HABITAT OF WINTER WRENS IN RIPARIAN AND UPLAND AREAS OF COASTAL FORESTS

by

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B.Sc., University of British Columbia, 1986

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

November 1998

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ABSTRACT

I studied the influence of water on placement of territories and selection of nest sites by Winter Wrens (*Troglodytes troglodytes pacificus*) in the Coastal Western Hemlock Dry Maritime subzone forests of British Columbia. Male Winter Wrens preferred to place their territories in habitats influenced by water (riparian and moist), although access to these sites for some males was likely limited by the spatial arrangement of territories. Strength of the association between Winter Wren territories and water depended on local annual weather and likely available food. In wet years, Winter Wrens preferred habitats influenced by water; whereas in dry years, Winter Wrens preferred habitats with large volumes of downed wood. Males chose nest sites in relatively open patches that had fewer trees and snags than the surrounding forest, and they preferred to build their nests near riparian systems. Creek banks and upturned root masses were preferred by male Winter Wrens as nest substrates compared to logs, snags and branches. Riparian habitats may provide superior nesting opportunities for males because these habitats have moister microclimates, preferred nest substrates, and more diverse stand structure than other sites in the stand. Because of habitat selection by males, most potential nests available to females were near riparian systems. However, among these nests, female Winter Wrens did not select nests that were closer to riparian systems, nor did they prefer any particular type of nest substrate. Nests occupied by females were more secure and easier to access than were unoccupied nests. I located song perches of Winter Wrens along transects in young (40 to 60-year-old) and mature (80 to120-year-old) forest and compared them with randomly selected locations to examine habitat use over a range of forest conditions. Even at this broad scale, Winter Wrens selected structurally complex patches of open forest. These patches were associated with riparian systems and likely influenced by light and moisture from gaps in the overstory canopy. Uprooted trees may have produced habitat patches for Winter Wrens that compensated for lack of riparian habitat in some stands. Because of its abundance, broad distribution, and habitat flexibility, the Winter Wren is an appropriate species for examining effects of forest practices on wildlife habitat in coastal forests of the Pacific Northwest.

Acknowledgements

This study received financial support from the British Columbia Ministry of Forests and through the Canada-British Columbia Forest Resource Development Agreement: FRDA II. Support was provided in part through the Silvicultural Systems Research Program and Forest Renewal British Columbia because the study area overlapped the Alternative Silvicultural Systems Research Site in the Roberts Creek Study Forest. I thank Drs. A. Harestad, N. Verbeek, K. Lertzman and A. Derocher for their time, advice, and insight into the study of wildlife habitat ecology. Peter Ott, Wendy Bergerud and Vera Sit of the B.C. Ministry of Forests (Research Biometrics Section) and Amanda Nemec (International Statistics and Research Corp.) provided me with essential statistical support on all aspects of my research. Invaluable field assistance was provided by Kevin MacPherson, Kate Hagmeier, Duane Sept, Rebecca Boettger and Karen Leonard. Alex Inselberg conducted the ecological mapping of the research site, and Peter Pitsakis from the Vancouver Forest Region provided GIS support. Personnel of the Sunshine Coast Forest District, Sechelt field office, provided logistical support. Researchers of the Vancouver Forest Region including Paul Courtin, Gerry Davis, Brian D'Anjou and Fred Nuszdorfer advised and helped me with the forestry aspects of this project. I am grateful to the Stillwater Division (Powell River) of MacMillan Bloedel Co. Ltd. for assisting in locating sites and supporting my research in TFL 39.

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General Introduction

Winter Wrens (*Troglodytes troglodytes*) occur in the Northern Hemisphere of both the Old and New Worlds and are a common resident (*T. t. pacificus*) in coastal British Columbia (Peterson 1961, Godfrey 1986, Ehrlich et al. 1988). They are insectivorous birds preyed upon in southwestern British Columbia by Douglas squirrels (*Tamiasciurus douglasi*, pers. observ), hawks (*Accipiter* sp., pers. observ.) and marten (*Martes americana*, Nagorsen et al. 1989). Our knowledge of the ecology and habitat use of Winter Wrens relies largely on European studies (Armstrong 1956, Garson 1980a, 1980b, Wesolowski 1983), community studies and incidental observations because there have been few studies of the Winter Wren in the Pacific Northwest of North America (McLachlin 1983, Van Horne and Bader 1990). Yet, the Winter Wren is ubiquitous in this region and an understanding of its autecology would contribute to our knowledge of coastal ecosystems and their bird communities.

Although Winter Wrens use a range of habitats, their abundance is correlated positively with habitats influenced by water, including those with free water or those with moist soils (McLachlin 1983, Carey 1988, McGarigal and McComb 1992). However, little is known about whether these habitats are important to Winter Wrens when they select territories and whether these habitats enhance reproductive success (Scoullar 1980, McLachlin 1983, Wesolowski 1983, Godfrey 1986, Manuwal 1991). Riparian and moist habitats may be more desirable to Winter Wrens for foraging, nesting, and thermoregulation than drier habitats because of the more complex stand structure typical of such areas, stand microclimate, and presence of water (Hawthorn et al. 1971, Armstrong and Whitehouse 1977, McLachlin 1983, Barrows 1986, Ehrlich et al. 1988).

The difficulty in assessing why riparian habitats may be preferred by Winter Wrens occurs because of the inter-relationships between water and forest stand structure. Winter Wrens use areas of localized disturbance (e.g., tree fall) that are associated with canopy openings and characterized by dense understory vegetation, downed wood, and upturned roots (Wesolowski 1983, Godfrey 1986, Holmes and Robinson 1988, Tobalske et al. 1991). Because riparian habitats are subject to these localized disturbances, it is difficult to determine if Winter Wrens prefer riparian habitats or if they prefer the disturbed areas that occur in riparian habitats, or both.

Riparian ecosystems are characterized by water flowing in channels and the riparian area adjacent to the channels. For this study I refer to the 'riparian ecosystem' as the 'riparian system', because my definition is limited to particular features or communities of the ecosystem. Typically, riparian areas have a high ratio of forest edge to area, a moister and cooler microclimate, standing water during all or part of the year, variable soil moisture with periodic flooding, and greater horizontal and vertical stand structure. Combined these features induce distinct plant communities and a diversity of niches compared to the upland areas (Raedeke 1988, Stevens et al. 1995). The upland area begins where decreased moisture availability creates accompanying changes to plant species composition and physiognomy (Raedeke 1988).

For the purposes of my study, I separate riparian systems into two classes creeks and streams. In my study area, creeks, compared to streams, usually have water throughout most of the breeding season, undercut banks along most of their length, gullied topography, strong gradients in microclimate (moisture, temperature, humidity), and overstory canopy gaps (edaphic gap, *sensu* Lertzman et al. 1996). Creeks channels were approximately 5-10 m wide, while stream channels were generally <5 m wide (and included noticeable seeps). Although streams vary, they are usually seasonal with sporadic undercut banks and canopy gaps. Generally, the banks of narrower water channels compared to those of wider channels have: vegetation with a greater influence on the aquatic zone; a narrower edge, with up to 100% canopy cover; a less distinct change in plant species composition; greater amounts of terrestrial organic debris that enters into the channel; and, greater accumulations of downed wood (Bilby 1988). Many narrow riparian systems, unlike wide riparian systems, do not appear as visually distinct zones, but have subtle trans-riparian gradients within the forest matrix (Gregory et al. 1991, McGarigal and McComb 1992).

Soil moisture is important to consider when assessing the relationship of water to wildlife habitat because stand structure, microclimate, plant communities and some animal communities can change with the amount of moisture in the soil (McLachlin 1983). Moist sites have higher water content in the soil compared to dry sites (Green and Klinka 1994). I refer to these sites and their associated features and communities as 'moist, mesic, or dry systems'. The terrestrial habitat in the riparian area of creeks and streams may have dry to moist systems present because quantity of soil moisture depends on the influence of slope and slope position on ground water.

The Winter Wren, because of its association with riparian habitats, may be a good species for understanding the contribution that small riparian ecosystems make to wildlife habitat, and whether this contribution changes with features associated with channel size. As well, because forest management regimes are often regulated by the occurrence of riparian habitats, the Winter Wren may provide insight for understanding the effects of forest management practices on riparian habitat and for testing specific hypotheses about operational forestry treatments at the stand-level (Green and Klinka 1994, British Columbia Ministry of Forests and British Columbia Ministry of Environment 1995a, 1995b). Rotations of stands for timber change the availability and distribution of structural attributes for wildlife depending on the management regime (Oliver 1981, Franklin and Spies 1991, Hansen et al. 1991, Keenan and Kimmins 1993), and thus potentially change the rate and direction of ecological succession and value of habitat (Hayes et al. 1997).

For my thesis, I use a hierarchical, multi-stage approach to study habitat use and selection over several spatial scales (Van Horne 1983, Aebischer et al. 1993, Orians and Wittenberger 1991, Manly et al. 1993). I examine microhabitat (nest site and song perch) and macrohabitat (territory) patch use by the Winter Wren in relation to riparian systems of unmanaged second-growth forest stands in coastal British Columbia. In Chapter 1, I examine placement, spatial arrangement, and habitat of Winter Wren territories relative to systems influenced by water, as an example of macrohabitat use in stands of mature forest. In Chapter 2, I examine selectivity by both male and female Winter Wrens for nest substrates and nest sites relative to locations of riparian systems and availability of forest attributes. In Chapter 3, I further examine the relationship between territories of males and riparian systems. I assess the importance of riparian systems to Winter Wrens for a broader area, and I determine whether riparian systems are equally important to Winter Wrens in both young and mature forests. I also describe microhabitats selected by Winter Wrens within their territories. In Chapter 4, I discuss the validity of my approach and the application of my research to forest management.

Study Area

My study area is located along the Sunshine Coast from the Sechelt Peninsula to Powell River, British Columbia (Fig. 1). It lies mostly within the Coastal Western Hemlock Dry Maritime subzone (CWHdm) (Meidinger and Pojar 1991, Green and Klinka 1994). The CWHdm ranges in elevation from sea level to approximately 650 m and is characterized by warm, relatively dry summers, moist, mild winters, and little snowfall. Forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*), with an understory of salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parvifolium*) and sword fern (*Polystichum munitum*) (Green and Klinka 1994). Part of the study area (Roberts study block) is transitional between the CWHdm and the Coastal Western Hemlock Submontane Very Wet Maritime variant (CWHvm1). The CWHvm1 variant ranges in elevation from sea level or above the CWHdm to approximately 650 m and is characterized by a wet, humid climate with cool summers, mild winters, and little snowfall (Meidinger and Pojar 1991, Green and Klinka 1994). In the CWHvm1, forests are dominated by western hemlock and amabilis fir (*Abies amabilis*) with lesser amounts of western redcedar. The understory is dominated by red huckleberry and Alaskan blueberry (*Vaccinium alaskaense*), and characterized by having a well-developed moss layer (primarily *Hylocomium splendens* and *Rhytidiadelphus loreus*) and sparse herbs.

The research discussed in Chapters 1 and 2 focuses on an unmanaged, mature (approximately 80 to 120 years old) stand in the Roberts Creek Study Forest (49°35'N, 123°38'W; elevation 100 to 200 m). Riparian systems within this stand have channels generally <10 m in width. One advantage of working in the Roberts Creek Study Forest was the mostly drier subzone, CWHdm, rather than the moister CWHvm1. The drier habitat may better express effects of riparian factors on habitat associations of Winter

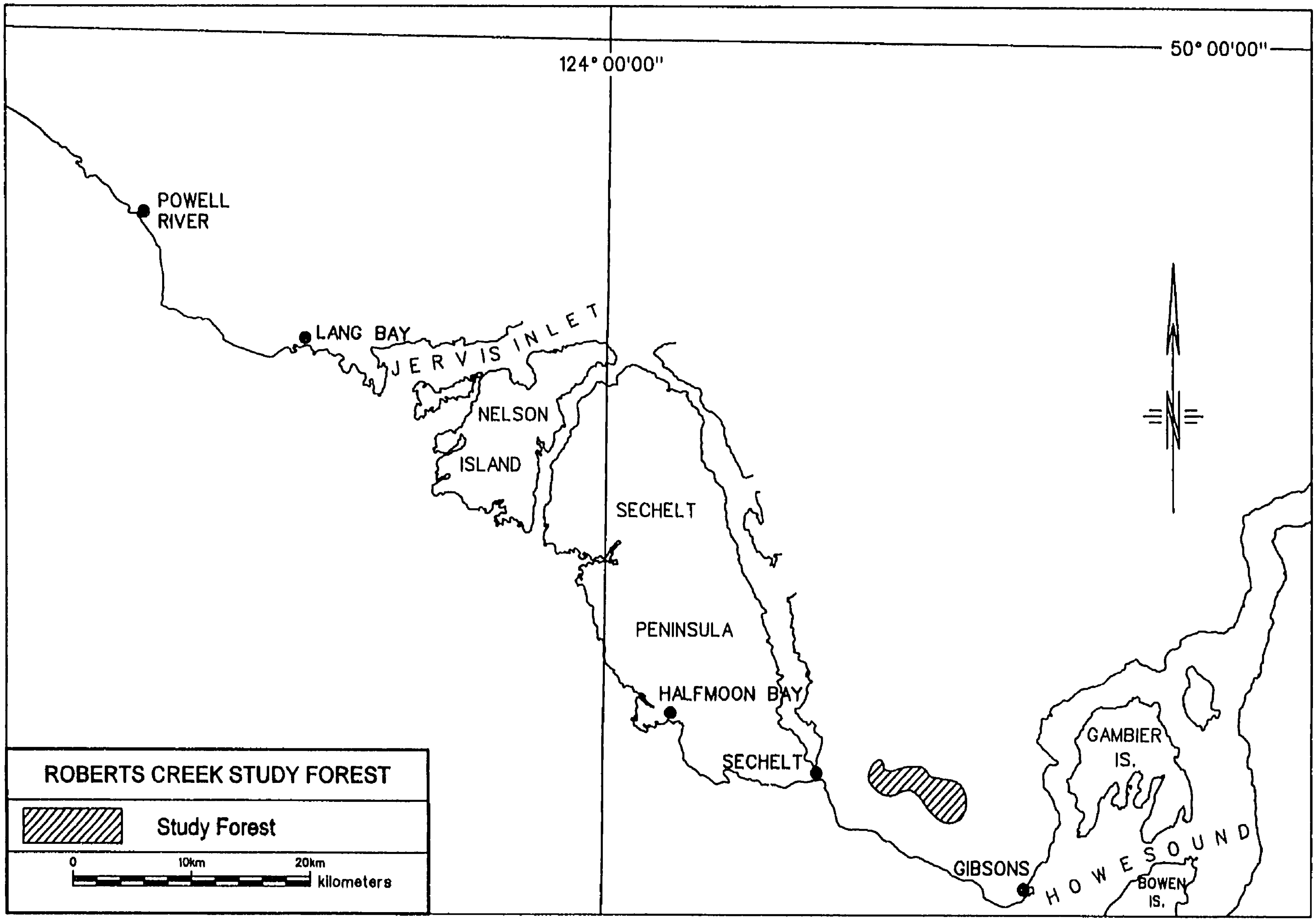


Fig. 1. Location of Roberts Creek Study Forest on the Sunshine Coast of British Columbia.

Wrens because habitat associations should be stronger and easier to detect when resources are limited. Other advantages were the mature forest, indicative of rotation age forest, and the homogeneity of the forest which would reduce confounding effects of age, slope, and aspect among study blocks. The disadvantages were altered quantities and distributions of snags and downed wood due to extraction of cedar for shakes, including the associated road beds.

In Chapter 3, I compare the distribution of Winter Wrens between two seral stages: young forest (40 to 60 years old) and mature forest (80 to120 years old). These seral stages represent different disturbance regimes, in addition to different stages of growth. In the mature forest, remnant burnt snags and burnt downed wood indicate these stands originated after fires. Most young stands originated after clearcutting. Amounts and distributions of residual trees, snags and downed wood (including cut logs) may differ among stands in both seral stages. My study sites were on Crown land (Small Business Forest Enterprise Program) and within TFL 39 of MacMillan Bloedel Co. Ltd.

Chapter 1. Territories and Habitat of Winter Wrens in Mature Forest

Introduction

Variation among individuals as well as environmental variation over time must be understood to identify the habitat needs of a species (Brown 1969, Sherry and Holmes 1985, Ruggiero et al. 1988). Habitat within a territory can provide food, cover and breeding sites, and the quality of this habitat affects reproductive success and survival of individuals (Roth 1976, Finch 1989a, Bibby et al. 1992). In coastal forests of British Columbia (CWHvm1), Winter Wrens show preference for particular types of habitat; although territorial behaviour may cause some individuals to occupy less desirable habitats (McLachlin 1983). For male Winter Wrens, size (Cody and Cody 1972, Wesolowski 1983) and location (McLachlin 1983, Van Horne and Bader 1990) of territories may depend on habitat quality. Therefore, if water has a strong influence on habitat quality, it should affect the location, size and shape of territories chosen by male Winter Wrens (Wiens 1985, Urban and Smith 1989).

The territory that a male Winter Wren occupies may also be influenced by the order in which individuals arrive at the breeding site, site tenacity of individuals, social dominance of individuals, and intraspecific competition between individuals (Brown 1969). Social dominance of an individual depends on age, previous experience and vigour (Armstrong 1956, Brown 1969). Thus, social dominance directly affects size and shape of territories, and indirectly affects locations of territories through intraspecific competition. Intraspecific competition mediated by social dominance, can constrain sizes and shapes of territories including their locations relative to one another. Territory size of Winter Wrens ranges from 0.2 ha to 1.9 ha in mature second-growth forest (CWHvm1) in coastal British Columbia (McLachlin 1983). Gaps (interterritorial spaces) between territories of Winter Wrens appear to contain unused habitat. But these gaps may occur because males can be stimulated to sing in defense, against one another, over distances of more than 20 m, and this reduces aggressive encounters on territory boundaries with neither male defending the gap (Armstrong and Whitehouse 1977, McLachlin 1983, Wesolowski 1983). Surplus males without territories may then be prevented from using these gaps due to the territorial singing behaviour of the adjacent males, and/or because the gaps may have unsuitable habitat (Armstrong 1956, McLachlin 1983, Wesolowski 1987).

In this chapter, I determine whether male Winter Wrens prefer sites influenced by water: creeks, both creeks and streams (as riparian systems in general), and moist systems. Next, I determine if habitat selection by male Winter Wrens changes with characteristics of the local systems and if it varies among years. Although normally, structure of habitat does not change substantially between years, local weather (precipitation and temperature) does change and could affect the availability of life requisites such as food (e.g., arthropods). As well, because territory holders and spatial configurations of territories change annually, the social context can vary between years. I use randomization tests to examine whether suitable habitat is likely available, but unused by male Winter Wrens because access to habitat is limited by social dominance and intraspecific competition.

Methods

Study Design and Data Collection

I established 5 study blocks ranging from approximately 380 m to 550 m in elevation at the Roberts Creek Study Forest, British Columbia (Fig. 2). To delineate the territories of male Winter Wrens, I located their observed behaviours on maps of the study blocks (Verner 1985, McLachlin 1983, Bibby et al. 1992). I centered each study block on a creek to facilitate examination of the spatial distribution of territories in relation to riparian habitats of these systems (Fig. 3). The study blocks in 1995 were 12 ha in size, extending, approximately 200 m beyond each side of the channel and 300 m along the channel. I enlarged the study blocks to 27 ha in 1996 and 1997 (300 m on each side of the channel and 450 m along the channel) to map the territories more accurately and increase my sample of whole territories. In all years, I mapped locations of Winter Wrens both inside and outside of the study blocks to ensure that territories along the boundaries were mapped as whole territories. Study blocks of 10 to 20 ha have been recommended as adequate for reducing edge effect and for censusing populations of breeding passerines (Verner 1985, Bibby et al. 1992). My study blocks were gridded using slope correction (planimetric, 25 m x 25 m), and flagged at 25-m intervals so that Winter Wrens could be located accurately on field maps.

Male Winter Wrens were captured in mist nets (30 mm mesh, 6 m long, 4 m high) from April to June 1995 and 1996. I played a taped song (Ward and Hall 1984) every 5-10 min to imitate rival conspecifics and draw territorial males to the net (Falls 1981, McLachlin 1983, Porneluzi et al. 1993). Winter Wrens were banded with coded aluminum bands (size 0 in 1995, size 0a in 1996, Environment Canada) and with coloured plastic

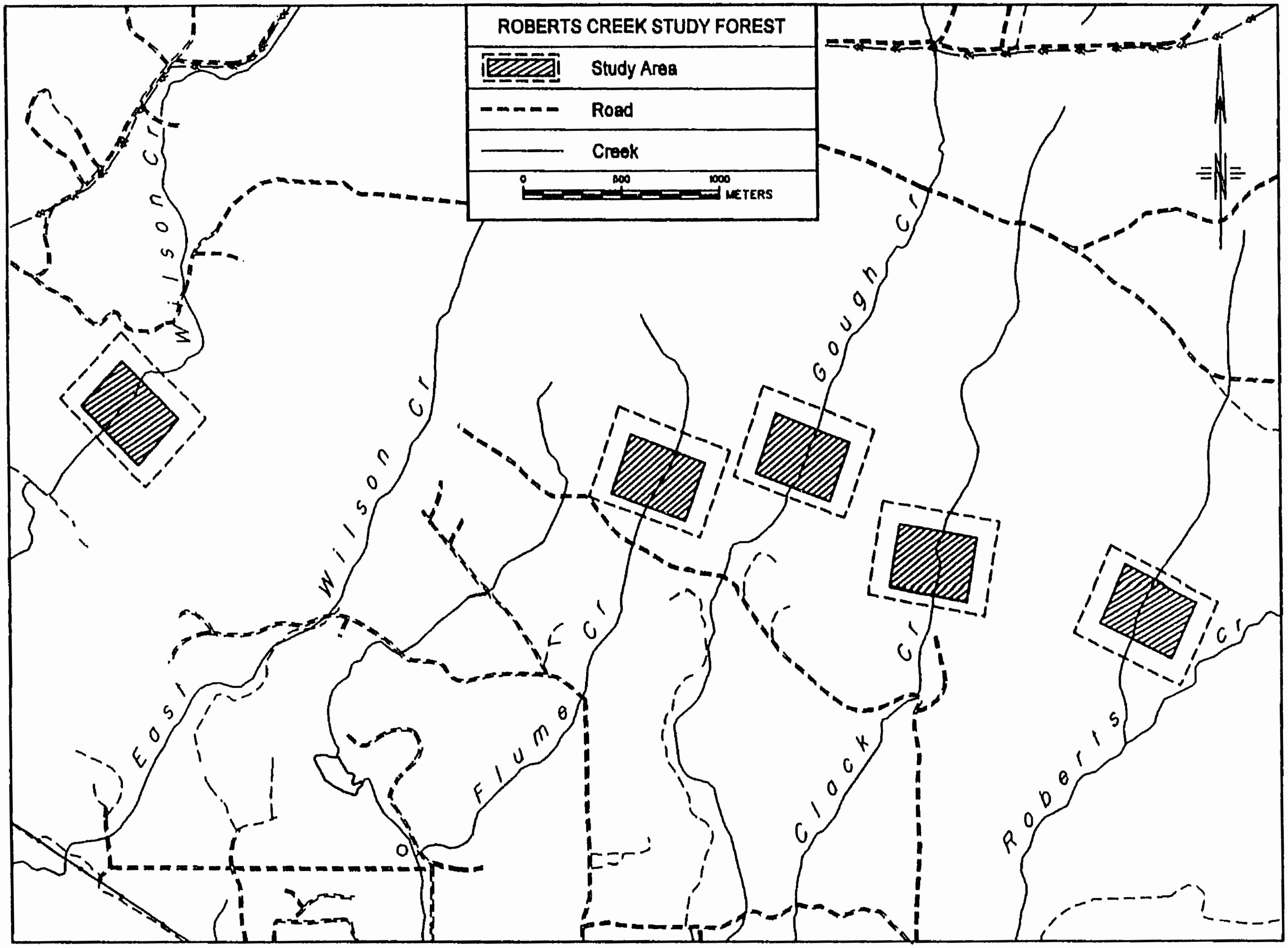


Fig. 2. Location of study blocks in the Roberts Creek Study Forest showing both 12-ha grids (shaded) and 27-ha grids (dashed line).

