

THE EFFECTS OF HABITAT DISTURBANCE ON THE
REPRODUCTIVE BEHAVIOUR OF THE BLACK-CAPPED CHICKADEE
(*POECILE ATRICAPILLA*)

by

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Abstract

This thesis examines the effect of habitat disturbance on reproductive behaviour in the black-capped chickadee (*Poecile atricapilla*), a resident cavity-nesting songbird known to breed disturbed habitats. I investigated whether reproductive success was lower in disturbed habitats, how habitat quality affected the intensity of territorial behaviour, and the extent to which chickadees exhibited consistent preferences for habitat types associated with increased reproductive success.

Nest success was lower in the disturbed habitat than in the undisturbed habitat. Abandonment was the most common cause of nest failure. A within-habitat comparison of the social rank of birds revealed that low ranking birds had lower nest success than high ranking birds in the disturbed, but not the undisturbed, habitat. Breeding pairs occupying the disturbed site were subject to higher amounts of territorial overlap than pairs in the undisturbed mature woodlands. Birds in disturbed habitat had larger territories, intruded more often into neighbouring territories than those in undisturbed habitat, and their intrusions were more extensive. There was no evidence that chickadees preferred or avoided specific habitat types in my study area. However, birds breeding in territories containing high proportions of disturbed habitat experienced lower reproductive success.

Thus, birds breeding in disturbed habitat may be altering their reproductive strategies to compensate for poor habitat quality. Nevertheless, evidence for maladaptive habitat selection and differential reproductive success suggest that disturbed habitats may be functioning as population sinks.

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1. General Introduction

1.1. Behavioural Ecology and Conservation Biology

The potential contribution of behavioural ecology to landscape-level processes, population biology and conservation biology has, until recently, been largely ignored (Caro 1999; Sutherland and Gosling 2000). However, over the past decade, behavioural ecologists have started to take a more applied approach to their discipline; for example, researchers have begun to investigate the extent to which information about individual behavioural responses to differing environmental conditions might increase the predictive power of large-scale population models used in conservation planning. This can be especially useful when anthropogenic change creates environmental conditions significantly different from those forming the empirical basis for statistical population models (Pettifor et al. 2000).

Behavioural approaches have advantages over statistical approaches because assumptions of optimality in behavioural models allow organisms to respond to environmental changes in ways that will maximize their fitness. However, the habitat conditions in some anthropogenically-disturbed environments may result in maladaptive behaviours, as organisms which have evolved in undisturbed habitat conditions may apply decision rules inappropriate to the novel environment (Lima and Zollner 1996). Still, an understanding of how such organisms behave in both disturbed and undisturbed environments may lead to insights about decision rules

being used, and the extent to which the maladaptive use of these rules will affect survival, reproductive success and, ultimately, population dynamics.

One area in which behavioural ecologists have taken strides to bridge the gap between large-scale patterns and individual behavioural decisions is in the effects of landscape fragmentation on movement patterns in birds. Desrochers et al. (1999) recently reviewed the empirical evidence for disruption of normal movement patterns in fragmented habitats and ways in which this information can be used to drive simple, testable landscape-level predictions. For instance, a number of studies (Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998) have shown a reluctance of some songbird species to cross habitat gaps. Consequently, one would expect to see a negative relationship between isolation and species abundance in habitat patches.

Alternatively, information from empirical studies on the behavioural responses of organisms to, for example, habitat edges can be incorporated into spatially explicit behaviour-based models. Such models can be used to predict movement patterns in fragmented landscapes. For example, individual-based models have been developed which assess the utility of habitat corridors between suitable patches by including behavioural responses to edges as important parameters (Tischendorf and Wissel 1997, Haddad 1999).

Although behavioural research has increased our understanding of how species may react and adapt to landscape alteration, it is only one facet of the growing body of work investigating the interaction between behavioural ecology and conservation

research. It has long been realized in behavioural research that variation in the natural habitat structure can lead to differences in reproductive strategies and reproductive success (Krebs 1971, Perrins 1979). It is likely then that anthropogenic disturbance may alter behavioural responses of animals through changes in habitat quality. This will be the predominant theme of this thesis.

1.2. Reproductive Decisions, Territoriality, and Habitat Quality

The term habitat quality is used to refer to the characteristics of the environment that allow birds inhabiting a particular patch to maximize their fitness. Thus, features such as food resource availability (for adults and for nestlings), access to suitable safe nesting sites and predation risk are all factors that contribute to habitat quality. Habitat quality has sometimes also been used to refer simply to the reproductive output of birds breeding in a particular patch or territory (e.g. Pulliam 1988, Muller et al. 1997). Unless otherwise noted, however, I will be using this term to denote the former meaning throughout this study.

Habitat quality is known to influence reproductive decisions in birds. Hogstedt (1980) argued that flexibility in clutch size in birds was adaptive and that variation in territorial quality was the most important factor in determining optimal clutch size. In an experimental study, Siikamäki (1995) found that female pied flycatchers (*Ficedula hypoleuca*) relocated to poor quality territories laid smaller clutches and were more likely to break the pair bond with their mate than those relocated to good quality territories. Habitat quality also has been shown to influence dispersal decisions; female pied flycatchers were more likely to disperse to other habitat

patches if either they had previously experienced poor reproductive success in that patch or if the overall reproductive success of the patch was low (Doligez et al. 1999). Disturbed environments or small habitat fragments assumed to be of lower habitat quality often contain higher proportions of young and inexperienced males (Hatchwell et al. 1996, Zanette 2001), suggesting that habitat quality also drives intraspecific competitive interactions.

Habitat quality also is known to affect territorial behaviour in birds. Gill and Wolf (1975a) found that nectarivorous sunbirds (*Nectarinia rechenowi*) adopt territorial defence of a patch of flowers if the patch resource levels were sufficiently high, but refrain from active defence when resource levels are low. Carpenter et al. (1983) found that migrating rufous hummingbirds (*Selasphorus rufus*) alter feeding territory size to maximize daily rate of weight gain. Further, optimality models predict that organisms should adjust the size of their feeding territories based on changes in local resource levels (although the relationship between size adjustment and resource availability depends crucially on the shape of cost and benefit curves- Schoener 1983).

These studies suggest that even minor variation in habitat quality can have large impacts on the behavioural responses and, ultimately, reproductive success of birds. As many of these same species are resilient enough to anthropogenic disturbances to continue breeding in these areas, it is pertinent to determine whether such alterations to the landscape are having similar effects on the remnant populations.

1.3. Sources, Sinks, and Habitat Disturbance.

Restricted movement of animals due to avoidance of habitat gaps, and changes that leave intervening 'matrix' habitats of such poor quality that they remain unoccupied can lead to fragmentation of avian populations. Such *metapopulations* can be defined as a set of local populations within some larger area, where typically dispersal from one local population to at least some other patches is possible (Hanski and Simberloff 1997). One component of the metapopulation model is the source/sink system formalized by Pulliam (1988). As with other versions of the model, regional metapopulations are divided into local populations or compartments. Source populations are characterized by birth rates in excess of death rates, and emigration rates in excess of immigration rates. Thus, they are net exporters of surplus individuals. Conversely, sink populations are characterized by death rates in excess of birth rates, and immigration rates in excess of emigration rates. As sink populations suffer from negative local recruitment, such populations would not persist in the absence of an influx of immigrants from local sources. Theoretically, for metapopulations in dynamic equilibrium (i.e. when population size is constant in all compartments, and there is no net population change in the assemblage of compartments), large sinks can be maintained by relatively small source patches. In such circumstances, removal of source patches or restriction of inter-patch dispersal rates may result in the decline and eventual extinction of sink populations as well as a general decline of the metapopulation.

Anthropogenic habitat disturbance has the potential to impact metapopulations in at least two ways. First, the disturbance may take the form of a matrix of unsuitable habitat, creating isolated fragments or ‘islands’ of usable habitat that are no longer connected by inter-patch migration. If certain habitat islands consist of sub-optimal habitats acting as population sinks, local recruitment cannot be supplemented with immigration and the population will decline to extinction. Alternatively, disturbed habitats (such as early seral habitat regenerating after logging activity) may themselves represent sink habitats if organisms breeding in such sub-optimal habitats experience lower reproductive output or survival rates (Blondel et al. 1994). Individuals may settle in these areas as a result of interference competition stemming from overcrowding in source habitats (Sutherland 1998, Caro 1999) or due to an inability to recognize their sub-optimality (Pulliam and Danielson 1991, Remes 2000, Delibes et al. 2001). Regional resource extraction activities may alter the proportion of the landscape in source and sink habitats to such an extent that existing sources will be unable to restock sink populations and the metapopulation will decline. Such a scenario may be difficult to predict in organisms whose patch population dynamics are not well understood, yet the ramifications of failing to account for this could potentially be high.

1.4. Limits of Traditional Habitat Sensitivity Protocols and Assumptions

From an evolutionary perspective, if a particular habitat patch does not meet the life-history needs of a particular organism as well as other available patches, the organism should avoid that environment. Also, population density has commonly been used as a proxy for reproductive success or resource levels in a particular patch, as low densities would presumably be an indicator of the decreased productivity of the local breeding population. Thus, the sensitivity of bird species to habitat disturbance has traditionally been assessed using presence/absence and species abundance census methods (e.g. point counts, line transects, spot-mapping).

However, a number of studies have questioned the utility of using density as an indicator of reproductive success or habitat quality. Van Horne (1982) found that deer mouse (*Peromyscus maniculatus*) density was highest in sub-optimal habitat, and argued that intraspecific competitive interactions explained this result. Thus, Van Horne contended (1983) that population density was an unreliable measure of habitat quality. Vickery et al. (1992) concurred with this assessment, in a study that showed no correlation between territory density and reproductive success in three emberizine sparrows. Roberts and Norment (1999) found that density did not differ, although reproductive success did, between populations of breeding scarlet tanagers (*Piranga olivacea*) in habitat fragments of varying size. In a recently published long-term study of productivity in a wood thrush (*Hylocichla mustelina*) population,

Underwood and Roth (2002) determined that density was a poor predictor of nest success.

These results indicate that a deeper understanding of the mechanisms controlling population density and habitat-specific reproductive success will be required if we are to determine the extent to which animals are affected by habitat disturbance. A greater emphasis on determining behavioural responses of individuals breeding in both disturbed and undisturbed habitats will contribute to greater accuracy in predictions of population responses to habitat disturbance.

The aim of my thesis is to investigate the impacts of habitat disturbance on the reproductive and territorial behaviour of black-capped chickadees (*Poecile atricapilla*). This species is commonly found in mixed woodlands, but also breeds in a variety of disturbed habitats including urban settings and early successional forests. It, therefore, serves as a perfect model to investigate how habitat alteration can impact retained species. In addition, a large body of work exists for this species where it breeds in undisturbed habitats, and so many aspects of its social structure, territorial behaviour and natural life history are known. I studied two adjacent local populations occupying differing habitats, a mature mixed sub-boreal woodland (undisturbed) and a forest in regeneration following logging/land clearing (disturbed). My goal was to determine whether habitat altered reproductive success in the species and to what extent habitat disturbance had cascading effects on territoriality and habitat selection in the species.

1.5. Study Site

The study location was immediately west of the University of Northern British Columbia, Prince George, BC (53°E 55' N, 122°E 50'W, and 850 m elevation), within the Sub-boreal Spruce (SBS) biogeoclimatic zone. The study area was composed of two adjacent habitat types: 1) an 85 hectare block of mature forest and 2) two sites (total area: 65 hectares) which have been disturbed as a result of forest management practices (Fig. 1.1). The undisturbed habitat is a continuous forested area composed of patches of various mature forest types. Canopy species represented in this area are trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), black cottonwood (*Populus balsamifera* ssp *trichocarpa*), hybrid spruce (*Picea glauca* x *Picea engelmannii*), lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*) and subalpine fir (*Abies lasiocarpa*). Canopy height is 25-30 m. The understory stratum is dominated by green alder (*Alnus crispa*), willow (*Salix* sp.), prickly rose (*Rosa acicularis*), low-bush cranberry (*Viburnum edule*), and twinberry (*Lonicera involucrata*).

The primary disturbed site (~ 75 hectares) was logged in 1962 and cleared to agricultural standards for the purposes of horse and cattle pasturing. The site was designated a model forest in 1985, and many areas were cleared and replanted with lodgepole pine and other conifers from 1986-89. Other sites regenerated naturally, and still others were never harvested. Consequently, the disturbed habitat was characterized by a mosaic of different habitat types, ranging from young managed lodgepole pine stands, somewhat older aspen/birch/willow stands, and isolated

patches of mature forest. Although species composition was similar to that of the undisturbed site, canopy height was lower (5-15 m), there were fewer large trees, and there was a much larger understory component. Where small patches of mature forest existed, they were similar in composition and structure to the undisturbed site. However, these exist as isolated patches of 1-4 hectares in the surrounding landscape. None of the birds classified as settling in disturbed habitat were able to establish territories exclusively in these patches. In all cases, the majority of the territory of any bird classified as breeding in disturbed habitat consisted of various early seral habitat types. The smaller disturbed site (~9 hectares) was a stand of mature birch that had been subjected to selective harvesting practices, in which many trees had been left standing. As a result, canopy height was similar to that found in the undisturbed site, but canopy cover is drastically reduced and there is a more pronounced understory component.

1.6. Study Species

The black-capped chickadee (*Poecile atricapilla*) is a small (~ 11 g) resident songbird. Chickadees are territorial during the breeding season (mid-April to early July locally), but forage and travel in small flocks consisting of 2-5 mated pairs during most of the non-breeding season. During most of the year, chickadees consume a mixed diet of seeds, berries, and invertebrates, but switch to a completely insectivorous diet during the breeding season (Smith 1991).

A weak cavity excavator, chickadees nest in hardwood snags, dead limbs or knotholes of live trees. Thus, they are dependent on significant densities of trees or

snags with advanced decay, and have evolved primarily in mature forests of North America. However, this species is known to breed in fragmented and otherwise disturbed habitats (Smith 1991) and preliminary investigations revealed that population densities in disturbed and undisturbed portions of my study site are roughly equivalent.

Nest sites are chosen in late April, at which time both pair members excavate the cavity. The bottom of the cavity is then lined with a nest cup, and the female begins egg-laying (in my study site, egg-laying commenced during the first or second week of May). One egg is laid daily until the clutch is complete (average clutch size is 6 eggs in my study area). Incubation begins on the day prior to the laying of the last egg, and lasts for a period of 12-13 days (Smith 1991). Only the female incubates the eggs, although the male will devote considerable effort to feeding the female at the nest during this phase.

Once the eggs hatch, both male and female will deliver food to the nestlings, although the female will also spend much of her time in the nest cavity, especially when fledglings are young and unable to thermoregulate effectively. Fledging typically takes place 16 days after hatch, although disturbance at the nest after Day 13 will likely trigger an early fledge. In my study area, most nests fledged in mid- to late June, although a few nests did not fledge until early July. Post-fledge, juveniles will remain with and continue to be fed by their parents for a period of 2-4 weeks, and then disperse in random directions, usually settling a few kilometres from the nest site as low-ranking members of winter flocks (Smith 1991).

Chickadees maintain a rigid social hierarchy in winter flocks, which can be used as a measure of male resource holding potential (Ficken *et al.* 1990). Because this species is resident year-round, dominance rankings of colour-banded birds may be determined in the non-breeding season by means of aggressive interactions at winter feeders (Ficken *et al.* 1990).

1.7. Thesis Outline

1.7.1. Area-Sensitivity, Reproductive Success, and Habitat

Although present in densities similar to those found in undisturbed habitat, chickadees breeding in disturbed habitats may nevertheless be experiencing lower reproductive success. This may be a consequence of lower habitat quality relating to features of the environment local to the nest site. In chapter 2, I investigate whether reproductive success differs between disturbed and undisturbed habitats, and to what extent nest tree and nest site variables are predictive of fledge success.

