzluff *et al.* 1994).

Study results

In assessing the risk that Steller's Jays pose to murrelets of Carmanah-Walbran, I explored how and why jays do well in human-altered landscapes and described responses by jays to artificial edges and clearcut habitat. Results indicate that edge habitat is ideal for jays. Jays were significantly more abundant at the stand edge than at the stand core, and overall jay abundance was greater in stands bordering artificial edges (Fig. 6, Chapter 1). Telemetry and habitat analyses revealed that both cutblock and forest-interior jays were attracted to forest edges and that they used them in a similar manner (Fig. 12, Chapter 2). There were no statistical differences in any of the parameters tested such as range size, number and size of core areas used, and patterns of micro-habitat use. Cluster cores, representing areas of intense use by jays, were situated at or near stand edges for 90% of tagged jays (Table 11, Chapter 3). Compositional analysis revealed that tagged jays selected edge habitat, defined in this study as 50 m on either side of any abrupt stand edge, at study-area (forest-interior and cutblock jays) and home-range scales (cutblock jays only).

Jays are likely drawn to areas where the juxtaposition of open areas or gaps and old-growth stands occurs. These areas best serve the habitat requirements of jays. Jays specifically used old-growth stands for caching food and nesting, but frequently foraged on substrates associated with edges such as road shoulders, shrubs, saplings, deciduous trees and logs along creek beds and in clearcuts. The results of this study indicate that Steller's Jays benefit from the creation of edges through forestry activities and that this edge habitat supports greater numbers of jays. This is occurring either because existing jays have moved from forest core habitat to artificial edges or because new jays have moved in to these modified landscapes thereby increasing the overall number of jays there. The scope of my study precluded a determination of which scenario existed on the southwest coast of Vancouver Island.

IMPLICATION OF STUDY RESULTS

It is important to determine whether jays are merely shifting from one location to another or whether jay numbers across the landscape are actually increasing. In the former situation the number of murrelet nests found could be the same, just where nests were found would differ. In the latter situation, an increase in the overall density of jays will lead to an increase in the total number of murrelet nests exploited across the landscape. However, fragmentation of murrelet nesting habitat may in itself, still result in a greater risk of predation at murrelet nests because it leads to a greater proportion of edge per unit area of habitat. This would increase the likelihood of jay predation at murrelet nests in two ways: 1) by increasing the probability that a jay will be in the same habitat as a murrelet nest and; 2) by increasing the probability of a jay actually encountering a murrelet nest.

Probability of jays near nests

Logging activities reduce or bisect murrelet habitat

Jays are brought in closer proximity to murrelet nests through forestry activities. Logging removes murrelet breeding habitat. If stands of nesting habitat become isolated patches on the landscape, surrounded on all sides by a matrix of regenerating forests, they will likely have minimal core areas, and will offer no protection from penetration of the core by jays (Temple 1986). A murrelet nest (or nests depending on the size of the patch) within this patch would be near several jays (Ralph *et al.* 1995). The construction of roads is also detrimental, particularly access roads through unlogged sections of forest. Although forest habitat is not greatly reduced by construction of these roads, they may bisect murrelet nesting habitat and draw jays into the forest interior. This would increase jay numbers in the forest interior above previous levels, and at the same time would bring existing nest trees and nesting stands in closer proximity to edges.

Distribution of murrelet nests relative to edges

Augmenting the probability that jays would be near murrelet nests is the apparent edge-related distribution of murrelet nests. In Desolation Sound, British Columbia, Manley (1999) found that murrelets selected nest trees adjacent to canopy gaps caused by tree mortality, lack of vegetative growth, rivers and streams, and in openings created by forestry activities. Artificial gaps were preferred presumably because they were larger than the other gap-types. Hamer and Nelson (1995a), reviewed characteristics of murrelet nest trees and nesting stands, and found that 66% of known nests ($n = 68$) were ≤ 100 m from the nearest forest opening. However, these results may reflect an observational bias. Observers may have been spending >66% of their time searching for nests near edges. In areas managed for timber harvesting, compensating for this bias may not change the outcome. Even if murrelets nested randomly relative to edges, in fragmented habitat, a greater percentage of the forest is near edges and therefore murrelet nests would more likely be near edges as well.