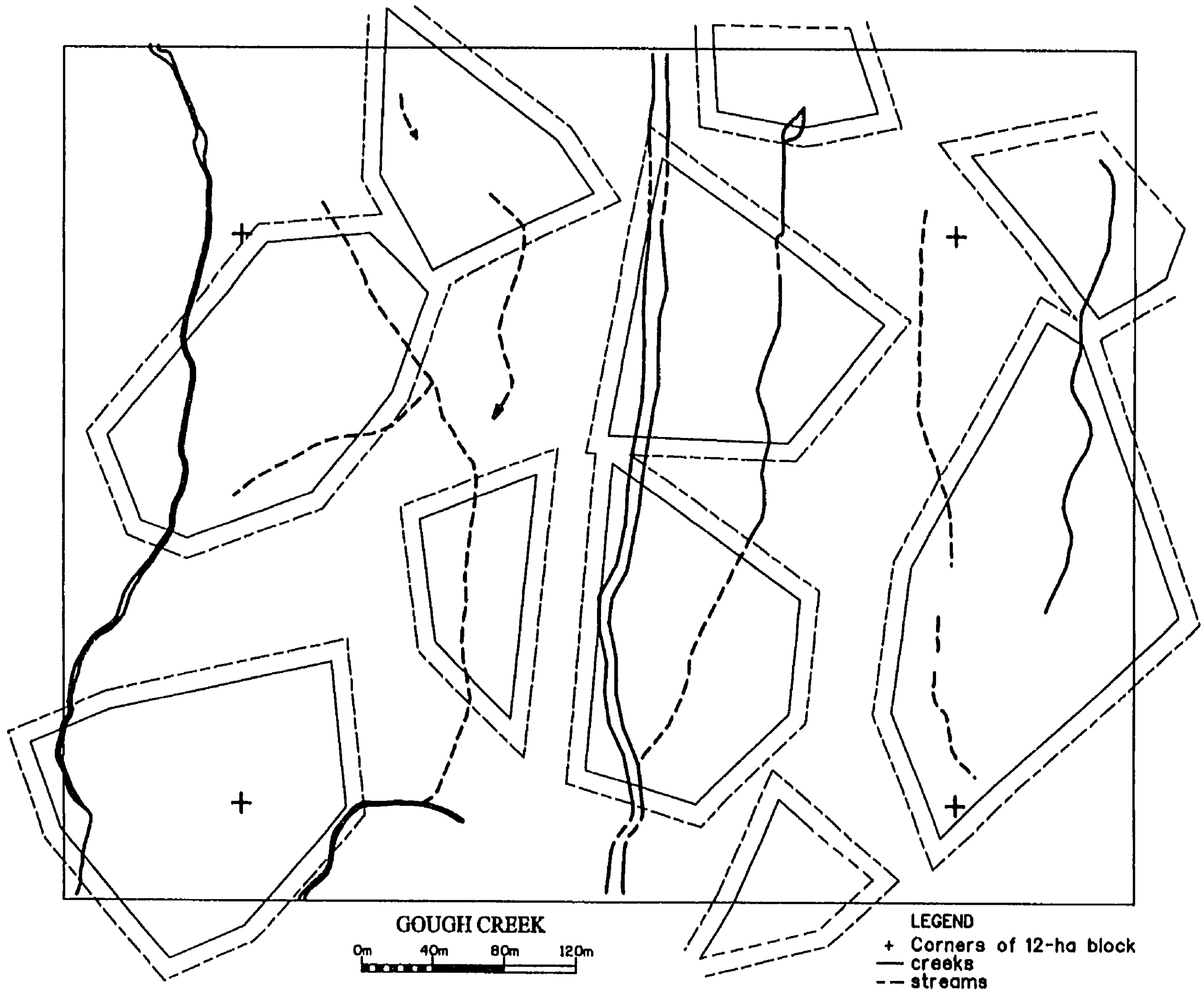


Fig. 3. Representative study block (1996 Gough) at Roberts Creek Study Forest showing block layout, creeks, streams, and core territories of Winter Wrens. To estimate potential boundaries (dashed line) of territories I extended territory borders beyond the outermost boundary locations using one half of the minimum distance between territories (Wesolowski 1983).

bands (2.3 mm inside diameter). I attached a maximum of 2 bands per leg.

I determined the sex and age class, and measured the weight (g) and left wing chord (mm) of each captured individual. Winter Wrens are difficult to age and sex, and reliability is reduced with the darker colouration of *T. t. pacificus*. I used the following criteria to distinguish adult males from adult females during the breeding season: males by song, sexual display, and cloacal protuberance; females by incubation or presence of a brood patch (McLachlin 1983, Pyle et al. 1987). I used the following characteristics to separate hatching-year juveniles from after-hatching-year or second-year adults: yellow/orange gape, down or evidence of moult, member of a brood, and immature song of males used from June to October (McLachlin 1983, Pyle et al. 1987).

For general surveys, I walked study blocks 2 to 3 times weekly, just after dawn, from the middle or last week of April until the end of June. Surveys were systematic, but because bird behaviour changes over the day, I rotated route directions ensuring that coverage of the study blocks was not biased. I used a compass bearing and the horizontal distance from the nearest grid marker to map locations of birds with an accuracy of ± 1 m. In 1995 and 1996, each individual bird was followed for up to 30 min each week. This improved my detection of territory boundaries by increasing the sample of behavioural observations. Because of financial constraints, I only conducted 5 general surveys per study block in 1997, 1 per week from the last week of April. These surveys included following birds for up to 30 min as in earlier years. I did not band individuals in 1997, but played taped songs at intervals throughout each study block to detect birds banded in 1995 and 1996. In each study block, winter survey routes were walked once a week to locate banded individuals during November 1995 (total of 3 surveys), February-March 1996 (total of 3 surveys), and November 1996 (total of 2 surveys).

I defined territory boundaries as the outermost detections of territorial and other behaviours including: conspicuous singing by males and counter-singing males, aggressive encounters between 2 males and agonistic counter-chipping, nest locations, male displays to attract females, and carrying of food for young. I observed few aggressive encounters between males. However, counter-singing males were common and generally 20 m or farther apart as observed in other studies (McLachlin 1983, Wesolowski 1983). Gaps of undefended areas, outside of the territory boundaries, occurred between adjacent Winter Wren territories. These undefended areas are described as areas of "no man's land" for the Shetland Wren (*T. t. zetlandicus)*, and as neutral areas between territories for the St. Kilda Wren (*T. t. hirtensis*) (Armstrong and Whitehouse 1977). Although these undefended areas may be used by the males for activities such as foraging, I did not have enough detailed observations to delineate foraging areas, hence, I refer to territories in my study as core territories.

I had some incomplete territories in 1997 because I conducted fewer surveys than in previous years. To construct the boundaries of these incomplete core territories, I assumed a core territory was a standard rectangular shape, and used dimensions calculated from the average width and the average length of complete core territories for that study block in 1997. The estimated core territory was positioned to include the existing observations. Where I lacked sufficient information to direct orientation of the territory, I randomly determined orientation with respect to the slope of the study block.

Territory boundaries fluctuated during the breeding season. In 1995 and 1996, some males vacated their territories following successful breeding, others had successive broods and extended their territory boundaries with the second brood. The complete area used by a male over the season, with or without successive broods, was delineated as the core territory, except in one case, where a boundary shifted into an area vacated by a bordering male. I did not use this individual's new boundary to ensure that total area covered by core territories of Winter Wrens was not accounted for twice in the stand-level analyses of habitat.

Habitat Measurements

I measured site characteristics to describe microclimate and forest structure that would provide security cover, escape cover, song perches, nest substrates, and foraging substrates for Winter Wrens. Site characteristics included descriptions of water and topography. Forest structure included measurements of amounts and dispersion of trees, snags and upturned root masses, and amounts of downed wood and vegetation. In my habitat analyses, the size categories that I devised for downed wood, snags and trees reflect both field observations of Winter Wrens (e.g., nests were in downed wood generally >30 cm dbh, and large diameter snags were often used for song perches or nest substrates) and typical forestry practices (e.g., harvest of trees generally >50 cm dbh, thinning of suppressed small trees, utilization standards for removing large pieces of wood, potential removal from second-growth forests of large, solid wood left after first-pass harvesting).

Soil moisture was assessed through site series classification, a tool developed for forest management (Luttermerding et al. 1990, Green and Klinka 1994). Site series classification quantifies soil moisture content and soil nutrients, in addition to using indicator plant species. I had the area of moist (high soil moisture content, site series 06 and 07), mesic (medium soil moisture content, site series 01 and 05), and dry systems (low soil moisture content, site series 03 and 04) mapped for the 12-ha study blocks (Green and Klinka 1994). For the 27-ha study blocks, I mapped with an accuracy of ± 1 m all the creeks and streams, and recorded locations of undercut banks. Creeks and streams were usually flowing at the beginning of the field season in April, but many dried during the breeding period.

I established 63 habitat grid points at the 50-m x 50-m grid intervals of each 12-ha study block to systematically sample site characteristics and forest structural attributes. Sampling was limited to the 12-ha study blocks because funds were not available to collect data on the 27-ha extended study blocks. I recorded presence or absence of moist and riparian systems (creek, stream, seep if noticeable; Fig. 4) in a 0.02-ha circular plot at each habitat grid point. I also measured: horizontal distance to closest riparian system (creek or stream channel), slope, and aspect (Appendix A) at each habitat grid point. I describe the detailed methods used to measure forest structural attributes at habitat grid points in Appendix A because these methods are referred to in the all chapters of my thesis.

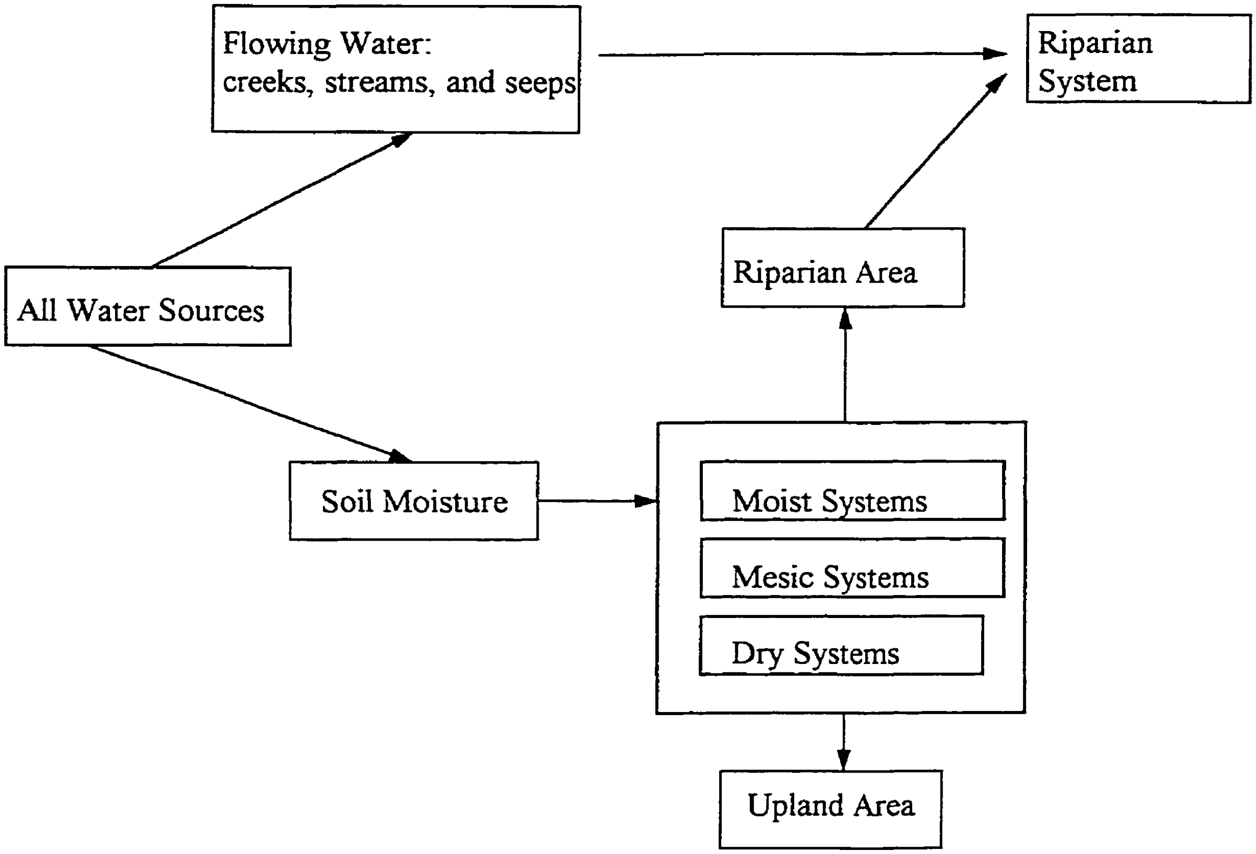


Fig. 4. Relationships of different water sources available in the Roberts Creek Study Forest. In my analyses, I examined habitat selection in relation to: a) all water - any site influenced by high soil moisture content or free flowing water; b) moist systems (moist) - a site with high soil moisture content (site series 06, 07); and c) riparian systems (riparian) - creeks, streams and seeps. The riparian system is comprised of the flowing water and the riparian area.

Habitat Analyses

I used three approaches to examine the association between Winter Wrens and riparian systems. First, I simply compared the length of creek and stream channels that occurred in territories (observed) with those that occurred overall in the study blocks (expected). Second, I used a randomization test to analyze whether habitats influenced by water (riparian and moist systems) occurred in territories of Winter Wrens (observed) more than in randomly placed individual territories within study blocks (expected). I retained size and shape of the territories in this test, when I calculated the expected occurrence of these habitats, because size and shape of territories reflect social dominance and thus may constrain the availability of riparian systems (or other attributes) to Winter Wrens. Third, I used another randomization test in which I calculated expected amounts of habitats influenced by water, when the observed configuration of territories (i.e., their spatial location relative to one another produced by intraspecific competition), as well as size and shape of territories, is maintained during random placement. I maintained territory configuration because intraspecific competition could further constrain availability of riparian systems (or other attributes).

Riparian index

If water is an important feature of Winter Wren habitat then core territories of Winter Wrens should be associated with riparian systems. I determine whether the total length of riparian channel (m/ha) found within territories is the same as that within the study block. I examined the length of riparian channels within Winter Wren territories for two categories: ‘creeks’ and ‘creeks and streams’. For each study block, I calculated the following riparian index (R):

$$R = (\Sigma^{t}{}_{1}L_{t} / \Sigma^{t}{}_{1}A_{t}) / (L_{B}/A_{B}) \qquad (1)$$

where, for each study block:

L_t is the length (m) of the riparian channel within a core territory (*t*);
A_t is the total area (m^2) within a core territory;

L_B is the total channel length (m) within the study block; and

A_B is the total area (m^2) within the study block.

A riparian index of >1 indicates core territories of Winter Wrens in the study block are associated positively with the riparian systems. The greater the riparian index is above 1, the stronger the positive association of Winter Wrens with the riparian systems. I calculated riparian indices for both 'creeks', as well as for 'creeks and streams' within each study block to determine if creeks, as riparian systems (Fig. 4), influenced behaviour of Winter Wrens differently than all the creeks and streams together as riparian systems. Total area of each study block varied each year because it was calculated as actual area traversed by observers. If part of a study block was inaccessible and not traversed, it was not included. I enlarged the areas of study blocks to include movements of Winter Wrens along the boundaries of the study blocks. Generally, if a study block was enlarged the whole boundary line was extended to maintain the rectangular shape and to ensure that the outermost activities were detected by observers. If riparian systems are important for Winter Wrens, then I expected that in all study blocks the riparian indices for 'creeks' and for 'creeks and streams' should be >1 indicating positive associations. However, if only 'creeks' were important for Winter Wrens, then for all the study blocks, the riparian indices for 'creeks' would be >1, but the riparian indices for 'creeks and streams' would not be consistently >1.

Randomization tests

I used two randomization tests (Edgington 1995) to determine if core territories were selected by Winter Wrens with respect to specific habitat attributes. These randomization tests generated random placement of core territories on the habitat grids for each study block. This enabled me to statistically test for spatial cross-correlation between the locations of the core territories and an identified habitat attribute of interest (e.g., volume of downed wood) (Nemec 1997). Randomization tests are non-parametric, and measurements (continuous or discrete) do not have to be transformed for normality. Randomization tests can accommodate different random assignment procedures using data collected by non-random sampling (e.g., systematic sampling as with my habitat grid points) (Edgington 1995). In addition, these tests make an allowance for spatial autocorrelation (i.e., my habitat samples within territories are clustered); whereas standard (parametric and non-parametric) two-sample tests do not make this allowance and ignore the spatial distribution of the two samples (i.e., sample points within territories and sample points outside of territories).

In addition to the statistical reasons cited previously, I retained territory size and shape (social dominance as a social factor) in the first randomization test (Ranhab1) to incorporate the potential influence of Winter Wren behaviour on selection of habitat. The size and shape of territories could affect habitat availability when testing for habitat selection. These territory features could limit access of Winter Wrens to normally available habitat. Hence, the amount of available habitat would be overestimated. If I fail to account for this social factor, my test for preference or avoidance would be compromised.

The random coordinates in Ranhab1 were generated for each territory polygon so that: 1) core territories did not overlap, and 2) sizes, shapes, and densities of core territories were fixed such that at least part of the boundary of each core territory remained within the habitat grid. The random placements of core territories in Ranhab1 resulted in many different configurations of territories.

In the second randomization test (Ranhab2), I retained territory size and shape, but I also retained the observed configuration of territories. This fixed configuration of territories was then randomly placed in the study block. I did not vary the spatial location of territories relative to one another because I wanted to account for intraspecific competition. This social factor may further limit access to habitat (Fig. 5). Random coordinates were generated in Ranhab2 such that densities of core territories were fixed and at least part of the boundary of each core territory remained within the habitat grid. If I used Ranhab1 and found a non-significant relationship for selectivity, then I retested with Ranhab2 (Fig. 5) to determine if available habitat for Winter Wrens was limited by intraspecific competition.

I conducted separate tests to determine if Winter Wrens show selectivity for the following attributes: water, riparian system, moist system and downed wood. I included volume of downed wood because downed wood is important for nesting and foraging habitat of Winter Wrens (Holmes and Robinson 1988, Van Horne and Bader 1990, Savard et al. 1995). Each habitat attribute was analysed separately by study block and by year (Aebischer et al. 1993).

To test whether there was more than a chance alignment of the core territories with a habitat attribute, I calculated the mean value of each habitat attribute of interest for

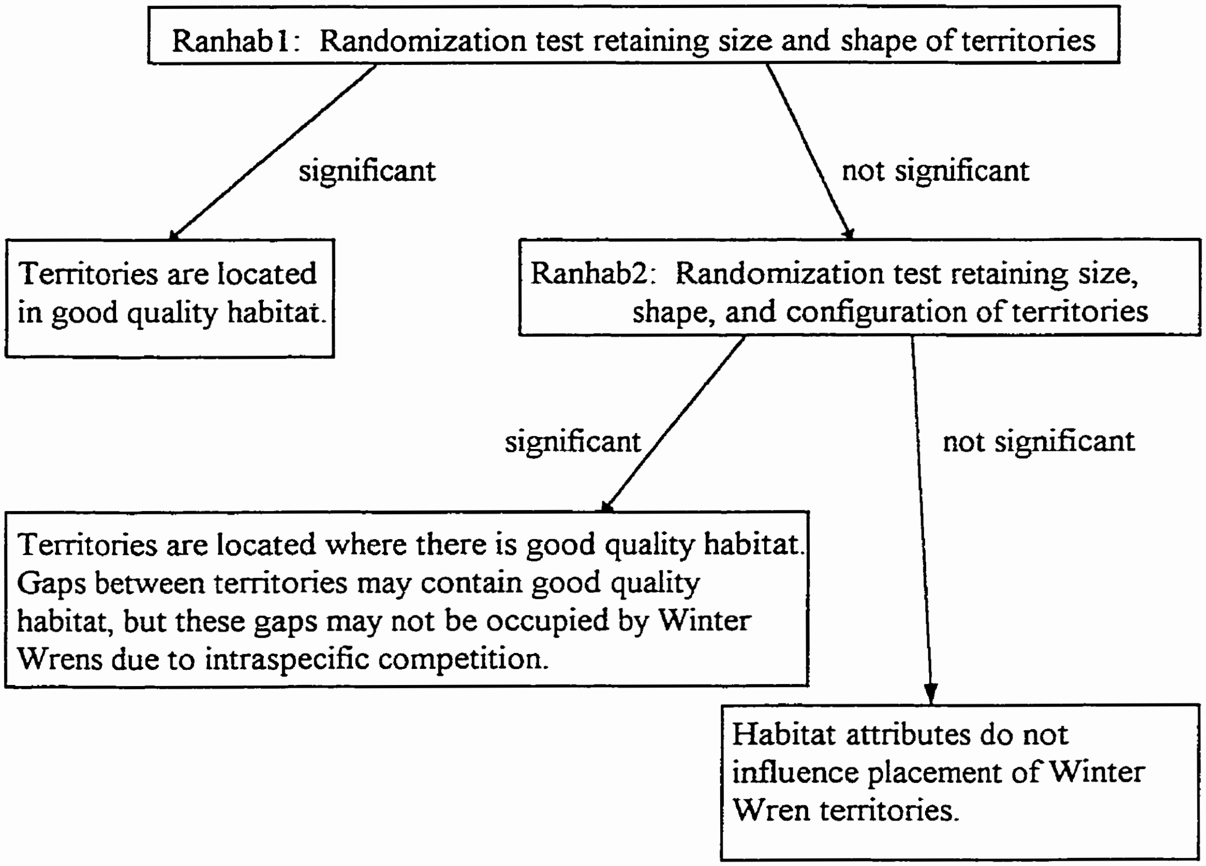


Fig. 5. Ecological interpretations of habitat use and selection based on significant outcomes of statistical programs Ranhab1 and Ranhab2.

the observed placement of the core territories, and for each of 1000 random placements of the core territories for each study block. I used the habitat grid points that were within the boundaries of each core territory to calculate the mean value for the habitat attribute of interest in the territory. Then, I calculated the grand mean from the means of individual core territories for a given random placement. For the randomization test, I calculated the grand mean values for 1000 random placements of core territories, and I produced an empirical distribution of these grand mean values. I used this distribution to assess the statistical significance of the observed grand mean, by determining the proportion of the grand mean values in the empirical distribution, less than or equal to the observed grand mean value that I had calculated (e.g., if 10 of the 1000 grand means were $\leq$ the observed grand mean, then P=10/1000=0.01). If this proportion (i.e., estimated P-value) was $\leq$0.10, I rejected the null hypothesis at the alpha=0.10 level of significance that there is no association between territory location and the habitat attribute. I used a critical value of alpha=0.10, rather than the traditional alpha=0.05, because these are exploratory analyses. I interpreted a significant probability in the upper tail portion of the empirical distribution as meaning that the observed core territories were more likely located where there was more of the habitat attribute, than if core territories were randomly placed (e.g., core territories are more likely to be located where there is greater volume of downed wood). I interpreted a significant probability in the lower tail portion of the empirical distribution as meaning that core territories were more likely located where there was less of the habitat attribute, than if core territories were randomly placed.

Habitat attributes and riparian systems within study blocks

I used Spearman correlations to determine which habitat attributes (dependent variable) were associated with riparian systems (distance to water as the independent variable). To increase my sample size from the creeks (n = 63-71 per study block) for these analyses, I used additional samples from along the main creek channels centered in the study blocks. I chose to present only the significant correlations (alpha=0.05) for a subset of attributes because of the large number of variables (see Appendix A). To reduce the number of variables, I eliminated: one of a pair of highly correlated variables; attributes with similar ecological interpretations; those that did not show trends across study blocks (potentially spurious correlations).

Results

Banded Winter Wrens and Returns of Individuals

I banded male Winter Wrens later during the breeding season in 1996 than in 1995 because of rain and low temperatures. I captured most Winter Wrens within several attempts in 1995, but in 1996, I was unable to capture an individual if my initial attempt was unsuccessful. Winter Wrens were not caught and banded in 1997. The percent of male Winter Wrens that had leg bands and held territories were: 69% (24/35) in 1995, 42% (19/45) in 1996, and 12% (5/42) in 1997 (Table 1). Forty-two percent (10/24) of all banded males from 1995 returned to the study area in 1996. Three of these males, however, did not reestablish territories at their previous territory location or anywhere else within the study blocks. In 1997, there was a 21% (4/19) return of banded

Table 1. Number of male Winter Wrens banded during 1995 and 1996 and percent return during the breeding seasons in 1996 and 1997.

Study block	Year	Study block area (ha)	Number of territory holders	Number of territories (percent) with banded wrens	Number of banded wrens returning from previous years with territories
Wilson	1995	16.9	7[3]	5 (71)	n/a
	1996	27.0	9	4 (44)	2
	1997	24.0	5	0 (0)	0
Flume	1995	24.4	8[3]	5 (63)	n/a
	1996	27.0	7	4 (57)	2
	1997	27.0	7	0 (0)	0
Clack	1995	17.5	7[3]	4 (57)	n/a
	1996	32.5	10	4 (40)	0
	1997	27.0	10	2 (20)	2
Gough	1995	19.0	6	6 (100)	n/a
	1996	32.5	10	2 (17)	1
	1997	27.0	10	1 (10)	1[1]
Roberts	1995	20.6	7	4 (57)	n/a
	1996	28.9	9	5 (55)	2
	1997	24.0	10	2 (20)	2
Total	1995	98.4	35	24 (69)	n/a
	1996	144.9	45	19 (42)	7[2]
	1997	132.0	42	5[1] (12)	5[1]

[1] One of the males that returned was banded in 1995 but had not returned in 1996.

[2] Number does not include the 3 males that returned but did not reoccupy territories in the study blocks.

[3] Includes a territory in which a male was banded (or attempt made) but <5% of the territory area was in the study block.

males from 1996: 3 were banded in 1996 and 1 was banded in 1995. A fifth banded male that returned in 1997 (5%, 1/19) was captured and banded in 1995, but had not returned in 1996.

Winter Wrens at the Roberts Creek Study Forest may move to lower altitudes during winter and return to higher altitudes during spring. Winter surveys during November 1995, February/March 1996 and November 1996 resulted in few detections of Winter Wrens, all unbanded (0-6 per study block). During surveys in November 1996, 2 banded Winter Wrens were seen together in Wilson, the lowest elevation study block (380 m). Neither of these birds returned to Wilson in 1997. Other possible evidence of seasonal movement by Winter Wrens was that most Winter Wrens, banded from the previous years, were gradually reobserved in the spring during the first 3 weeks of surveys. Ninety-one percent (32/35) of territories in 1995 and 84% (38/45) of territories in 1996 were known to be occupied by successfully breeding males. Twenty-three percent (8/35) of successfully breeding males had at least 2 broods in 1995, while 24% (11/45) of successfully breeding males had at least 2 broods in 1996. Some core territories had nests located near their boundaries: 27% of territories had nests within 1 m of their boundary in 1995 and 37% in 1996.

Both males and females fed nestlings. Males fed arthropods to newly fledged broods regardless of whether the fledglings were accompanied by a female. New fledglings followed the male as he issued a distinctive song. Occasionally, a male with a female and their brood entered other males' territories to forage. Several males with their broods disappeared from the study blocks, and I observed most of these males again on their territories later in the same season. In June 1995 and 1996, several new males established themselves in unoccupied areas or areas that territory holders had abandoned in the study blocks. These may have been surplus males or males that had unsuccessful territories in other locations.

Systems Influenced by Water, Habitat Attributes and Annual Weather

Although predominantly mesic, the 5 study blocks had various amounts of riparian and moist systems (Fig. 6). Clack, Flume and Wilson had small amounts of their area in moist systems (2-8%), and various amounts of total length of riparian systems (685-1197 m). Roberts and Gough both had greater representation of moist systems (15-28%) and riparian systems (1140- 1455 m). The 5 study blocks formed 2 broad groups: Roberts and Gough were relatively moist study blocks and Clack, Flume and Wilson were relatively dry.