1.7.2. Does Habitat Disturbance Influence Territorial Behaviour?

Most songbird species defend exclusive territories during the breeding season. If resources levels are low, benefits associated with exclusive access to resources necessary for reproduction may no longer outweigh energetic expenditures associated with territory defence. In chapter 3, I investigate whether birds breeding in disturbed habitats alter their territorial behaviour by comparing the frequency of anomalous territorial behaviour in disturbed and undisturbed habitats. Two methodologies are used to accomplish this goal: 1) a radio-telemetry study and 2) a comparison of territory intrusion rates observed during daily territorial surveys.

1.7.3. Territory Size, Habitat Selection, and Reproductive Success

In chapter 2, I looked at the extent to which habitat features in and around the nest site are predictive of nest success. However, territorial habitat quality may also be an important factor determining songbird reproductive success. Certain available habitat types will likely offer more of the resources critical to nest success than others. Consequently, birds should seek to maximize their fitness by including these habitats in their territories in greater proportion to their availability in the landscape. If birds are prevented from utilizing favoured habitat types, they may respond by increasing territory area to encompass enough low-quality habitat to meet their reproductive requirements. In chapter 4, I investigate whether territory size differs for birds breeding in disturbed and undisturbed habitats, if chickadees show clear preferences for certain habitat types, and if there are any relationships between habitat type and nest success.

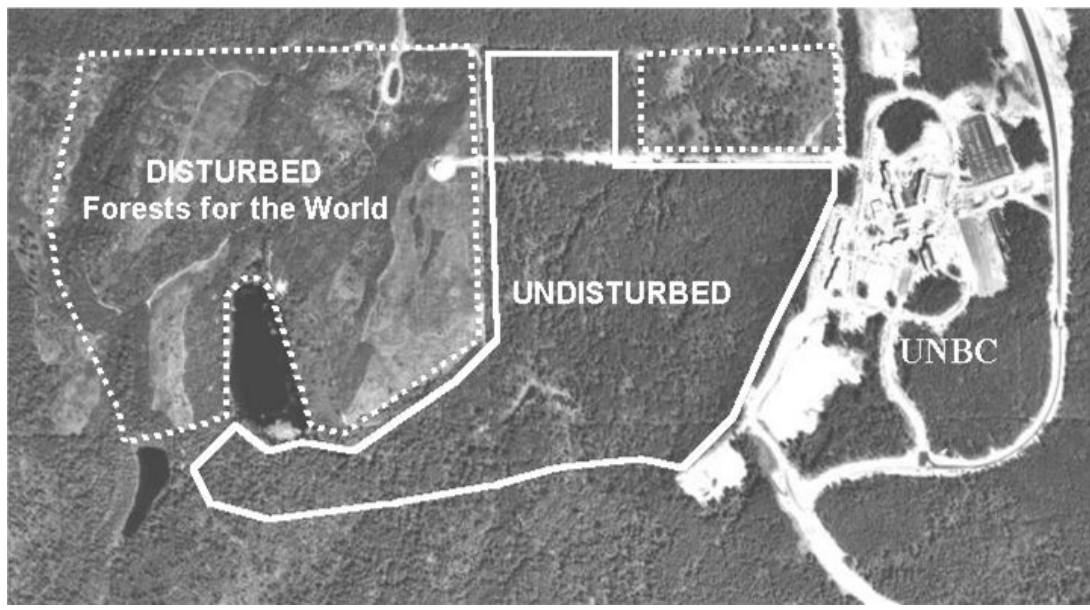


Fig. 1.1. Aerial photo of the study site, showing areas of disturbed and undisturbed habitat.

2. Area sensitivity in an "area-insensitive" songbird: the impact of habitat disturbance on reproduction of chickadees.

2.1. Abstract

Avian species that persist in breeding in disturbed habitats are often thought to be unaffected by disturbance, yet there is growing evidence that altered environments may negatively affect reproductive behaviour and nest success. I compared chickadee nest success in two adjacent habitats, a mature mixed wood forest (undisturbed) versus a forest regenerating post-logging (disturbed). Despite similar breeding densities, nest success was lower in the disturbed habitat than in the undisturbed habitat. Abandonment was the most common cause of nest failure. A within-habitat comparison of the social rank of birds revealed that low-ranking birds had lower nest success than high-ranking birds in the disturbed, but not the undisturbed, habitat. However, clutch size, brood size, and total fledgling productivity did not differ significantly between habitats. Nests situated in snags with lower amounts of internal decay were more successful. Successful nests were also located in sites with higher canopy height, low understory density less than 1 m, and higher understory density between 2 and 3 m. This study provides evidence that disturbed habitats may potentially function as habitat sinks, despite their ability to retain species at normal densities. Therefore, seemingly stable metapopulations

may experience rapid population declines if suitable source habitats of mature forest become uncommon across the landscape.

2.2. Introduction

Research on habitat disturbance and its effects on the reproductive success of forest songbirds typically focuses on community-level effects and is primarily determined by presence/absence census methods (Schmiegelow et al. 1997). Also, studies of focal-species are often restricted to species deemed “area sensitive” (*i.e.* species no longer present following habitat disturbance) (Gibbs and Faaborg 1990). However, recent single-species studies suggest that altered environments negatively affect various aspects of reproductive behaviour (Chase 2002, Ruiz et al. 2002, Zanette 2001).

There are potential dangers of assessing the degree to which a species is affected by habitat disturbance based solely on presence/absence methods. Specifically, reproductive output could be diminished in disturbed habitats in comparison to undisturbed habitats, despite similar breeding densities. This could arise as a result of reproductive decisions made by animals breeding under sub-optimal and stressful conditions. A number of studies have shown that birds breeding in poor-quality territories will compensate for the lowered resources by adjusting clutch size downward (Dhondt et al. 1992, Dhondt et al. 1990, Slagsvold and Lifjeld 1990). However, birds experiencing extremely stressful conditions may opt to forgo breeding altogether if the perceived survivorship risk is too high relative to the

potential fitness benefit of a successful nest. Such conditions might arise either naturally (as a result of stand-level disturbance such as fire or insect outbreak, in which birds begin to re-colonize the area of disturbance from adjacent undisturbed areas) or as a result of anthropogenic disturbance (such as when birds re-colonize regenerating clearcuts).

From a landscape perspective, subpopulations of birds breeding in disturbed habitats may represent population sinks that are dependent on adjacent sources (relatively undisturbed patches) for their continued persistence (Pulliam 1988). The entire metapopulation will persist as long as population sources can export individuals to nearby sinks. Once disturbance levels are too high across the landscape, the number individuals emigrating from source subpopulations may be inadequate to maintain the large number of sink populations, resulting in a large-scale population collapse. This could also happen if certain patches become inaccessible to colonizers, due to behavioural avoidance of intervening habitat. Black-capped chickadees (*Poecile atricapilla*), for example, are known to avoid crossing habitat gaps such as clearcuts (St. Clair et al. 1998).

The black-capped chickadee, a resident cavity-nesting songbird, is known to breed in fragmented and otherwise disturbed habitats (Smith 1991). While its breeding behaviour in pristine woodland habitats has been well studied (Otter and Ratcliffe 1996, Otter et al. 1998), the effects of breeding in disturbed habitats are not well understood. Despite the presence of black-capped chickadees in disturbed habitats, these populations could experience reduced reproductive success as a result

of habitat alteration. This may be due to effects traditionally considered to impact species in disturbed habitats, such as increased predation rates, lower food availability, and a decrease in appropriate nesting sites. It may also stem from more subtle impacts; reproductive strategies of birds based on social ranks (Otter et al. 1998, Otter et al. 1999a) may interact with habitat effects to impact overall reproductive success of populations. For instance, breeding in sub-optimal habitats may differentially impact high-ranking and low-ranking birds if competitively superior high-ranking birds are able to secure better breeding territories. The purpose of this study is to determine whether chickadees do in fact experience lower reproductive success in disturbed habitats than in undisturbed habitats, and to what extent this can be attributed to specific characteristics of that habitat.

2.3. Methodology

2.3.1. Winter Banding and Dominance Assessment

Adult chickadees were captured at established feeding stations using box (Potter) traps mounted on platform feeders and banded during December through February of both years. The banding protocol consisted of applying one numbered aluminum band (under Canadian Wildlife Services license) and three colour plastic bands. Each bird was given a unique colour combination, allowing individuals to be identified from a distance. At the time of banding, body measurements were taken (length of rectrices, flattened wing chord, and mass). Sex of the bird can be determined with 90% accuracy at time of banding using a combination of these three

measures (Desrochers 1990), and this was confirmed by behavioural observations during the breeding season. The age of the bird was determined by examining the shape of the rectrices (Meigs et al. 1983). Birds were classified as either second-year (SY) or after-second-year (ASY). SY birds are entering their second calendar year, and are therefore approaching their first breeding season. ASY birds are any birds entering their third or higher calendar year (i.e. second or higher breeding season).

Once the birds were banded, dominance ranks were assessed by monitoring aggressive interactions between birds at winter feeding stations. A bird was considered dominant to another if it "won" the majority of dyadic interactions. Three behaviours were used to assess dominance. If a focal bird 1) supplants or chases away its opponent, 2) gives a display which elicits a submissive posture in an opponent, or 3) the opponent waits for the bird to leave before approaching a feeder (Ficken et al. 1990, Otter et al. 1998), that bird was considered dominant to its opponent. Flock membership was determined by observing patterns of feeder use and by tracking foraging activities throughout the flock range. These data were collected using a voice-activated recorder (Optimus CTR-116) at a distance of not less than 10 m from the station to minimize the risk of influencing feeding behaviour. A linear dominance matrix was determined for each flock. Birds were classified either as low, mid, or high rank, depending on their position within the flock. As female rank is known to be correlated with rank of their social mate (Otter et al. 1999a, Smith 1991), I concentrated on determining relative rank of males

within flocks. In flocks consisting of three pairs, the mid-rank was applied to the male submissive to the alpha male but dominant over the low-ranking male. No flocks consisting of greater than three mated pairs were observed in my study area over the course of the two-year study period. In flocks consisting of two mated pairs (the most common flock size in my study area), the dominant male was assigned the high rank while the other male was considered low-ranking. This relative ranking system is likely a more biologically accurate measure than absolute ranks, because high-ranking birds from one flock tend to dominate low-ranking individuals from other flocks. As interactions between birds from each habitat type were relatively rare (K. Fort unpubl. data), it was not feasible to assess whether birds from one habitat type were consistently dominant to birds from the other habitat type (i.e. evidence for a habitat-induced settling bias, such that high-quality birds competitively exclude low-quality birds from undisturbed habitat).

In early spring (prior to flock breakup) of the first year, a 50 m by 50 m grid system was created in the undisturbed habitat, and grid points were marked with flagging tape. All grid points were recorded using a Trimble Geoexplorer III (Trimble, Sunnyvale, CA) handheld GPS unit. Thus, the location of bird observations and territory boundaries in relation to aerial photos of the study site could later be determined with a high degree of accuracy. By also marking locations of specific landmarks in either habitat, the GIS images could be superimposed onto satellite images of the area to give a high resolution of accuracy in marking animal movements. It was unnecessary to establish a grid system in the

disturbed habitat, as existing trails and other landmarks were sufficient to determine locations of territory boundaries and nest sites.

2.3.2. Breeding Season

After the breakup of flocks in early spring, three field assistants and I conducted surveys of the study area from 0800–1600 hours daily to determine settling patterns, territorial boundaries, and nest locations. Territorial boundaries were determined by recording locations of territorial disputes between neighbouring males, male singing posts, and the geographical extent of foraging bouts by mated pairs. During this period, mated pairs will excavate nest-cavities, and these sites were recorded and monitored to determine when pairs initiated incubation. All nest sites were marked with flagging tape at a random distance (minimum 5 m away) and direction (indicated on the marker flag, to facilitate relocation of the nest) from the actual cavity tree to minimize the risk of attracting potential nest predators. I also maintained a minimum distance of 5 m away from the nest during all monitoring activities.

Once a nest-site had been determined, it was monitored every 3-4 days for changes in status (i.e. excavation, nest-lining, egg-laying, incubation, hatch, fledge). Change in nesting status can often be determined (within a range of accuracy of 1-2 days) by noting certain characteristic behaviours. During the nest-lining phase, females will bring nest-material such as animal hair or dried plant material to the cavity. The egg-laying phase is accompanied (a few days prior to onset) by the use of the ‘broken-dee’ call by the female (D. Mennill pers. comm.). Once incubation

begins, the female spends the majority of her time within the cavity, and the male feeds the female at the nest entrance. After the eggs have hatched, both male and female feed the young, although the female still spends much of her time brooding within the cavity. However, when the male arrives with food, the female will often leave the cavity to allow the male to enter, feed the young, and remove any fecal sacs.

All accessible nests were visited on or around day 7 post-hatch for the purposes of banding nestlings. Nests were accessed in one of three ways. The majority of nests were accessed using a 10 m extension ladder, a tree-climbing belt, or with the help of an experienced tree-climber. Inaccessible nests could still be monitored to determine whether a successful fledge took place.

Once at the cavity, a small saw was used to cut a square portal in the side of the tree several cm above the level of the nest cup. Whenever possible, chicks were removed in two stages in order to minimize the risk of nest abandonment (no nests were abandoned as a result of my activities). Fledglings were enumerated and the nest cup was examined for unhatched eggs. Once the fledglings were returned to the nest, the portal was re-inserted and held in place with duct tape. Using this methodology, clutch size (# hatched + # unhatched eggs) is a valid measure, as chickadees are not known to remove unhatched eggs or dead nestlings – Otter et al. 1999a), brood size, and proportion hatched (# hatched/ clutch size) could be determined. A successful nest was defined as a nest that was still active at day 14 post-hatch; although fledging does not normally take place until day 15 or 16, any

disturbance in the vicinity of the nest at or beyond day 14 will trigger fledging. Failed nests were classified according to the cause of failure (abandonment, nest predation, weather event) whenever possible. Nest predation events could be determined easily, as local nest predators (red squirrels and, in one instance, a young black bear) leave signs of forced entry in and around the cavity entrance. Abandoned nests were further classified according to the nesting phase (pre-incubation, incubation, or nestling) at which abandonment occurred.

2.3.3. Vegetation Sampling Protocol

Nest-site habitat characteristics were assessed using, at each established nest site, 0.04 ha (11.3 m radius) circular plots centred on the cavity tree. Vegetation sampling took place within two weeks after fledging had occurred. As the vegetation is fully developed well before the time of fledging, my vegetation plots should be an accurate reflection of habitat conditions at the nest during the nestling phase. Characteristics of the cavity tree itself as well as the surrounding habitat were recorded. With respect to the cavity tree, species, diameter at breast height (dbh), tree height (using a clinometer), cavity height, and cavity type (top or side entrance, knothole, or branch) was recorded. Within the plot, species and dbh (in six size classes) of each tree was recorded. The height, species, and dbh of a representative canopy tree were also recorded. Canopy cover was measured using a convex densiometer at the edge of the plot in the four cardinal directions. For all snags within the plot, species, dbh size class, height, and decay class was recorded. The understory component was assessed by estimating the overall percent cover (in

seven cover classes) of all shrub species (including young trees) at four vertical height classes (0-1 m, 1-2 m, 2-3 m, 3-4 m).

2.3.4. Statistical Analyses

I used G-tests to determine whether nest success differed between disturbed and undisturbed nests, between high- and low-ranking birds, and to assess whether birds responded differentially by rank within each habitat type. When cell frequencies were less than five, I used Fisher Exact tests. As rank is known to influence reproductive output (Otter et al. 1999a), I included rank as an additional factor in analyses of nest data. I also included year as a factor in ANOVA models. If annual variation was detected, I standardized the data by determining the average value of the variable for each year and then expressed the data as a deviation from the yearly average. Two-factor ANOVA was used where assumptions were met. Poisson multiple regressions were used for count variables. Year was included as a factor in these models. As Incubation Date (commencement of incubation of the clutch) was also not distributed normally and is known to be highly correlated with rank (Smith 1991), a nonparametric comparison of high-ranking birds only was used to control for this factor.