Probability of jays encountering an active murrelet nest

Use of canopies by jays

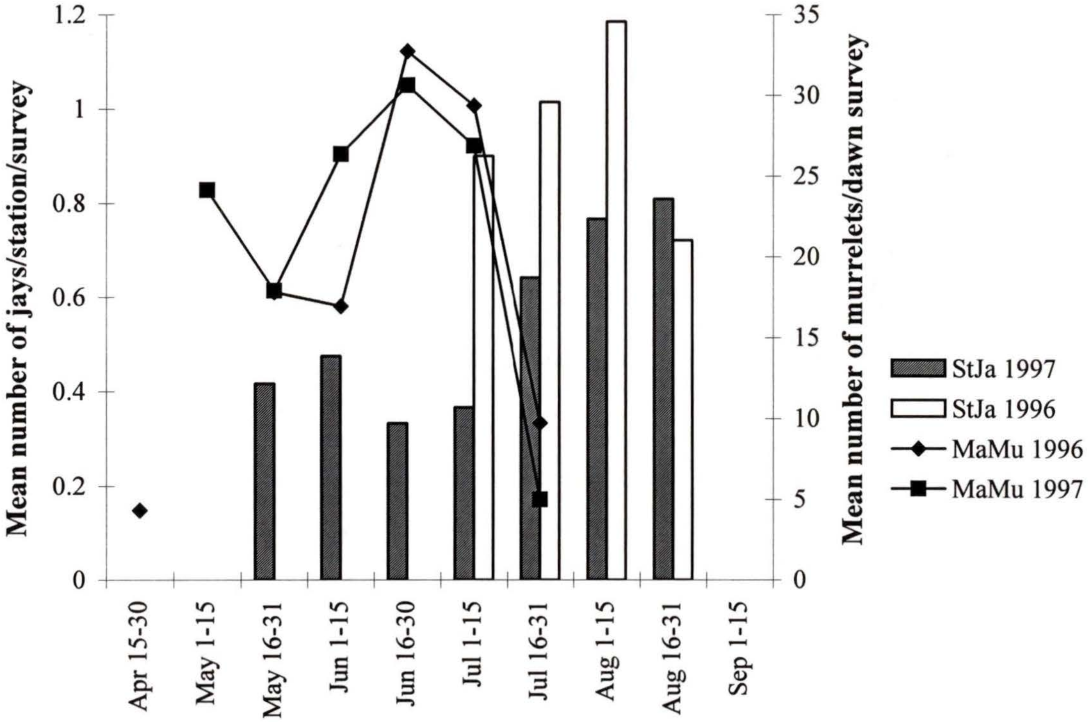
Given the low densities of murrelet nests, the probability of a jay encountering a murrelet nest may seem unlikely. However, there have been frequent sightings of jays at or near murrelet nests throughout the Pacific Northwest (reviewed in Nelson and Hamer, 1995a). In my study, the ground and shrub layers were used more intensively than the subcanopy and canopy layers relative to the volume of space in the latter two categories. However, jays were observed in the canopy stratum (mean percentage of locations for all tagged jays was 28%; Fig. 15, Chapter 3) and further examination of cutblock jays revealed that almost 20% of foraging observations were in the canopy (Fig. 16). Caching activity, not included with foraging behaviours, repeatedly brought jays up into the sub-canopy and canopy strata where murrelets nest as well. In addition, it is possible that once jays encounter an active murrelet nest, they repeatedly "visit" it. Jays exhibit spatial memory, particularly evident in their use of caching for their own food storage (Greene *et al.* 1998) and in "pirating" the caches of other birds (Burnell and Tomback 1985). Therefore, although the canopy layer represents a rather large area for jays to search for murrelet nests, it is plausible, given their behaviour in the canopy, that they would encounter murrelet nests at a greater rate than absolute time in that layer would dictate.

Breeding season of murrelets

The murrelet's long breeding season potentially increases the probability that jays will encounter murrelet eggs and chicks at the nest. Murrelet breeding is asynchronous among individuals and incubation through to fledging takes 106-170 days (Nelson 1997). Lougheed (2000) used telemetry, at-sea observations and physiological techniques to estimate murrelet breeding chronology and egg laying dates, and found that the murrelet breeding season in British Columbia extends from mid-April to mid-September. Although there is a distinct peak in inland breeding activities (mid-June through mid-July in Carmanah, Fig. 18, Burger 1994), it is possible to find murrelet nests containing eggs and chicks throughout the summer (Hamer and Nelson 1995b). For jays, this lengthy window of opportunity could potentially be used by both adult and fledged jays.