Riparian habitats are characterized by a suite of attributes (Table 2), thus I could not separate whether Winter Wrens were selecting for the habitat type, specific attributes of the riparian channel, or both. Cover of vegetation (ferns and deciduous shrubs) occurred in higher densities near riparian systems; whereas small and medium live tree stems, small snags and cover of low shrubs (mostly evergreen salal - *Gaultheria shallon* - except in Roberts) occurred in greater densities away from riparian systems. Although correlations between the habitat attributes and distance to water varied in magnitude among study blocks (Table 2), they reflect general relationships for the Roberts Creek Study Forest.

I ranked years based on weather during the breeding season and weather during the preceding winter: 1995-dry/mild, 1996-wettest/mild, and 1997-wet/severe (Table 3).

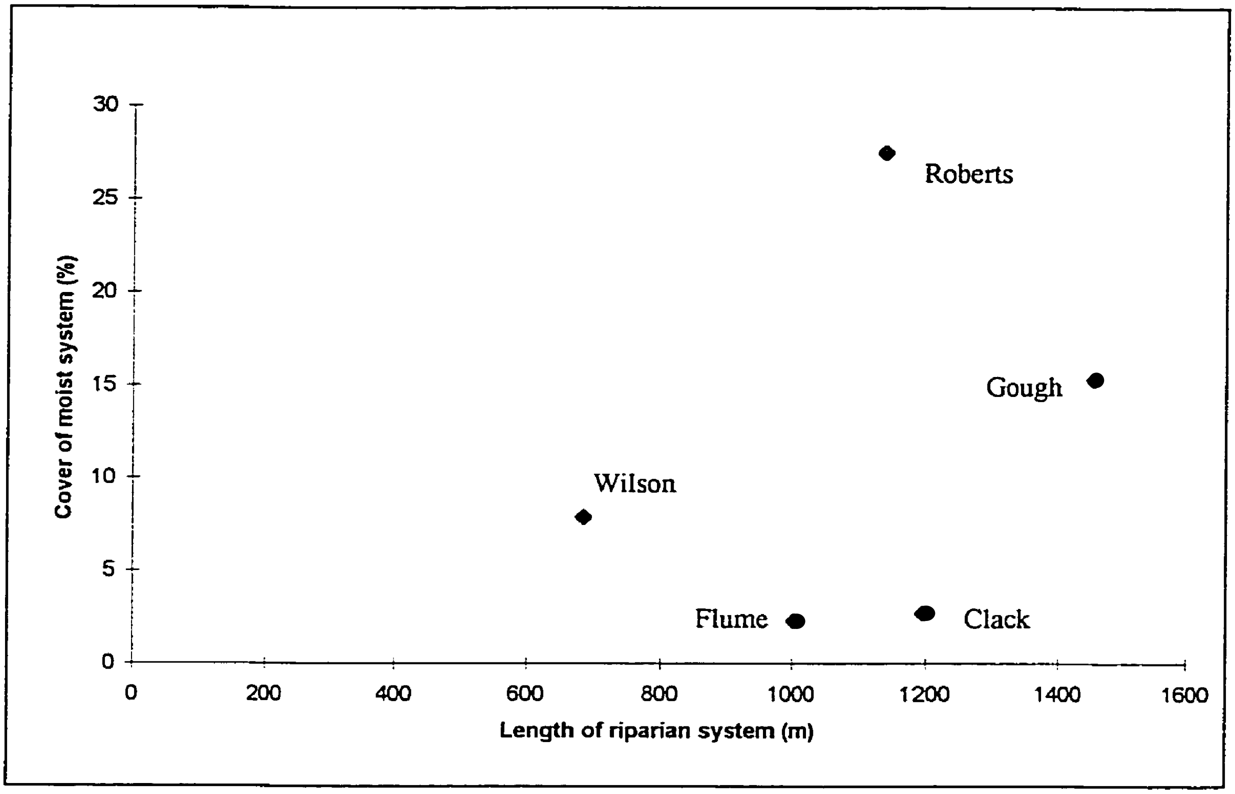


Fig. 6. Length of riparian systems as metres of creeks and streams and percent cover of moist systems (site series 06, 07) in the 5 study blocks.

Table 2. Spearman correlation coefficients between habitat attributes and distance to riparian systems for $P \leq 0.05$.

	Study blocks				
	Wilson	Flume	Clack	Gough	Roberts
Attribute	r_s	r_s	r_s	r_s	r_s
ferns and deciduous shrubs (%)	-0.27	-0.59	-0.45	-0.26	-0.23[1]
ferns (%)	-0.37	-0.50	-0.42		-0.29
shrubs <0.5 m high (%)[2]			0.40	0.50	
snags ≤10 m high (stems/ha)	0.50	0.43[1]	0.23[1]		0.34
live stems < 10 cm dbh (stems/ha)	0.32	0.51			
live stems 30-49 cm dbh (stems/ha)	0.48	0.42[1]	0.29		0.30

[1] Indicates $0.05 < P \leq 0.10$.

[2] Mostly evergreen species (salal) in this estimate of cover.

Table 3. Precipitation (PPT.) and temperature (Temp.) at the Sechelt Weather Station 0307 during the breeding season of Winter Wrens 1995 to 1997 and snowfall during the previous winter (Environment Canada, Sechelt 5W (1995 and 1997) and Merry Island (1996)).

April 16 to May 31 (n=46 days)	Mean temp. (°C)[1]	Temp. range (°C)[1]	Total PPT. (mm)[2]	Total days of PPT. (mm)	Snowfall in previous winter (cm)	Ranking by PPT. and winter conditions
1995	15.3	8.1-22.5	41	8	16	Dry/Mild
1996	12.0	7.3-17.3	150	30	14	Wettest/Mild
1997	14.4	7.4-23.4	131	24	151	Wet/Severe

[1] From daily maximum temperatures

[2] Rain

Weather data for the main breeding season (April 15 - May 30) were collected at Sechelt Weather Station 0307 (elevation 100 m) approximately 8 km from the Roberts Creek Study Forest. Weather during the breeding season in 1995 was warmer and drier than for the same period in 1996 and 1997. The mild winters (November-March) preceding each breeding year were typical for the CWHdm during 1994-1995 and 1995-1996 with 16 and 14 cm of snow, respectively (Environment Canada Sechelt 5W data). The winter of 1996-1997 was unusually severe with 151 cm of snow (Environment Canada, Merry Island data adjusted as 30 % less than Sechelt 5W for November and December 1996).

The temperatures and precipitation (rain) for 1995 and 1996 were in the extremes of their ranges for the past several decades. At the Gibsons Gower Point Station (Environment Canada), located approximately 10 km from the Roberts Creek Study Forest, the monthly average of mean daily temperatures for May from 1970 to 1997 ranged from 10.3 to 14.2 °C, (average 12.33 °C, 1.03 SD, n=27 years). The warmest year in this period was 1995 (14.2 °C), while 1997 (13.7 °C) was mid-range, and 1996 (11.2 °C) was in the lower-range. The total amount of precipitation for May from 1961 to 1997 ranged from 12.7 to 153.6 mm (average 70.76 mm, 39.67 SD, n=36 years) with 1995 (25.5 mm) in the lower-range, 1997 (89.6 mm) mid-range, and 1996 (139.9 mm) in the upper-range.

Influence of Water and Weather on Spatial Distribution of Territories

Distribution of territories on study blocks

During 1995 to 1997, core territories of male Winter Wrens that were completely mapped ranged from 0.37-2.38 ha. The average size of core territories per study block ranged from 0.72 - 1.46 ha: 1.04 (0.38 SD, n=7) - 1.46 (0.70 SD, n=6) ha in 1995, 0.72 (0.19 SD, n=8) - 1.44 (0.61 SD, n=7) ha in 1996, and 0.68 (0.32 SD, n=4) - 1.15 (0.32 SD, n=4) ha in 1997. Collectively, core territories (those completely and partially mapped) covered only a portion of each study block in any year (Table 4). The unused portions of study blocks occurred as gaps between the core territories in both riparian and upland areas (Fig. 3). The presence of gaps supported the hypothesis (Fig. 5) that undefended gaps occur among territories.

The proportions of the study blocks occupied by core territories were lower in 1996 than in 1995, and this may be due to changes in behaviour related to changes in annual weather. The density of Winter Wrens was slightly higher in 1995, suggesting that more birds may have been able to use the same area (Table 4). However, my calculation may have overestimated density because smaller study blocks were used in 1995 and I assumed that edge territories made equal contributions to density of Winter Wrens as did whole territories (i.e., smaller blocks and thus more edge effect). If I count partial territories as contributing 0.5 of an individual and whole territories as contributing 1.0 of an individual, and use a fixed 12-ha study block each year, there was no consistent trend in density by year and block (Table 4). In 1997, there was a further decrease in the proportion of study blocks occupied by core territories of male Winter Wrens (Table 4),

Table 4. Total areas of study blocks, proportions of study blocks within core territories, densities of Winter Wrens, and riparian indices (Equation 1) by study block and year.

Study block	Year	Study block area (ha)	Proportion of study block in territories	Winter Wrens/ha (full block)	Winter Wrens/ha (12-ha block)[2]	Riparian index[3]	
						Creeks	Creeks and streams
Wilson	1995	16.9	0.34	0.36[1]	0.33	2.04	2.22
	1996	27.0	0.22	0.33	0.42	2.78	3.70
	1997	24.0	0.21	0.21	n/a	2.86	2.63
Flume	1995	24.4	0.37	0.29[1]	0.33	1.47	1.47
	1996	27.0	0.27	0.26	0.33	1.33	1.89
	1997	27.0	0.23	0.26	n/a	3.33	2.63
Clack	1995	17.5	0.33	0.34[1]	0.42	1.33	1.28
	1996	32.5	0.31	0.31	0.33	1.85	1.92
	1997	27.0	0.23	0.37	n/a	1.69	1.41
Gough	1995	19.0	0.36	0.32	0.42	1.69	1.75
	1996	32.5	0.35	0.31	0.38	1.69	1.47
	1997	27.0	0.20	0.37	n/a	1.15	1.82
Roberts	1995	20.6	0.35	0.34	0.38	2.38	1.54
	1996	28.7	0.32	0.31	0.42	2.17	1.49
	1997	24.0	0.28	0.42	n/a	1.22	1.89

[1] Excluded a territory where <5% of the territory area was in the study block.

[2] Counted partial territories (i.e., those on boundary edges) as only contributing 0.5 to density of Winter Wrens.

[3] See Methods.

and my short field season limits my ability to explain this decrease. The size of core territories may have decreased in 1997 because I conducted fewer surveys and under estimated some boundaries of the core territories. Alternatively, the decrease in the proportions of study blocks in core territories may be related to the higher turnover of territory holders (e.g., Flume) and/or low return of territory holders (e.g., Wilson) following the deep snow in 1996/1997 (Tables 1 and 3).

Do Winter Wrens select riparian systems?

The riparian indices for the patterns of territories in the 5 study blocks were consistently >1.0 (Table 4), indicating core territories had positive associations with both ‘creeks’ and ‘creeks and streams’ in the 5 study blocks. Hence, Winter Wrens were associated with ‘creeks and streams’ and, although male Winter Wrens occupy areas along the creeks, selection for territory is best explained by considering the broader definition of riparian systems (i.e., ‘creeks and streams’).

Does seasonal weather influence importance of riparian systems to Winter Wrens?

Territorial male Winter Wrens were associated positively with riparian systems, but the values for the riparian indices, thus strength of the association, varied among study blocks and years. I expected variation among riparian indices because variation in habitat, turnover of individual territory holders, and weather could affect patterns of habitat use. A comparison of riparian indices for ‘creeks and streams’ for each study block by year demonstrates how weather may influence the importance of riparian systems to Winter Wrens (Fig. 7). Riparian indices (‘creeks and streams’) were smaller in 1995 than in 1996

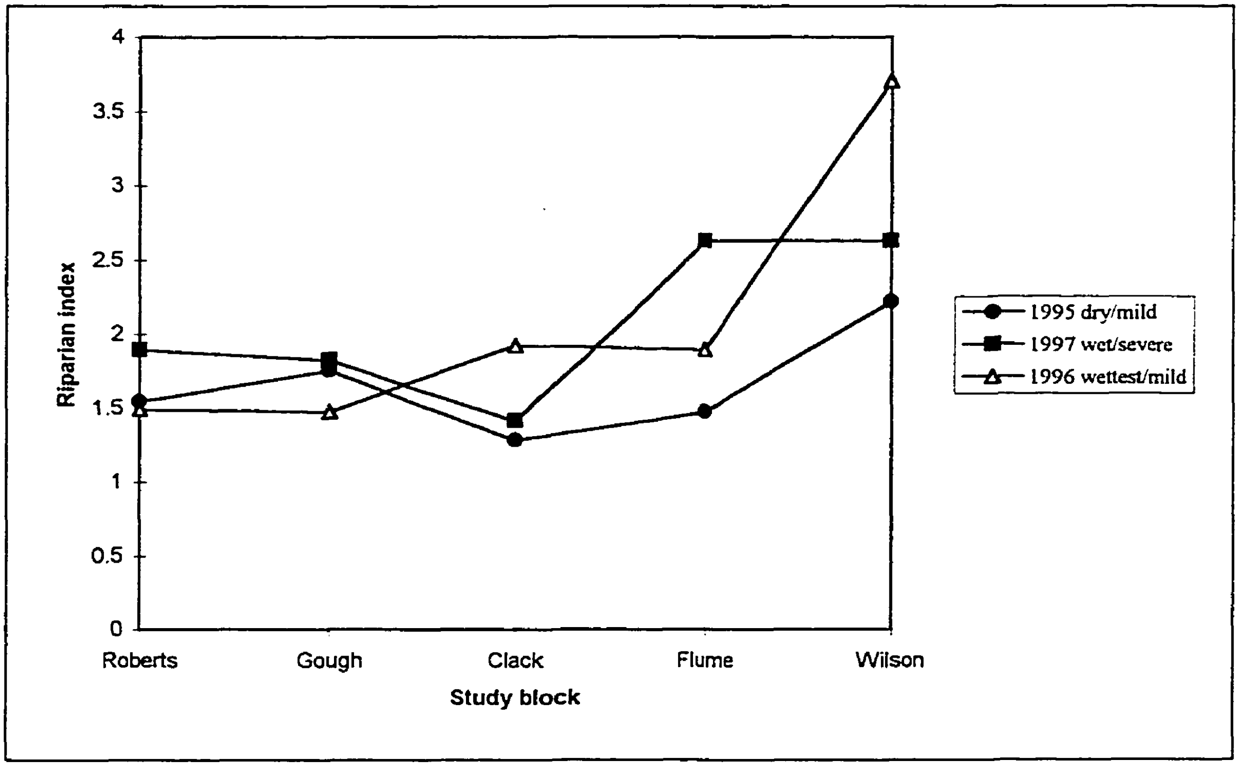


Fig. 7. Effects of riparian systems ('creeks and streams') and weather on riparian index of Winter Wrens. Study blocks are ordered from the greatest amount of riparian and moist systems (Roberts) to the least amounts of riparian and moist systems (Wilson) (Fig. 6). The larger the riparian index the stronger the positive association of the core territories with riparian systems. Years are ranked based on weather during breeding season (dry, wet, wettest) and winter prior to breeding season (mild or severe) (Table 3).

for the dry study blocks (Wilson, Flume and Clack) although the portion of study block occupied by core territories was greater in 1995. The 1995 summer was characterized by a warmer, drier climate that had been preceded by a mild winter; whereas the 1996 summer was characterized by a wetter, cooler climate also proceeded by a mild winter. Thus, male Winter Wrens in dry study blocks appear to be less strongly associated with riparian systems in drier, warmer years, but more strongly associated with riparian systems in wetter, cooler years. The riparian indices for 'creeks and streams' in the moist study blocks (Gough and Roberts) were greater in the drier, warmer year (1995) and smaller in the wetter, cooler year (1996). Thus male Winter Wrens in moist study blocks appeared more strongly associated with riparian systems in drier, warmer years than in the wetter, cooler years. This opposite trend to that in the dry study blocks is unexpected because core territories of Winter Wrens in moist study blocks, similar to those in dry study blocks, tended to occupy a larger portion of the study block in the drier, warmer year. Wilson, the study block with the least amounts of riparian and moist systems had the highest indices, and showed the strongest associations between Winter Wrens and riparian habitat in all years.

The riparian indices for Clack and Wilson were smaller in 1997 than in 1996 indicating associations of Winter Wrens with riparian systems were not as strong in 1997 as in 1996. But, the riparian indices for Gough and Roberts were larger in 1997 indicating a stronger association of Winter Wrens with riparian systems. Except for Flume, the riparian indices showed the same patterns of Winter Wren association with riparian systems by study block in 1997 as in 1995. This coincided with a warmer, slightly drier summer in 1997. The riparian index for Flume increased substantially in 1997 (Table 4,

Fig. 7) because one half of the study block lacked any riparian or moist systems and contained a single territory, while all the other new territory holders used the other side of the study block which had riparian and moist systems available to Winter Wrens.

Do Winter Wrens select for all water, riparian systems or moist systems?

To further examine the importance of habitat influenced by water and the variation of response at the local scale, I used randomization tests with the following variables: all water (both riparian and/or moist systems), moist system, and riparian system (Fig. 4). The results from Ranhab1 (retains size and shape of territories) show that although the importance of all water, riparian systems, and moist systems varies by year and by study block, mean observed use was significantly greater than random expected use ($P \leq 0.10$) for these variables (Table 5). The importance of habitats influenced by water was more apparent in dry study blocks (Wilson 1996; Clack and Flume 1996, 1997; Table 5), as was suggested by the largest riparian indices occurring in the driest study block 'Wilson' (Table 4). All water, riparian systems, and moist systems were selected by Winter Wrens in Wilson and Flume, but Winter Wrens in Clack selected only all water and riparian systems during the 3-year study period. In Gough and Roberts, the moist study blocks, Winter Wrens showed selectivity for all water in 1995 (Table 5). Gough ranked highest for representation of riparian systems, yet, I found that Winter Wrens in Gough, selected only moist systems (1995 and 1997). Roberts ranked highest for representation of moist systems, but Winter Wrens selected only riparian systems (1995). Selection was for the most part detected with Ranhab1. Ranhab2 (retains size, shape and configuration of territories) revealed significant relationships in Wilson and Flume (dry study blocks), and

Table 5. Importance of habitat variables that reveal the influence of water in study blocks. Study blocks ranked by representation of moist and riparian systems are compared to rankings of results of randomization tests. Mean observed use was consistently greater than random use for those categories with significant P-values ($P \leq 0.10$). Total number of significant responses and number of categories with significant responses are shown for all years combined.

Study block	Type	Moist system (% cover)	Riparian system (m)	Number of significant responses	Number of categories significant responses	All water			Riparian			Moist		
						Years			Years			Years		
		Rank[2]	Rank[2]	Rank[3]	Rank[4]	95	96	97	95	96	97	95	96	97
Wilson	Dry	1	1	3	1.5		0.05			0.08[1]			0.08	
Flume	Dry	3	2	1	1.5		0.10[1]	0.01		0.08	0.01		0.07	0.01
Clack	Dry	2	3	2	4		0.07	0.07		0.01	0.09			
Gough	Moist	4	5	4	4	0.09[1]						0.05[1]		0.09[1]
Roberts	Moist	5	4	5	4	0.03			0.01					

[1] Not significant using Ranhab1, only significant using Ranhab2.

[2] Rank where 1 is driest and 5 is wettest.

[3] Rank based on total number of significant responses for the 3 categories over all years combined; 1 is highest and 5 is lowest.

[4] Rank based on significant response in each of the 3 categories over all years combined; 1 is highest and 5 is lowest.

Gough (a moist study block). In these study blocks the configuration of territories constrained availability of riparian and moist systems.

Study blocks varied in the abundance of riparian and moist systems (Fig. 6) yet, the physical factor water (all water) best described areas occupied by Winter Wrens. Some riparian systems with weak trans-riparian gradients did not always have moist systems as adjacent habitat in the riparian area. Although representation of moist systems was low in all study blocks, these systems, together with riparian systems, provided preferred habitats for Winter Wrens. This result is consistent with the observed occurrence of these systems in territories: 64% of core territories over all years had riparian systems (with or without moist systems); an additional 23% of core territories were associated with only moist systems; and 13% of core territories had neither system.

The results of the randomization tests (Table 5, Ranhab1 and Ranhab2) were consistent with the inter-annual variation that I found for riparian indices (Table 4). Significant associations with riparian systems occurred for the same year that I observed the larger riparian indices for 'creeks and streams'. Results of the randomization tests in 1997 are consistent in interpretation with the riparian indices for Clack, Flume and Gough.

Selection of Downed Wood by Local Populations of Winter Wrens

Using the randomization tests, I found that in all study blocks but Wilson, Winter Wrens showed preference ($P \leq 0.10$) for total volume of downed wood in the driest year 1995: Clack P=0.06 (Clack also in 1996, P=0.07), Gough P=0.05, Roberts P=0.09, and Flume P=0.03. Winter Wrens also preferred habitat with greater volumes of harder, downed wood attributable to large pieces, including: 50-74 cm dbh in Clack (1995, P=0.08) and Roberts (1995, P=0.06), and 75+ cm dbh in Flume (1995, P=0.05; 1996, P=0.09; 1997, P=0.08) and Gough (1995, P=0.04). Winter Wrens in Wilson in 1997 avoided areas with large volumes of downed wood (P<0.01), but this may be a spurious result because of the turnover of individuals on the study block. The relationships for Wilson, Flume and Clack were determined using Ranhab2.

Discussion

Riparian and moist systems provide important habitats for Winter Wrens in the Roberts Creek Study Forest. Winter Wrens preferred to occupy habitats influenced by either creeks or streams, although characteristics of riparian habitats can vary with channel width (amount and duration of water flow, undercut banks, topography, strength of microclimate gradients, plant and invertebrate communities, and forest structure). Habitats associated with moist systems were also preferred by Winter Wrens suggesting these systems are important because of habitat features similar to those in riparian systems (e.g., vegetation and microclimate). The suite of attributes associated with riparian areas in the Roberts Creek Study Forest were typical of those described for riparian areas of coastal Douglas-fir forests (Carey et al. 1991, McGarigal and McComb 1992). It is possible that selection for these attributes, as microhabitat patches within riparian systems, influenced Winter Wren selection of territories (Pedlar et al. 1997, Matsuoka et al. 1997).

Birds may select territories based on criteria that are indirectly related to food density. For example, each year Ovenbirds (*Seiurus aurocapillus*) cue into habitat features that are correlated with expected prey abundance rather than directly assessing prey abundance when selecting territories (Smith and Shugart 1987). Winter Wrens may also exhibit such processes of habitat selection. They may select systems influenced by water, if these systems have a range of resources that will supply their long-term needs.

Long-term needs are important because Winter Wrens are site tenacious and occupy the same territories in successive years. Winter Wrens could use riparian or moist systems as criteria for placing themselves in high quality habitat at the stand-level (Fretwell and Lucas 1969, Cody 1981, Orians and Wittenberger 1991). Habitats associated with water may be valuable to Winter Wrens and water is just a proximate factor (Fretwell and Lucas 1969).

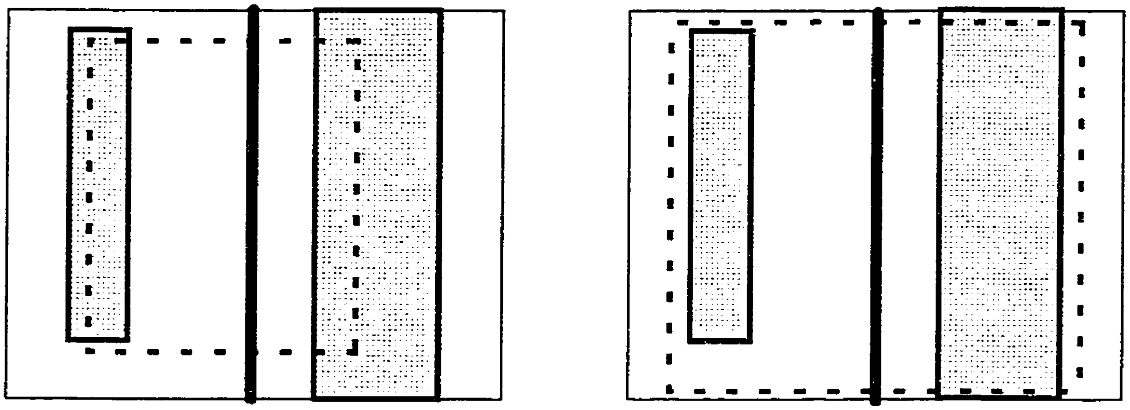
The availability of arthropods can affect habitat selectivity and dispersion of Winter Wrens (Armstrong 1956, McLachlin 1983, Holmes and Robinson 1988, Van Horne and Bader 1990). The abundance and composition of arthropod communities varies with temperature, site conditions (moisture, nutrients), stand structure, and vegetation (Mattson and Haack 1987). Generally, there are more arthropods in habitats influenced by water than in drier upland habitats (McLachlin 1983, Van Horne and Bader 1990, Gray 1993). But over short periods, variation in weather may alter the presence and abundance of arthropods. Thus food availability within the system can vary, while the forest structure and topography remain stable (Coulson and Witter 1984). The annual shifts in importance of riparian and moist systems for Winter Wrens may be related to the interaction between annual weather, their local environment, and their food base (arthropods) (McLachlin 1983, Van Horne and Bader 1990). Winter Wrens may establish their territories near riparian and moist systems as a long-term strategy because these are higher quality systems that provide food and other important resources (e.g., nest sites). However, Winter Wrens must also exhibit habitat flexibility because short-term fluctuations in food availability are induced by variation in weather. If the quality of their preferred habitats changes temporarily, Winter Wrens, like other bird species (Gray 1993), may increase their survival by exploiting other habitats.