I employed backward stepwise multiple logistic regression to determine which, if any, habitat variables were predictive of nest success, both with respect to cavity-tree and nest plot-level characteristics, irrespective of overall habitat type. This analysis allows differentiation of success based on microhabitat, within larger landscape categories. Data were collected from 69 nest plots in 2000 and 2001. The

following cavity tree variables were entered into the cavity tree model: tree height, tree diameter at breast height, cavity height, decay class at Cavity, number of cavities in the cavity tree. Decay class was assessed using the Wood Classification system outlined in the Field Manual for Describing Terrestrial Ecosystems (Ministry of Forests 1999). The nest plot vegetation variables that I entered into the model were canopy height (distance from ground to the top of the canopy layer), canopy cover, understory cover (in four 1 m vertical classes), basal area of all trees, snag density, density of large hardwoods.

A Kolmogorov-Smirnov test was used to determine whether the distribution of snags in each decay class differed between the disturbed and undisturbed sites. Also, I used a t-test to determine whether the ratio of cavity height to canopy height differed significantly between disturbed and undisturbed habitats. Non-parametric tests were used when distributions were not normal. All statistical analyses were performed using SYSTAT 9.0 (SPSS Inc. Chicago, IL).

2.4. Results

2.4.1. Overall Reproductive Success between Habitats

I collected nest success data for 68 breeding pairs over the two-year study period. Birds breeding in disturbed habitat had significantly lower nest success than did those in undisturbed habitat (G-test, $P = 0.02$), and this pattern did not differ between years (G-test, $P = 0.14$). For the 52 breeding pairs where dominance rank was known, high-ranking birds were significantly more successful than low-ranking

birds (G-test, $P = 0.02$). For clarity, this analysis also excluded the small number of mid-ranked birds. In order to look for a possible interaction between habitat and rank, I examined the ratio of successful to failed nests in each habitat separately by rank (Fig. 2.1). Rank influenced patterns of nest success to a much greater extent in disturbed habitat (G-test, $P = 0.05$) than in undisturbed habitat (Fisher Exact test, $P = 0.26$) in that the majority of successful nests in disturbed habitat were attributable to high-ranking birds.

Breeding densities were not appreciably different between habitats or years. There were 0.25 pairs per hectare breeding in the disturbed habitat averaged over two years, compared with 0.33 pairs per hectare in the undisturbed habitat. However, the density of *successful* pairs in the undisturbed habitat was 0.26 pairs per hectare, twice the density of 0.13 in the disturbed habitat.

2.4.2. Comparisons of Nesting Chronology and Reproductive Output between Habitats

Nest failure due to predation was a relatively rare event (less than 5% of all nests were depredated) and does not appear to differ between habitats. The majority of nest failure occurred through abandonment. High-ranking birds nesting in disturbed habitat started incubating earlier than those in undisturbed habitat (Mann-Whitney U-test, $U = 10.5$, $P = 0.01$, $n = 11$ undisturbed vs. 7 disturbed nests). However, hatch date, incubation period, and fledge date did not differ between habitats or ranks (Table 2.1). Decreasing sample sizes in these analyses are due to nest failures and instances of abandonment accumulating over the breeding season.

Clutch size and brood size did not differ between habitats (Table 2.2). For this analysis, nests that failed pre-incubation were excluded (N= 14), as were failed nests where males abandoned (N= 2) and a single nest where behavioural and genetic evidence implicated conspecifics brood parasitism (Otter et al. in prep.).

2.4.3. Overall Productivity in Each Habitat

To compare productivity between disturbed and undisturbed areas, I calculated the average number of fledglings per pair over two years in both habitats. In this analysis, I did not consider pairs for which the number of fledglings was not known (i.e. inaccessible nests), but did include all nests where pairs initiated a clutch and abandoned either pre-hatch or post-hatch. In undisturbed habitat, 3.33 ± 0.49 fledglings were produced per pair (or 1.67 fledglings per breeding individual), whereas only 2.30 ± 0.56 fledglings per pair (1.15 fledglings per breeding individual) were produced in the disturbed site over the same period. These estimates did not differ statistically (Mann-Whitney U-test, $U= 323$, $P = 0.17$, $n = 30$ undisturbed and 27 disturbed). Note, that I have no information on rates of post-fledging juvenile survivorship.

As total area of each habitat type was known, and the reproductive output of nearly all pairs within the study area was also known, I was able to calculate the productivity in each habitat in terms of the number of fledglings produced per hectare. In this analysis, I inserted average values for number of fledglings produced per successful nest for those successful nests (N=10) for which brood size

was unknown. In undisturbed habitat, 0.92 fledglings per hectare were produced compared to 0.53 fledglings per hectare in the disturbed habitat.

2.4.4. Nest Success and Habitat

The cavity tree multiple logistic regression model was significant (Chi-square = 8.447, $df = 1$, $P < 0.01$), although only Cavity Decay was retained after the stepwise analysis. Successful nests were those that were in nest sites with lower decay (Table 2.3). The nest plot vegetation model was also significant (Chi-square = 9.665, $df = 3$, $P = 0.02$). Canopy Height, Understory <1m, and Understory 2-3 m were significantly associated with nest success (Table 2.4).

2.4.5. Distribution of Decay Class among Snags

Cavity Decay was negatively associated with Nest Success and pairs breeding in disturbed habitats experienced nest failure more often than birds in undisturbed habitat (Figure 2.1). Therefore, I hypothesized that snags in the lower decay classes would be relatively less abundant in disturbed habitats than in undisturbed habitats. I used snag information collected from 69 nest plots to calculate average snag decay class distributions for nest sites in disturbed and undisturbed habitats (Figure 2.2). I excluded snags under 10 cm dbh, as these are known to be unavailable as nest sites for chickadees (Smith 1991). However, I found no significant differences between average decay class distributions in disturbed and undisturbed habitats (Kolmogorov-Smirnov test, $P = 0.52$).

2.4.6. Ratio of Canopy Height to Nest Height

Canopy Height was positively associated with Nest Success (Table 2.4), although Cavity Height was not predictive of nest success, nor did it differ significantly between habitats (Mann-Whitney U-test, $U = 466.0$, $P = 0.15$, $n = 39$ in undisturbed and 30 in disturbed). If the nest sites in disturbed sites are relatively closer to the height of the canopy they may be more exposed, possibly resulting in sub-optimal cavity microclimates. The difference in meters between the height of the cavity and the surrounding canopy height was greater around undisturbed nests than disturbed nests (Mann-Whitney U-test, $U = 423.0$, $P = 0.05$, $n = 39$ in undisturbed and 30 in disturbed), suggesting that nests in disturbed habitats may be more exposed.

2.5. Discussion

2.5.1. Nest Success

Overall, birds nesting in disturbed habitats experienced lower nest success than those breeding in undisturbed habitats. High-ranking birds were generally more successful than low-ranking birds, irrespective of habitat. However, low-ranking birds appear to experience much lower overall reproductive success in disturbed habitat than in undisturbed habitat. By contrast, the reproductive success of higher-ranking birds appears less sensitive to habitat disturbance. The majority of nest failure is due to nest abandonment, not predation, in my study site. Additionally,

most nest failures occurred early in the breeding season (i.e. before the onset of the incubation phase).

The difference between habitats with respect to rates of nest success may best be explained by the relative availability of suitable breeding habitat. As chickadee density did not differ markedly between the disturbed and undisturbed habitats, good quality nest sites and breeding territories may have been more limited in the disturbed than undisturbed habitat. Within the disturbed site, this may have created increased competition among males for access to these patches containing desired resources. Dominance rank in male chickadees is known to be a good measure of quality and therefore resource-holding potential (Smith 1991). Also, other studies have shown that female chickadees seek opportunities to pair with high-ranking males (Otter and Ratcliffe 1996) and that these females gain reproductive benefits from such pairings (Otter et al. 1999a). In disturbed sites, competitively superior high-ranking males may be better able to incorporate remnant mature forest patches into their territories which might provide favoured nest sites for their mates, excluding lower-ranking birds from these resources. The undisturbed habitat is not likely to be as limiting in good quality habitat, so one would expect competitive interactions between pairs for nesting sites and good quality territories to be much reduced. Thus, intraspecific competition for reproductive resources biased in favour of high-ranking birds could explain the high incidence of nest-attempt abandonment in disturbed habitat relative to undisturbed habitat.

In other studies, poor territory quality has been associated with such nest data variables as low clutch size and clutch productivity (Dhondt et al. 1990, Dhondt et al. 1992), and delayed onset of laying (Bromssen and Jansson 1980). However, I found no differences between habitats with respect to any nest data variables with the exception of the estimated start of incubation, which was earlier in the disturbed habitat. Thus, those pairs in disturbed habitat that did establish nests did not appear to be suffering from decreased resource availability in comparison to birds in undisturbed habitat. This suggests that these predominantly high-ranking birds were able to obtain territories and nest sites comparable to those in undisturbed habitat. However, the high rate of nest abandonment by low-ranking birds in the disturbed site suggests that there is a greater disparity between good and poor-quality territories in disturbed habitat. Low-ranking birds forced into sub-optimal territories in the disturbed site may be confronted with a breeding territory so resource-depauperate that attempting a clutch becomes prohibitively costly. Thus, lower-ranking birds may elect to forgo breeding attempts altogether rather than lower either their clutch size to accommodate decreases in resource availability or their own future survival prospects by attempting to breed in sub-optimal conditions.

2.5.2. Productivity by Habitat

Across the two habitat types in the study area, successfully nesting birds do not differ in number of young in their nests. Instead, the disparity between habitats lies in the number of pairs that successfully reproduce. Ultimately, this could lead to differences in reproductive output potential if the two habitats were viewed as

somewhat isolated subpopulations (a view supported by low rates of inter-habitat movement in winter flocks- Fort and Otter unpubl. data).

The overall density of breeding pairs does not differ between the two habitats, but the low success rates of pairs trying to establish in the disturbed site resulted in a fledgling habitat production rate that was substantially lower than that in the surrounding woodland. This creates the potential for regenerating woodlands to function as sink habitats, despite their apparent ability to retain species at normal densities. Within the mosaic of regenerating forests that characterize the forestry practices of the north central region of BC, the small isolated stands of mature woodland may feed the overall population structure. Loss of these older stands may have high impacts if younger seral forests cannot keep up to overall production. This could be compounded if the fewer young produced in these areas also showed lower survival prospects, something not studied here but which has been found in other species occupying sub-optimal habitat (Przybylo et al. 2001, Magrath 1991, Walsberg 1985).

2.5.3. Factors Associated with Nest Success

In order to investigate the underlying mechanisms responsible for patterns of nest success in my study site, I chose to look for nest site habitat characteristics that were predictive of nest success irrespective of habitat type. I found that successful nest sites in disturbed habitat were often structurally similar to undisturbed nest sites, as successful birds tended to find remnant patches of mature forest in which to

situate their nest. Similarly, unsuccessful nests in the undisturbed site were situated in locations more similar to typical habitat conditions in the disturbed site.

Birds nesting in cavity trees with lower stages of internal decay were more successful. This may be due to increased protection from predation afforded by such nesting substrate (Hooge et al. 1999). However, I think that this is an inadequate explanation of patterns of nest success in my data, as predation rates within my study site were generally low. Successful nests were surrounded by a higher canopy and unsuccessful cavities were closer to the level of the canopy than were successful nests. Hooge et al. (1999) found that greater cavity tree integrity was correlated both with more stable microclimates and higher rates of nest success. Nest microclimate is also known to influence incubation demands on parents (Hoi et al. 1994). As canopy height is generally lower in disturbed areas, smaller crown areas could also result in lower caterpillar abundance, the primary food source of the birds. Some preliminary evidence from my study site points to lower feeding rates among pairs in disturbed habitat (Z. McDonnell unpubl. data).

It is likely that body condition is the primary proximate mechanism driving both pre-incubation and post-incubation abandonment decisions. Females breeding in sub-optimal habitat may be in poor condition due to lower food intake levels. If the nest site is also sub-optimal in terms of providing a stable microclimate, and is more exposed to weather conditions, female body condition will decrease further as a result of increased thermoregulatory costs. These factors may act in concert to reduce body condition to such an extent that females may elect to forgo a breeding

attempt altogether. Differences in microclimate of the nest and condition of breeding pairs are currently being investigated.

Songbirds breeding in disturbed habitat may be experiencing reproductive losses despite their continued presence in such habitats at densities comparable to those found in adjacent undisturbed woodlands. Disturbed habitats may act as population sinks (*sensu* Pulliam 1988) due to reproductive decisions made by individuals breeding in sub-optimal conditions. Specifically, low food resource levels combined with increased thermoregulatory costs associated with poor nest microclimate may lower body condition to such an extent that breeding becomes too energetically costly. In order to understand the mechanisms underlying source-sink dynamics in disturbed habitats, it may be important to investigate how individual animals make reproductive decisions under sub-optimal conditions.

Table 2.1. 2-way ANOVA comparing effects of Habitat and Rank for nest data variables, Spring 2001 and 2002. Values are means \pm SE. Sample sizes are in parentheses. None of these differences were significant at $P < 0.05$.

Variable	Habitat		Rank		P_H	P_R	P_{Int}
	Disturbed	Undisturbed	High	Low			
Standardized Hatch Date	-0.55 ± 1.72 (11)	0.94 ± 1.38 (14)	-1.38 ± 1.38 (14)	1.78 ± 1.73 (11)	0.51	0.17	0.31
Incubation Period	13.87 ± 1.65 (11)	16.56 ± 1.30 (14)	15.68 ± 1.31 (14)	14.75 ± 1.63 (11)	0.31	0.96	0.51
Standardized Fledge Date	0.15 ± 1.37 (16)	0.90 ± 1.20 (18)	-0.82 ± 1.18 (19)	1.87 ± 1.39 (15)	0.68	0.15	0.21

Table 2.2. Poisson regressions comparing effects of Habitat, Rank and Year on nest data variables, spring 2001 and 2002.

	<i>Parameter</i>	χ^2	<i>P</i>
Clutch Size	Habitat	0.13	0.51
	Rank	-0.01	0.97
	Year	-0.34	0.05
Brood Size	Habitat	0.18	0.53
	Rank	-0.11	0.68
	Year	-0.51	0.06

Table 2.3. Results of Backwards Stepwise Multiple Logistic Regression using cavity tree variables as predictors of nest success.

Variable	Estimate	SE	t-ratio	P
Constant	2.493	0.830	3.002	0.003
Cavity Decay	-0.386	0.149	-2.585	0.010

Table 2.4. Results of Backwards Stepwise Multiple Logistic Regression using nest plot vegetation variables as predictors of nest success.

Variable	Estimate	SE	t-ratio	P
Constant	2.11	2.32	0.91	0.36
Canopy Height	0.07	0.04	2.09	0.04
Understory 1	-0.94	0.47	-2.02	0.04
Understory 3	0.64	0.32	2.01	<0.05

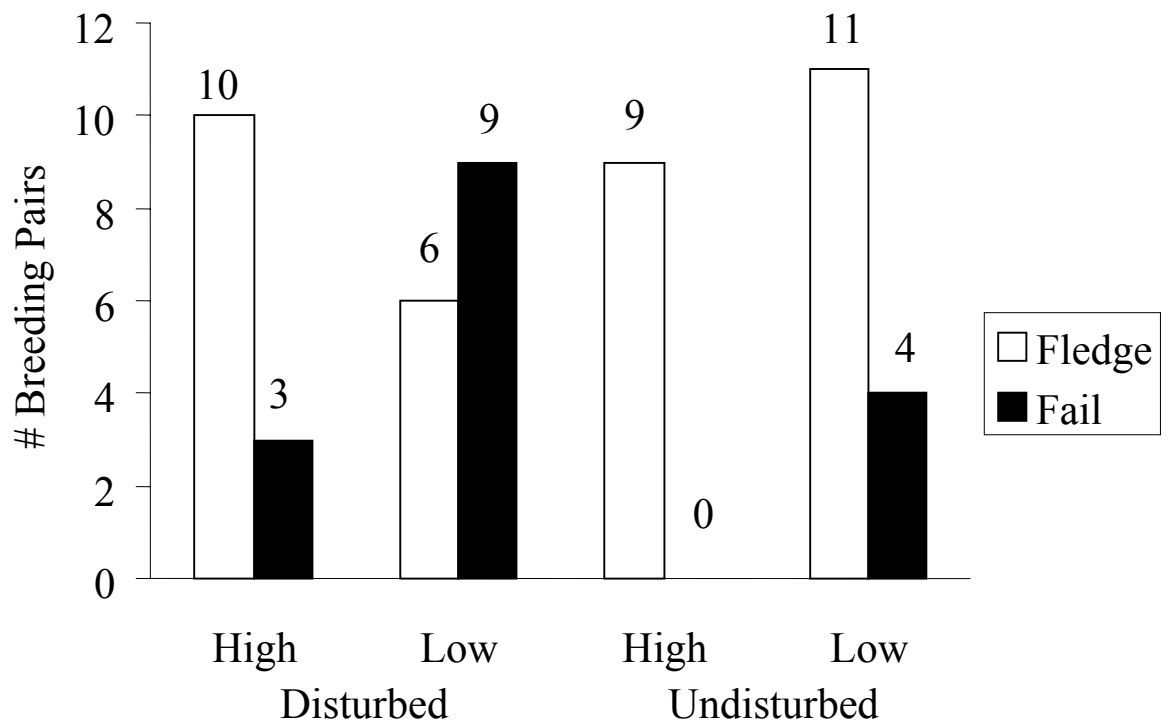


Fig. 2.1. Nest Success in disturbed and undisturbed habitats by rank for 29 and 24 pairs breeding in 2000 and 2001, respectively.