During the latter half of peak murrelet activity in Carmanah, adult jays are provisioning their chicks (Fig. 18). Later, near the end of the murrelet breeding season, straggling nesting murrelets may be at risk of being discovered by large groups of fledged jays (sometimes as many as a dozen individuals), which "roam" forest cores and edges. Based on observations of tagged individuals and plumage differences, adult jays never joined these groups. These juveniles were noisy and readily attracted to "new" objects, and would probably investigate a murrelet egg or chick if they encountered a nest.

Figure 18. The peak in murrelet detections in Carmanah-Walbran coincided with the Steller's Jay breeding season. See Figure 5 for information regarding data included for the Steller's Jay. Data for the Marbled Murrelet were based on the mean number of detected murrelets during dawn surveys (n = 0 - 29 surveys grouped into two-week intervals) conducted at 28 sites in the same valleys and in the same years (Burger, unpubl. data). Breeding chronology (covering all known dates) for the Marbled Murrelet was based on Lougheed (2000). Jay breeding period includes nest building, incubation, chick rearing and fledging (Campbell *et al.* 1997, pers.obs. this study).



|-----Jay breeding period-------|

|-Fledged jays present-|

|----------------Murrelet breeding season-----------------|

Limitations of this study

One important aspect of predation risk at murrelet nests that I was unable to address in this study is the probability of a jay taking a murrelet egg or chick when it encounters a nest. This would have required direct observation of jays at murrelet nests. Two nesting strategies decrease the probability of predation of eggs and chicks by jays: minimal exposure of the egg, and size of the nestling.

Protection of egg

Murrelet eggs are protected by the incubating adult. Studies have shown that adult murrelets are adept at defending themselves against jay-size predators (Singer *et al.* 1995, Nelson 1997), so it would be unlikely that a jay could take an egg while an adult was at the nest. Murrelets may occasionally leave the egg unattended for 3-4 hours at a time during the day in order to forage at sea (Nelson and Hamer 1995b), thereby providing a window of opportunity for a jay to take an egg. Egg neglect has resulted in the predation of eggs and chicks (Nelson and Hamer 1995a,b).

Small chicks are vulnerable

Murrelet chicks are brooded only until they can thermoregulate, usually in 1-2 days (there is some evidence of protective brooding past this point), at which point they are left on their own at the nest until they fledge 27-40 days later (Nelson 1997, Nelson and Hamer 1995b). Although semi-precocial, by day three when the adults leave them unattended, chicks only weigh roughly 50 g. At this size, chicks are vulnerable to predation by jays, as witnessed by Singer *et al.* (1991). However, chicks within days of fledging are able to defend themselves against jays (Singer *et al.* 1995). Therefore, jays have a limited window of opportunity in which to prey on chicks.

Predator community

Recent, multifaceted studies in Washington (Raphael *et al.* in press, Luginbuhl *et al.* in press, Bradley 2000) and Oregon (Luginbuhl, pers. comm.) emphasize the importance of understanding the behaviour and habitat use of all members of the predator community in order to properly assess predation risks to Marbled Murrelets of a given area. In Carmanah-Walbran, other potential predators of particular concern include the red squirrel (*Tamiasciurus hudsonicus*) and deer mouse (*Peromyscus maniculatus*). Common Ravens (*Corvus corax*), also known predators of murrelets (Manley 1999), were rarely seen in Carmanah, and Northwestern Crows (*Corvus caurinus*) were absent in interior forests presumably because they prefer the forests of the coastal fringe (Burger *et al.* 2000).

Many studies indicate that red squirrels are nest predators of forest birds (Darveau *et al.* 1997, Fenske-Crawford and Niemi 1997, Tewksbury *et al.* 1998, DeSanto and Willson 2001, Martin *et al.* 2001). Deer mice have also been observed preying on eggs and chicks of other alcids which nest in burrows (Gaston 1992, Blight *et al.* 1999) and quail eggs in artificial nests (Fenske-Crawford and Niemi 1997). In addition, deer mice have been trapped in the canopy of conifers in Carmanah (N. Winchester, pers. comm.). A study of these nest predators in Carmanah-Walbran would be worthwhile. However, unless these predators are preying on jays, they would not lessen the potential risk posed by Steller's Jays.