As water dried in riparian and moist systems in 1995, habitat quality may have declined because these systems no longer provided suitable conditions for arthropods. Winter Wrens may then have extended their activities into previously unused areas (dry and mesic systems and surplus riparian and moist systems) in search for food. As well, higher productivity of arthropods may have simultaneously occurred in mesic and dry upland areas because warmer temperatures, in these already drier systems, could produce stressful conditions for the plants inducing outbreaks of herbivorous insects (Mattson and Haack 1987). I found that Winter Wrens selected areas with high volumes of downed wood in 1995. Volume of downed wood in my study area was not correlated with distance to riparian channels, but was distributed across the study blocks. Downed wood provides important foraging sites for Winter Wrens because they retain water and thus the associated arthropods, even as soil and duff dry out (Harmon et al. 1986, Bunnell et al. 1991). The inter-annual variation in habitat selection by Winter Wrens may simply reflect their response to changing abundance and distribution of food. The reduced importance of riparian systems for Winter Wrens and other bird species during dry periods has been suggested in other regions (Barrows 1986, Gray 1993).

Temperature also affects the metabolic rates of birds, and Winter Wrens require more energy during cool temperatures (Armstrong 1956). In the cool breeding season (i.e., 1996), Winter Wrens may have benefited by focusing activities (e.g., foraging and nesting) in higher quality habitats (e.g., greater abundance of arthropods) such as riparian and moist areas, rather than expending more energy by maintaining larger territories for foraging or for having multiple broods spaced far apart. Winter Wrens appeared to sing more actively in defense of boundaries in the dry year (1995) than in the wet year (1996). In the wet year their activities appeared more focused around the nest. Quantitative data for analysis were not collected, but this also suggests that they may have extended their activities in the dry year and changed patterns of habitat use because locations of suitable habitat may have changed with the shift in the food base. This flexibility in habitat use has been suggested for other bird species (Cody 1981, Wiens 1981, 1985). I was unable to determine if mean size or shape of territories changed between years because of incomplete territories and my small sample sizes. However, my results suggest that although Winter Wren density per study block was relatively consistent between years, total areas of study blocks occupied by their core territories were greater in 1995. In 1995, Winter Wrens extended farther into upland areas than in 1996 (Table 4). If the habitat was not saturated, I would expect density to vary among years, if in some years low quality habitats could improve and support surplus males.

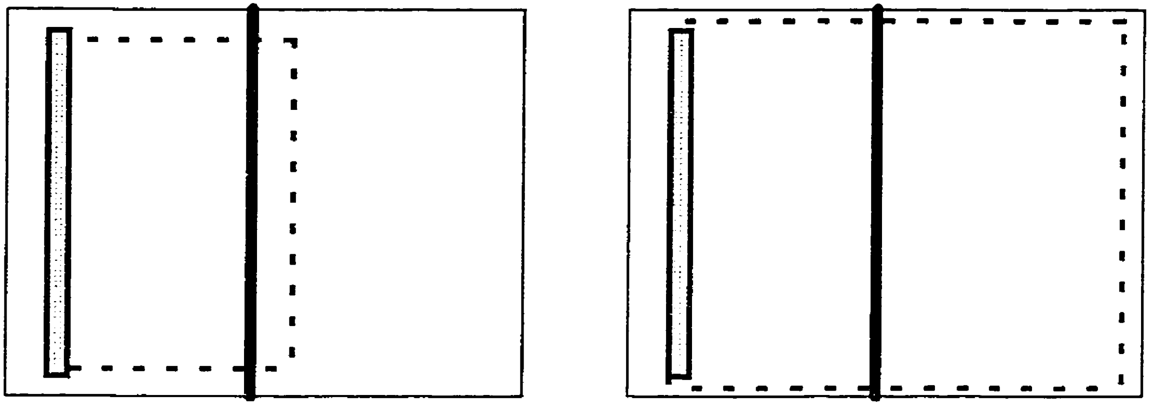
If Winter Wrens relied less on riparian and moist systems in the drier year (1995) as I previously suggested, I would not expect to observe preference for these systems by Winter Wrens in any of the study blocks. Instead, I detected preference of Winter Wrens for riparian and moist systems in the moist study blocks, during the dry year.

Inter-annual changes to habitat selection may be, in part, a consequence of the contagious dispersion of riparian systems in the landscape. If moist study blocks have more riparian and moist systems available than Winter Wrens could use in an 'average season' for their territories (e.g., 1996), I may have been unable to detect selectivity because selectivity is determined usually when preferred habitats are limited (Orians and Wittenberger 1991). Selectivity may have been exaggerated in 1995 if Winter Wrens in moist study blocks inadvertently included surplus riparian and moist systems when they extended their activities (Fig. 8; i.e., riparian channel length increased relative to total area of territories, Equation 1). This apparent disproportionately high use of riparian and moist



A. wet year, moist study block

B. dry year, moist study block



C. wet year, dry study block

D. dry year, dry study block

Fig. 8. Model of habitat selection by Winter Wrens that explains changes to the riparian index (Equation 1) under different conditions. The territory (dotted line) of most Winter Wrens includes a section of riparian channel (thick black line) and/or moist system (stippled area). During wet years, food density is high in riparian and moist habitats, and territories are small (A and C). During dry years, food density is diminished in riparian and moist habitats and territories expand (B and D). On moist study blocks, riparian and moist systems (stippled) are common (A). During dry years when the territory expands, large amounts of riparian habitats are included in the enlarged territory and the riparian index increases (B). On dry study blocks riparian and moist systems are uncommon (C). During dry years when the territory expands, additional riparian habitat may be included in the enlarged territory. However, this amount is small compared to the area added to the territory, hence, the riparian index decreases (D).

habitat would result in my measuring preference during a dry year. In dry study blocks in 1995, Winter Wrens could include only more mesic and dry systems when they extended their activities (Fig 8). This resulted in decreased riparian channel length relative to total area of territories. Interpretation of selectivity for riparian and moist systems must consider the spatial context, as well as multi-year patterns, otherwise habitat selection can be misleading (Haila et al. 1989).

The use of randomization tests that incorporated social factors, both social dominance (size and shape of territory) and intraspecific competition (configuration of territories), were helpful for understanding selection of habitat by Winter Wrens. If social factors limit access to areas of good quality habitat for birds (e.g., some Winter Wrens had territories without riparian and/or moist systems), these individuals may be forced to establish territories in lower quality habitat (Wiens et al. 1987). Habitat selectivity may fail to be detected because the amount of available habitat falsely appears higher than some mean 'threshold' amount of the attribute used by the local population of Winter Wrens. Inclusion of social factors may have given a more realistic measure of habitat availability for Winter Wrens, if social factors reduce levels of available habitat to below these 'threshold' levels. Social behaviour was important because it limited access to good quality habitat of riparian and moist systems.

My ability to determine habitat selection by Winter Wrens was also in part influenced by abundance of an attribute and its distribution within study blocks relative to the spatial configuration of territories of a given year (Manly et al. 1993). Selectivity occurs in the context of habitat suitability. Habitat suitability is influenced not only by availability of life requisites (food, cover, nest sites), but also by density of individuals, and habitat suitability may be density dependent (Brown 1969, Fretwell and Lucas 1969, Wiens et al. 1987). A high turnover of territory holders in all study blocks and lower densities in some study blocks followed the severe winter of 1996/1997. Winter Wren populations in other regions decreased following severe winters with deep snow falls (Szaro and Balda 1986, Peach et al. 1995). Research on the Winter Wren in England suggests these declines may be attributable to density dependent mortality of adults, immigration of adults or both (Peach et al. 1995). I was able to measure selectivity for some attributes in 1997, following the changes to the local population, because density declined in some study blocks, and new territory holders in other study blocks redistributed themselves in the higher quality habitats perhaps as equal competitors.

Chapter 2. Nest Sites and Nest Substrates Selected by Winter Wrens

Introduction

Territories of birds include various habitats which can provide food, nest sites, security cover, and shelter. Habitats associated with nesting are particularly important because they can affect reproductive success, and thus individual fitness (Van Horne 1991). Characteristics of nesting habitat can influence mate attraction, vulnerability to predators (concealment), and food supply. As well, the microclimate and the available shelter of the selected nesting habitat affects the amount of energy expended on thermoregulation and incubation (Martin and Roper 1988, Li and Martin 1991, Matsuoka et al. 1997). Selection of habitat for nesting by some species of birds is a major factor in the placement of territories (Matsuoka et al. 1997) and hence affects the distribution of a species in a landscape.

Winter Wrens occur throughout coastal forests of British Columbia, and they are common near creeks and streams (Carey 1988, McGarigal and McComb 1992). The association of Winter Wrens with these riparian systems is of particular interest because creeks and streams are featured in forest management guidelines (B.C. Ministry of Forests and B.C. Ministry of Environment 1995b) and are a major consideration in forest planning. I used the Winter Wren as a model species to examine relationships between wildlife habitat and riparian systems in managed forests. By examining habitat selection of Winter Wrens, I hope to identify key relationships that will enhance our understanding of the effects of forest harvesting on wildlife.

Winter Wrens are often monogamous, but polygyny occurs under some conditions in both North America and Europe (Armstrong 1956, Garson 1980a, McLachlin 1983, Wesolowski 1983, 1987). Winter Wrens can lay 5-7 eggs per clutch and raise one or more broods per season (Godfrey 1986, Ehrlich et al. 1988, Campbell et al. 1997). The breeding season for Winter Wrens in coastal British Columbia ranges from mid-April to mid-July (McLachlin 1983). In forests, Winter Wrens make nests out of moss and twigs, in upturned tree roots, in creek banks, beneath slabs of thick bark, and among piles of downed wood (Wesolowski 1983, Godfrey 1986, Ehrlich et al. 1988, Campbell et al. 1997). A male can build several nests in his territory, but fewer nests may be built in less favourable habitat (Armstrong 1956, Armstrong and Whitehouse 1977). During courtship, the male leads a female to one or more of the nests, and she inspects and occupies one that will be used for the breeding attempt (Garson 1980b). Some nests constructed by the male remain unused during the breeding season. Nests built in previous years that were occupied or remained unoccupied may be used for nesting in subsequent years (Wesolowski 1983). Females of polygynous males will often choose nests in different parts of the territory (Armstrong 1956). The female incubates the eggs for approximately 15 days, and both parents usually feed the nestlings for approximately 17 days before they fledge (McLachlin 1983).

I investigate nesting habitat of Winter Wrens at three scales: the nest site (the area around the nest), the nest substrate (the substrate to which the nest is attached), and the nest itself. I distinguish between two types of nests: occupied (nest in which a female laid eggs) and unoccupied (nests built by males but not used by females). My objectives are to examine how habitat is exploited by Winter Wrens for nesting (nest substrates and nest sites) and to determine if nesting habitat is an important factor for selection of territories by males. I examine location of nests relative to riparian systems and moist systems (Fig. 4, Chapter 1) at the stand-level, because these systems have distinct features such as microclimate, and they can be more structurally diverse than mesic and dry systems (Raedeke 1988). I could not test for habitat patchiness within territories in Chapter 1, however, in this chapter, I determine if habitats at nest sites are distinct from other parts of territories and whether nest sites differ between creek and non-creek areas. I compare nest sites to non-nest sites within territories to examine habitat selectivity by males. I also examine whether Winter Wrens prefer particular types of nest substrate. I compare occupied with unoccupied nest sites within territories to determine criteria that females might use to choose nests (Wesolowski 1983).

Methods

Nest Searches

I searched for nests of Winter Wrens in and around 5 study blocks at the Roberts Creek Study Forest (Fig. 2). Most nests were found when I observed displaying males and Winter Wrens carrying nesting material or food (Martin and Geupel 1993), and when I collected habitat data. I flagged and checked nests regularly from a minimum distance of 10 m to reduce disturbance and predation on nests. In each territory, I searched upturned root masses, downed wood (logs), stumps, snags and tree branches. My efforts were focused in the vicinity of song perches (Garson 1980b). I examined nest interiors after the young had fledged.

Measurement of Habitat Attributes

I measured the same habitat attributes at nest sites as I measured at habitat grid points in the study blocks (Chapter 1, Appendix A). Attributes that I used in my analyses were chosen to represent factors that could affect selection of nest sites (concealment from predators, food, thermal cover, and male's ability to advertise nests). These attributes included deciduous shrubs, ferns, downed wood, snags, and trees.

Nest Substrates

For each nest and nest substrate, I recorded: nest height, nest position, substrate type, hardness, decay, dbh (diameter breast height), species, and other characteristics, depending on the type of substrate. There were 5 main types of nest substrate: logs, snags, upturned root masses, creek banks (this includes a few nests in stream banks) and branches. For some analyses, I classified logs into 2 subcategories (log and log butt) and snags into 3 subcategories (bark, crevice, and stump).

I used log-likelihood Chi-square tests to test whether Winter Wrens showed selectivity for location of nest substrate, thus nest site, relative to riparian and moist systems, and for type of nest substrates. Bonferroni-adjusted Z tests (alpha = 0.05) showed preference or avoidance of classes with the 95% confidence intervals controlled for experiment-wise error (Neu et al. 1974, Alldredge and Ratti 1986, Thomas and Taylor 1990, Manly et al. 1993).

Locations of nest sites relative to water

In Chapter 1, I examined the locations of territories in relation to riparian systems (creeks and streams). Here, I determined how far nest substrates, thus nest sites, of Winter Wrens were from riparian systems (channels). I used 5 distance categories (0-5, 6-10, 11-50, 51-100, 101-300 m) chosen for ecological and management reasons. I chose 0-5 m for the first interval, because generally the influence of riparian channels on vegetation extended up to 5 m on each side of creeks and streams. The category of 6-10 m is transitional between riparian and upland areas. A category break of ≤50 m is less than the mean distance to water. This category was also chosen because proposed forest management zones of 20-50 m are designated in the Riparian Guidebook (B.C. Ministry of Forests and B.C. Ministry of Environment 1995b). I included categories 51-100 m and 101-300 m because a distance greater than 50 m is greater than the mean distance to water and because Winter Wrens were observed to fly between locations up to 100 m apart. Only 2 nests were located at ≥100 m from riparian systems, and 1 of these was at 300 m.

First, I tested if nest sites (n=99) selected by males were independent of distance to riparian systems. I used the proportion of nest sites in each distance category as my measure of habitat use. The number of habitat grid points that fell within each distance category was my measure of habitat availability (n=315, habitat grid points pooled from each 50-m x 50-m habitat grid in the 5 study blocks, Chapter 1). Next, I determined whether females showed selectivity for location relative to riparian systems and I assumed nests were equally available to females (n=99). I tested whether the proportions of occupied nests (n=55) in the 5 distance categories were different than the proportions of unoccupied nests (n=44).

If presence of water is important to Winter Wrens, I expected male Winter Wrens to have preferentially located their nests in both riparian and moist systems. I tested whether males locate their nests in systems in proportion to their availability: 1) riparian systems (creeks and streams); 2) moist systems (sites with high soil moisture content); 3) both of these systems together; and 4) neither of these systems. I calculated the proportion of nest sites (n=99) of males within each of 4 categories and I calculated availability as the proportion of habitat grid points (n=315) that fell within each category.

Selectivity for type of nest substrate

To determine whether male Winter Wrens showed selectivity for type of nest substrate (creek bank, root mass, log, snag (stump, crevice, bark), branch), I compared the proportions of types of nest substrates in which males built nests (n=95, nests within known territories) to proportions of types of nest substrates available within the stand (estimate based on the number of each type of nest substrate at the 315 habitat grid points). To determine if females showed selectivity for type of nest substrate (creek bank, root mass, log, snag, branch), I compared proportions of types of nest substrates for occupied nests (n=55) to proportions of types nest substrates for unoccupied nests (n=40) during the 2-year period. To further examine if particular types of substrates were preferred by males for nesting, I compared reuse of nests between 1995 and 1996. I excluded data from 1997 because I was unable to visit the study area at the end of the breeding season and verify nest reuse. Availability was calculated from nests still intact from the previous year (i.e., in 1996 based on availability from 1995). I excluded the branch category because the nests on branch substrates were not available from 1995.

The nest substrates could be divided into two general categories: creek banks and upturned root masses which are both comprised of soil and rootlets; and logs, snags, and branches which are all comprised of (or associated with) wood. Because creek banks are always associated with riparian systems and upturned root masses are often associated with areas influenced by water, and because soil has different physical properties than wood (e.g., higher moisture content), I decided to examine if use of nest substrates comprised of soil could benefit Winter Wrens differently from use of those nest substrates comprised of wood. I addressed whether nest substrates comprised of soil may be more valuable than those comprised of wood, if they generally occur in more structurally diverse areas, such as riparian systems. Structurally diverse areas may provide higher quality habitat for males if they offer more opportunities to build nests. I tested whether nests in substrates comprised of soil occurred more frequently in territories containing multiple nests, than in territories containing only a single nest. I compared proportions of multiple and single nest territories, with and without nest substrates comprised of soil, using my largest data set (1996, n=38 territories with nests).

Nest substrates that retain higher moisture content may provide better insulation, thus a more stable interior microclimate for nesting birds (McComb and Noble 1981). In the wet summer of 1996, I had noticed a fungus growing inside some occupied nests. I assumed that the presence of this fungus revealed a humid interior of the nest, and thus may indicate why particular types of nest substrates are preferred by Winter Wrens. I used occupied nests to compare the proportions of those nests with or without fungus (1996, n=32 occupied nests) between the two categories (nest substrates comprised of soil and those comprised of wood). I excluded branch nests (n=2) because I was unable to check them for fungus.

Comparisons of Habitats at Nest and Non-Nest Sites within Territories

To determine habitat selectivity by male Winter Wrens at nest sites, I used Multivariate Analysis of Variance (MANOVA, Tabachnick and Fidell 1989) to test for differences in amounts of habitat attributes between creek nest sites and non-creek nest sites ($P \leq 0.10$), and to test for differences between nest sites and non-nest sites. I use pairs of nest sites and non-nest sites as the multivariate response because these pairs are not independent, where they are within the same territory in the same year. I chose to use alpha=0.10, instead of alpha=0.05 as for the selection calculations, because this is an exploratory analysis that examines habitat associations for many attributes. I pooled sites of occupied and unoccupied nests because there were no identifiable criteria of unoccupied nests that distinguished them as "dummy nests" or as representing lower quality nest sites for males (Garson 1980b, pers. obser.). I pooled 1995 and 1996 nests because of reuse between years. I randomly selected ,with random number tables, 1 nest in territories with multiple nests. Nest sites and non-nest sites were paired by territory, year and habitat type (creek, n=10; non-creek, n=37) ensuring all samples were independent. I separated habitat type into creek and non-creek nest sites. Creek nest sites included nest substrates in creek channels and along the immediate edge of the creek bank because availability of habitat attributes at these sites may differ due to channel width, and the associated influence of slope and overstory canopy openings. Hence, non-creek nest sites included those in riparian habitats of streams, as well as those nests in upland areas. A non-nest site was selected as the closest habitat grid point $\geq$25 m within the territory that did not have any nests. A distance of $\geq$25 m was chosen because this was double the length of transects used to measure downed wood (12.5 m) and 25 m is approximately one-half standard tree height. If an interaction for a particular attribute occurred between creek and non-creek, then I tested for differences between nest and non-nest sites within each of these categories separately ($P \leq 0.05$, corrected for experiment-wise error). Residuals were examined for homogeneity of variance and normality. I reduced the number of habitat variables analyzed by eliminating strongly correlated pairs (Spearman rank correlation) and variables with similar ecological interpretations. Given the large number of attributes tested, I present only significant relationships in tables.

Occupied and Unoccupied Nest Sites within Territories

I did not find all the nests in the territories, and thus only a small sample of territories that had both occupied and unoccupied nests were available for analysis. I used a one-way randomized block design analysis of variance (ANOVA) to test for differences in habitat between these nest sites (n=16). I pooled years, controlling for independence of all sample units. On 6 occasions, I had observed females being shown 2 nests, from which only 1 nest was subsequently used to raise young. Thus, I reasoned that choice of nests should reveal habitat selectivity by females. In territories with either multiple occupied and/or unoccupied nests, I randomly selected 1 nest from each category. I examined residuals to ensure homogeneity of variance and normality. Six of the 16 pairs of occupied/unoccupied nest sites had at least 1 nest located within or along the immediate edge of a creek. Therefore to determine if including creek nest sites had affected my interpretation of habitat use, I reran the ANOVA tests and used only non-creek nests (n=10).

Results

Nests

I found a total of 99 nests during 1995 and 1996. Some territories had multiple nests (22% in 1995 and 53% in 1996), some territories had single nests (35% in 1995, 47 % in 1996) and in other territories, I was unable to find any nests (43% in 1995). Most nests were dome shaped with a moss lining. Nests were primarily woven from moss, twigs, and western redcedar needles. Nests in upturned root masses or creek banks had rootlets from trees and shrubs woven into the nest. I noticed a fungus growing in many nests after young had fledged in 1996. The occurrence of fungus in occupied nests was greater in the wetter and cooler year (50%, 16/32, 1996) than in the drier warm year (4%, 1/24, 1995). In 1996, the occurrence of fungus was significantly greater in occupied nest substrates comprised of soil (75%, 9/12) than in occupied nest substrates comprised of wood (35%, 7/20, G=54.1, v=1, P<0.01).

Locations of Nest Sites Relative to Water

All of the creeks in my study area had running water during most of the year, but most of the streams dried by late May to early June during the breeding season. Male Winter Wrens showed selectivity for riparian systems (both creeks and streams) when building nests (Fig. 9, G=30.2, v=4, P<0.01). Only 9.5% of the habitat grid points (n=315) were $\leq$5 m from riparian systems, but 55% of the nests (54/99) were $\leq$5 m from riparian systems. These nests included all nests in banks (n=12) and upturned root masses (n=20). The number of nests 6-10 m from riparian systems were in proportion to availability of this distance category. Fewer nests than expected were located in the 11-50 m category. The number of nests 51-100 m from riparian systems were in proportion to available habitat. Although some nests were >100 m from a riparian system, Winter Wrens tended to avoid these locations. There was no significant difference between proportions of occupied nests and unoccupied nests in relation to distance from riparian systems (G=3.6, v=4, P>0.10). This result assumes that the female makes the final choice and that availability is not constrained by occurrence of territories of males or locations of other females.

I examined the occurrence of riparian and moist systems within 8 m of each grid point (availability) and each nest (use). Most (75%) of the study area but only 27%

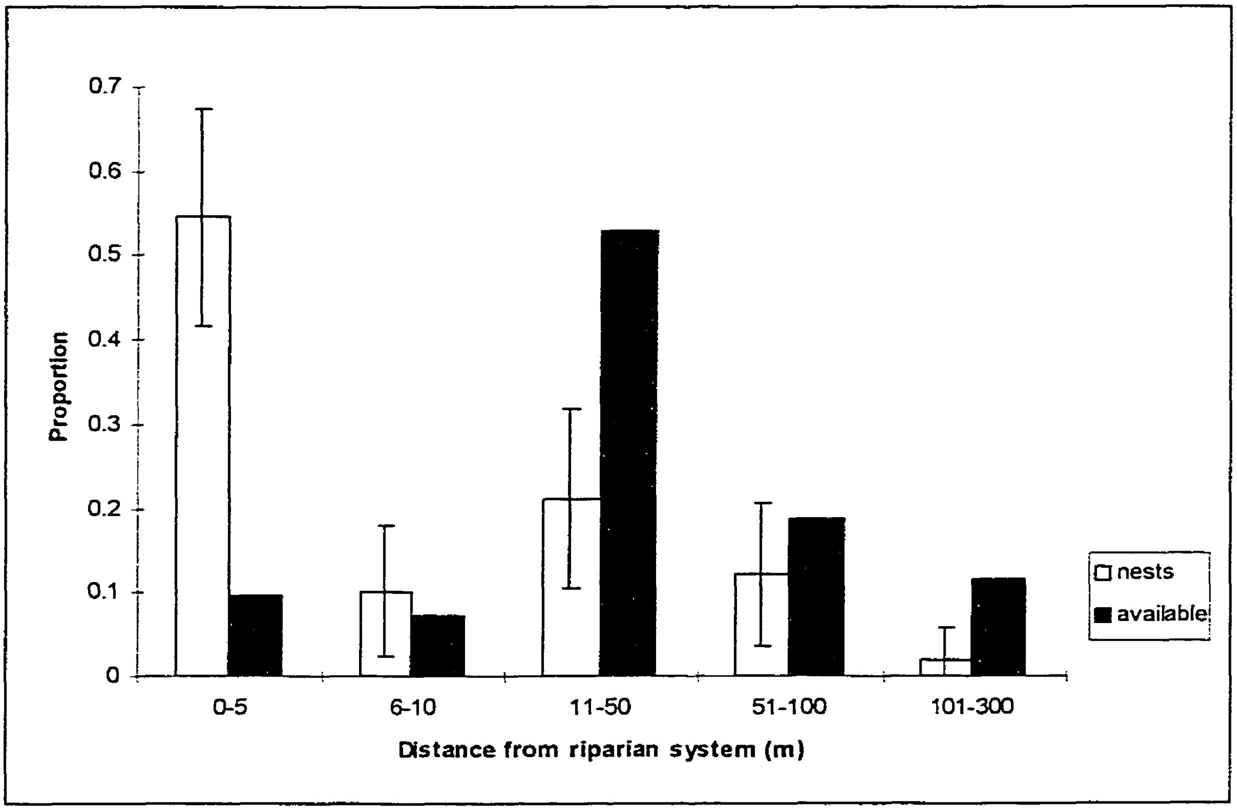


Fig. 9. Proportions of Winter Wren nests (n=99) and habitat availability (n=315 habitat grid points) at different distances from riparian systems (channels) in the Roberts Creek Study Forest. The 95% confidence intervals adjusted to control for experiment-wise error rates (Bonferroni - adjusted Z-tests, K=5) show a significantly higher proportion of nests located at 0-5 m (proportion available below lower confidence interval) and significantly fewer nests located at 11-50 and 101-300 m compared to availability (proportion available greater than upper confidence interval).

of the nests were >8 m from riparian and moist systems (Fig. 10). Winter Wrens avoided placing their nests >8 m from riparian and moist systems ($G=176.6$, $v=3$, $P<0.01$). Winter Wrens nested at sites where both riparian and moist systems were present but did not nest at sites where only moist systems were present.