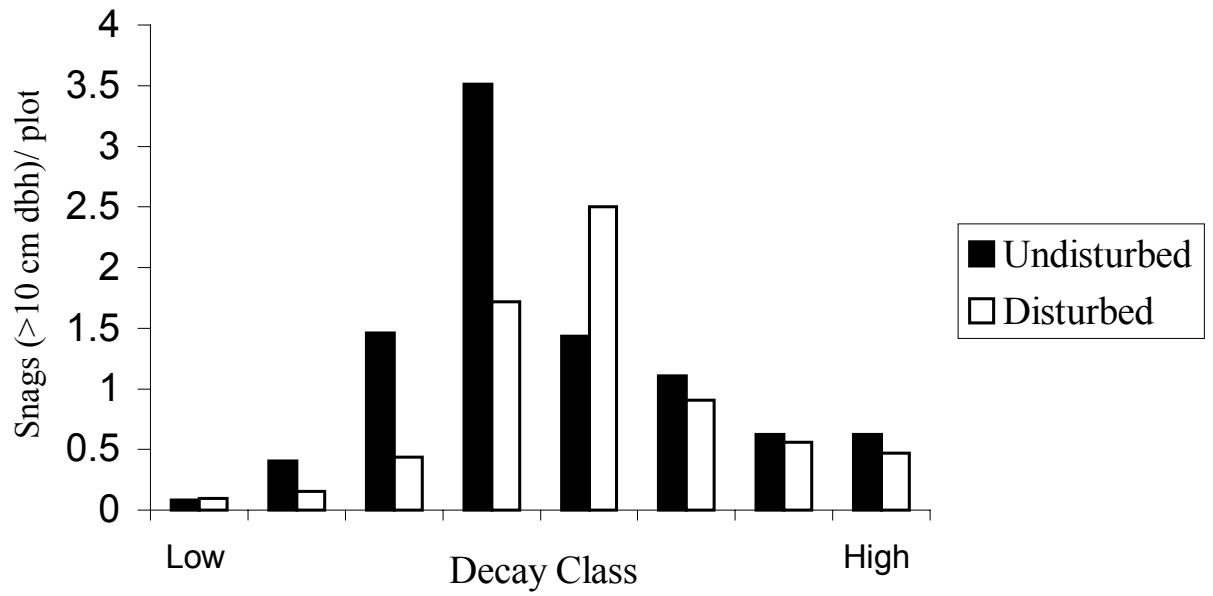


Fig. 2.2. Snag Decay Class Distributions for 69 nest plots in disturbed and undisturbed habitats. Despite an apparent shift in the distributions between habitats, the effect is not significant.

3. Territorial breakdown of black-capped chickadees (*Poecile atricapilla*) in disturbed habitats

3.1. Abstract

The propensity of males to act territorially may be greatly affected by the perceived quality of the habitat. In sub-optimal habitats, the cost of defence may be prohibitively large compared to the associated benefits, and territorial behaviour may be expected to decline. I tested this hypothesis in a population of chickadees breeding in adjacent habitats; an 85 ha patch of early seral forests regenerating after clearcut logging (disturbed site), which is surrounded by mature mixed wood forests (undisturbed site). Breeding success of pairs in the disturbed site is significantly lower than in the undisturbed site, suggesting a difference in the relative quality of the two habitats. During the spring of 2000 and 2001, I mapped the actively defended areas and song posts of colour-marked chickadees and found that males occupying the disturbed site were subject to higher amounts of territorial overlap than pairs in the undisturbed mature woodlands. Five pairs of chickadees in the disturbed habitat and five in undisturbed were radio-tagged and I conducted repeated focal observations on the movement patterns of the birds. All five pairs in the disturbed habitat regularly intruded into areas actively defended by neighbouring birds; only one of the five pairs in the undisturbed habitat ever intruded onto the known territory of another pair during an observation period. My results suggest that the quality of the disturbed habitat may be sufficiently low so as

to make normal levels of exclusive defence cost-inefficient. Conversely, birds in disturbed habitat may intrude more frequently into neighbouring territories because resource levels in their own exclusively-defended territories are insufficient to meet energetic requirements during the breeding season.

3.2. Introduction

Most songbirds defend breeding territories, defined as an area of habitat that a single bird or pair will defend against conspecifics. As territorial defence is costly (Marler and Moore 1989), it is assumed that there must be a compensatory reward in terms of reproductive output. Such benefits usually include securing exclusive access to resources such as food and/or nest sites found within that territory. In addition, males may further benefit from access to sites for mate attraction displays (Dale and Slagsvold 1990) and the existence of a buffer that prevents other males from obtaining access to their mates (Møller 1987, 1990).

Dhondt and Schillemans (1983) found that great tit (*Parus major*) intruders, non-territorial birds breeding within the territory of another bird, produced fewer offspring than territory owners, suggesting that territoriality is adaptive in songbirds under certain conditions. Territory quality is highly variable, however, and birds that establish territories in sub-optimal habitat often have lower reproductive success than those in preferred habitat (Krebs 1971, Hatchwell et al. 1996, Roberts and Norment 1999). There is also evidence to suggest that many songbirds are capable of a certain degree of behavioural plasticity with respect to territoriality. Birds may

switch from a territorial to non-territorial strategy if, for instance, the energetic cost of territorial defence outweighs the caloric benefits obtained via exclusive access to a food resource (Gill and Wolf 1975a, 1975b, Stamps and Buechner 1985, Schoener 1983, Perret and Blondel 1993). Additionally, Gill and Wolf (1975a, 1975b) showed that, although increased patchiness of a food resource tends to generate territorial behaviour, a concomitant increase in intrusion rates from neighbouring birds resulted in territory holders becoming *less* territorial. Thus, birds breeding in low-quality habitats may relax territorial defence because aggressive responses to higher intrusion rates will increase energetic costs, and the depleted value of the resource being defended may be insufficient to offset this increase.

Black-capped chickadees (*Poecile atricapilla*) defend exclusive territories during the breeding season (Smith 1991). However, in Chapter 2 I showed that birds living in disturbed habitats (habitats regenerating following past periods of logging) have significantly lower reproductive success than those in undisturbed mature forests. This may indicate poor resource availability within the disturbed areas, making them less energetically valuable to exclusively defend. Preliminary observations suggested that birds occupying disturbed areas within my study area had higher levels of overlap on their territory boundaries, creating areas that were not exclusively defended by any one bird. If this is indicative of reduced territory quality, I hypothesize that birds settling in disturbed habitats should also show decreased levels of territoriality even within areas that are solely defended by a

single pair. This may appear in the form of high levels of intrusions into neighbouring territories, and tolerance of these intrusions by residents.

I employed two methodologies to investigate this phenomenon. First, I examined daily breeding season survey maps in both 2000 and 2001 to compare relative frequencies of observed territorial intrusions between habitats. Second, I radio-tracked focal breeding females in both disturbed and undisturbed habitat to quantify the frequency and magnitude of intrusion behaviour in both habitat types. During these latter trials, I also monitored the behaviour of resident birds to determine whether intrusions elicited an aggressive response towards intruders.

Many telemetry studies involving songbirds have focused on the extent to which both males and females may increase their opportunities for extra-pair copulations (EPC's) by means of extra-territorial movements (Smiseth and Amundsen 1995, Stutchbury 1998, Neudorf et al. 1997), whether habitat fragmentation affects intra-territorial (edge vs. interior) habitat use (Norris et al. 2000), as well as comparisons of movement patterns through a fragmented landscape with respect to habitat specialist vs. habitat generalist species (C. Gillies unpubl. data). None, however, have addressed the potential impact of habitat disturbance on territorial behaviour during the breeding season.

3.3. Methodology

3.3.1. Capture, Flock Composition, and Rank Determination

Birds were captured at winter feeders and individually colour-marked as described in Chapter 2. During the winter, I determined the flock composition of birds and their linear hierarchies by watching interactions at feeders, also described in Chapter 2.

3.3.2. Determination of Territory Boundaries

Territorial information for each breeding pair of chickadees in the 170 ha site (Fig. 3.1) was determined from daily surveys conducted during May and June 2000 and 2001. Male song posts and locations of inter-pair boundary disputes were recorded on maps of the study site, with reference to 50 x 50 m grid point markers or other spatial reference points (trails, other geographic landmarks). Using the combination of grid points and spatial references, bird locations could be plotted on maps to approximately ± 10 m. These data, accumulated over the course of the early breeding season, allowed me to determine territory polygons for each breeding pair. Territory boundaries were defined as the Minimum Convex Polygon (hereafter referred to simply as MCP) created by the outermost set of song posts and boundary dispute locations. A small number of territory disputes were also witnessed during formal radio-tracking trials. These observations were incorporated into the data collected outside these times to help define the space that was actively defended by a pair, and aided by providing precise information on territorial boundaries during periods when intrusion behaviour was being monitored. All territory polygons in the

study area created by this process were digitized using ArcInfo (Environmental Systems Research Institute 1996), and superimposed over an orthophoto of the study area (Fig. 3.2). One map was created for each of the two years of the study.

3.3.3. Definition of Intrusion Events

An 'intrusion' was defined as a case in which an intruding bird travelled in excess of 25 m into an area known previously to be solely defended by another bird, and in which the latter bird was observed defending subsequent to the intrusion event. This definition eliminates cases of slight territorial shifting, which are known to occur on a regular basis during the course of the breeding season. It also excludes areas of territorial overlap (areas being defended by more than a single pair) from inclusion as an intrusion event by any of the contesting birds. The distance restriction (which effectively places a 25 m wide buffer around all territory boundaries) allows a conservative measure of intrusion behaviour. Given the estimated ± 10 m level of accuracy of territory boundaries, an intrusion of less than 25 m would be difficult to distinguish from a case in which a bird was simply foraging along its territorial boundary and occasionally 'straying' into areas defended by neighbouring pairs. As territories are roughly circular, a territory diameter estimate of approximately 180 m is reasonable. Therefore a 25 m intrusion may represent a movement nearly 1/3 of the distance to the territory centre.

3.3.4. Territorial Intrusions during Daily Surveys

During the breeding season, both disturbed and undisturbed sites were intensively surveyed every two to three days to determine territorial boundaries, nest

locations, and other information relevant to reproductive success of chickadees.

Surveys were conducted in two teams of two trained observers, and typically lasted from six to eight hours. Both habitat types were surveyed with equal intensity.

Intrusion events observed in the course of these daily surveys were noted and plotted on daily survey maps during the course of the entire study period. These intrusion events were then enumerated upon later examination of the survey maps.

3.3.5. Radio-telemetry Observations

Females mated to low-ranking males in either habitat were selected as focal individuals for the telemetry study. Low-ranking females were predicted to be more likely to engage in extra-territorial movements, as they are known to engage in more EPC's (Smith 1988, Otter et al. 1998) and resources within their territories are likely to be more limiting (Smith 1991). Platform feeders baited with sunflower seeds were placed near cavity excavations or centrally in territories of all telemetry candidates. Once the focal pair had located the feeder (usually within 1-2 days), females were captured in Potter traps mounted on the platforms. A Holohil LB-2 (0.52 g) transmitter (Holohil Systems Ltd., Woodlawn, Ontario) was attached by means of a figure-eight harness method (Mennill 2000) glued to the underside of the transmitter. As chickadees typically weigh approximately 11g, the transmitter constituted about 5% of the bird's body mass, and was in accordance with recommended maximum weight specifications (Bibby et al. 2000). The loops of the harness were fitted around the base of the legs so that the transmitter lay snugly on the back of the bird and the whip antenna extended down along the length of the tail.

There was no indication that the transmitter or antenna interfered with copulation, as focal females that established active nests did fledge young. After the installation of the transmitter, birds were observed for approximately 30 minutes to ensure that they were adjusting normally to the additional weight. In no cases was it necessary to re-capture the bird and remove the transmitter. The first observation period was conducted after a 1-2 day waiting period, to give the birds time to acclimatize to the additional weight of the transmitter.

As the fertile period commences during cavity excavation and extends to the laying date of the penultimate egg (Smith 1991), I attached transmitters mid-way through the cavity excavation phase and continued trials until birds began to incubate eggs. The fertile period of chickadees spans approximately 21 days, which is roughly equivalent to the functional longevity of the transmitters. In my study, territory quality is hypothesized to drive the observed patterns of territorial breakdown, so extending the tracking period beyond the start of incubation would be admissible. However, females drastically reduce their own foraging behaviour during the incubation phase, as they rely heavily on their mates to feed them at the nest during this period (Smith 1991). Consequently, post-incubation observations on female movements would not likely reflect food resource constraints in low-quality territories and so were not conducted.

I tracked female movements using a Communications Specialists Model R-1000 148-174 MHz telemetry receiver and YAGI antenna (Communications Specialists Inc., Orange, California). Hour-long observations were conducted for each focal bird

every 3-4 days throughout the fertile period. Observation periods began once the focal bird had been located. Focal females were often tracked visually and by sound, but when visual contact was lost the birds were re-located by means of radio-telemetry. I maintained a distance of at least 20 m at all times, so that I did not interfere with bird movement. Positions were recorded on study-site maps at 2-minute intervals, whenever possible. For a trial to be acceptable, the focal birds must have been tracked for a minimum of 40 minutes, although most observation periods ran the full 60 minutes. It was necessary to maintain visual contact with the birds, and if this contact was lost for greater than five consecutive 2-minute time intervals, observations were aborted and restarted from time zero upon relocation of the birds.

Telemetry observations were conducted in teams of two; one person operated the receiver and antenna while the other recorded bird positions and other relevant information (see below). Both team members were required to concur on bird positions to increase accuracy of mapping. Each team conducted two observation periods per day. All observations took place in the morning during one of two tracking periods (approx. 0800–0900 hours or 0930–1030 hours); exact start times depended on the ease with which birds were initially located. During each time period (first versus second), one pair from either habitat was tracked simultaneously by two separate teams, barring weather problems. Observation periods were not conducted in excessively inclement weather (high winds or rain), as birds tend to curtail their movements under such conditions. Observations were arranged so that birds were sampled equally during the early and late time periods, to control for

possible time-of-day biases in movement patterns. For each focal bird, 4-6 trials were conducted over the course of the study period. In total, I tracked ten pairs of birds over the two year period: two pairs, one each in disturbed and undisturbed habitats in 2000; and eight pairs, four each in either habitat in 2001.

For each 2-minute interval during the trials, I recorded: 1) the presence/absence of focal female's mate; 2) if mate was present, his distance (in metres) from the female; and 3) the presence/absence of neighbouring conspecifics and all information on their interaction with the pair (# present, sex, distance from focal female, presence/absence of aggressive interactions)

For analysis, bird positions during each trial were added as points to an orthophoto in GIS. Location of all grid markers and geographic landmarks were determined with a global positioning system and overlaid on the map for reference. A MCP was created in ArcView 3.1(Environmental Systems Research Institute 1996) using the Animal Movement extension software package, for each set of points in a trial, and superimposed over territory polygon ArcInfo coverages (see above) for comparison. With respect to the MCP for each trial I determined:

1. The total area of the MCP.
2. Whether the MCP was contained within the territory polygon associated with that breeding pair, or whether it straddled more than one territory.
3. If the MCP straddled more than one territory, whether it met the minimum requirements for classification as an intrusion.
4. When intrusions occurred, the proportion of the MCP for that trial that occurred within neighbouring territories.