Why is an increased predation risk important to murrelets?

Like most other Alcids, murrelets lay a single egg clutch (DeSanto and Nelson 1995). Although there is some evidence to suggest that murrelets will replace lost eggs or may attempt a second clutch in the southern portion of their range, overall reproductive rates are low (Nelson 1997, Hamer and Nelson 1995b). Recruitment is further diminished during the breeding season because in addition to predation, nest failure is caused by abandonment and by chicks dying from exposure or falling from the nest (Nelson 1997). Cooke *et al.* (2001) estimated that there are as few as 0.14 to 0.22 fledged female murrelets produced annually per breeding age female in Desolation Sound, British Columbia. Due to such low fecundity, it is theorized that any increase in predation rates caused by an aggregation of predators is likely to be additive to normal post-breeding losses, and could keep murrelet populations at levels below what would naturally occur in remaining breeding habitat (Nelson and Hamer 1995a).

Population modelling suggests that adult survival is pivotal in maintaining murrelet populations (Boulanger *et al.* 1999) but reproductive success may be important as well. Beisinger and Nur (1997) found that current levels of reproductive success throughout the murrelet's range were insufficient to sustain populations. Predation of eggs and chicks does not immediately affect the population of breeding adults but can be a limiting factor on prey numbers when predation levels prevent or slow the rate of population growth of the prey species (Newton 1993, Temple and Cary 1988).

In a recent study in southeast Alaska, DeSanto and Willson (2001) found that in general nest predation was highest in habitats with the greatest abundance of nest predators. A review of all active murrelet nests from Alaska to California with known outcomes indicated that only 38% of murrelet nests located within 50 m of an edge survived, compared to 62% of nests more than 50 m from an edge (Manley and Nelson 1999). If we assume that murrelets nest more frequently near edges, given the results of this study, it is possible that Steller's Jays of Carmanah-Walbran further reduce fecundity of the Marbled Murrelet and thereby limit its numbers in these watersheds.

MITIGATIVE MEASURES

If disturbed habitats attract jays and artificial edges reduce and bisect murrelet nesting habitat, the best way to mitigate potential nest predation risks caused by jays is to limit the creation of new edge habitat, reduce the contrast of existing man-made edges, and reduce opportunities for jays to be attracted to human refuse at picnic areas and campsites situated in stands occupied by murrelets. I discuss these concepts in the context of Carmanah-Walbran Provincial Park.

Reduce edge habitat

The silvicultural system (cycle of activities planned for a particular stand from harvest through to regeneration) chosen for an area can dramatically impact the extent of new edges created around parks. Small complexly shaped clearcuts and leave-areas (< 40 ha) like those located near the entrance to Carmanah-Walbran Provincial Park (16 -25 ha) reduce the contiguity of old-growth forests and shrink the area of forest core habitat in stands adjacent to the park boundary (Province of British Columbia 1995a). To reduce edge habitat and thereby reduce edge related nest losses, both Niemuth and Boyce (1997) and Gustafson and Crow (1994) suggested aggregating small clearcuts to create fewer larger openings.

Group-cut selection (where a series of 0.25 - 1.0 ha openings are created every 10 -20 years) and variable retention regimes (where groups of trees are left behind) are not viable alternatives. Both systems, which attempt to address the visual issues and biodiversity concerns of clearcuts, would actually cause more harm than good because they create more edge per unit area cut than clearcuts (Gustafson and Crow 1994, King *et al.* 1998).

Road construction within and adjacent to parks can reduce the contiguity of forests as well. In Carmanah-Walbran Provincial Park for example, there are 4.6 km of unused access roads. Based on a minimum 25 m road width (including ditches and deforested edges) and a conservative edge-effect penetration into the forest of 50 m, these roads represent 11.5 ha of open habitat and 57.5 ha of edge habitat. These roads reduce the area of forest core habitat and thereby modify the quality of protection provided by the park (Schonewald-Cox and Buechner 1992). Because roads are persistent features on the landscape even when no longer in use (it often takes decades for trees to establish), they would act as long-term, high contrast edges that would attract jays. In order to reduce edge habitat, unused access roads within parks should be removed, and to ensure a normal rate of succession, the topography restored. For the same reason, roads created for timber extraction should not run along park boundaries.