Comparisons of Habitats at Nest Sites and Non-Nest Sites within Territories

Some habitat attributes differed between nest sites and non-nest sites but these differences were not consistent between creek and non-creek areas (Table 6). Creek nest sites had small amounts of canopy cover from the live lower overstory trees (canopy position referred to as A4); whereas non-creek nest sites had no canopy cover in this layer. In non-creek areas, nest sites had significantly fewer live stems and snags (30-49 cm dbh) and fewer live stems ($\geq$50, 30-49 and $\geq$10 cm dbh) than did non-nest sites. These densities were similar to densities at both nest and non-nest sites in creek areas. In non-creek areas nest sites had lower densities of Wildlife-Trees-3 (these are snags with branches, twigs and needles present, sound roots, all dbh classes) than did non-nest sites. The density of Wildlife-Trees-3 at non-creek nest sites were similar to that found at both nest and non-nest sites in creek areas. Wildlife-Trees-3 occurred most often in the lower overstory canopy or below the overstory canopy. In non-creek areas, nest sites selected by male Winter Wrens had lower volumes of medium sized downed wood (30-50 cm dbh) than did non-nest sites. In creek areas, nest sites and non-nest sites did not significantly differ in volume of downed wood but tended to show the opposite trend. There were no interactions between creek and non-creek nest sites for 8 habitat attributes (Table 7).

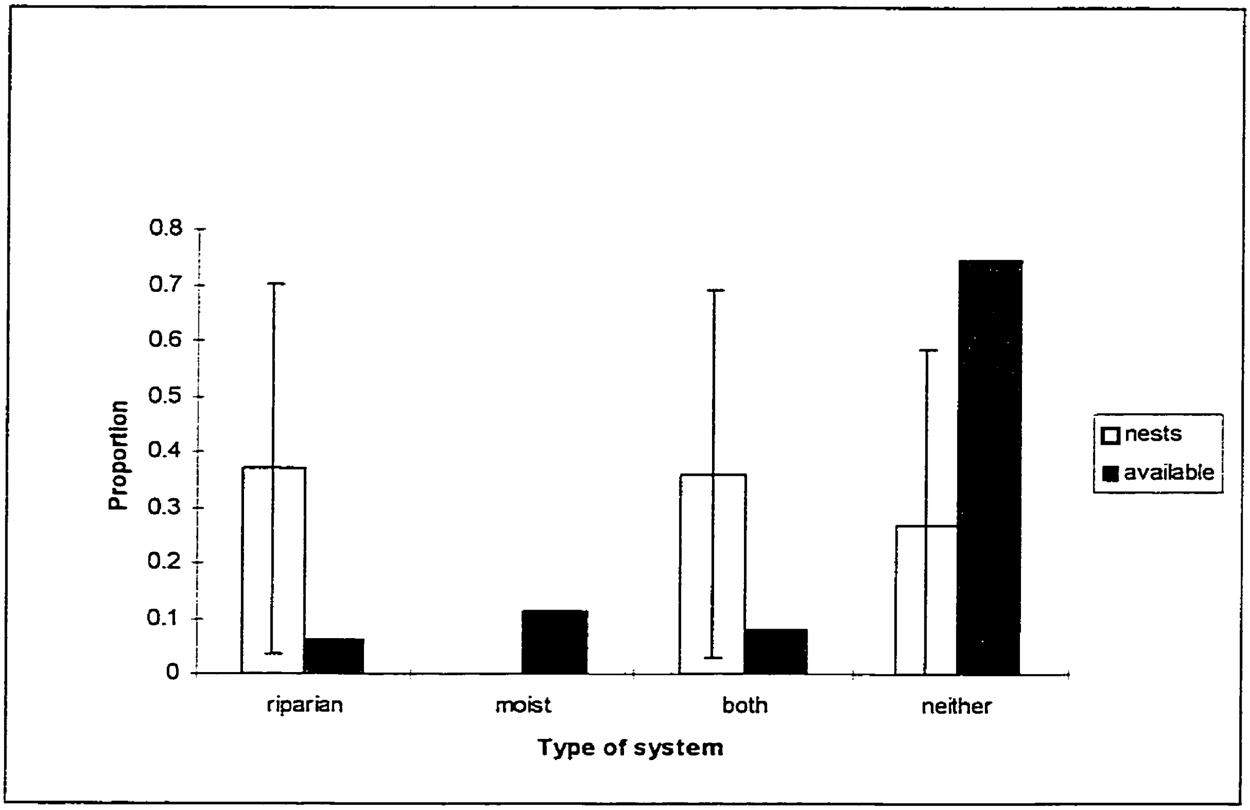


Fig. 10. Proportions of Winter Wren nests (n=99) and habitat availability (n=315 habitat grid points) within 8 m of riparian and moist systems. The 95% confidence intervals adjusted to control for experiment-wise error rates (Bonferroni-adjusted Z-tests, K=4) show avoidance of sites with neither riparian or moist systems. Nests were not located in moist systems without the presence of a riparian system.

Table 6. Mean habitat attributes at nest sites and paired non-nest sites (multivariate response) by habitat type (creek and non-creek). Values from the MANOVA are presented separately by habitat type because of an interaction between habitat types. Variables are presented only if significant ($P \leq 0.05$) differences occurred between nest and non-nest sites in either habitat type (creek or non-creek).

Habitat attribute	Habitat type	Nest site		Non-nest site		MANOVA		
		Mean	SE	Mean	SE	df (n, d)	F	P
Canopy cover lower overstory A4 trees (%)	Creek	1.30	0.28	0.00	0.00	1,9	21.4	<0.01
	Non-creek	1.68	0.22	1.93	0.20	1,36	1.11	0.29
Downed wood 30-49 cm dbh (m^3/ha)	Creek	140.6	28.4	77.6	18.8	1,9	4.45	0.06
	Non-creek	94.7	13.0	127.1	11.9	1,36	4.50	0.04
Live stems 30-49 cm dbh (stems/ha)	Creek	115	20	85	22	1,9	0.89	0.37
	Non-creek	99	11	232	27	1,36	24.96	<0.01
Live stems and snags 30-49 cm dbh (stems/ha)	Creek	145	25	110	27	1,9	1.15	0.31
	Non-creek	137	14	257	27	1,36	27.63	<0.01
Live stems ≥50 cm dbh (stems/ha)	Creek	95	23	85	22	1,9	0.13	0.73
	Non-creek	107	12	184	22	1,36	12.49	<0.01
Live stems ≥10 cm dbh (stems/ha)	Creek	400	47	325	62	1,9	0.871	0.36
	Non-creek	481	40	727	40	1,36	27.91	<0.01
Wildlife-Trees-3 (stems/ha)	Creek	10	10	10	7	1,9	0.0	1.0
	Non-creek	8	4	42	7	1,36	13.79	<0.01

Table 7. Mean habitat attributes at nest sites and paired non-nest sites (multivariate response) for both habitat types (creek and non-creek). Values from the MANOVA are presented for pooled habitat types (n=47) because no interaction was found between habitat types. Variables are presented only if significant ($P \leq 0.10$) differences occurred between nest and non-nest sites.

Habitat attribute	Nest site		Non-nest site		MANOVA		
	Mean	SE	Mean	SE	df (n, d)	F	P
Live stems < 10 cm dbh (stems/ha)	313	33	923	203	1,46	8.62	0.01
Live stems and snags < 10 cm dbh (stems/ha)	505	51	1127	204	1,46	8.40	0.01
Live stems and snags ≥ 75 cm dbh (stems/ha)	31	5	72	17	1,46	6.04	0.02
Live stems and snags ≥ 50 cm dbh (stems/ha)	137	11	204	20	1,46	12.35	<0.01
Distance to upturned root mass (m)	9.0	1.4	12.8	1.3	1,45	3.93	0.05
Fern cover (%)	6.6	1.2	3.7	0.8	1,46	3.36	0.07
Deciduous shrub cover (%)	5.4	1.0	3.4	0.6	1,46	5.02	0.03
Ground cover (%)	82.0	2.2	88.5	1.0	1,46	7.55	0.01

Nest sites had fewer live stems (<10 cm dbh) and fewer combined live stems and snags ($\geq$75, $\geq$50, <10 cm dbh) than did non-nest sites. Nest sites had greater cover of ferns and deciduous shrubs, but less exposed ground than did non-nest sites.

Occupied and Unoccupied Nest Sites within Territories

For creek and non-creek nest sites combined, occupied nest sites had lower volumes of large wood ($\geq$75 cm dbh), less cover of ferns, more snags and a more southerly aspect than did unoccupied nest sites (Table 8). When I restricted my analysis to non-creek areas, nest sites occupied by female Winter Wrens had less cover of shrubs $\geq$0.5 m high (deciduous and evergreen), more live stems and snags (10 - 29 cm dbh), and more live stems overall (>10, $\geq$75 cm dbh) than did unoccupied nest sites (Table 9). Live stems were more abundant at occupied nest sites when I excluded creek nest sites, and this may partly explain the change in the relationship from when I included creek nest sites. Aspect was no longer significant when I excluded creek nest sites, likely because of small sample size. Also, there were no longer significantly greater amounts of Wildlife-Trees-3 stems/ha at occupied compared to unoccupied nest sites.

Nest Substrates

Nests occurred at a range of heights but all were in the understory of the forest (Table 10). The lowest nest was 35 cm above the ground in a crevice of a log and the highest was 285 cm above the ground hanging from a branch on a snag. Mean heights of nests in each type of nest substrate ranged from 70 cm to 190 cm (Table 10).

Table 8. Results from one-way randomized block design (ANOVA) testing for differences between pairs of occupied and unoccupied nest sites blocked by territory and year ($P \leq 0.10$). The ANOVA was run with 6 pairs with creek nests and 10 pairs of non-creek nests (n=16).

Habitat attribute	Occupied nest site		Unoccupied nest site		ANOVA	
	Mean	SE	Mean	SE	F	P
Aspect (°)	201.6	6.2	212.0	4.9	4.60	0.04
Downed wood ≥75 cm dbh (m^3/ha)	22.3	12.7	141.2	29.3	10.3	0.01
Fern cover (%)	4.5	1.6	11.5	2.9	3.63	0.01
Wildlife-trees-3 (stems/ha)	13	7	3	3	3.46	0.08
Wildlife-trees-4/5(stems/ha)	84	16	31	10	4.73	0.05
Total snags - all dbh (stems/ha)	256	90	150	50	4.23	0.06
Mean distance to nearest canopy snag (m)	11.9	1.6	16.6	1.0	12.15	<0.01

Table 9. Results from one-way randomized block design (ANOVA; $P \leq 0.10$) using only non-creek nest sites to test for differences between pairs of occupied and unoccupied nest sites blocked by territory and year (n=10).

Habitat attribute	Occupied nest site		Unoccupied nest site		ANOVA	
	Mean	SE	Mean	SE	F	P
Downed wood $\geq$75 cm dbh (m^3/ha)[1]	35.6	19.4	155.6	40.2	4.74	0.06
Fern cover (%)[1]	2.3	1.0	10.6	3.6	5.14	0.05
Shrubs >0.5 m high (%)	0.5	0.3	2.8	1.0	4.56	0.06
Live trees and snags 10-29 cm dbh (stems/ha)	590	94	360	61	4.73	0.06
Wildlife-trees-4/5 (stems/ha)[1]	80	17	25	13	5.21	0.05
Live stems $\geq$75 cm dbh (stems/ha)	15	8	0	0	3.86	0.03
Total snags - all dbh (stems/ha)[1]	605	153	350	67	4.83	0.06
Mean distance to nearest canopy snag (m)[1]	10.3	1.1	18.1	1.2	26.3	<0.01
Live stems $\geq$10 cm dbh (stems/ha)	625	53	470	46	7.15	0.03

[1] Significant result was found when including creek nest sites (Table 3).

Table 10. The mean diameter of 8 nest substrates, and the mean heights of Winter Wren nests in these substrates. The dbh of trees (28.0 - 102.0 cm dbh) and snags (4.5 - 20.0 cm dbh) that had nests on branches was highly variable thus I do not include a mean (SE).

Nest substrate	n	DBH cm Mean (SE)	Nest height cm Mean (SE)
Creek bank	12	n/a	70 (6)
Upturned root mass	20	n/a	80 (6)
Log	36	50.7 (3.7)	70 (4)
Log butt	3	90.5 (14.0)	70 (4)
Stump	3	143.5 (29.4)	90 (11)
Snag crevice	8	53.7 (8.3)	111 (27)
Snag bark	11	29.3 (2.5)	160 (17)
Branch	6	n/a	190 (23)

Nests were usually woven into crevices. Nests beneath overhanging portions of creek and stream banks and in upturned root masses were located in crevices in the loose soil and fine rootlets. Nests in logs were usually in a crevice on the underside of the log. Logs were generally suspended above the ground which provided Winter Wrens with flight access to their nest. Most logs were western redcedar and Douglas-fir. They were hard and intact on the outside with decayed centers, and 75% of them had been burned during earlier fires. Although mean diameter of logs suggested that large pieces were favoured (mean dbh 50.7±3.7 SE cm), Winter Wrens did not show selectivity for any size class (logs and log butts of size classes: 17.5-29, 30-49, 50-74, 75+ cm dbh; $G=2.8$, $v=3$, $P>0.10$).

There are 3 subcategories of snags used by Winter Wrens for nesting. I included these subcategories when testing for selectivity of nest substrates because each subcategory has different implications for forest management. A few nests were in remnant old-growth stumps of western redcedar. These nests were located in cracks in the hollow, decayed centers of the stumps. Other nests were located in crevices in large diameter snags that were predominantly western hemlock, well decayed and with broken tops. Some nests were behind large slabs of peeling bark on broken-top snags from well decayed red alder (*Alnus rubra*) and some amabilis fir. Nests were generally woven onto the branches of suppressed western hemlocks snags that had most of their branches remaining. Nests were also woven onto the branches of live trees, including: suppressed western hemlocks, old Douglas-fir "vets", and among the sucker branches of red alder.

Male Winter Wrens showed selectivity for type of nest substrate ($G=124.9$, $v=6$, $P<0.01$, Fig. 11). Upturned root masses and creek banks were used more than expected

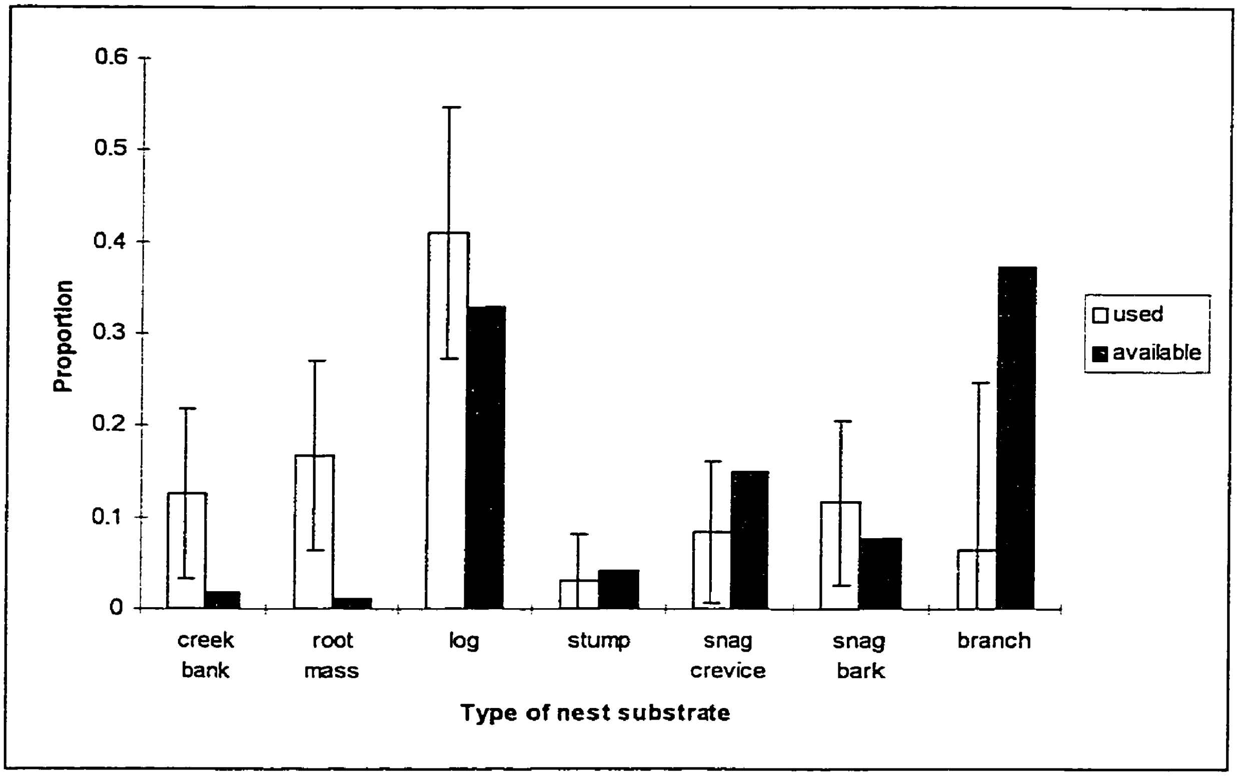


Fig. 11. Proportions of substrates in which male Winter Wrens built 95 nests and proportions of substrates available (n=845) in the Roberts Creek Study Forest. The 95% confidence intervals are adjusted to control for experiment-wise error rates (Bonferroni-adjusted Z-tests, K=7). If proportion available is greater than the upper confidence interval then the substrate is avoided (e.g., branch category) and if the lower confidence interval is greater than proportion available then the substrate is preferred (e.g., creek banks and upturned root masses).

whereas branch substrates were used less than expected. Logs and snags (bark, crevice and stump) were all used in proportion to their availability. Females did not show selectivity for the type of nest substrate that they used (G=2.8, v=4, P>0.10). But I am cautious in this interpretation of preference because availability for females may be overestimated, if location of males territories or other breeding females constrain female choice. Ninety-four percent (44/47) of nest substrates found in 1995 remained available for use in 1996. Sixteen of 44 nests available from 1995 were reused by male Winter Wrens in 1996 (Fig. 12), and 5 of these were known to be reused by the same territory holders from 1995 (i.e., banded birds). Male Winter Wrens preferred to reuse nests in creek banks (G=31.8, v=3, P<0.01).

Nests in substrates comprised of soil (creek banks and root masses) were not used evenly among territories. Nests in nest substrates comprised of soil occurred more frequently in multiple nest territories than in single nest territories in 1996, whereas single nest territories more often had nest substrates comprised of wood (multiple nest territories, 12/20 territories nest substrates comprised of soil compared to 8/20 territories without this substrate type; single nest territories, 5/18 territories with nest substrates comprised of soil compared to 13/18 territories without this substrate type; G=4.4, v=1, 0.025<P<0.05). I did not test the 1995 data because of small sample sizes.

Discussion

Male Winter Wrens preferred to build nests close to riparian systems, often locating their nests within substrates in the riparian channel or in the adjacent riparian area. By selecting territories that include riparian systems, males ensure their access to riparian

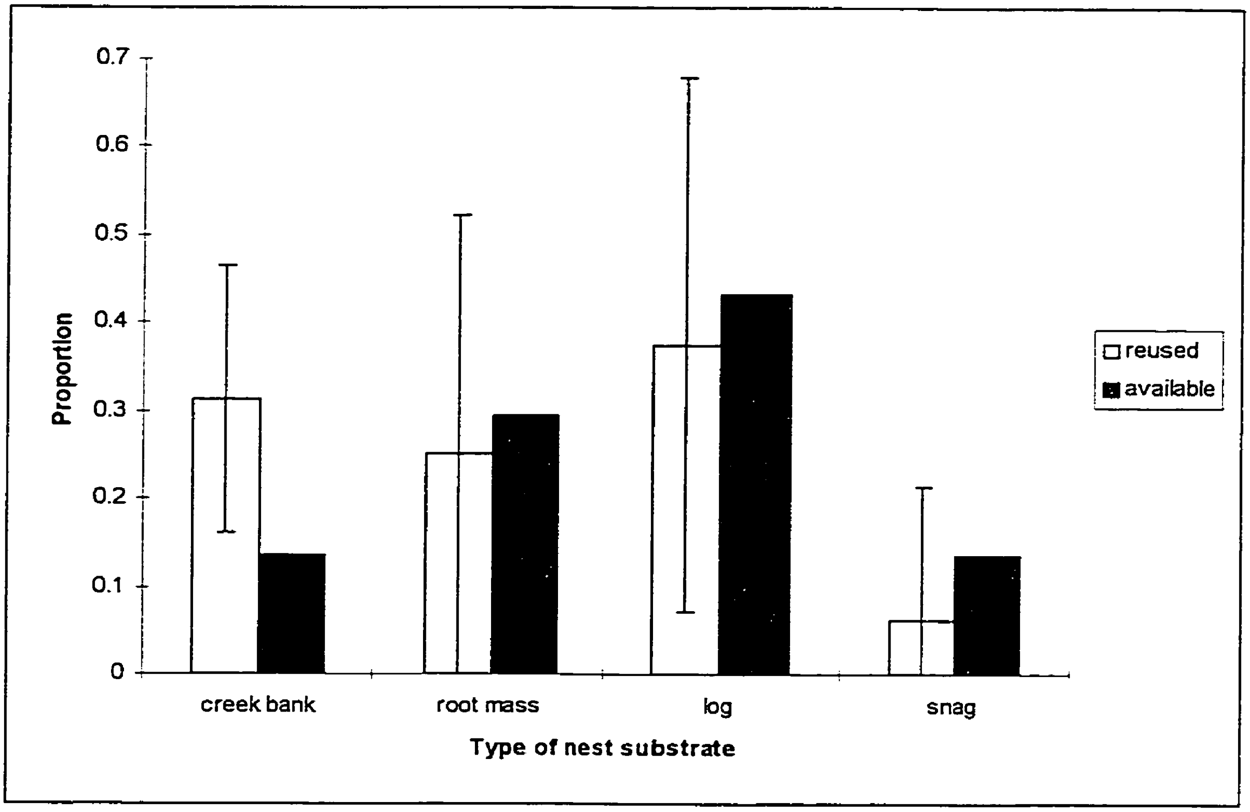


Fig. 12. The proportion of nest substrates with nests, that remained available from 1995 to 1996 (n=44) and the proportion of nests in these substrates that were reused (n=16) by males in 1996. The 95% confidence intervals adjusted to control for experiment-wise error rates (Bonferroni-adjusted Z-tests, K=4) show that creek bank nests were reused more than expected.

areas. However, nest sites selected by males were not limited to riparian systems, and nests were also located in mesic and dry upland systems. Positions of nests relative to territory boundaries may be just as important for males as type of system, if males gain breeding advantages by dispersing nest sites. I found nests near the centres as well as near the borders of territories. Alternate nesting sites may increase opportunities for males to attract females, as well as increase their chances of mating, even when they are in lower quality sites (Finch 1989b). Male Winter Wrens may attract females by dispersing nests because home ranges of females overlap territories of several males (Garson 1980b, McLachlin 1983, Evans and Burn 1996). Female Winter Wrens may also avoid occupying nests close to one another, therefore dispersion of nests throughout the territory increases opportunities for multiple nesting by males (Armstrong 1956). Use of nests positioned farther apart, may be a strategy to avoid predators. Female Winter Wrens did not show selectivity for riparian systems when selecting nests. This finding supports the hypothesis that the spacing of nests is an important factor in nest selection by female Winter Wrens (Armstrong and Whitehouse 1977).

Selectivity for nest sites at the stand-level suggests that moist systems are not preferred by males unless riparian systems are present as well. Therefore, free flowing water, and the associated riparian channels and habitats, may have more value to nesting Winter Wrens than habitats influenced by ground water only. To explore why male Winter Wrens showed selectivity for riparian systems at the stand-level, I examined both nest sites and nest substrates. The habitat attributes of nest sites used by males may reflect the association with riparian systems, rather than the attributes themselves providing preferred habitat. Yet, although amounts of habitat attributes varied between riparian areas of creeks and other areas, Winter Wrens selected similar nest sites in both these areas. Alternatively, this finding suggests that selectivity for nest sites with particular habitat attributes, may be more important than simply selecting any site in a riparian system. But, there may be a greater likelihood that males can find a preferred nest site in riparian areas of creeks, than in riparian areas of streams or in upland areas because nest sites near creeks were more similar to non-nest sites near creeks, than non-nest sites elsewhere. Selectivity for riparian systems rather than upland systems by males may be an expression of this greater opportunity for locating preferred nest sites.

Winter Wrens may prefer to nest in structurally heterogeneous patches in the forest. Males built nests in sites that had fewer live tree stems and snags than the surrounding forest, and thus these sites had relatively more open than closed understories. Furthermore, although I did not measure canopy gaps directly, some of these nest sites likely had gaps in the overstory canopy above the nest substrates: edaphic gaps above creek banks, and developmental gaps above uprooted trees and large dead snags (Spies et al. 1990, Lertzman et al. 1996). More open areas in the understory and overstory contribute to structural diversity in the stand by providing heterogeneous patches. These patches not only include a shift in horizontal structure with the lower density of stems, but may have a more diverse vertical structure, if understory vegetation develops beneath a gap in the canopy that lets in more light and moisture than normally penetrates a closed canopy. Nest substrates such as creek banks, upturned root masses, downed wood, and snags may themselves also contribute to vertical structural diversity. Additional evidence that males select heterogeneous areas was provided by my finding that uprooted trees were significantly closer to nest sites than non-nest sites. This indicates that male Winter

Wrens may prefer to use disturbed areas that are more structurally heterogeneous because of the uprooted trees.

There may be several advantages to males if they locate their nests in sites that are relatively open in the understory and overstory. Openings would enable the male to better advertise his nest with visual displays and because his song would carry farther. He would also remain in better vocal contact, over greater distances, when the female is laying and incubating eggs. Openings with greater cover of ferns and deciduous shrubs, such as those associated with nest sites, can have a greater potential prey base, especially when associated with moister habitats (McLachlin 1983, Wesolowski 1983, Van Horne and Bader 1990). However, nest sites were not centered in gaps because male Winter Wrens preferred some overstory canopy, for example in riparian areas of creeks, nest sites had significantly more lower overstory canopy than did non-nest sites. Overstory canopy may provide protection from predators that use the edges of openings (Paton 1994) or from weather (e.g., sun, rain or possibly wind). Open areas may also be associated with preferred nest substrates because these substrates produce (e.g., snags) or are associated with (e.g., creek banks) overstory gaps.