5. The total area of a neighbour's territory over which the focal pair travels

Territory and MCP areas were calculated in Arc View (using the Xtools extension software package). Proportional data were calculated by creating coverages in ArcInfo, which consisted of the territory coverage for that year overlapped with the MCP for each telemetry trial. This effectively divided each MCP into sub-polygons corresponding to the proportion of the entire MCP spent in each territory or undefended area.

3.3.6. Statistical Analyses

We used a Fisher Exact test to compare the number of focal birds known to intrude at least once during the set of x trials in disturbed and undisturbed habitat. Mann-Whitney U-tests were used to compare subjects in disturbed and undisturbed habitats with respect to the proportion of trials featuring intrusions and the proportion of area of the entire MCP that was in designated intrusion areas. Mann-Whitney U-tests were also used to determine if average MCP area differed between habitats. A Fisher Exact test was used to determine if dominance rank influences which birds engage in intrusions (or are intruded upon) with respect to the survey map data. All statistical analyses were performed using SYSTAT 9.0 (SPSS Inc. Chicago, IL).

3.4. Results

3.4.1. Intrusion Events during Daily Surveys

During the two breeding seasons, I observed 26 intrusion events during daily territorial surveys. Of these, 25 involved pairs occupying disturbed habitat, while only one involved pairs occupying undisturbed habitat, showing a significant difference in intrusion rates based on habitat (Binomial test: $P < 0.001$). Of the intruding birds that occupied disturbed habitats, the majority of birds intruded into other territories within the disturbed habitat, although there were three cases of birds possessing territories in disturbed habitat intruding on birds breeding in undisturbed habitat. There was no relationship between intruder and neighbour rank and intrusion rates in disturbed habitat (Fisher Exact test, $P = 1.00$) for the 20 intrusion events involving birds whose rank was known, in that both intruders and those intruded upon were equally likely to be of either high or low rank. Intrusion events were detected by the resident pair in 13 of 26 cases. Of these, residents responded aggressively in only five instances, or 38% of the time.

3.4.2. Phenomenon of Early Flocking

Another phenomenon relating to territoriality observed in the course of daily nest surveys was a pattern of early flock formation. Typically, chickadees begin to aggregate in loose flocks in the late summer, as fledglings leave their parents and disperse to new locations (Smith 1991). During the 2000 breeding period in my study area, flocks were formed by pairs and single birds that experienced reproductive failure in the disturbed site as early as mid-May, and three such flocks

were present by early June, ranging in size from four to seven individuals. No such behaviour was observed in the undisturbed site. Daily nest survey map data documented 14 separate events interpreted as evidence of early flocking behaviour (defined as single birds or pairs aggregating with others during the course of the breeding season, not behaving aggressively, and no longer engaging in breeding/nesting behaviour). The first such event took place on May 18 (Flock 1 identified), the second flock was first observed on May 27, and subsequently was observed two more times. The third flock was observed on June 11 and again on June 18. Flock membership in each flock was consistent between sightings, suggesting that these flocks were stable. In total, 18 of 37 (49%) birds breeding in disturbed sites participated in early flocking behaviour. No early flocking behaviour was observed during the 2001 breeding season. Six of the ten pairs in 2000 that abandoned breeding attempts and joined early flocks had previously engaged in intrusion behaviour.

3.4.3. Telemetry Study

Birds in disturbed habitat (5 of 5 radio-tracked female chickadees) were more likely to intrude into neighbouring territories during at least one set of trials than birds in undisturbed habitat (1 of 5 pairs-Fisher Exact test, $P = 0.048$) (see, for comparison, Figs. 3.2 and 3.3). Females were accompanied by their mates in 100 % of intrusion events recorded in disturbed habitat, and males maintained an average distance of 6.39 m from their mate during these times. Intruders encountered resident pairs in 65% of intrusions. However, in only 45% of those cases where

intruders were detected did the residents respond with aggression, despite approaching within 25 m of intruders in all cases. No EPC's were ever observed during intrusions, nor were intruding females ever observed entering the nest cavities of resident pairs.

Proportion of trials in which intrusions occurred also differed by habitat type. Subjects breeding in disturbed habitat intruded into neighbouring territories during more individual trials than those in undisturbed habitat (Mann-Whitney U-test, $U = 24$, $P = 0.013$, $n = 5$ in each habitat). The average size of the intrusion area was also larger in disturbed than undisturbed habitats (Mann-Whitney U-test, $U = 22$, $P = 0.034$, $n = 5$ in each habitat). A higher proportion of the total average area of the MCP for each trial consisted of intrusion areas in disturbed habitats (Mann-Whitney U-test, $U = 22$, $P = 0.034$, $n = 5$ in each habitat). I also compared average areas of minimum convex polygons in disturbed versus undisturbed habitats, and found that the average area of the MCP's is larger for birds in undisturbed than disturbed habitats (Mann-Whitney U-test, $U = 3$, $P = 0.047$, $n = 5$ in each habitat).

The preceding analyses included birds for which no intrusions were observed during any trial. Thus it is arguable that comparisons of proportional area spent within neighbouring territories might merely reflect the fact that subjects in undisturbed habitat intrude far less frequently than those in undisturbed habitat, but that intrusions in undisturbed habitat are of the same magnitude as those in disturbed habitat when they do occur. A comparison between the subjects actually known to have intruded into neighbouring territories at least once is desirable, to see if the

magnitude of the intrusion differs between habitats. As only one of five birds was observed to engage in territorial intrusions in the undisturbed habitat, it is only possible to compare actual values obtained for this subject to the average values of the four subjects in the disturbed habitat, but a comparison of these values suggests that the magnitude of intrusion behaviour is much greater in disturbed habitat (Table 3.1).

3.5. Discussion

Birds in disturbed habitat intruded more often than those in undisturbed habitat, and their intrusions were more extensive. Intrusion events observed during daily surveys, like those observed in the course of the telemetry study, were not covert. Rather, intruding birds traveled as a pair and engaged in typical foraging behaviour, with concomitant vocal behaviour (i.e. intra-pair contact calls). In addition, the majority of intrusions were not accompanied by aggressive responses from territory holders, despite the fact that in many instances intruders were foraging in close proximity to resident pairs.

Theoretical models have predicted that when defence time reaches a threshold beyond which the bird cannot support its maintenance and defence requirements, territorial defence will be abandoned (Schoener 1983, Stamps and Buechner 1985, Perret and Blondel 1993). In my study site, habitat quality in areas where intrusions are common may be so poor that these areas are not economical to defend. That is, the energetic cost of territory defence is in excess of the anticipated benefits of

exclusive control of these areas. Additionally, birds may be forced to intrude into neighbouring territories, as they are unable to obtain sufficient resources within their own territory.

Birds breeding in disturbed habitat in my study site experience lower reproductive success than those breeding in undisturbed habitat (chapter 2). Low site-specific reproductive success is frequently taken to be an indicator of low habitat quality (Siikamäki 1995, Muller et al. 1997), encompassing such possible environmental factors as low food availability, high predation rates, and low nest-site availability. Thus, territorial breakdown may be occurring as a result of energetic stresses caused by pairs engaging in breeding attempts in sub-optimal habitat conditions.

Birds breeding in disturbed habitat do not fully abandon territorial defence. Territorial boundaries could be defined in the traditional ways and aggressive interactions between neighbouring pairs were observed on a regular basis. However, intrusion events were often not accompanied by aggression. Intruders appeared to be engaging in typical foraging behaviour. Resident males might be responding to sub-optimal habitat conditions by 'scaling back' territorial behaviour. For instance, birds may restrict aggressive responses to intruders that approach the mate or nest site directly. Dhondt and Schillemans (1983) observed that great tits tolerated intruders establishing nests within their territories as long as the intruders themselves did not engage in territorial behaviour.

Early flocking behaviour observed in 2000 is also best explained by resource limitation. Flocking in general is thought to occur under circumstances in which resources are low and patchily distributed (Crook 1964). The energetic savings in terms of decreased search time for resource patches is thought to offset the cost of having to share that resource with flock members. Early flocks consisted almost exclusively of pairs and single individuals that had been unable to establish an active nest during the breeding season. That flocking was observed to occur among failed breeders only in the disturbed site suggests that habitat quality may be playing an important role in generating this anomalous behavioural pattern.

The resource limitation hypothesis may also explain why neighbouring pairs are willing to engage in intrusion behaviour. Breeding pairs in disturbed habitat may be unable to procure enough resources in their own territory, and are consequently forced to risk the energetic costs of increased foraging distances and potential aggressive encounters so that a threshold rate of daily resource acquisition can be maintained. Alternatively, females may be assessing neighbouring males for future extra-pair copulation (EPC) solicitations (Smith 1988, Otter et al. 1998). Their mates would consequently be performing a mate-guarding function. However, one would anticipate that the motivation for such female assessment behaviour would be equivalent in both habitats, as extra-pair mate quality assessment is thought to rely on relative performance measures (Otter et al. 1999b). Consequently, I would not have observed such a large bias towards intrusion behaviour in disturbed habitats. Also, female-initiated EPC intrusions in this and other passerine species are

characterized by rapid and cryptic behaviour (Smith 1988, 1991, Smiseth and Amundsen 1995, Neudorf et al. 1997). In contrast, intrusion events observed during the course of this study did not differ qualitatively from typical territorial foraging behaviour, nor were any attempted copulations witnessed.

If birds in disturbed habitat are more energetically stressed than those in undisturbed habitat, females may 'anticipate' nest failure, and engage in intrusions to look for partners for future divorce and re-pairing (Wagner 1992). To test this, one would have to determine if patterns of intrusion behaviour match patterns of future pairings. I have insufficient data to investigate this hypothesis.

Females just prior to or during the egg-laying phase, anticipating nest failure, may be engaging in nest-searching activities to 'dump' their eggs in the active nests of neighbouring pairs as part of a mixed reproductive strategy. Egg dumping is not a common practice in this species although there is some evidence that it may be a reproductive decision made by females in dire circumstances (Otter et al. 1998). The majority of intrusion events did occur in disturbed habitats during or prior to egg laying, indicating that these forays could be related to egg-dumping behaviour, but more than half of the intruders had active nests at the time of intrusion. Also, egg dumping in chickadees typically involves low-ranking birds dumping their eggs into the nests of high-rankers (Otter et al. 1998), but intruders in my study showed no low-rank bias. These considerations suggest that the resource limitation hypothesis provides a better explanatory fit. The two hypotheses are also not mutually exclusive, as resource limitation is likely to be the root cause of

hypothesized increased rates of egg dumping. I have no paternity data available to test these ideas, but studies are currently underway to provide this information in the future.

The telemetry study focused on the movements of low-ranking females. However, the data set of informal observations revealed that many birds that were classified as high-ranking during winter dominance assessments also engaged in intrusion behaviour. It is likely that the disturbed habitat is patchy in terms of optimal breeding habitat, and high-ranking birds will presumably have a competitive advantage when it comes to territory acquisition (high-ranking birds, by definition, are ones which tend to win in aggressive encounters). This presents a challenge to the resource limitation hypothesis in that high-ranking birds would be expected to establish and actively defend a territory that contained suitable food and/or other resources to meet their energetic needs, and thus would not need to engage in intrusion behaviour. However, it may be that resource-rich 'optimal' patches are distributed so sparsely across the landscape that active defence of an area encompassing enough patches to support the resource requirements of a breeding pair would be energetically inefficient (Hinsley 2000). Thus, high-ranking pairs might actively defend a smaller area encompassing only a few high-quality patches insufficient for the energetic their total energetic demands, and compensate by occasionally foraging beyond their territory boundaries in patches within the boundaries of neighbouring pairs.

Table 3.1. A comparison of average intrusion behavioural data collected during formal telemetry trials, Spring 2000 and 2001, for pairs that intruded at least once during a set of trials. Only one experimental subject in undisturbed habitat actually engaged in intrusion behaviour, so $n = 5$ in disturbed vs. $n = 1$ in undisturbed. Means are given \pm SE.

	Undisturbed	Disturbed
Proportion of trials in which intrusion occurs	0.33	0.53 ± 0.11
Proportion of total average area of each minimum convex polygon spent in neighbouring territories	0.03	0.20 ± 0.07
Average area (m ²) of intrusion into neighbouring territories	1571.0	3085.6 ± 655.8
Average area (m ²) of the minimum convex polygon derived from each radio-telemetry trial.	14753.4	8058.2 ± 1263.8

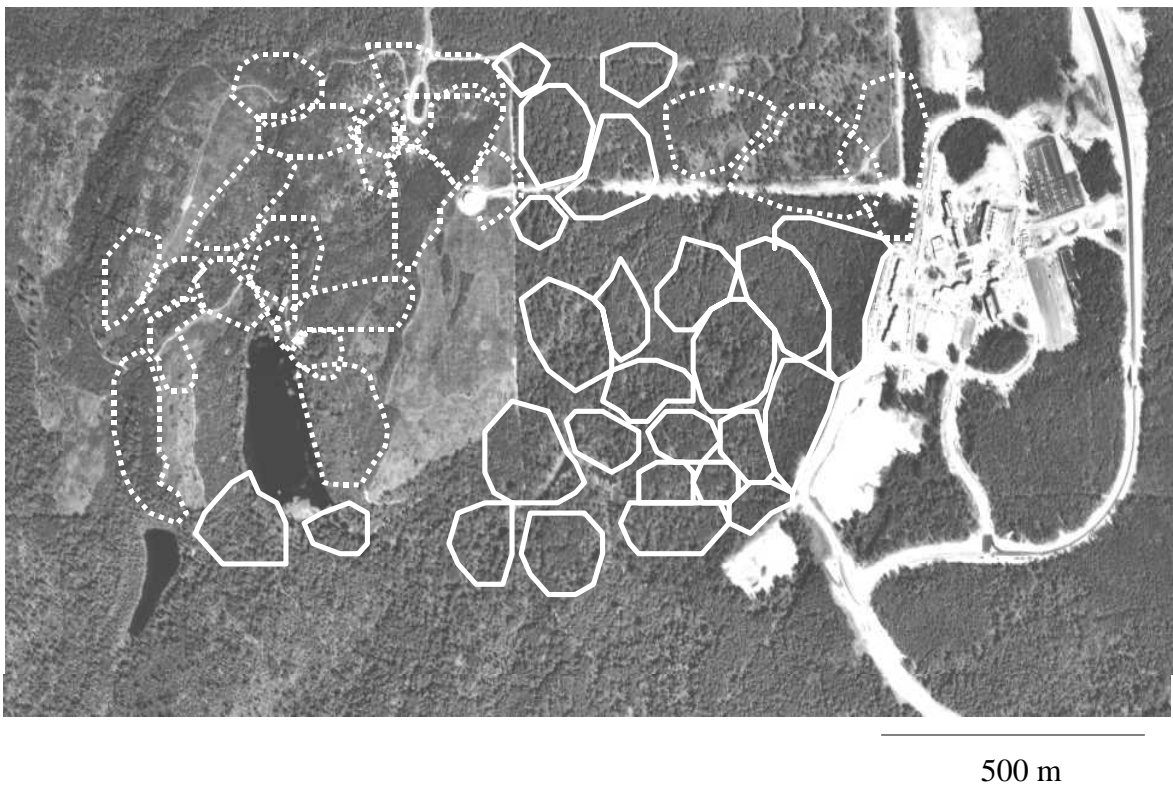


Fig. 3.1. Map of study site showing breeding territories for birds breeding in undisturbed (solid lines) and disturbed (broken lines) habitat, Spring 2000.