Reduce edge contrast

Angelstam (1986) suggested that the "steepness of the productivity gradient between an habitat island and the surrounding matrix" was the main factor influencing predation rates in fragmented environments. In studies that specifically examined edge contrast and nest predation, abrupt edges had higher predation than "feathered" edges (Ratti and Reese 1988) or edges that acted as transition zones (Chasko and Gates 1982). Yahner and Mahan (1997) reported that nest fate was related to the type of induced edge.

In their study, 84% of artificial nests at clearcut plot edges were disturbed as opposed to only 22-64% at various road edges.

In many areas, timber harvesting has reached the Carmanah-Walbran Park boundary, creating long stretches of high-contrast edge (old-growth forests adjacent to early seral-stage stands). A study by Marzluff *et al.* (2000) found that stands of simple structure support the least predators. Such results suggest that if stands which are adjacent to the Park were selectively logged in a manner which would simplify their structure, they could reduce edge contrast at the Park boundary and act as a buffer against jays.

Existing high contrast edges along park boundaries could also be reduced by extending the time allowed for the regeneration of previously harvested stands adjacent to leave-areas or proposed cutblocks. Currently, second and third cuts in an area take place roughly when "green-up" of previously harvested stands reaches 3 m in height (Province of British Columbia, 1995b). At this height, edge contrast is still attractive to jays and food resources plentiful due to the abundance of deciduous trees and berry producing shrubs (pers. obs. this study). By allowing conifers to reach 10-15 m in height (pole-sapling stage) before going back in to harvest leave-areas, the shrub component is eliminated or in decline, thereby limiting the amount of food and high contrast edge available at any given time adjacent to the Park.

Reduce disturbance and access to human food

New or additional trail systems and camping areas in murrelet nesting habitat require careful planning and should be located in areas of low murrelet detections and away from natural travel corridors like rivers. Incidents of direct human disturbance of murrelet nests by park visitors are few (Nelson 1997, Long and Ralph 1998). However, human activities such as hiking, picnicking and camping become a concern when corvids, and in particular Steller's Jays, become attracted to food left by people. On numerous occasions I witnessed jays foraging in campsites and parking lots, anywhere where crumbs could be found or an obliging tourist was giving handouts. In park settings, people are drawn to natural edges such as rivers, but this edge type usually supports prime murrelet nesting habitat. It would therefore be better to place trails and campsites beyond the riparian zone, where possible, to reduce a tourist-season influx of jays. At the same time, efforts should be made to educate tourists in the consequences of feeding corvids.

Conclusion

In general, forest fragmentation does not alter how Steller's Jays respond to their environment. Jays that have access to new open habitat such as clearcuts make use of edges and behave in a similar manner to jays which do not use clearcuts. However, the creation of edges through timber harvesting activities does augment the numbers of jays in these areas while at the same time exposing more murrelet nests to edges. Therefore, eggs and chicks of murrelet nests are at greater risk in fragmented landscapes. This risk could be greatly minimized by reducing the amount of edge habitat and the contrast of existing edges, and by careful placement of trails and campsites in stands used for nesting by murrelets.

An assessment of predation risk is a major step toward making more informed decisions regarding the management of predators like the Steller's Jay and prey species such as the threatened Marbled Murrelet. Attempts are being made to obtain actual measurements of predation rates at murrelet nests. However, many researchers have found that it is costly and logistically difficult to obtain a large enough sample of active murrelet nests for study (Manley 1999, Lougheed 2000). In addition, methods necessary to observe nests (e.g., climbing adjacent trees, setting up cameras) are often disruptive (Nelson 1997, Long and Ralph 1998). Other studies that would aid in assessing the predation risk posed by jays include an examination of changes in jay abundance with stand regeneration and an investigation of jay predation at the nests of other species of forest birds. With such information, managers would have a better understanding of how jay numbers change over time and the effect that jays have on other bird populations. Of particular importance would be a large scale and long term census of jays on southwest Vancouver Island to determine if the jay population is indeed increasing in areas managed for timber harvesting.

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