Nest security is a major determinant in the breeding success of the Winter Wrens, and females may prefer to occupy more secure nests (Garson 1980a, 1980b). Winter Wrens are likely therefore to optimize forest attributes to achieve maximum security for their nests. Females selected nest sites from those already selected by males. Females chose to occupy nest sites with less cover of tall vegetation, including shrubs and ferns, and a lower volume of large downed wood when compared to unoccupied nest sites. Less cover at the nest implies that the nest is less secure from predators. But, for House Wrens

(*Troglodytes aedon*) in Wyoming, less cover (i.e., downed wood) and more open ground, with sparse overstories, at nest sites may have benefited the incubating females (Finch 1989b). These sites may have enabled females to detect predators from a distance, and limited predators' access to nests (Finch 1989b). Female Winter Wrens may select their nest sites for similar reasons, because most nests are situated below 2 m in the lower forest strata and they may be more vulnerable to predation, particularly if some substrates such as large downed wood attract predators. In the Roberts Creek Study Forest, Douglas squirrels commonly used logs as pathways and feeding sites, and I observed one preying on nestlings of Winter Wrens.

Nest substrates used by the Winter Wrens provided good places to nest, but they were also prominent features in a stand. Female Winter Wrens preferred nest sites with high densities of live tree stems and snags. These sites had a diverse tree structure comprised of large trees and snags, as well as small understory trees and snags. The forest structure at sites preferred by female Winter Wrens provided greater concealment without obscuring flight paths, as might occur if they preferred sites with more shrub cover. On the other hand, sites with more standing stems and snags will also tend to have reduced cover from vegetation and downed wood.

Female Winter Wrens must also choose nest sites that have sufficient food, and an appropriate thermal regime for the young in addition to security. Feeding conditions near the nest may be crucial in determining female Winter Wren reproductive success (Garson 1980b). Diverse forest structure is preferred by Red-breasted Nuthatches *(Sitta canadensis*) and Brown Creepers (*Certhia familiaris*) because it provides high arthropod abundance and better protection from inclement weather (Adams and Morrison 1993).

Badly situated or ill-constructed nests (too high from the ground, poor seclusion, inconvenient entrance) are liable to be rejected by female Winter Wrens (Armstrong and Whitehouse 1977). Female Winter Wrens in my study area selected nests with more southerly aspects but there was a limited range available (170-260 degrees). Nest boxes in sparse habitats receive greater solar radiation than nest boxes in densely vegetated habitats (McComb and Noble 1981, Finch 1989b). The more southerly aspect and openings in the canopy may provide warmer conditions for nest microclimate. Nest microclimate is important for incubating females, especially when nesting earlier in the season or when occupying nests near creeks, which tend to be cooler than the surrounding stand.

Male Winter Wrens used a variety of nest substrates, revealing that their habitat use is flexible. Except for branch nests, all nest substrates had a natural crevice or cavity, and the substrate itself concealed the nest, rather than the nest being obscured by other vegetation. The substrate selected also had a convenient entrance that allowed for a quick exit from the nest (Armstrong and Whitehouse 1977). Males avoided using branch substrates for nests. Nests on branches are exposed and did not often last between years as those in crevices and cavities. Males preferred two types of nest substrates comprised of soil: root masses of uprooted trees and overhanging banks of creeks and streams. Both of these types were associated with riparian systems in my study area and thus preference for these 'soil nest substrates' may in part be owing to the preference of Winter Wrens for riparian systems. Further evidence for this preference comes from territories with multiple nests. Forty-five percent of males in 1996 had territories with nest substrates comprised of soil and there was a greater likelihood of males having multiple nests in these territories, than in territories where nest substrates comprised of soil were not used by Winter Wrens. Soil nest substrates may be preferred because they are associated with high quality sites that are able to support more nests. The number of vacant nests in a territory is a criterion that females may use to judge territory quality, including her need for alternative nests for double brooding (Garson 1980b, Wesolowski 1987, Evans and Burn 1996). Winter Wrens build fewer nests in lower quality habitats (Armstrong 1956, Armstrong and Whitehouse 1977).

The preference that male Winter Wrens exhibited for creek bank nest substrates was further illustrated by their reuse of nests in this substrate rather than root mass, log, or snag substrates, thus supporting the notion that substrate itself is important or that characteristics associated with creeks are important. The microclimates of both nest substrates and riparian systems could also contribute to nest site and nest substrate selectivity. Nest substrates comprised of soil tend to be moister than nest substrates comprised or associated with wood (logs, snags, branch nests). Substrates with higher moisture content have greater heat capacity (McComb and Noble 1981). Occurrence of fungus, which I used as an indicator of higher humidity, was significantly greater in nest substrates comprised of soil compared to those comprised of wood. Although, more heat is required to raise the temperature of soil than wood, heat stored during the day is lost slowly from soil because of its higher heat capacity. As air temperatures change, internal temperatures of nest substrates comprised of wood, that have less moisture, will fluctuate more than the more stable internal temperatures of the nest substrates comprised of soil. If variable ambient temperatures (e.g., day and night) influence internal nest temperatures, the metabolic rates of cavity users will be affected (McComb and Noble 1981). For example, female Winter Wrens require high amounts of energy to incubate and greater energy is required at cooler temperatures (Armstrong and Whitehouse 1977).

Another advantage for males locating nests near riparian systems is the condition of the nest building materials: wet materials may be more easily manipulated for weaving nests (Armstrong 1956, Wesolowski 1983). Although cedar needles, moss and rootlets are pliable, small twigs are not normally pliable and these were used for weaving nests in the Roberts Creek Study Forest.

Females did not show selectivity for type of nest substrate in my study area. This finding differs from research, in forest stands of eastern Poland, where female Winter Wrens preferred upturned root masses for nest substrates only in mesic to dry habitats which had limited availability of these nest substrates (Wesolowski 1983). I may have been unable to detect female preference in my study because measuring selectivity relies on having variability among habitats (Orians and Wittenberger 1991). As well, choice of nest substrate may already be incorporated by the habitat selection of males.

Chapter 3. Habitat Selection by Winter Wrens in Young and Mature Forest

Introduction

The densities of most species of birds vary across seres (Morrison 1986). Although there is some correspondence between these densities and stand age, stronger correlations exist between bird density and stand structure (Rotenberry and Wiens 1980, Hayes et al. 1997). In the Pacific Northwest of North America, Winter Wrens are most numerous in structurally diverse stands, such as mature, old-growth and hardwood forests, whereas they are least numerous in more structurally uniform, immature forests (Carey et al. 1991, Eckert et al. 1992, Bryant et al. 1993, Hansen et al. 1995, Savard et al. 1995). The density of Winter Wrens is correlated with abundance of particular habitat attributes (e.g., snags, downed wood and canopy gaps) within and among these seral stages (Carey et al. 1991, Savard et al. 1995).

Young stands, especially if they are even-aged, may provide fewer resources to many species of wildlife than mature or uneven-aged stands, and thus have diminished value as wildlife habitat (Hunter 1990, Franklin and Spies 1991). However, many young and mature stands contain structures such as large trees, snags and downed wood that remained following natural (e.g., fire) and human induced (e.g., operational harvesting) disturbances. The number and distribution of these structures varies with the type of disturbance and they change over the course of the stands' development (Spies et al. 1988, Carey et al. 1991, Franklin 1992, Wells 1996, Hayes et al. 1997). Besides remnant structures (biological legacies), the structural homogeneity of young and mature stands is interrupted by physical features such as topography and streams. These physical features provide specific habitat (e.g., water for drinking, stream banks for nests) for wildlife and also contribute structural diversity to the stand. Riparian systems offer resources to wildlife which add to those available in upland portions of both young and mature stands. The importance of riparian habitat for enhancing the stand's capability to support wildlife varies among stands, but is likely greater in structurally uniform forests.

To determine the generality of my results in Chapter 1, I examine habitat use of Winter Wrens in two seral stages, young (40 to 60-year old) and mature (80 to 120-year old) forest, located along the Sunshine Coast (Fig. 1). My sampling design did not include old-growth stands because little accessible old-growth remains in the Coastal Western Hemlock Dry Maritime subzone (CWHdm). Nor, did I sample stands younger than 40 years because this age class was concentrated at mainly higher elevations and most are managed intensively by spacing or thinning. In this chapter, I sampled over a broader area than I examined in the previous chapters. Habitat selection may be constrained in places where particular habitats are unavailable (Sherry and Holmes 1985, Ruggiero et al. 1988). Hence by sampling over a broader area, I could determine the generality of my results. As well, an understanding of variability in habitat selection over the landscape provides a basis for testing the generality of species-habitat relationships and should reveal how broadly these relationships can be applied as management (prediction) tools (Brennan et al. 1984, O'Neil et al. 1988).

My objective was to determine whether riparian systems are selected by Winter Wrens over a broader range of conditions, and if so, are riparian habitats preferred to upland habitats because of the unique characteristics associated with water channels (e.g., microclimate, stand structure). If riparian systems influence the spatial distribution of

Winter Wrens, there should be a significant response to riparian habitat by Winter Wrens in both seral stages. However, if riparian systems provide only favourable habitats under particular conditions of disturbance history or stage of stand development, then the responses of Winter Wrens to riparian systems are likely to differ between seral stages.

I walked transects to locate singing Winter Wrens and identify their song perches. I chose to use song perch locations because Winter Wrens exhibit a range of vocalizations and they have a loud, far-carrying song (Van Horne 1995). Song has two main functions for birds, including to advertise and defend a territory, and to attract a mate (Best 1981). Song perches and the area surrounding song perches are microhabitats that Winter Wrens select within their territories, the macrohabitat patch (Collins 1981). First, I compare whether density of Winter Wrens and habitat structure is different between the two seral stages. Next, I determine if microhabitats around song perches of Winter Wrens are different from randomly selected sites, and whether these differences are consistent between the two seral stages.

Methods

Transect Method

Forest stands were identified in areas of young (40 to 60-year old) and mature (80 to 120-year old) forest along the Sunshine Coast from the Sechelt Peninsula to Powell River. These stands were accessible, at least 500 m apart and usually large enough to walk 2 transects. Transects were 500 m in length with 150-m buffers along each side. I selected a transect length of 500 m because most stands were not consistent in shape, and usually a maximum of 1 km could be surveyed during a day. I estimated that 2 Winter Wrens would be located per transect, thus 4 per survey day.

I randomly selected a distance from the edge of each stand that would allow placement of the full transect. Next, I selected a random distance perpendicular to the start of the transect that ensured the 150-m buffers to each side of the transect. I placed transects across the slope of the stand to obtain a range of distances from riparian systems. I walked along each transect and located singing Winter Wrens (wren locations) during the active breeding season from late April to early June 1996. Transect width was based on aural location of singing Winter Wrens and this generally did not exceed 150 m (pers. obser.). For each wren location, I randomly selected a location (random location) on the same transect. The sample of random locations gave me an estimate of habitat available to Winter Wrens that I could compare to the observed habitat used by singing Winter Wrens. On the transects, I located each random location by first selecting a random distance along the transect with a random number table. I then selected a second random distance perpendicular to the transect within the 150-m buffers. For analyses, I grouped stands within the same general area (usually a watershed) as blocks, and these blocks were nested within seral stage. There were a total of 40 wren locations and 37 random locations in 10 blocks (19 transects) in young forest, and 37 wren locations and 38 random locations in 9 blocks (19 transects) in mature forest.

I surveyed for Winter Wrens from sunrise to 4 hours after sunrise because this is the most active singing period for birds (Verner 1985). My methods did not account for possible non-breeding singing males or individuals' singing away from territories (Haila et al.1989) and I did not distinguish between different songs. During the survey at each wren location, I recorded type and height of each song perch, the height at which the Winter Wren was singing, and I flagged the locations to later revisit for measuring habitat attributes.

Habitat Attributes Measured on Transects

I assessed habitat attributes on plots centered at both wren and random locations to determine habitat use and affinity of Winter Wrens for riparian and moist systems (Appendix A, Chapter 1, Fig. 4). I chose habitat attributes that were associated with Winter Wren activities, including: foraging (downed wood, snags, ferns and shrubs, horizontal and vertical structure); nesting (upturned root masses, logs, trees and snags, horizontal and vertical structure); singing (horizontal and vertical structure); and concealment (horizontal and vertical structure). I chose subcategories based on Winter Wren behaviours (e.g., use of wood structures > 30 cm dbh for nesting) and forestry practices (Chapter 1).

I measured distance to the nearest riparian system (channel) of creeks and streams (or seeps) and any bodies of free water. I used distance to riparian system for assessing the influence of riparian systems on the spatial arrangement of territories (macrohabitat) as represented by the song perches. As well, this distance enabled me to examine relationships of other habitat attributes to riparian systems. Measurements for other attributes are described in Appendix A.

Analyses

If density of Winter Wrens was greater in the mature forest, as reported in other studies, I expected to encounter more Winter Wrens (wrens/transect length) in the mature forest than in young forest. As well, I expected that the mean detection distance to Winter Wrens would be greater in the younger forest than in mature forest. I used the Mann-Whitney test to determine if number of Winter Wrens per km of transect (n=19 transects for young forest, and n=19 transects for mature forest) differed between the two seral stages. I used the normal approximation to the Mann-Whitney test (Zar 1984) to test whether there was a difference in detection distance (mean perpendicular distance from the transect to a Winter Wren location) between young (n=40 locations) and mature (n=37 locations) forests.

I used a log-likelihood Chi-square test to test for differences between types of song perches used by Winter Wrens (downed wood, root mass, snag, tree; n=71). I used contingency tables (3 dimensional, n=152) to test for differences between the presence of water near random locations and near wren locations in each seral stage. First, I tested whether type of location, seral stage and presence of moist systems were mutually independent. Next, I replaced presence of a moist system with presence of water (either a riparian or moist system) and re-ran the test. Presence was defined as a moist system (or water) within a 0.20-ha plot around the song perch or random location.

I used analysis of variance (ANOVA) to determine if Winter Wrens in young and mature forest placed their territories closer to riparian systems and if they selected for other habitat attributes at their song perches. The ANOVA determined which habitat attributes (response variables) had significant between group differences for: a) the 2 seral stages (young and mature); and b) the 2 types of locations (wren and random). The data were analyzed as an unbalanced, completely randomized, split-plot, factorial design (Sit 1995) in which seral stage was the whole-plot factor and location was the split-plot factor. The experimental units for the whole-plot factor were the 'blocks' that were nested within seral stage. The split-plot ANOVA tested the following 3 null hypotheses separately for each of several habitat attributes:

(1) H_0: There is no interaction of seral stage (young and mature) and type of location (random and wren) on the amount of a habitat attribute (α=0.10);

(2) H_0: There is no effect of seral stage on amount of a habitat attribute (α=0.10);

(3) H_0: There is no effect of type of location on amount of a habitat attribute (α=0.10).

I used alpha=0.10 for the ANOVA because the exploratory nature of the analysis involved many variables. I did not test habitat attributes that were infrequent across locations. I also eliminated one attribute for pairs of attributes that were highly correlated ($r > 0.70$) and had a similar ecological function. A rank transformation was used on all habitat attributes to normalize the residuals. However, estimated least-square means and standard errors were calculated using the unranked data. If riparian systems (distance to riparian) were optimal habitat for Winter Wrens, I expected that wren locations would be associated with riparian systems in both seral stages. However, if an interaction occurred, this would indicate that Winter Wrens may use riparian habitats differently as the forest matures, or where different disturbances to the stands resulted in different patterns of habitat use by Winter Wrens. I did not use power tests for non-significant results because I could not provide accurate estimates of expected ranked differences needed for determining power.

Next, I used logistic regression models to identify those habitat attributes that best predicted the probability of a wren location in these forest stands (Brennan et al. 1984). The logistic regression model is used as a 'resource selection *probability* function', and the 'selection probability' normally used to predict this function is estimated by comparing those locations with a given set of attributes being used by Winter Wrens (wren locations) to those locations not used by Winter Wrens (Manly et al. 1993). My random locations may or may not be used by Winter Wrens; therefore the 'selection probabilities' are unknown, and instead I estimate the 'resource selection *probability* function' using a 'resource selection function', which is directly proportional to the 'resource selection *probability* function'. The resource selection function is estimated by modeling the conditional probability that an observation having a particular set of habitat attributes will be found at a wren location rather than at a random location, given that the observation is at one of the two locations (McCullagh and Nelder 1989, p.101; Manly et al. 1993, p.126). The habitat attributes that I selected as covariates for the logistic regression model were those for which the ANOVA revealed significant differences in their amounts between wren and random locations at $P \leq 0.05$. I chose to use alpha=0.05 to reduce the number of variables for the modeling, and because I was using the model as a predictive, rather than an exploratory tool.

Logistic regression analysis proceeded in two steps. First, I used a mixed model logistic regression to determine whether seral stage had a significant effect on the conditional probability outlined above. The SAS macro GLIMMIX (SAS 1988), was used to find restricted (residual) pseudo likelihood (REPL) parameter estimates (P. Ott, pers. com.). The full model is defined as follows:

$$\log\left(\frac{\tau_{ijk}}{1-\tau_{ijk}}\right) = \mu + s_i + a_{(i)j} + \beta_1 x_{1(ij)k} + \beta_2 x_{2(ij)k} + \ldots + \beta_p x_{p(ij)k} \qquad (2)$$

where,

τ_{ijk} is the probability that an observation having a particular set of habitat attributes x_{ijk} will be found in the wren location rather than the random location, given that it is one of these locations;

μ is the overall intercept;

s_i is the effect of seral stage ($i = 1,2$);

$a_{(i)j}$ is the (random) block effect $a_{(i)j} \sim N(0,\sigma_a^2)$ ($j = 1,2,\ldots,19$), which is *nested* within seral stage;

$\beta_1, \beta_2, \ldots, \beta_p$ are the regression parameters, and the observations are indexed by $k = 1,2,\ldots,148$; and

x_{ijk} the set of attributes modeled included moss cover, mean distance to overstory tree, distance to riparian system, cover of small vegetation (<0.5 m high).

Following the non-significant effect of seral stage, I eliminated it from the model and incorporated all random and wren locations in a simple logistic regression. Non-significant habitat attributes were also dropped, thus producing a simplified model with only $q \leq p$ regression parameters:

$$\log\left(\frac{\tau_k}{1-\tau_k}\right) = \mu + \beta_1 x_{1_k} + \beta_2 x_{2_k} + \ldots + \beta_q x_{q_k}, \qquad (3)$$

where all parameters are defined as in Equation 2. I used Spearman rank correlations with the random locations to examine relationships between these attributes including distance to riparian systems in both seral stages.

Results

The abundance of some habitat attributes differed between seral stages. Overstory tree canopy cover, including a more prominent deciduous overstory component, was significantly (P<0.01) greater in the young stands compared to the mature stands, and these closed stands had significantly shorter mean distances to both overstory tree (P=0.06) and understory snag (P=0.02) (Table 11). The cover of understory tree canopy (P=0.08), shrubs <0.5 m high (P=0.07), and total vegetation <0.5 m high (P=0.02) were significantly greater in the mature stands compared to the young stands (Table 11). The mature stands had more developed vertical and horizontal structure. The reduced cover of overstory canopy in mature stands was in part due to gaps in the canopy, and the greater amounts of the vertical understory shrub <0.5 m high, vegetation <0.5 m high, and understory tree canopy were likely a response to light from these gaps. There were no significant differences between the volume of downed wood per hectare in the two seral stages (Table 12). However, distance to the upturned root masses was significantly shorter (P=0.01) in the young stands indicating a greater abundance of root masses (Table 11).

Forty Winter Wrens were located along 9.12 km of transect in the young forest compared to 37 along 9.30 km in mature forest. The encounter rate of Winter Wrens in the young forest (4.39 wrens/km) was not significantly different (Mann-Whitney Test, n_y=19 and n_m=19, U=226, P>0.10) from that in mature forest (3.98 wrens/km). Mean detection distance to Winter Wrens in young forest was 40 m (SD 27.5) compared to 50 m (SD 37.3) in mature forest. There was no significant difference (Z=0.984, P>0.10) between these mean distances (normal approximation for Mann-Whitney Test, Zar 1984).

Proportions of types of structures used as song perches by Winter Wrens were not significantly different between young and mature forest (G=5.93, v=3, P>0.10; Fig. 13). There were 5 unidentified structures in young forest and 1 in mature forest (i.e., I only

Table 11. Results from split-plot ANOVA (df 1, 17) for differences between seral stages (main effect), and interaction between seral stage and location type using rank transformed habitat attributes for the ANOVA. Least-square means and standard errors were calculated using untransformed data.

		Seral stage				Main effect		Interaction	
Habitat attribute		Young n=77		Mature n=75				Seral stage X Location type	
	Units	Mean	SE	Mean	SE	F[1]	P[1]	F	P
distance to riparian	m	242	87	49	91	0.66	0.42	0.65	0.43
mean distance to overstory tree	m	3.6	0.4	4.8	0.4	**3.82**	**0.06**	2.59	0.12
mean distance to overstory snag	m	15.0	2.7	17.9	2.8	0.25	0.63	0.15	0.70
mean distance to understory tree	m	4.9	0.5	4.3	0.5	1.74	0.21	0.07	0.79
mean distance to understory snag	m	5.3	0.8	8.3	0.8	**6.46**	**0.02**	2.46	0.13
distance to root mass	m	9.7	1.4	18.2	1.4	**9.37**	**0.01**	0.04	0.85
overstory canopy cover	%	96.1	0.9	92.5	0.9	**3.70**	**0.07**	0.02	0.88
deciduous overstory canopy cover	%	21.8	4.0	3.3	4.3	**25.77**	**<0.01**	0.03	0.86
understory canopy cover	%	25.2	5.6	42.2	5.8	**3.47**	**0.08**	2.11	0.16
fern cover	%	4.1	2.9	9.4	3.1	0.42	0.53	0.04	0.85
shrub ≥0.5 m high cover	%	6.7	3.5	14.2	3.7	1.23	0.28	2.51	0.13
shrub <0.5 m high cover	%	3.1	0.9	5.0	1.0	**3.86**	**0.07**	0.63	0.43
vegetation cover <0.5 m high	%	3.1	0.9	5.7	0.9	**6.43**	**0.02**	1.24	0.28
moss cover	%	24.9	7.0	41.7	7.4	1.02	0.33	1.83	0.19

[1]Significant ($P \leq 0.10$) relationships bold type

Table 12. Results from split-plot ANOVA (df 1, 17) for differences in volume of downed wood between seral stages (main effect) and for interaction between seral stage and location type. Rank transformed downed wood variables were used for the ANOVA. Least-square means and standard errors were calculated using untransformed data.

Size of downed wood[1] (cm)	Decay /hardness	Seral stage				Main effect		Interaction	
		Young volume (m^3/ha) n=77		Mature volume (m^3/ha) n=75				Seral stage X Location type	
		Mean	SE	Mean	SE	F	P	F[2]	P[2]
7-29 dbh	fresh	12.8	4.4	13.8	4.6	0.28	0.60	2.19	0.15
	hard	55.8	4.6	60.3	4.7	0.23	0.63	1.43	0.24
	soft	17.5	3.1	19.2	3.2	0.20	0.66	0.22	0.64
	Total	86.1	6.7	93.7	6.9	0.15	0.70	0.41	0.52
30-49 dbh	hard	88.7	11.3	65.5	11.6	1.75	0.20	0.04	0.85
	soft	36.6	7.2	40.0	7.5	0.08	0.77	0.08	0.78
	Total	139.1	13.2	118.0	13.5	1.19	0.18	0.24	0.63
50-74 dbh	hard	63.6	13.5	78.5	13.9	0.03	0.87	0.10	0.75
	soft	20.9	8.1	33.2	8.3	0.65	0.43	1.28	0.72
	Total	96.5	17.3	124.0	17.8	0.08	0.78	0.10	0.75
75+ dbh	hard	74.0	30.2	78.8	31.1	0.26	0.61	2.00	0.17
	Total	80.8	29.7	87.8	30.6	0.36	0.56	**4.57**	**0.04**
7+ dbh	Total	389.1	40.8	423.5	41.8	0.06	0.81	0.75	0.38

[1] 7+=total volume of downed wood

[2] Significant ($P \leq 0.10$) relationships bold type

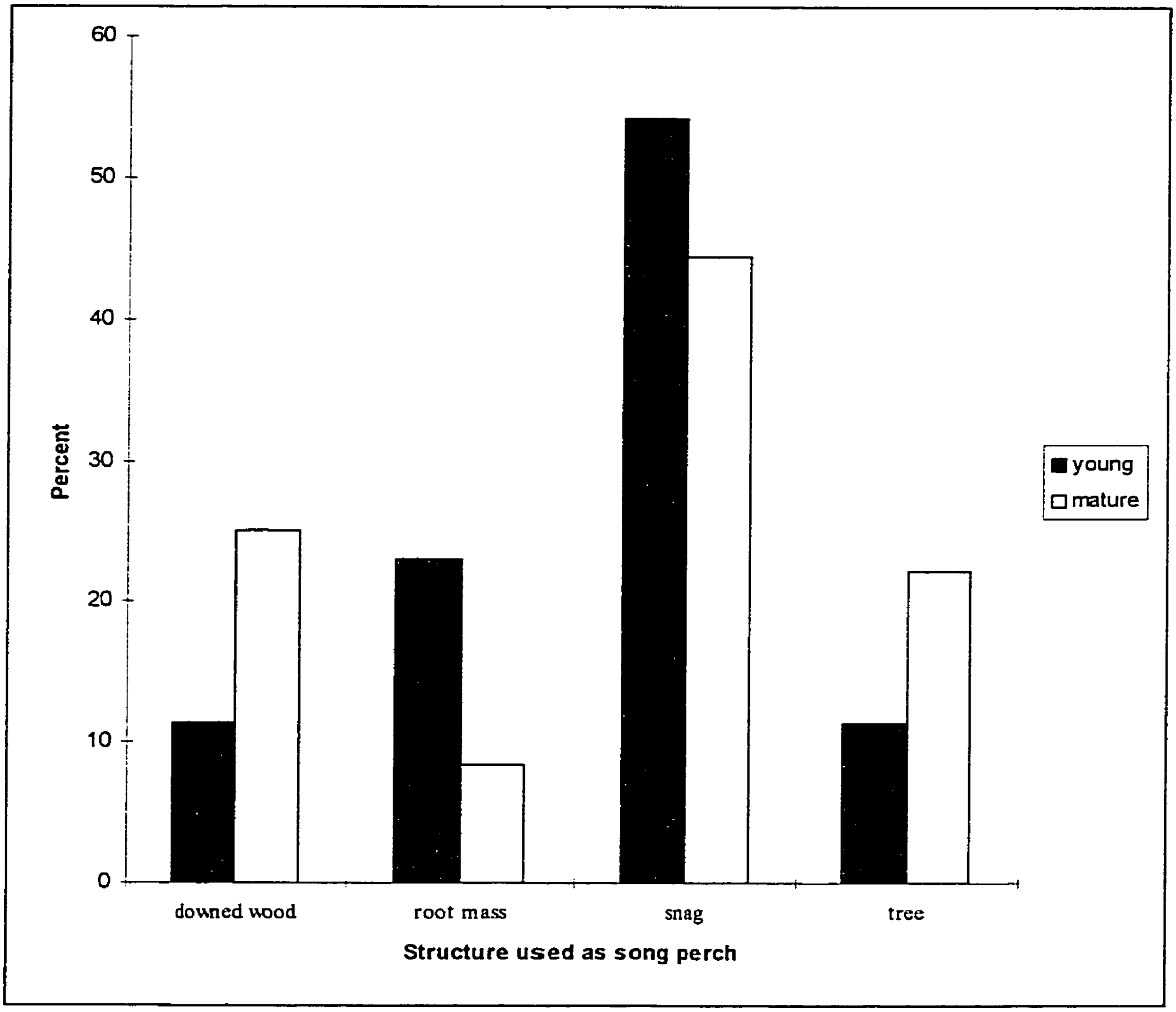


Fig. 13. Forest structures used for song perches by Winter Wrens in young (n=35) and in mature forest (n=36) in 1996.

located these Winter Wrens within +/- 5 m of their song perch). Except for trees, song perches used by Winter Wrens were in the understory layer, generally <5 m high above the ground, often at the highest location available on the structure. All song perches on downed wood were below 2 m high in the lowest stratum of the forest. Song perches on root masses and snags were also in the understory stratum, mostly in the 2-10 m high, B1 layer. Trees used as song perches were up to 40 m high but Winter Wrens sang from branches <25 m high in these trees. Several of the young stands were dry, with riparian systems at distances >400 m from any wren location or random location. Seventy-five percent (6/8) of the song perches in these dry stands were root masses.