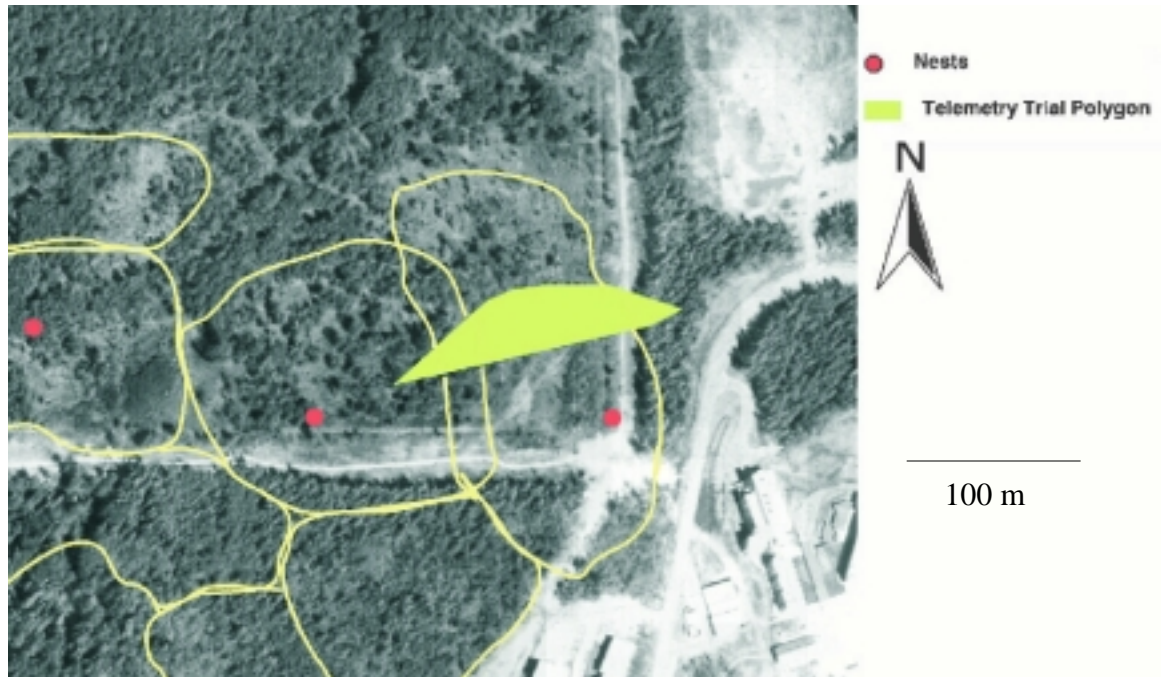


Fig. 3.2. A typical intrusion telemetry trial in disturbed habitat, Spring 2000. Solid lines indicate territory boundaries. The central territory in this figure belongs to the focal bird. The movement polygon is almost entirely within the territory defended by the neighbouring pair to the east.

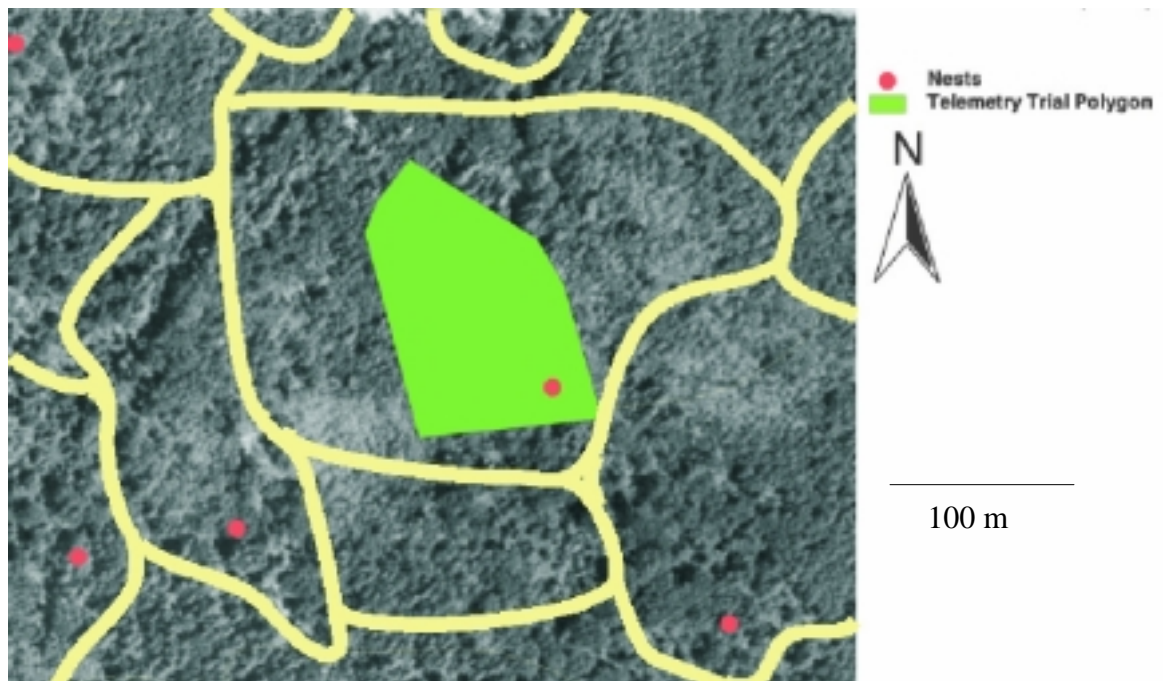


Fig. 3.3. A typical trial in undisturbed habitat, Spring 2001. Solid lines indicate territory boundaries. Note that the movement polygon is entirely within the territorial boundaries of the focal bird.

4. Lack of habitat preference may prove maladaptive in disturbed habitats.

4.1. Abstract

As reproductive success is known to vary among habitat types, it may be adaptive for birds to develop preferences for those habitat types that optimize reproductive success. In addition, birds constrained to breed in sub-optimal habitats may adjust territory size to offset lower resource levels. Using compositional analyses, I assessed the extent to which birds demonstrate preference or avoidance of a range of distinct habitat types found in my study site. I evaluated the adaptiveness of these preferences by determining if birds preferred or avoided those habitats associated with increased reproductive success or failure, respectively. Birds breeding in disturbed habitats had larger territories than those in undisturbed habitats, suggesting that resource levels were limiting in these areas. There was no evidence that chickadees preferred or avoided specific habitat types in my study area. However, birds breeding in territories containing high proportions of disturbed habitat experienced lower reproductive success. This result is discussed in terms of a maladaptive response to habitat disturbance.

4.2. Introduction

The term ‘habitat quality’ is often used to describe the availability of food resources (Siikamäki 1995), suitable nest sites (Alatalo et al 1986), and protection from predators (Robinson et al. 1995). Variation in habitat quality is an important

factor affecting reproductive success in birds. Burke and Nol (1998) found that pairing success in ovenbirds (*Seiurus aurocapillus*) was higher for birds breeding in food-rich territories in large fragments. Lower reproductive output in a population of blue tits (*Parus caeruleus*) breeding in an insular evergreen habitat compared to a mainland mixed habitat is attributed to poorer food conditions (Blondel et al. 1991). As variation in habitat quality has the potential to impact individual fitness, evolution of behavioural responses to habitat variability is therefore adaptive. Thus, in addition to merely correlating reproductive success with particular habitat characteristics, it is valuable to determine whether organisms recognize and respond to variation in habitat quality in terms of active preference or avoidance of certain habitat types.

Birds may have evolved preferences for habitat types that allow them to maximize their access to critical breeding season resources. If so, birds should target particular habitat types available to them, and include them in their territories at levels disproportionate to their availability (Lack 1933, Bergin 1992, Esely and Bollinger 2001). A number of different methodologies have been suggested to assess habitat preferences, including Discriminant Function Analysis (Clark and Shutler 1999), Chi-square goodness-of-fit analysis (Neu et al. 1974), rank-based methods (Quade 1979, Johnson 1980), resource selection functions (Meyer et al. 1998, Boyce and McDonald 1999), and compositional analysis (Aitchison 1986, Aebischer et al. 1993). Resource selection functions were not used because annual shifting of territory locations made it difficult to determine which areas were

actually unutilized. Also, logistical constraints prevented the intensive sampling effort that would have been required to implement this approach. Compositional analysis has been used widely in recent years (e.g. Stoate 1998, Genovesi et al. 1999), as it is closely related to Johnson's (1980) rank-based method, but involves actual log-transformed ratios of use and availability proportions, thereby making use of all available information (Aebischer et al. 1993). In addition, birds breeding in poor quality habitat may have the ability to partially compensate by increasing the size of their territories, thus increasing their access to resources, albeit at an energetic cost.

A failure to respond to habitat variability may have additional negative impacts at the population level, especially if poor quality habitat is abundant in the landscape. In a metapopulation model, Pulliam and Danielson (1991) show that, when habitat selectivity is low, the presence of birds breeding in poor quality sink habitats will result in a decline in the overall metapopulation.

In chapter 2, I showed that chickadees breeding in early seral habitat recovering from anthropogenic habitat disturbance experience lower levels of fledging success than those in undisturbed habitat. This habitat-dependent variability in reproductive success constitutes evidence that conditions exist for an evolutionary response in terms of territory-size adjustments and development of habitat preferences.

By assessing territory size, reproductive success in relation to habitat type, and habitat composition within territories in relation to the surrounding area, I will address three main questions: 1) do chickadees breeding in disturbed habitats have

larger territories than those breeding in undisturbed habitats, 2) does chickadee reproductive success vary with relative proportion of habitat types and 3) do chickadees have consistent preferences for habitat types associated with increased reproductive success?

4.3. Methodology

4.3.1. Capture, Flock Composition & Rank Determination, and Territorial Mapping

Birds were captured at winter feeders and individually colour banded as described in Chapter 2. During the winter, I determined the flock composition of birds and their linear hierarchies by watching interactions at feeders, as described in Chapter 2. By monitoring the song post locations and areas of exclusive use of pairs following spring flock breakup, I mapped the territorial boundaries of individual pairs during the breeding season (see Chapter 3).

4.3.2. Determination of Habitat Zone Boundaries

In order to assess habitat selection at a landscape level, the entire area of the study site was classified into ten different habitat types, or 'zones'. Habitat zones were classified on the basis of canopy tree composition and structure (Table 4.1). During the summer of 2000, the entire study area was mapped in the field on the basis of these zones, using existing grid markers and geographical landmarks as reference points. These maps were further refined using GIS (see below).

4.3.3. Vegetation Sampling Protocol

I assessed habitat zone characteristics using, at 3-5 random locations within each zone, 0.04 ha (11.3 m radius) circular plots. The decision as to the number of plots within a given habitat was based on the proportion of each habitat in relation to the overall study area. Plot location was determined by using a random number table to determine distance (in metres) and direction from the centre of a representative habitat zone polygon. Sample plots were taken from a number habitat zone polygons, except where only one such polygon existed in the study site. Vegetation sampling took place within two weeks after fledging had occurred. As the vegetation is fully developed well before the time of fledging, my vegetation plots should be an accurate reflection of habitat conditions in territories during the nestling phase. Within the plot, I recorded species and dbh (in six size classes) of each tree. The height, species, and dbh of a representative canopy tree were also recorded. I measured canopy cover using a convex densiometer at the edge of the plot in the four cardinal directions. For all snags within the plot, species, dbh size class, height, and decay class were recorded. I assessed the understory component by estimating the overall percent cover (in seven cover classes) of all shrub species (including young trees) at four vertical height classes (0-1m, 1-2 m, 2-3 m, 3-4 m).

4.3.4. Inter-nest Distances

I recorded GPS locations for all known nests in both years of the study using a Trimble Geoexplorer III (Trimble Navigation, Sunnyvale, CA) handheld GPS unit. All nest locations consisted of a minimum of 10 consecutive points. Consequently,

accuracy was estimated at $\pm 2-3$ m. Nest location GPS data were downloaded into Pathfinder Office (Trimble Navigation, Sunnyvale, CA) and subsequently converted into ArcView files for spatial analysis.

4.3.5. Territory Size and Inter-nest Distance Determination

I calculated the area of each breeding territory in both years in ArcView using the territory polygon maps. Inter-nest distances in both years were also calculated in ArcView using the nest location data maps. For each nest, the average distance to the nearest four neighbours was calculated, to mitigate biases associated with spatial clumping in the data.

4.3.6. Habitat Use and Availability Determination

I used the habitat zone classification map as the template for creation of a habitat zone theme in ArcView, consisting of a set of contiguous habitat polygons covering the entire study area. This theme was refined further with reference to habitat zone boundaries visible from an orthophoto of the study area, and converted to ArcInfo coverages for further analysis.

Territorial polygons from 2000 and 2001 were superimposed upon this habitat zone map, which allowed me to calculate the total area of each habitat type within each breeding territory. From these data, I calculated the proportional representation of habitat use with respect to each habitat type for each territory.

To determine whether particular habitats were secured disproportionately to their availability, I calculated habitat availability in two ways. First, habitat availability was determined at the level of the treatment (disturbed vs. undisturbed), by

calculating the proportional representation of each habitat type within each treatment area. For these purposes, both undisturbed areas were amalgamated, as they were essentially contiguous. Thus, it seemed plausible to suggest that all habitat types within these two areas were available to the resident birds. Conversely, I determined habitat availabilities for the two disturbed sites separately, as these sites were not contiguous and available habitat types differed markedly between them.

In the second analysis, I calculated habitat availability based on a measure of flock range. Unfortunately, total flock ranges in my study population were only approximately known. Therefore I opted, for the purposes of this analysis, to conservatively define flock range as the sum of breeding territory area for all pairs within a flock. As members of flocks generally subdivide the flock range into the individual territories of the breeding pairs (Smith 1991), my use of combined territories is likely a close reflection of availability of habitats to flock members.

4.3.7. Analyses

Cluster Analysis

The 10-zone classification scheme was somewhat subjective, in that it was based primarily on dominant canopy species and overlooked structural similarities between zones to which breeding birds may be responding. Reducing the number of habitat zones would have the additional benefit of simplifying flock-level compositional analyses and territory-level success analyses. To accomplish these aims, I performed hierarchical cluster analysis on the original 10-zone classification. This procedure treats each habitat zone as a case. Associated with each habitat zone

are average values for eight vegetation variables measuring canopy-level and understory species composition and habitat structure. Cluster analysis 'linkage algorithms' group cases on the basis of relative distances in multivariate Euclidean space. Thus, members of a particular cluster will possess structural and compositional similarities with each other, while being distinct from members of other clusters.

Compositional Analysis

Compositional analysis is a methodology commonly employed to determine whether animals show preferences for particular habitat types, by comparing proportional data of habitat use and availability. As proportions are non-independent (i.e. proportional values sum to one over all habitat types), an analysis using proportional data must transform the data to remove this dependence. In compositional analysis, this is accomplished by means of log-ratio transformations (Aitchison 1986, Aebischer et al. 1993). The analysis produces, for each animal, a matrix with **D** rows and columns (where **D** equals the number of habitat types), in which each matrix element consists of a log-ratio of availability subtracted from a log-ratio of use. Columns in the matrix are indexed by the habitat type used as denominator in the log-ratio, and the habitat type used in the numerator indexes rows. A positive value for any matrix element indicates preference for the habitat type in the numerator over the reference (denominator) habitat type. Matrix elements are then averaged across all individuals in the sample population. From this, a ranking of habitat zones from 'most preferred' to 'least preferred' can be

calculated. Individual elements in the average matrix and their standard errors can be used to pinpoint where nonrandom use occurs, indicating which ranks give a reliable order and which are not statistically distinguishable in terms of preference.

A full analysis at the level of the entire study site, comparing all ten habitat zones, was not possible because it did not seem biologically accurate to define certain zones as available to breeding birds in cases where the nearest patch of that habitat type might be more than a kilometre away. Two distinct sets of compositional analyses were performed. In the first set, habitat availability was defined at the level of the treatment for three treatment blocks (undisturbed, main disturbed, small disturbed). This analysis allowed a standard compositional analysis comparison of preferences for all birds within each treatment, for all habitat zones defined as available within that treatment. Nine of ten zones were represented in the undisturbed treatment, whereas seven of ten zones were represented in the main disturbed treatment. Only four zones were available in the smaller disturbed treatment.

In the second set, habitat availability was defined at the level of the flock and the analysis was restricted to the alpha pair in each flock only. This analysis was performed because habitat availability may be defined more realistically with reference to flock range. The rank restriction was implemented because high-ranking birds, by definition, out-compete lower ranking birds for valuable resources, and so may establish territories that encompass the majority of the preferred habitat within the flock range. Lower ranking birds, excluded from these areas, would be

forced to settle in less preferred habitats, biasing the results of the compositional analysis.

As the area in the average flock range was quite small, the flock-level analysis was particularly vulnerable to availability values of zero for habitat zones or clusters, which results in problematic undefined values for elements in the matrix. As no discernible core of habitat zones was used by all birds in the analysis, compositional analysis was performed for each bird separately using only habitats available within the flock range of that bird. No attempt was made to determine an average preference ranking. Instead, for all birds whose territories include each habitat type X, the proportion of pairs for which that habitat type was most and least preferred was recorded. If birds consistently prefer/avoid specific habitat types, those habitat types should consistently receive the highest/lowest ranking across the sample population.

Territory Area and Inter-nest Distances

To test for relationships between habitat and territory size, dominance rank was first included as a potential covariate in the statistical model. As rank was not a significant factor ($F_{1,56} = 0.89$, $P = 0.35$), it was removed from subsequent analysis, as an incomplete knowledge of rank for all territorial birds in the dataset would result in a concomitant loss of power. Consequently, I ran a two-factor ANOVA to investigate the possibility that birds breeding in disturbed vs. undisturbed habitats may differ with respect to territory area. The factors included in the model were Year and Habitat. Histograms revealed a lack of normality in both habitat types with

respect to the dependent variable, so log-transformations were performed. Rank could not be included in the ANOVA testing for a relationship between habitat and inter-nest distance, as breeding pair identities were not associated with nest locations in this dataset.

Territory Composition and Nest Success

I investigated the relationship between territory composition (in terms of the proportional representation of habitat types within a breeding territory) and nest success using Mann-Whitney U-tests, comparing the average proportions of each habitat type for successful vs. unsuccessful territorial pairs. Proportions were used instead of raw area scores to control for the potentially confounding effect of territory area on the response variable.

4.4. Results

4.4.1. Territory Size and Inter-nest Distances

Territories were larger in disturbed than undisturbed habitats ($F_{1,71} = 8.35$, $P = 0.005$; Fig. 4.1a), and larger in the second year of the study ($F_{1,71} = 22.908$, $P < 0.001$; Fig. 4.1b). There was no significant interaction effect ($F_{1,71} = 0.45$, $P = 0.51$). Inter-nest distances were higher in disturbed than undisturbed habitats ($F_{1,58} = 12.34$, $P = 0.005$; Fig. 4.2a), and in the second year of the study ($F_{1,58} = 8.68$, $P = 0.001$; Fig. 4.2b). There was no significant interaction effect ($F_{1,58} = 0.076$, $P = 0.78$).

4.4.2. Cluster Analysis

Hierarchical cluster analysis using the single linkage method produced a six-cluster grouping based on similarities in vegetation characteristics (Fig. 4.3). DECMATURE contains Aspen, Birch, and Mix zones. WETMATURE contains Riparian and Marsh zones. VRPINE contains Variable Retention and Lodgepole Plantation zones. CONIFER contains only the conifer zone, REMNANT contains only the Mature Remnant zone, and EARLYSERAL contains only the Willow-Alder zone. Cluster means \pm SE of all eight habitat variables used in the analysis are reported in Table 4.2.

4.4.3. Compositional Analysis- Treatment Level Analyses

The compositional analysis ranked undisturbed habitats in the following order: Mix>Aspen>Lodgepole>Conifer>Variable Retention>Willow-Alder>Marsh>Riparian>Birch. Of these, Mix is preferred significantly over Willow-Alder, Riparian, and Birch habitats. Aspen, Lodgepole, Conifer, Variable Retention, Willow-Alder, and Marsh are all preferred significantly over Riparian and Birch habitats, while being interchangeable in rank with each other. Riparian and Birch habitats are interchangeable in rank (Table 4.3).

The compositional analysis ranking of disturbed (D1) habitats was in the following order: Willow-Alder>Lodgepole>Marsh>Remnant>Riparian>Conifer>

Mix. Of these, Willow-Alder is preferred significantly to all other habitats. Lodgepole and Marsh are preferred significantly over Conifer and Mix, but are interchangeable with each other as well as with Remnant and Riparian. Remnant and

Riparian habitats are preferred over the Mix zone only (Table 4.4). D2 site compositional analysis produced the following ranking: Variable Retention>Conifer>Marsh>Birch. Variable Retention is preferred over Marsh only (but not Birch, despite the ranking). All other rankings are interchangeable (Table 4.5).

4.4.4. Compositional Analysis- Flock Level Analyses

Compositional Analysis with reference to the six habitat clusters was performed on territories of alpha pairs for 25 flocks. Although an average ranking matrix could not be performed in this analysis, the proportion of times each habitat cluster, when available, was the most preferred and least preferred habitat was calculated. No strong patterns of preference or avoidance were detected for any habitat using this method, although there is some weak evidence for preference of WETMATURE and DECMATURE habitats and avoidance of VRPINE habitats. Each habitat assessed was ranked both as 'most preferred' and 'least preferred' by different pairs. No one habitat ranked consistently high or low (i.e. always in the top two most preferred or least preferred habitats). Rather, habitats were scattered from highest to lowest rank among birds (Table 4.6).

4.4.5. Territory Composition and Nest Success

Birds experiencing nest failure had higher proportions of VRPINE (Mann-Whitney U-test, $U = 547$, $P = 0.048$, $n = 37$ successful and 23 failed; Fig. 4.4a), while those experiencing nest success showed a trend towards higher proportions of DECMATURE habitat in their territories (Mann-Whitney U-test, $U = 316$, $P =$

0.085, $n = 37$ successful and 23 failed; Fig. 4.4b). Despite this, the amount of VRPINE incorporated into territories in the disturbed site did not differ between high and low ranking pairs (Mann-Whitney U-test, $U = 72.5$, $P = 0.554$, $n = 14$ high ranking and 12 low ranking).

4.5. Discussion

4.5.1. Territory Size and Inter-nest Distances

Territories were larger and inter-nest distances were greater in disturbed than undisturbed habitats. Such larger territory sizes have been linked to poor habitat quality and lower reproductive success in other studies (Krebs 1971, Conner et al. 1986, Smith and Shugart 1987, Hunt 1996, Roberts and Norment 1998, Jones et al. 2001). This may arise because birds should defend a territory that provides sufficient food and nesting resources for successful reproduction, while minimizing energetic expenditure (Carpenter et al. 1983, Hixon et al. 1983). Increased territory size will amplify energetic costs associated with defence, as well as foraging and delivery of food to the nestlings, and thus larger territory size in disturbed habitats suggests that birds are experiencing lower resource levels in comparison to those in undisturbed habitats.

4.5.2. Compositional Analysis

Compositional analysis at the treatment level produced few significant preferences, counter-intuitive results, and a lack of consistency in rankings between habitats. This suggests that chickadees do not exhibit strong habitat preferences in

my study area. Alternately, these site-level analyses may be uninformative due to inherent flaws in large-scale analyses when working with chickadees. Two assumptions are implicit in these kinds of analyses: 1) the definition of habitat availability at the level of the treatment accurately reflects habitat type options and 2) intraspecific competitive interactions do not influence settlement patterns. Violation of either of these assumptions will impact results of the analysis in unpredictable ways.

The life history patterns of chickadees could lead to violations of both assumptions. First, uncommon habitat types were present in certain territories at proportions much higher than their availability in the treatment overall, due to their clumped spatial distribution in my study area. Unless these birds sampled the entire treatment block, habitat rankings for such birds would tend to result in an artificial ‘preference’ for these rare habitats, whereas birds settling in territories distant from such habitat types would appear to be ‘avoiding’ them. Chickadees are known to establish breeding territories within the home range of the winter flock with which they were associated (Smith 1991, personal observations). As the flock ranges are much smaller than treatment blocks, definition of availability at the treatment level will be inaccurate when habitat types are not evenly distributed across the landscape. Second, as black-capped chickadees have a well-defined hierarchical social structure (Smith 1991), intraspecific interactions may influence settlement patterns. Low-ranking birds forced into sub-optimal habitat types in greater proportion to

availability of those types will appear to ‘prefer’ them and, conversely, to ‘avoid’ optimal habitats from which they are excluded.

The flock level compositional analysis is a far better test of habitat selection in this species, as it involves a more biologically accurate determination of habitat availability and considers only high-ranking birds, thus eliminating potential biases associated with intraspecific competition. Unfortunately, average matrices could no longer be calculated to look for significant preferences across all birds. Therefore, I looked for strong patterns of preference or avoidance of each habitat type, for all birds containing that habitat type. No strong patterns emerged in this analysis, so I still conclude that there is little evidence for territory-level habitat selection in my population of chickadees.

Alternatively, differential response to habitat preferences in disturbed and undisturbed habitats may compromise my ability to detect strong habitat preferences. This may occur if organisms breeding in each type: 1) have evolved adaptations to the local environment, or 2) as a result of behavioural plasticity in habitat selection. An evolutionary response to local habitat conditions can only take place under conditions of restricted gene flow (Blondel and Dias 1994). Given the dispersal mechanisms of chickadees (Smith 1991) and the local spatial distribution of disturbed and undisturbed sites, gene flow between habitat types is likely to be unrestricted. Thus, there is no strong evidence for a genetic basis for differing habitat preferences between birds breeding in different disturbed and undisturbed habitats.

Behavioural plasticity in habitat preferences has been inferred in other studies in the context of response to natural disturbances. Jones et al. (2001) showed that cerulean warblers (*Dendroica cerulea*) demonstrated a significant shift in nest-site location patterns following a large-scale natural habitat disturbance. Pellech and Hannon (1995) hypothesized that black-capped chickadees may shift foraging strategies to spend more time in the understory following severe tent caterpillar (*Malacosoma disstria*) outbreaks, as canopy-level food abundance decreased drastically. Myserud and Ims (1998) formalized this phenomenon in a model of functional response in habitat use in which habitat preference is conditional on habitat availability such that birds might 'switch' to preferring certain habitats, if their availability is very high. However, disturbed habitats, which are characterized by low canopy heights, contain a much smaller foraging volume per hectare than a mature habitat. It is unlikely that birds in disturbed areas would prefer early seral habitats, as these habitats are likely to have lower food abundances.

Thus, factors other than habitat selection must determine territory composition in chickadees. Many studies have shown consistent habitat preferences for migratory songbirds (Oliarnyk 1996, Stoate et al. 1998, Esely and Bollinger 2001). However, site tenacity may affect territory composition in resident songbirds, which spend the entire year in the breeding habitat, as the benefits of familiarity with habitat features in the territory may outweigh benefits of obtaining higher-quality, but less familiar, areas (Krebs 1971, Stamps 1987). For example, familiarity with a territory may decrease search times in foraging bouts, as birds may already be familiar with areas

of high arthropod abundance. There is some evidence that pairs breeding in both years of my study tend to locate their territories in the same general area, despite a concomitant upward shift in dominance rank (K. Fort unpubl. data).

Alternatively, breeding chickadees may focus only on obtaining an appropriate nest site, and defend a territory that encompasses it regardless of habitat composition. Nest-site selection in birds has been demonstrated in other studies (Clark and Shutler 1999, Chase 2002). If appropriate nest sites are limiting, and undisturbed chickadee habitat is reasonably homogeneous with respect to food abundance and predation risk, such a strategy may be adaptive. Although I did not test for selection for certain nest site characteristics, I found that certain variables associated with the cavity tree and the habitat immediately surrounding the nest site predicted nest success (chapter 2).

4.5.3. Territory Composition and Nest Success

Unsuccessful birds had higher proportions of VRPINE habitat and tended to have lower proportions of DECMATURE habitat than successful birds. Chickadees breeding in disturbed habitat also had lower fledge success than those in undisturbed habitat (Chapter 2). Together, these results suggest that, although chickadees show no strong habitat preferences, birds breeding in territories containing high proportions of disturbed habitat experience lower reproductive success. In this context, their lack of strong preference or avoidance of particular habitat types may be seen as maladaptive. That is, birds are not responding to environmental features that lower their fitness. Such a scenario is unlikely to persist in evolutionary

timescales, as organisms will tend to develop more adaptive habitat preferences ('niche conservatism' *sensu* Holt 1995) or, alternatively, adapt to habitat conditions in their new environments (Holt 1996).

However, at ecological timescales, the phenomenon of maladaptive habitat selection may be quite common (Remes 2000, Delibes et al. 2001), especially when anthropogenic influences are considered. Blondel and Dias (1994) concluded that gene flow between populations of blue tits living in optimal (source) and sub-optimal (sink) habitats explained maladaptive timing of breeding in the sink habitat (see above). Recapture data in my study site show that juvenile birds fledged in one habitat have settled in the other (K. Fort unpubl. data). As dispersal mechanisms in chickadees also allow free gene flow between disturbed and undisturbed habitats, and there is no evidence of settling bias based on condition in natal habitat (H. van Oort unpubl. data), maladaptive habitat selection behaviour may persist indefinitely.

In general, resident species may be more at risk with respect to maladaptive behaviours, as evolutionary processes may have resulted in selection for site tenacity or nest-site preferences over specific territory-level habitat preferences in certain environments. If the environment is altered by anthropogenic disturbance, the advantages of territory familiarity may no longer outweigh the costs associated with breeding in sub-optimal habitat.

If a maladaptive lack of habitat preference exists, it has population-level implications. Delibes et al. (2001), using a modelling approach, showed that hypothetical metapopulations that fail to avoid 'sink' habitats due to a lack of habitat

preferences experience steadily declining growth rates. Such metapopulations will eventually decline to extinction, especially if sink habitats increase in abundance across a landscape. Similarly, Pulliam and Davidson (1991) argue that the extent to which the presence of habitat sinks is damaging to metapopulation size depends critically on the selectivity of the organism. As anthropogenic disturbance continues to alter natural landscapes, the inability of organisms to respond to these changes may have serious conservation implications.

Table 4.1. 10 zone habitat classification system, Spring 2000.

Zone	Dominant Canopy Species and Site Description
Aspen	Mature trembling aspen. Moderate understory.
Conifer	Mature hybrid spruce, subalpine fir, lodgepole pine. Sparse understory.
Mix	Mature deciduous/coniferous mix. Moderate understory.
Marsh	Mature black cottonwood, senescent willow. Dense understory.
Birch	Mature paper birch. Moderate understory.
Willow-Alder	Early seral mix of willow, green alder, young aspen and conifers. Low canopy height.
Lodgepole	Early seral monoculture, lodgepole pine plantation. Low canopy height.
Variable Retention	Mature birch and aspen, low stem density due to partial harvesting. Dense understory.
Mature Remnant	Mature douglas fir, lodgepole pine, birch. Sparse understory.
Riparian	Mature birch, senescent willow. Dense understory.

Table 4.2. Cluster membership and mean values \pm SE for 8 habitat variables for six clusters. Cluster sample sizes are reported in parentheses. Vegetation data collected Summer 2000.