One significant interaction was found using the split-plot ANOVA between seral stage and location types (Table 12). The general lack of interactions indicate that differences between wren locations and random locations for all habitat attributes were the same in both seral stages (Tables 13 and 14). I conclude that Winter Wrens were selecting similar microhabitats for song perches, although forest structure changed with seral stage. The significant interaction ($P=0.04$) was for the total volume of downed wood ≥ 75 cm dbh (Table 12). Although volumes of large downed wood were similar between seral stages (Table 12), and although selectivity by Winter Wrens for this large downed wood also occurred in both seral stages (Table 13), this interaction shows that the importance of large downed wood to Winter Wrens varied between seral stages (i.e., differences between amounts at random and wren locations were not the same in the two seral stages).

Amounts of several habitat attributes differed significantly ($P \leq 0.10$) between wren locations and random locations in both seral stages. Wren locations were closer to

Table 13. Results from split-plot ANOVA (df 1, 17) for differences in volume of downed wood between random and wren locations (split-plot effect). Rank transformed downed wood variables were used for the ANOVA. Least-square means and standard errors were calculated using untransformed data.

Size of downed wood[1]	Decay /hardness	Type of Location Random volume (m^3/ha) n=75		Wren volume (m^3/ha) n=77		Split-plot effect	
(cm)		Mean	SE	Mean	SE	F[2]	P[2]
7-29 dbh	fresh	14.1	3.5	12.5	3.6	2.20	0.15
	hard	58.5	4.6	60.3	4.7	0.02	0.88
	soft	21.2	2.8	15.5	2.8	2.35	0.14
	Total	93.8	6.3	85.9	6.3	1.21	0.28
30-49 dbh	hard	74.4	10.7	79.9	10.6	0.06	0.81
	soft	41.9	7.3	34.6	7.4	0.78	0.38
	Total	128.2	13.4	128.8	13.3	0.00	0.99
50-74 dbh	hard	50.9	13.6	91.2	13.6	1.94	0.18
	soft	27.1	8.2	27.0	8.2	1.15	0.29
	Total	84.0	17.5	136.5	17.6	**2.97**	**0.10**
75+ dbh	hard	60.1	27.4	92.8	27.3	**3.68**	**0.07**
	Total	69.0	27.9	99.7	27.2	**3.34**	**0.09**
7+ dbh	Total	374.6	38.7	437.9	38.5	0.69	0.42

[1] 7+=total volume of downed wood

[2] Significant ($P \leq 0.10$) relationships bold type

Table 14. Results from split-plot ANOVA (df 1, 17) for differences between random and wren locations (split-plot effect). Rank transformed habitat attributes were used for the ANOVA. Least-square means and standard errors were calculated using untransformed data.

Habitat attribute	Units	Type of Location				Split-plot effect	
		Random n=75		Wren n=77			
		Mean	SE	Mean	SE	F[1]	P[1]
distance to riparian	m	150	64	142	64	**10.44**	**0.01**
mean distance to overstory tree	m	3.9	0.3	4.5	0.3	**11.77**	**<0.01**
mean distance to overstory snag	m	16.6	2.0	16.4	2.0	0.04	0.85
mean distance to understory tree	m	4.1	0.4	5.1	0.4	2.7	0.12
mean distance to understory snag	m	6.5	0.6	7.0	0.6	**3.27**	**0.09**
distance to root mass	m	15.2	1.4	12.7	1.4	1.68	0.21
overstory canopy cover	%	94.1	0.8	94.6	0.8	0.98	0.34
deciduous overstory canopy cover	%	11.6	3.4	13.5	3.4	**3.15**	**0.10**
understory canopy cover	%	35.3	4.3	32.1	4.3	1.71	0.20
fern cover	%	5.6	2.3	8.0	2.3	0.5	0.49
shrub ≥0.5 m high cover	%	11.0	2.9	9.8	2.9	1.71	0.21
shrub <0.5 m high cover	%	4.8	0.9	3.2	0.9	**4.29**	**0.05**
vegetation cover <0.5 m high	%	5.3	0.8	3.5	0.8	**6.34**	**0.02**
moss cover	%	38.1	5.4	27.9	5.5	**7.77**	**0.01**

[1] Significant ($P \leq 0.10$) relationships bold type

riparian systems than random locations (P=0.01), although the mean differences appear to be small (Table 14). There was high variance associated with distance from riparian systems. This variance may occur because song perches have several behavioural functions and can be situated anywhere from the boundary to the centre of the territory. Also several transects were >400 m from riparian systems and a few were almost close to 1000 m from riparian systems. Distance to riparian system did not significantly differ between seral stages (Table 12), but high variance between blocks may have resulted in low power of the test.

Wren locations had significantly less cover of shrub <0.5 m high (P=0.05), total vegetation <0.5 m high (P=0.02) including shrubs, ferns and herbs, and less cover of moss (P=0.01), than did random locations (Table 14); but had significantly greater cover of deciduous overstory canopy (P=0.10) and lower density of understory snags (P=0.09, Table 14). Mean distance (n=4) from the song perch to overstory trees at wren locations was significantly (P<0.01) greater than that at random locations, indicating Winter Wrens were using sites with overstory trees that were spaced further apart (Table 14).

Significant negative Spearman correlations showed that mean distance to overstory trees and mean distance to understory snag at the random locations decreased with distance from water; whereas significant positive Spearman correlations indicated that cover of moss increased with distance from water (Table 15). Cover of moss was positively correlated with cover of vegetation and both of these were also positively correlated with mean distance to overstory tree. These correlations indicate that overstory trees spaced further apart, generally resulted in an understory with greater cover of moss and/or vegetation <0.5 m high, except when close to riparian systems, where there

Table 15. Spearman rank correlations between distance to water and habitat attributes at random locations (n=75). Habitat attributes are those that Winter Wrens preferred or avoided (Tables 13 and 14)[1].

Habitat attributes		r_s	P-value[3]
Distance to riparian	mean distance to overstory tree	-0.20	**0.08**
	moss cover	0.39	**<0.01**
	mean distance to understory snag	-0.24	**0.04**
	deciduous overstory canopy cover[2]	-0.15	0.24
	vegetation cover <0.5 m high	0.08	0.47
	volume downed wood 50-74 dbh	-0.25	**0.07**
	volume hard downed wood ≥75 dbh	-0.27	**0.02**
	volume downed wood ≥75 dbh	-0.30	**0.01**
Mean distance to overstory tree	moss cover	0.22	**0.07**
	vegetation cover <0.5 m high	0.33	**<0.01**
	deciduous overstory canopy cover[2]	0.00	1.0.
	mean distance to understory snag	0.70	**<0.01**
	volume downed wood 50-74 dbh	0.02	0.87
	volume hard downed wood ≥75 dbh	0.04	0.74
	volume downed wood ≥75 dbh	0.09	0.46
Moss cover	vegetation cover <0.5 m high	0.46	**<0.01**
	deciduous overstory canopy cover[2]	-0.33	**0.01**
	mean distance to understory snag	0.14	0.23
	volume downed wood 50-74 dbh	0.10	0.42
	volume hard downed wood ≥75 dbh	-0.33	**<0.01**
	volume downed wood ≥75 dbh	-0.38	**0.01**
Vegetation cover <0.5 m high	deciduous overstory canopy cover[2]	-0.71	**<0.01**
	mean distance to understory snag	0.32	**0.01**
	volume downed wood 50-74 dbh	0.06	0.60
	volume hard downed wood ≥75 dbh	-0.06	0.60
	volume downed wood ≥75 dbh	0.03	0.79
Deciduous overstory canopy cover[2]	mean distance to understory snag	-0.08	0.53
	volume downed wood 50-74 dbh	0.12	0.35
	volume hard downed wood ≥75 dbh	0.10	0.45
	volume downed wood ≥75 dbh	0.02	0.90
Mean distance to understory snag	volume downed wood 50-74 dbh	-0.04	0.76
	volume hard downed wood ≥75 dbh	0.15	0.18
	volume downed wood ≥75 dbh	0.21	**0.07**

[1] I did not include shrub cover <0.5 m high.

[2] n=65.

[3] Significant (P≤0.10) relationships bold type

was a decrease in cover of moss. Cover of both moss and total vegetation <0.5 m high were negatively correlated with the cover of deciduous overstory canopy.

Winter Wrens were in areas that had slightly more volume of downed wood in the large size classes: hard wood $\geq$75 cm dbh (P=0.07) and total volume $\geq$75 cm dbh (P=0.09), and total volume for the 50-74 cm dbh class (P=0.10) (Table 13). However, these relationships were significant only within $0.05<P\leq0.10$ and an interaction occurred with the total volume of downed wood for the largest size class ($\geq$75 cm dbh). Large wood volume was correlated negatively with distance to riparian systems showing that greater volumes were associated with riparian systems (Table 15). The largest pieces ($\geq$75 cm dbh), both hard and total, were also negatively correlated with cover of moss.

Winter Wrens did not appear to use habitat differently as the forest developed from young to mature, although some of the habitat attributes associated with wren locations were more abundant in the young forest compared to the mature forest, and viseversa. For example, greater mean distances to overstory trees and understory snags were characteristic of wren locations and the mature forest, not the young forest (Table 12); whereas greater mean cover of deciduous canopy and lower mean cover of shrubs and total vegetation <0.05 high were characteristic of wren locations and the young forest, not the mature forest. Therefore Winter Wrens, independent of stand age and stage of development, selected for a suite of habitat attributes to provide optimal habitat.

Seral stage, type of location (random or wren) and moist systems within a 25-m radius of the song post were independent of each other (X^2=4.75, v=4, P>0.10). Seral stage, type of location (random or wren), and presence of water within a 25-m radius were also independent of each other (X^2=5.25, df=4, P>0.10). The lack of a significant relationship between wren locations and presence of water in the 0.20-ha plot likely resulted because this measure only described the microhabitat patch around the song perch not the macrohabitat used by the Winter Wren.

I selected habitat attributes, representing different elements of forest structure, that had significant differences ($P \leq 0.05$) between random locations and wren locations in the split-plot ANOVA (Table 14). These attributes were mean distance to overstory tree (Over), cover of moss (Moss), cover of total vegetation <0.5 m high (Veg), and distance to nearest riparian system (Rip). Using the full mixed model logistic regression (Equation 2), I found that seral stage did not have a significant effect in the model (Table 16). This allowed seral stage to be eliminated from further analyses. In the full model (Equation 2), both distance to overstory tree and cover of moss were significant predictors for estimating the probability that Winter Wrens would use a location in either seral stage. For this model, the adjusted or least square mean (Lsmean) probability of a location being occupied by a Winter Wren, given that it is either a wren or random location, was similar in the young and mature forest: (young Lsmean=0.54; mature Lsmean=0.47; Table 17).

The simple logistic regression best-fit model (Equation 3) also resulted in both mean distance to overstory tree and cover of moss being identified as the best predictors of Winter Wrens using a location (Table 18, Figs. 14 and 15). The collective significance of these two factors is reflected by the high Reduction of Deviance (13.958, $P=0.0009$). Both distance to riparian system and cover of vegetation <0.5 m high did not contribute significantly to the model. The non-significant Hosmer and Lemeshow

Table 16. Analysis of (restricted pseudo likelihood) estimates for the full model (Equation 2). The fixed independent variables are seral stage classification (1 or 0), mean distance to overstory tree (m, Over), cover of moss (%, Moss), cover of vegetation < 0.5 m high (%, Veg), and distance to riparian (m, Rip). Plot-to-plot variability is treated as a random factor. The intercept represents the mature seral stage and S represents the additional effect of the young seral stage over-and-above the mature seral stage. The estimate of the variance component is $\sigma_a^2 \cong 0.000$.

Parameter	Estimate	SE	df	t	P-value
Intercept	-1.0851	0.6732	17	-1.61	0.12
S	0.2679	0.4307	17	0.62	0.54
Over	0.3706	0.1328	125	2.79	0.01
Moss	-0.0100	0.0100	125	-1.98	0.05
Rip	0.0001	0.0006	125	0.17	0.86
Veg	-0.0400	0.0400	125	-1.12	0.26

Table 17. Least-square Means (Lsmeans) of seral stage for the full model (Equation 2). The difference in the two Logit Lsmeans is 0.268 (SE=0.431). A t-test of their equivalence yields t = 0.62 (17 df, P=0.54), which as expected, corresponds exactly to the test result for S in Table 16.

Seral Stage	Lsmean probability	Lsmean logit	Lsmean logit SE
young	0.54	0.154	0.277
mature	0.47	-0.114	0.289

Table 18. Analysis of (maximum likelihood) estimates for the simplified model using mean distance to overstory tree (Over) and cover of moss (Moss) (Equation 3). The Reduction in Deviance = $-2[\mathrm{LogL}(\mu) - \mathrm{LogL}(\mu, \beta_1, \beta_2)] = 13.958$ with 2 df (P=0.0009), and the Hosmer and Lemeshow Goodness-of-fit Statistic = 7.2871 with 8 df (P=0.5060).

Parameter	Estimate	SE	Wald Chi-Square	P-value
Intercept	-0.7835	0.4720	2.7551	0.097
Over	0.3193	0.1148	7.7398	0.005
Moss	-0.0170	0.0058	8.2356	0.004

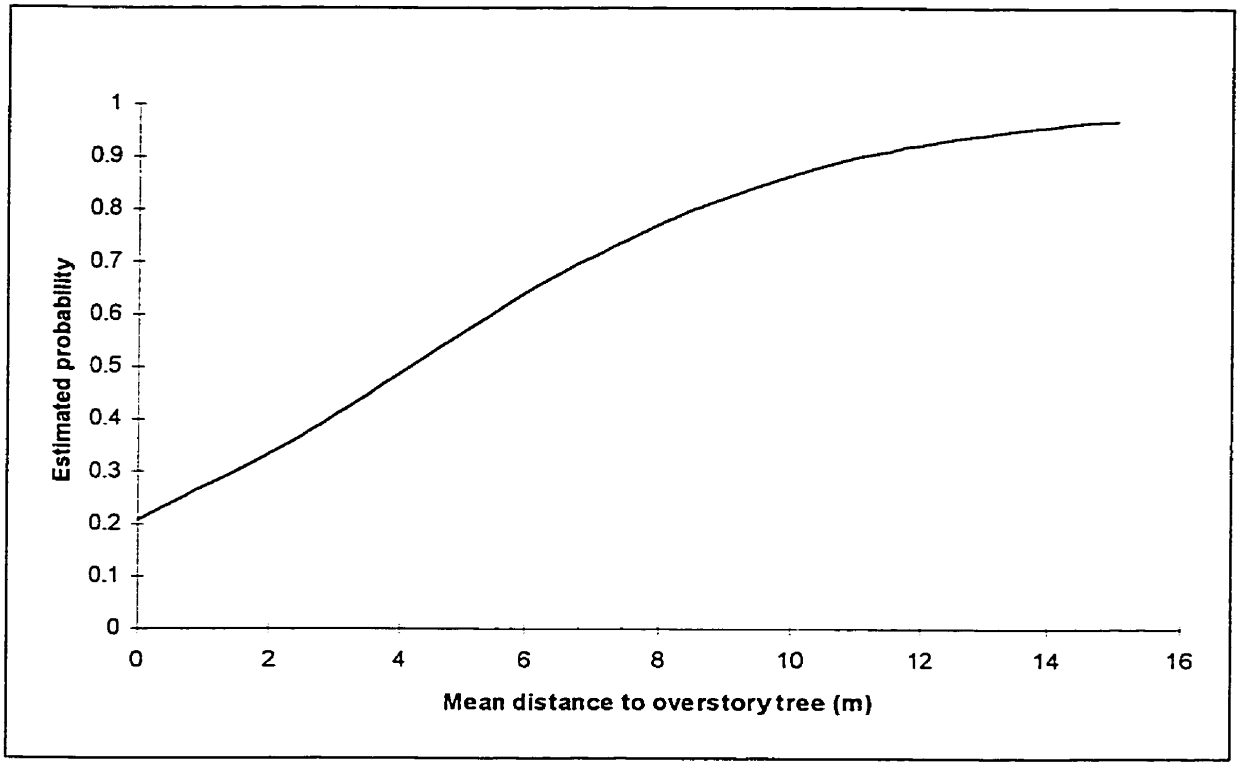


Fig. 14. Estimated probability (based on Equation 3) of a Winter Wren occupying a location: $\tau_k = e^{-0.784 + 0.319\text{over}_k - 0.017 mean(moss)} / (1 + e^{-0.784 + 0.319\text{over}_k - 0.017 mean(moss)})$ as mean distance to nearest overstory tree (*over*$_k$) changes from 0 to 15 m while moss coverage (*mean*(*moss*)) is held at its estimated mean (32%).

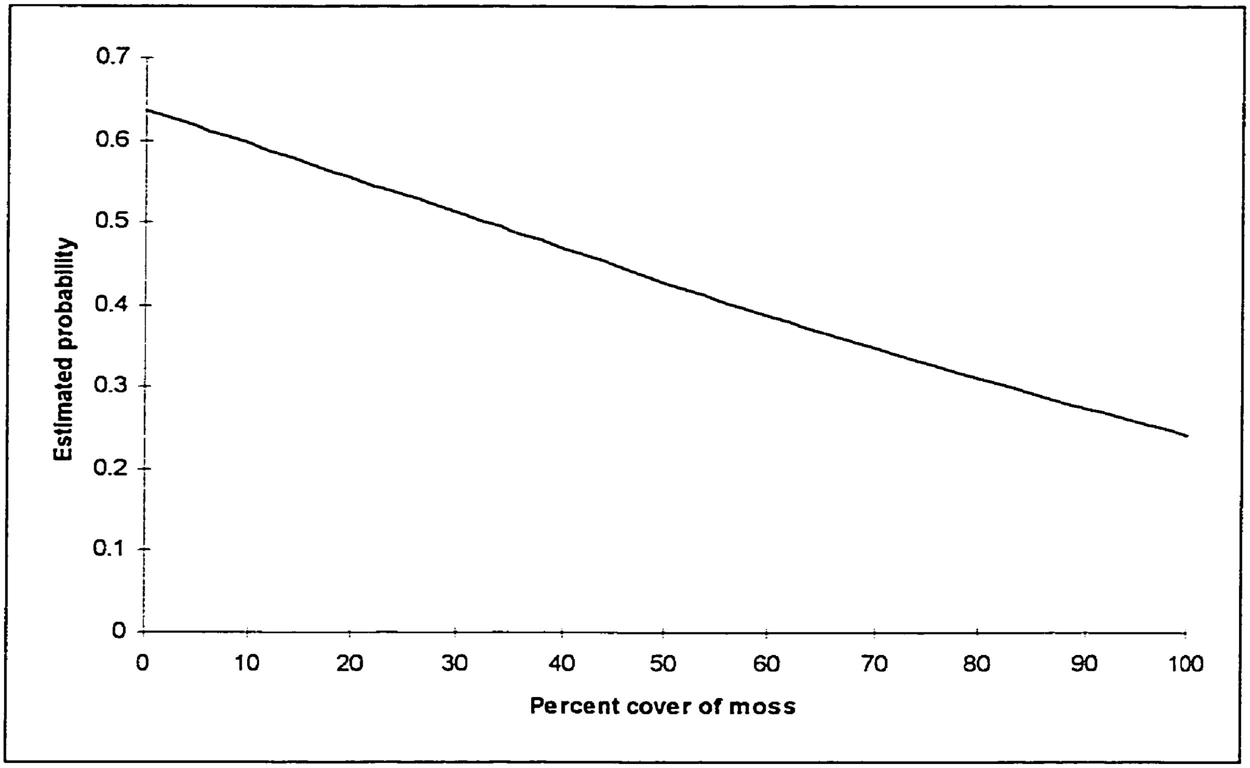


Fig. 15. Estimated probability (based on Equation 3) of a Winter Wren occupying a location: $\tau_k = e^{-0.784 - 0.319 mean(over) - 0.017 moss_k} / (1 + e^{-0.784 - 0.319 mean(over) - 0.017 moss_k})$ as cover of moss ($moss_k$) changes from 0 to 100 % while mean distance to overstory tree ($mean(over)$) is held at its estimated mean (4.2 m).

Goodness of Fit statistic (7.29, 8 df, P=0.51) indicates the closeness between predicted and observed probabilities, and suggests that the model is a good fit.

The estimated probabilities of the logistic regression model (Figs. 14 and 15) show that there is a higher probability that Winter Wrens will use the location as mean distance to overstory trees increases (e.g., 80% probability at 10 m), and this is a non-linear relationship because the rate of increase, decreases with increasing distance to overstory trees. In these forests, a mean distance to overstory tree of ~15 m from a Winter Wren song perch, in any direction, suggests possible gap in the overstory canopy, rather than a closed overstory. The lower limit (20 % probability) that a Winter Wren will occur in areas with overstory trees spaced closely together, likely having a dense overhead canopy, shows that Winter Wrens are flexible in habitat use and exploit a range of conditions. The relationship for cover of moss is linear, but it covers a smaller range of probability estimates for predicting a Winter Wren location. There is a 20-30% probability a Wren can be found with 100% cover of moss, while presence of a Wren is greater (~63%) with 0% cover of moss.

Discussion

The spatial locations of territories of Winter Wrens, in both young and mature forest, were influenced by the locations of riparian systems over a broad area covering many watersheds. However, Winter Wrens were able to use drier stands and exploited upland habitats. The microhabitat patches around Winter Wren song perches were relatively more open with overstory trees spaced further apart, but these patches did not have a developed lower strata of shrubs/vegetation, nor were they characterized by mossy ground. Instead these habitat associations suggest that the ground in these patches was covered by downed wood, or exposed soil or rock as may be associated with riparian systems or upturned root masses. Winter Wrens did not exhibit different habitat use patterns between young and mature forest, although abundance of habitat attributes changed with stand development and age.

Stand Structure of Mature and Young Forests on the Sunshine Coast

Differences in forest structure between the two seral stages along the Sunshine Coast were typical of developing forests and the silvics of dominant tree species in the CWHdm (Krajina et al. 1982, Franklin and Spies 1991). Young (40 to 60-year old) stands had higher densities of trees and snags, more closed canopies, and less well developed horizontal/vertical structure than did mature (80 to 120-year old) stands. The young stands were self-thinning, thus creating the higher densities of small snags. The deciduous component remaining in the young stands was primarily red alder (*Alnus rubra*), a shade intolerant species that can dominate during early successional stages, but dies as the stand matures because competing conifers reduce available light (Krajina et al. 1982). Uprooting of more trees, thus higher densities of upturned root masses, in the young stands either occurred during harvesting or stand development. Uprooting can be more common on drier and wetter sites than on mesic sites (Lertzman et al. 1996). Several stands in the young seral stage were dry with few water sources.

Location of Winter Wren Territories Relative to Riparian Systems

The spatial distribution of Winter Wrens was influenced by riparian systems in both young and mature stands. Riparian systems may add spatial heterogeneity to forest stands with the diverse forest structure, associated with riparian habitats, providing preferred habitat for Winter Wrens over a broad range of stand conditions and stand ages. However, Winter Wrens are not strictly tied to riparian systems and do use other types of habitat (Chapter 1). Some of the microhabitat patches around song perches did not have riparian systems because Winter Wrens do not need to be adjacent to water when singing in their territories. Furthermore, several stands in the young forest lacked riparian systems but Winter Wrens occupied these stands. My results indicate that Winter Wrens do not require riparian systems within their territories. Instead, they are flexible in their use of habitats (Carey 1988) and other sources of structural diversity may provide suitable habitat for Winter Wrens.

Microhabitat Patches of Song Perches

In general, Winter Wrens exploit similar microhabitat patches around song perches in both seral stages. Microhabitat patches selected by Winter Wrens had overstory trees, understory trees and understory snags all spaced further apart than elsewhere in the stands. These attributes describe a more open stand structure ranging from an open understory (openings) to overstory canopy gaps (gaps, Spies et al. 1990). Edaphic gaps can form over creeks and streams, while developmental gaps are more commonly formed by mortality of standing canopy dominants and less commonly formed by uprooted trees (Lertzman et al. 1996). There appeared to be a greater probability that a Winter Wren would use a location if it was a gap. In addition, Winter Wrens preferred openings or gaps that had either more deciduous canopy, downed wood or were in areas near creeks or streams. They avoided openings and gaps that had greater cover of moss and/or short vegetation. There was no evidence that Winter Wrens preferred or avoided any of these particular attributes for the value of the attribute itself. Rather those attributes selected may simply be correlated with the sites, not the cause for selection.

Microhabitat should influence the allocation of time and energy of the individual (Morris 1987). The advantages to Winter Wrens of using a habitat patch with open area in the understory or overstory for singing may include: 1) better ability to project the song thus limiting attenuation due to obstruction from trees and shrubs (Richards 1981) and 2) better visibility for displaying when defending the territory or attracting mates. Several attributes that were associated with microhabitat patches also relate to breeding or foraging by Winter Wrens. Small shrubs and vegetation included a large component of salal. Salal is associated with drier sites and it may be avoided by Winter Wrens because it is difficult to move through and obscures foraging substrates (McLachlin 1983). Riparian and moist systems have greater densities of arthropods (McLachlin 1983, Van Horne and Bader 1990). Downed wood is moist, and the associated arthropod communities may provide good feeding sites (Harmon et al. 1986, Lofroth 1998). Selection for deciduous patches by some bird species is linked to abundance of some taxa of insects (Bunnell et al. 1991). Thus, Winter Wrens may prefer areas influenced by water and areas associated with deciduous trees or downed wood because they are prime feeding sites.

Microhabitat patches around song perches were similar in riparian and upland areas, hence, selectivity of Winter Wrens for riparian systems may be due to the structure of streamside habitat. The structure of the riparian areas in the young and mature forest was similar in structure to riparian areas in other Douglas-fir dominated forests (Spies et al. 1988, Carey et al. 1991, McGarigal and McComb 1992). Although I had determined that the percent cover of deciduous trees (mostly red alder) was not correlated with riparian systems, red alder is associated with wetter sites and areas of light penetration (Krajina et al. 1982, McGarigal and McComb 1992). In New Hampshire, Winter Wrens used canopy gaps formed from fallen trees that had upturned roots and dense understory vegetation (Holmes and Robinson 1988).

Developmental gaps in forests may have higher light intensities and greater moisture because the canopy no longer shades the site, intercepts rain, and fewer roots remove less water (Schaetzl et al. 1989). Pits and mounds are created in the microtopography when trees are uprooted. Pits in poorly drained soils flood and become locally wet sites (Beatty and Stone 1986). During the breeding season in 1996, water collected in pits from upturned trees throughout the study area following heavy rains. Developmental gaps may produce patches of wetter habitats, with uprooted trees providing potential water sources. Developmental gaps, like edaphic gaps may have distinct microclimates as well as vegetation creating heterogeneity in the stand. In the young stands that did not have nearby riparian systems, 6 of the 8 song perches were root masses. This suggests that upturned root masses and their associated developmental gaps provide suitable habitats for Winter Wrens in upland areas, and habitat in these patches may compensate for lack of riparian habitat.

Riparian and Upland Habitats Selected by Winter Wrens in Young and Mature Forests

In my study area, the density of Winter Wrens in young forest was similar to that in mature forest. This lack of difference conflicts with other studies that reported lower densities in young forests (Carey et al. 1991, Eckert et al. 1992, Bryant et al. 1993, Hansen et al. 1995, Savard et al. 1995). However, densities of Winter Wrens in the southern Washington Cascades were only higher in wet, more structurally complex, old-growth stands, while densities in young (55 to 80-year-old), mature (95 to 190-year-old) and mesic to dry old-growth stands did not differ (Manuwal 1991). If young stands provided sub-optimal habitat for Winter Wrens (Van Horne 1983, Pulliam 1988) because of lower structural diversity and limited environmental resources (Franklin and Spies 1991), I would have expected either that these stands support fewer Winter Wrens or that Winter Wrens would use alternative kinds of microhabitat. Instead, Winter Wrens in both young and mature stands used similar habitats, preferring riparian habitats for macrohabitat, but exhibiting flexibility and using upland habitats, by exploiting microhabitat patches with similar habitat characteristics to those in riparian areas. Preferred habitat is provided in the young stands and mature stands, in riparian and upland areas, because both edaphic and developmental gaps contribute spatial heterogeneity and distinct microclimates, and thus resources that are desirable to Winter Wrens in these relatively homogenous forests. Stand structure rather than stand age is the better criterion for wildlife habitat (Bunnell et al. 1991), and habitat relationships of Winter Wrens along the Sunshine Coast are consistent with this hypothesis.

Chapter 4: Summary of Conclusions and Management of Coastal Forests

To maintain habitat capability for wildlife in coastal forests, some guidelines focus on riparian systems (B.C. Ministry of Forests and B.C. Ministry of Environment 1995b). At the stand-level, riparian systems, which I defined for my study area as creeks (5-10 m) and streams (<5 m, including seeps), provide important habitat variation in generally homogeneous stands of second-growth forests. This variation is coincident with forest attributes that provide food, nesting sites, and cover for wildlife such as Winter Wrens. My results indicate that the distribution of territories in mature forest and the singing locations of male Winter Wrens in young and mature forest were associated with riparian systems of both creeks and streams. Thus, the correspondence between Winter Wrens and riparian systems is expressed in both young and mature forests across a range of landscapes in the Coastal Western Hemlock Dry Maritime subzone. Winter Wrens also respond to habitats influenced by ground water. Moist systems are important to Winter Wrens because they offer similar habitat values to riparian systems (i.e., forest structure and microclimate). Other studies of birds and riparian systems (LaRue et al. 1995, Wiebe and Martin 1998) also suggest that complex forest structure (e.g., inherent edge and vegetation) associated with narrow riparian ecotones provides valuable habitat for wildlife. However, these studies do not separate the presence of water from the structure of streamside habitats.

Riparian and moist systems may be preferred by Winter Wrens as habitat because they have higher productivity of arthropods and greater numbers of nest sites due to moisture, microclimate, and particular forest attributes including deciduous shrubs and ferns. However, Winter Wrens can meet their life requisites in mesic or dry upland habitats and hence, are not strictly associated with moist and riparian systems (McGarigal and McComb 1992). Upland habitats may in part provide important alternative habitats because access to preferred riparian or moist systems may be constrained by social factors, and because habitat preferences of Winter Wrens may vary with local, annual weather. In upland areas, structurally heterogeneous patches (e.g., developmental gaps) that are influenced by light and water (e.g., precipitation) can exhibit conditions similar to those near riparian systems, and Winter Wrens may use upland areas because of the occurrence of these patches and other habitat attributes (e.g., downed wood with arthropods in the drier years). Furthermore, my results suggest that uprooted trees in young forest and the associated developmental gap may provide habitat that compensated for the lack of edaphic gaps in some stands. Birds that maintain territories year round or show site tenacity by returning one year to the next, such as the Winter Wrens in my study, must choose habitats that can satisfy their needs under variable, often unpredictable environmental conditions (Ruggiero et al. 1988). Winter Wrens thus cue into riparian and moist systems as a strategy that ensures they can meet their long-term needs within an environment that varies annually.

Selection of riparian systems by male Winter Wrens for territories (macrohabitat level) affects availability of nest structures and nest patches for both males and females, and the importance of nest structures may dominate habitat selection for the territory (Orians and Wittenberger 1991, Matsuoka et al. 1997). Selection for riparian systems at the macrohabitat level may be partly explained by the strong association between nest structures and riparian systems. Moist systems do not appear to be as important as riparian systems for providing nest sites to Winter Wrens. In mature forest, both heterogeneity of stand structure near riparian systems and strong association of two of the most preferred nest structures (creek bank and root mass) with riparian systems likely provided superior nesting opportunities for males.

Gaps in the forest canopy may provide greater densities of food, more diverse stand structure, and moister microclimates than the surrounding closed-canopy forest. As well, gap makers (e.g., uprooted trees, snags) provide nest substrates (Wesolowski 1983, Campbell et al. 1997). Males selected relatively open patches compared to the surrounding forest for nesting and song perches, and these patches may be associated with canopy gaps. The characteristic open understory with downed wood, deciduous shrubs, and ferns that was selected as nest sites by males enabled them to advertise their nest, provide abundant food, and possibly reduce nest predation. Nest sites selected by females are confined to those provided by males, but even with this restriction, females selected sites that were more secure and easy to access. The variety of substrates used for nests reveals that habitat flexibility by Winter Wrens can enable them to adapt to managed forests. However this resilience is limited because most of the nest substrates selected by Winter Wrens are created through the processes of succession and natural disturbance and are linked directly to gaps.

Forest Management

Winter Wrens are an appropriate species to study to understand effects of stand-level forestry because they are found in a variety of habitats and occur in densities large enough to obtain a statistical sample. Winter Wrens are also appropriate for studying stand-level effects because they are managed under general guidelines (B.C. Ministry of Forests and B.C. Ministry of Environment 1995a, 1995b) and not under special strategies for species at risk (B.C. Ministry of Forests and B.C. Ministry of Environment 1998). In addition, Winter Wrens over-winter in coastal forests, and some annual and seasonal comparisons can be made without the confounding effects associated with neo-tropical migrants.

Animals can be used to monitor environmental quality because factors that affect an animal's distribution can be used to predict the animal's response following a disturbance (Morrison 1986). Insight into the potential implications of forestry activities on the system can be obtained by studying Winter Wrens because this species uses specific structural attributes within the forest for nesting, feeds on arthropods, and relies on cover for security at nest sites. The distribution of Winter Wrens reflects the availability of these resources at the stand-level.

Because of the plasticity of the species, abundance of Winter Wrens may not be an appropriate indicator of habitat change (Van Horne 1983). But, I expect that changes in habitat use and behaviour of the Winter Wren (e.g., location of nest sites, type of nest substrates) may provide more sensitive criteria for detecting short and long-term changes in stand-level habitat, than those of other wildlife species (e.g., habitat dependents, invasive species, sedentary species). For example, polygyny is more commonly observed in Winter Wrens in England compared to Winter Wrens in Poland. This increased frequency of polygyny coincides with deforestation and the clumping of individuals along linear hedgerows in England (Wesolowski 1987). Winter Wrens could act as indicators of indirect, secondary environmental changes, as has been suggested for bird species in general (e.g., change in microclimate) (Morrison 1986). In addition, occurrence of species relative to environmental gradients, such as successional chronosequences, may identify thresholds for the amounts of attributes that are required by wildlife. Knowledge of these thresholds would be useful to understand the biology of the species and helpful to forest management (Hansen et al. 1995, Kremsater 1998). My results apply to the Coastal Western Hemlock Dry Maritime subzone and likely other coastal subzones, but they may not apply beyond these subzones because behaviour of an animal can vary among broader systems and geographic location (Ruggiero et al. 1988).

Forest managers require immediate feed-back on the effects that different forest practices impose on wildlife habitat and they require operational criteria and advice to achieve biodiversity and riparian objectives (B.C. Ministry of Forests and B.C. Ministry of Environment 1995a, 1995b). I contend that through short-term studies of some generalist species, insight may be gained into how biological mechanisms within local systems (Wiens 1989) are affected by different forest practices. These studies should enable us to predict biological implications for long-term forest management. If for example, Winter Wrens of the Pacific Northwest have evolved to exploit gaps, then an observed change in Winter Wren behaviour or habitat use between second-growth stands that are differentially managed for spatial distribution of gaps, could provide a mechanism to evaluate how different forest practices alter the value of wildlife habitat. However, I caution that this single species approach should only be a tool to guide forest management because extrapolation of effects to other species can ignore variation associated with these species and must be applied judiciously (Bunnell and Kremsater 1990, Noss 1990).

I undertook my research on the Winter Wren with the intent of using the results to develop more specific questions that compare present and proposed management practices in second-growth forests. My results support the importance of managing for stand-level habitat components and riparian areas as suggested in several management guidebooks (B.C. Ministry of Forests and B.C. Ministry of Environment 1995a, 1995b). Based on my research and these guidelines, several recommendations are apparent.

Both edaphic and developmental gaps appear to have critical habitat roles for Winter Wrens and this emphasizes the need to manage for the structural heterogeneity that these gaps contribute to the stand. Important attributes used by Winter Wrens include those associated with gaps such as creek banks, upturned root masses, logs, and snags. My research on the Winter Wren emphasizes: the value of biological legacies for wildlife including various stages of decay and sizes of logs and snags; creek banks and upturned root masses, two substrates that have had limited research to date for habitat values; the utility of retaining a deciduous component as both live standing and dead trees for nest sites; and the distribution of all components within the stand. Stand-level management to retain forest structure through microhabitat patches and biological legacies must include a mixture of retaining structural components to contribute to future rotations and using silvicultural practices to imitate both vertical and horizontal heterogeneity across the stand.

My research on the Winter Wren supports the need to use ecological stratification (Green and Klinka 1994) when managing for structural attributes within the stand, particularly where properties of the coarser scale system may act as a cue identifying higher quality habitat for a species. The Riparian Guidebook and Operation Planning

Regulations of the Forest Practices Code (B.C. Ministry of Forests 1995b) require a combination of permanent reserves and management areas to be left as linear buffers adjacent to aquatic systems. Many of the small riparian systems in my study area would only need, if any, a narrow management area. The abundance of small riparian systems and the narrow trans-riparian gradients, patchily associated with the creeks and streams, emphasizes that these narrow corridors should not be separated over time from the forest matrix. Furthermore, the value of riparian systems for many wildlife species, such as I found for the Winter Wren, could be important at a fine scale (e.g., annual streams or large seeps that would not necessarily be managed for under the general guidebook) with values varying by environmental conditions (e.g., weather). My research on Winter Wrens suggests that although linear buffers may be used to meet some management objectives (e.g., fish), patches of habitat that are not necessarily linear and include upland areas adjacent to smaller riparian systems are also of value (McGarigal and McComb 1992, Wiebe and Martin 1998) because they provide habitat components for Winter Wrens over the long-term. Patches that capture a cross-section of riparian areas and upland areas may be more effective for managing habitat associated with these smaller streams that have unspecified management objectives, rather than a stream by stream classification with linear zones. Over time, patches will recruit habitat components such as upturned root masses, snags and logs. Retaining unharvested areas that overlap riparian systems will retain edaphic gaps and retaining patches of upland habitat will retain developmental gaps during the rotation.

Amount and distribution of patches or structural elements (e.g., downed wood) for wildlife habitat could be stratified by occurrence of riparian systems, but moist site series as the finest scale for the influence of water should also be considered. One method of including upland areas under present guidelines could be through retention of patches of trees (B.C. Ministry of Forests and B.C. Ministry of Environment 1995a). In the short-term, attributes that are managed as single components or in isolated patches may be diminished in value if moist habitats are disrupted, for example, by changes in canopy cover or edge (Ruggiero et al. 1988) but over the long-term, they should regain their value and support species such as Winter Wrens.

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Appendix A. Methods for Measuring Site Characteristics and Habitat Attributes.

I used nested circular plots to sample habitat attributes. At habitat grid points and nest sites, I used: 0.002-ha plots (2.65 m radius) for strata <0.5 m high; 0.01-ha plots (5.64 m radius) for strata ≥0.5 m high or count stems of trees and snags <10 cm dbh; and 0.02-ha plots (7.98 m radius) to count stems of trees and snags ≥10 cm dbh or to count number of upturned root masses (Stickney 1985, Finch 1989a, 1989b, Luttmerding et al. 1990, Morrison et al. 1992, Backhouse 1993, G. Davis pers. comm.). For wren and random locations on transects (Chapter 3), I estimated canopy cover on 0.20-ha circular plots (25 m radius) and cover of all other vegetation variables on 0.01-ha circular plots.

At sample plots, two observers independently estimated vertical projections of habitat attributes using a visual (ocular) method. I took the mean of these two estimates as the percent cover for the plot. Estimates of overstory canopy for trees (deciduous and coniferous) included divisions for codominants, intermediates, and suppressed. Estimates of understory canopy included divisions for higher strata and lower strata. Estimates of understory included percent cover of trees (coniferous and deciduous), shrubs (evergreen, deciduous, combined), ferns, herbs, mosses, and downed wood. Most species of ferns were characteristic of moist to wet sites (e.g., sword fern, lady fern *Athyrium felix-femina* and small amounts of deer fern *Blechnum spicant*). The most common deciduous shrubs in my study blocks, red huckleberry and salmonberry *Rubus spectabilis* are also characteristic of moist to wet sites (Klinka et al. 1989). I combined percent cover of ferns and deciduous shrubs into the variable 'Ripall' because it represented moister areas. Evergreen shrubs such as salal characterize drier, open canopy forests (Klinka et al. 1989).

I recorded, as appropriate, for trees and snags: species, dbh, canopy class, wildlife tree status, percent bark retained, and decay class. Decay and hardness were combined into two decay classes hard outside or soft outside. These data allowed me to estimate density of stems per ha by species, amount of bark retained, and frequency of decay and canopy classes. Number of prime (loose soil and rootlets) upturned root masses or other root masses were recorded separately because prime are the preferred type of structure for Winter Wren nests. I did not measure live stems or snags or count root masses for transect measurements (Chapter 3).

Distance can be used to describe stand characteristics including horizontal forest structure. I measured distance to nearest upturned root mass. I measured mean distance to overstory canopy and understory canopy ($\geq$0.5 m to 10 m high) trees and snags using a plotless method (i.e., unlimited distance). Each location was divided into 4 (90°) quadrants from a random orientation. I then measured nearest distance to each of the attributes in each of these quadrants and used the mean distance (n=4). Mean distance describes spatial dispersion, and is an indirect estimate for density (Roth 1976, Noon 1981, Finch 1989a, 1989b, Morrison et al. 1992).

Three adjoining 12.5-m transects were used at each location to estimate number of pieces and volume of downed wood. The first transect was placed at a random direction from the grid point and the next two transects were each laid out at 120° angles to either side of the first from the grid point (Marshall 1994, Gerry Davis pers. comm.). Pieces of downed wood $\geq$2.0 cm dbh were counted if the mid-point intersected the transects. In addition to dbh, I recorded angle of wood, height of wood above ground, percent decayed (0; 1-$\leq$5; >5-$\leq$50; >50), and hardness class (hard fresh, hard intact, soft blocky, or soil wood). Downed wood is presented as volume per ha (calculated from 37.5 m of transect per sample plot) for decay-hardness classes of soft (>50% decay, blocky or soil wood) and hard (≤50% decay hard, intact). I modified this method for Chapter 3 because of limited funds. I only used 2 12.5-m transects at a 90° right angle; I only measured pieces ≥7 cm dbh; and I used a third decay-hardness class (fresh) because I expected greater amounts of newly fallen trees in the younger stands.

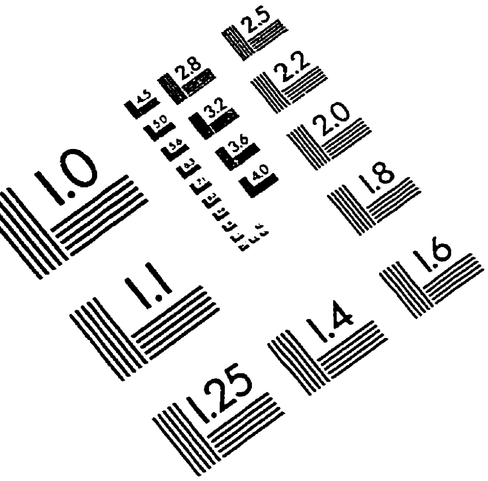
The area of nested plots or length of downed wood transects were not adjusted if intersected by streams, creeks or old road tracks. Unlike inventory methods where plots are often adjusted to ensure comparisons of equal growing areas, the measurements from my sampling reflect site variability. I included this variability in my sampling scheme because it could affect distribution of Winter Wrens. I applied slope correction with all sampling methods.

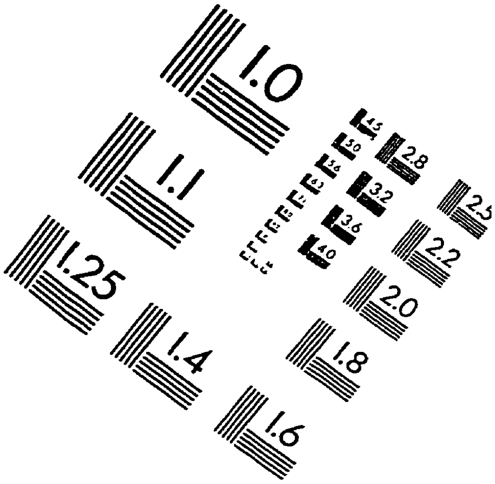
To increase number of samples from the main creeks at the center of each study block, I placed additional nested circular plots (0.01 and 0.02 ha) in these creek channels. To obtain larger sample sizes of streamside ground vegetation (moss, herbs and small shrubs <0.5 m high) in the lower strata, additional 0.002-ha plots were centered 2.65 m to the side of the creek (randomly selected side) at the 25-m intervals along the main creek. All of these supplemented plots were placed to avoid overlap with other sampling plots.

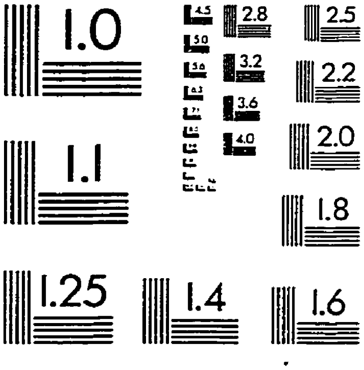
Site characteristics and habitat attributes measured at habitat grid points and at nest sites.

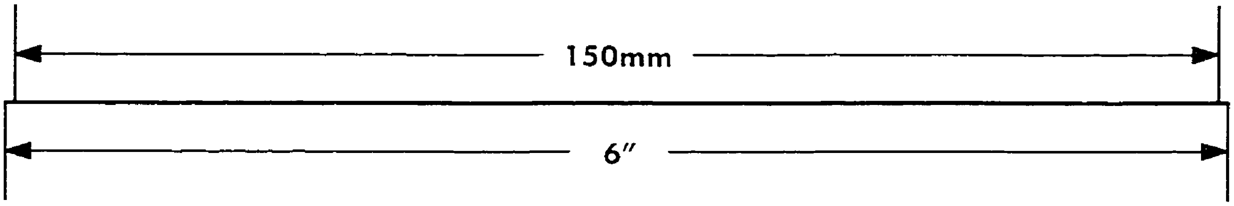
	Classes	Description of class
Site Characteristics		
Slope (%)		
Aspect (170^0-260^0)		
Riparian systems	main creek	creek only (study block center)
	all creeks and streams	creeks and streams only
	riparian	evidence of water as creek, steam or seep
Moist systems	moist	very moist site series (06, 07) over a range of nutrient regimes (very poor to very rich)
Riparian and moist systems	all water	site influenced by water as indicated by site series or evidence of water
Forest Structural Attributes		
Vegetation Cover (%)		
Ground		duff and rock
Moss		
Total cover	< 0.5 m high	herbs, ferns, shrubs
Ferns	< 0.5, ≥0.5, total, m high	
Shrubs	< 0.5, ≥0.5, total, m high	evergreen, deciduous
Riparian layer (Ripall)		ferns, and deciduous shrub
Tree Canopy (%)		
Understory canopy	B=understory, B2=0.50-1.99 m, B1=2.0-10.0 m high	
Overstory canopy	A=overstory, A2/A1=codominants, A3=intermediates A4=supressed below canopy but >10 m high	
Downed Wood		
Volume (m^3/ha)	dbh class cm 2-<7, 7-29, 30-49, 50-74, ≥75, ≥50, ≥30, ≥7	decay-hardness: Hard, Soft (fresh)
Percent cover	dbh class cm ≥7, 2-<7, <2	coarse wood fine wood (twigs branches)
Wildlife Trees and Snags (stems/ha)		
Trees and total trees and snags	dbh class cm <10, 10-29, 30-49, 50-74, ≥75, ≥50, ≥30, ≥10, total	species height classes by canopy
Snags	dbh class cm <10, 10-29, 30-49, 50-74, ≥75, ≥50, ≥30, ≥10, total	decay-hardness: hard or soft species, height wildlife tree classification
Root Masses (present/absent)		
	prime (loose soil, rootlets, gaps in soil) or other	
Horizontal Distance (m)		
	overstory tree, overstory snag, understory tree, understory snag, upturned root mass, nearest water source	

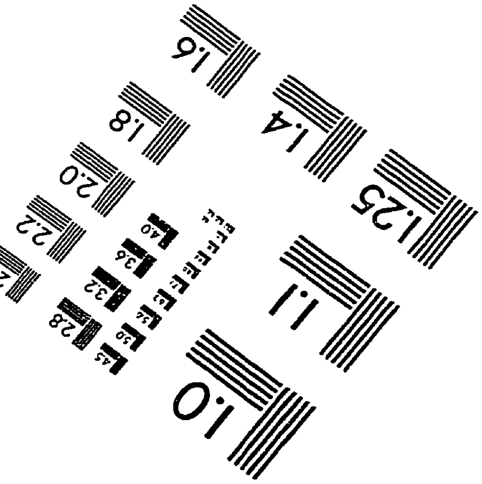
IMAGE EVALUATION
TEST TARGET (QA-3)

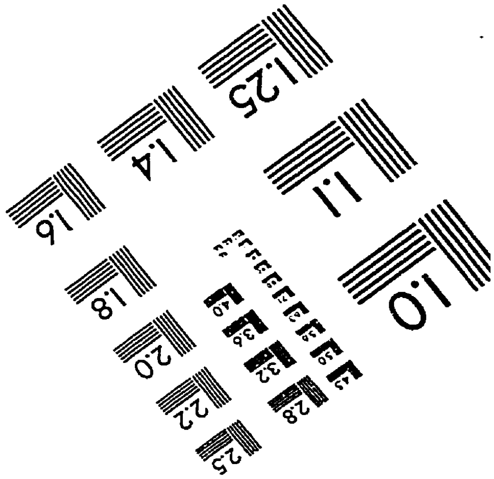












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