Cluster	Zone(s)	Canopy Height (m)	Canopy Cover (%)	Shrub Cover <1m	Shrub Cover 2-3 m	Snag Density (stems/ha)	Canopy Tree Density (stems/ha)	Willow Density (stems/ha)	Large Conifer Density (stems/ha)
Conifer (3)	Conifer	27.3 \pm 1.2	63 \pm 1.0	4.3 \pm 0.2	1.0 \pm 0.8	41.7 \pm 16.7	1043.3 \pm 433.8	0.0 \pm 0.0	550.0 \pm 75.0
DecMature (9)	Aspen Birch Mixed	26.0 \pm 1.2	55.1 \pm 5.0	5.6 \pm 0.2	3.0 \pm 0.3	169.4 \pm 44.4	769.4 \pm 95.9	0.0 \pm 0.0	105.6 \pm 58.6
Remnant (3)	Mature Remnant	34.1 \pm 0.3	65.5 \pm 0.3	5.4 \pm 0.1	4.0 \pm 0.3	50 \pm 0.0	375.0 \pm 75.0	0.0 \pm 0.0	275.0 \pm 75.0
WetMature (6)	Marsh Riparian	25.5 \pm 3.7	48.4 \pm 5.4	5.0 \pm 0.4	3.4 \pm 0.2	130 \pm 47.0	230.0 \pm 41.4	20.0 \pm 9.4	45.0 \pm 33.9
VRPine (6)	Variable Retention Lodgepole	13.2 \pm 3.7	22.7 \pm 9.7	5.6 \pm 0.3	4.0 \pm 0.4	20.8 \pm 16.4	275.0 \pm 98.3	0.0 \pm 0.0	108.3 \pm 80.0
Early Seral (3)	Willow- Alder	12.6 \pm 1.4	37.8 \pm 13.3	5.6 \pm 0.3	4.3 \pm 0.5	66.7 \pm 44.1	75 \pm 38.2	75.0 \pm 62.9	58.3 \pm 36.3

Table 4.3. Compositional Analysis Ranking Matrix of t-values for 34 birds in undisturbed habitat, Spring 2000 and 2001. Statistically significant departures from random use are in bold, indicating that the habitat type indexed by the row is more preferred (positive value) or less preferred (negative value) than the habitat type indexed by the column. Ranks can be determined by the count of positive values in each row of the table. Rank indicates the degree of preference, from 'least preferred' to 'most preferred'.

Zone	Aspen	Conifer	Mix	Marsh	Birch	Willow/Alder	Lodgepole	Variable Retention	Riparian	Rank
Aspen	X	0.049	-0.799	0.855	2.513 *	0.630	0.017	0.467	3.878 **	7
Conifer	-0.049	X	-1.098	0.669	2.732 *	0.605	-0.032	0.472	4.042 **	5
Mix	0.799	1.098	X	1.856	4.146 **	2.134 *	1.323	1.944	6.020 **	8
Marsh	-0.855	-0.669	-1.856	X	2.163 *	-0.337	-0.914	-0.368	3.242 **	2
Birch	-2.513 *	-2.732 *	-4.146 **	-2.163	X	-4.321 **	-4.862 **	-5.305 **	-0.101	0
Willow/Alder	-0.630	-0.605	-2.134 *	0.337	4.322 **	X	-1.588	-0.219	303.579 **	3
Lodgepole	-0.017	0.032	-1.323	0.914	4.862 **	1.588	X	1.065	10.286 **	6
Variable Retention	-0.467	-0.472	-1.944	0.368	5.305 **	0.219	-1.065	X	8.804 **	4
Riparian	-3.878 **	-4.042 **	-6.020 **	-3.242	0.101	-303.579 **	-10.286 **	-8.804 **	X	1

*, $P < 0.05$; **, $P < 0.01$

Table 4.4. Compositional Analysis Ranking Matrix of t-values for 26 birds in disturbed (D1) habitat, Spring 2000 and 2001.

Zone	Conifer	Mix	Marsh	Willow- Alder	Lodgepole	Remnant	Riparian	Rank
Conifer	X	1.919	-2.744 *	-8.873 **	-3.403 **	-1.102	-0.957	1
Mix	-1.919	X	-7.812 **	-10.986 **	-5.284 **	-2.442 *	-2.323 *	0
Marsh	2.346 *	7.812 **	X	-6.113 **	-0.946	1.057	1.049	4
Willow-Alder	8.873 **	10.986 **	6.113 **	X	2.963 **	4.645 **	5.001 **	6
Lodgepole	3.403 **	5.284 **	0.767	-2.963 **	X	1.499	1.226	5
Remnant	1.102	2.705 *	-1.057	-4.645 **	-1.499	X	0.045	3
Riparian	0.613	2.323 *	-1.049	-5.001 **	-1.051	-0.045	X	2

*, P< 0.05; **, P< 0.01.

Table 4.5. Compositional Analysis Ranking Matrix of t-values for 5 birds in smaller disturbed (D2) habitat, Spring 2000 and 2001.

Zone	Conifer	Marsh	Birch	Variable Retention	Rank
Conifer	X	0.833	0.515	-1.250	2
Marsh	-1.377	X	0.151	-2.585	1
Birch	-0.515	-0.151	X	-1.774	0
Variable Retention	1.250	2.585	1.774	X	3

*, $P < 0.05$; **, $P < 0.01$.

Table 4.6. Compositional Analysis results, flock level analysis, for alpha pairs of 25 flocks, Spring 2000 and 2001.

Habitat Cluster	CONIFER	DECMATURE	REMNANT	WETMATURE	VRPINE	EARLY SERAL
Territories containing cluster	14	16	6	16	17	14
Most Preferred Cluster	3	6	1	8	3	4
Proportion	0.21	0.375	0.17	0.5	0.18	0.29
Least Preferred Cluster	3	5	3	5	7	2
Proportion	0.21	0.3125	0.5	0.3125	0.41	0.14

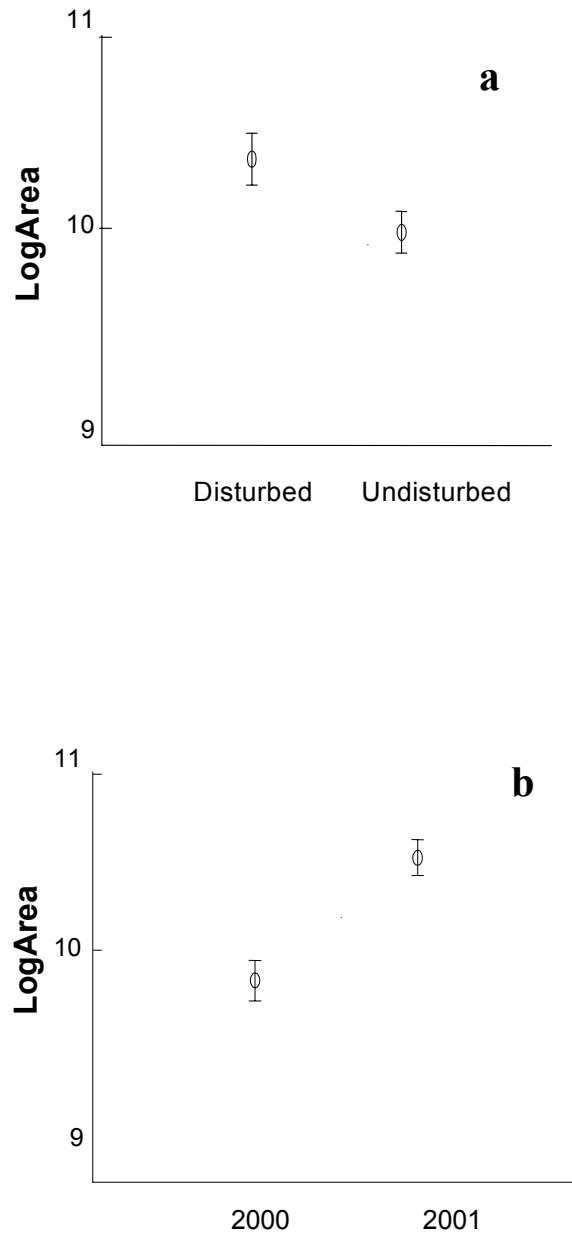


Fig. 4.1. a) Mean \pm SE LogArea of territories (n=61) in disturbed and undisturbed habitats. b) Mean \pm SE LogArea of territories (n=61) in 2000 and 2001.

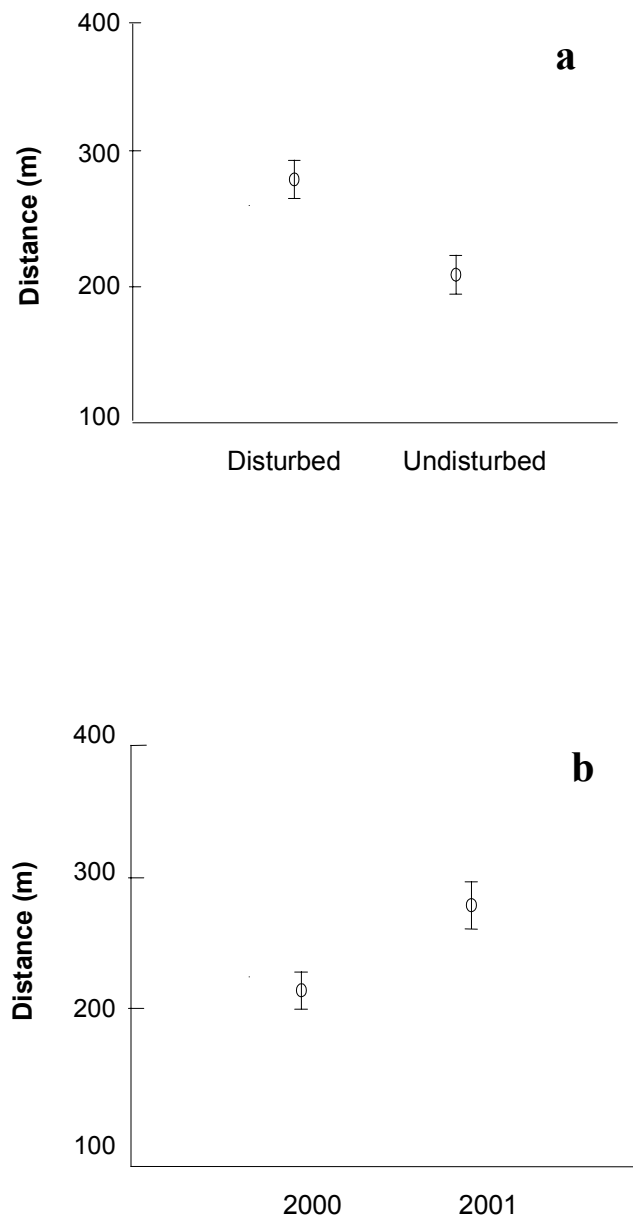


Fig. 4.2. a) Mean \pm SE Interest Distance of territories (n=61) in disturbed and undisturbed habitats. b) Mean \pm SE Interest Distance of territories (n=61) in 2000 and 2001.

Cluster Tree

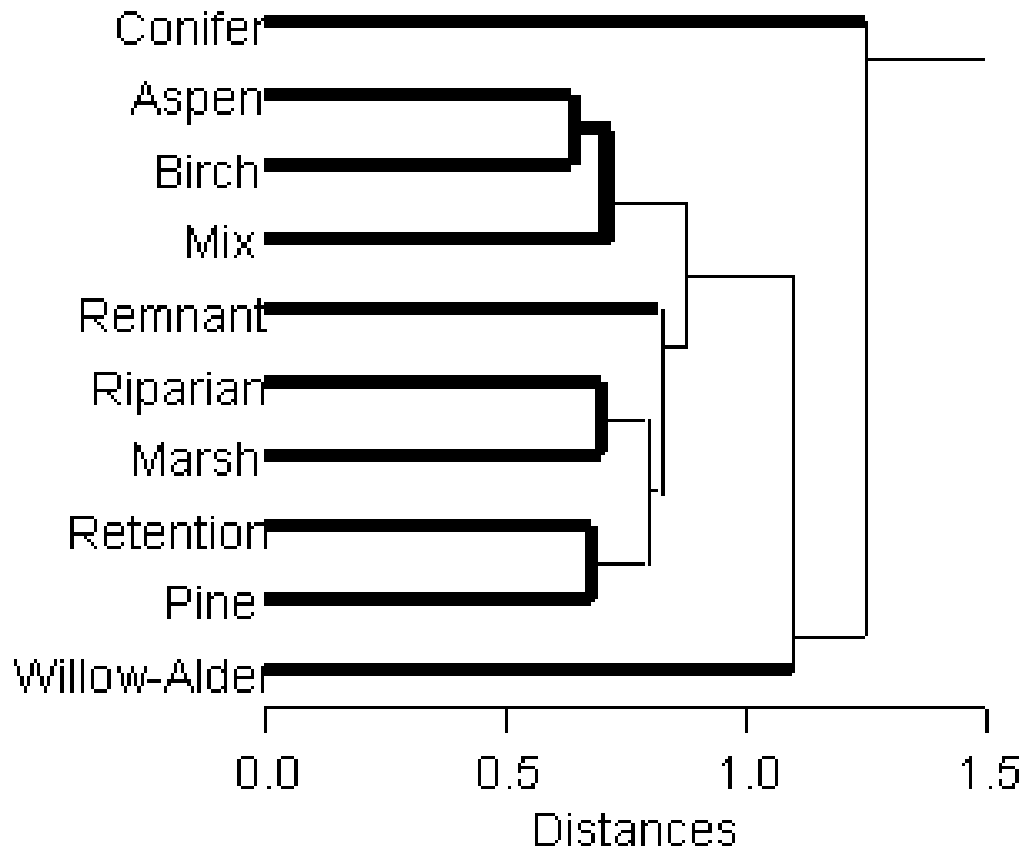


Fig. 4.3. 6-Cluster dendrogram produced by Hierarchical Cluster Analysis of 10 habitat zones. Vegetation data collected Spring 2000. Scale at bottom refers to Euclidean distance.

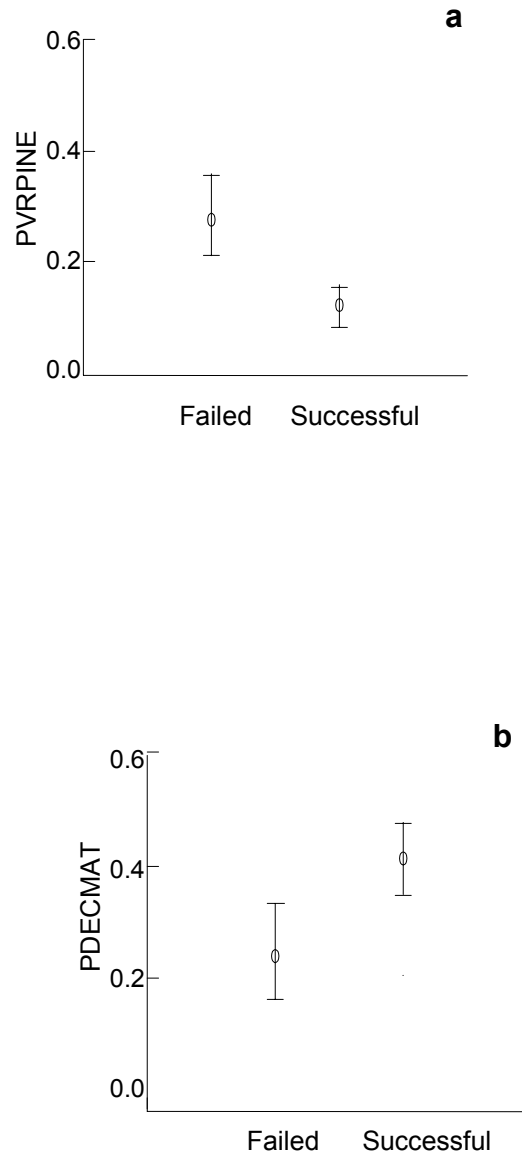


Fig. 4.4. a) Mean \pm SE proportion of VRPINE cluster in Failed vs. Successful breeding territories, Spring 2000 and 2001. b) Mean \pm SE proportion of DECMAT cluster in Failed vs. Successful nests, Spring 2000 and 2001.

5. General Discussion

5.1. Habitat Quality, Abandonment, and Reproductive Decisions

Birds breeding in disturbed habitats experienced lower fledging success than those breeding in undisturbed habitats (chapter 2). Thus, breeding birds in disturbed habitats are confronted with a choice: 1) attempt to breed in sub-optimal habitat or 2) abandon the breeding attempt in the hopes of securing a better quality territory in the subsequent breeding season. Breeding attempts are known to affect subsequent adult survival in birds, as body condition deteriorates due to the energetic costs associated with producing and rearing a brood (Hörak 1995, Ots & Hörak 1996, Murphy 2000). Consequently, birds breeding in poor habitat may first attempt to reduce energetic costs associated with reproduction. In chapter 3, I showed that birds were more willing to permit territorial intrusions in disturbed habitats, but that most intruders appeared to be engaged in foraging behaviours. Subsequent studies indicate that birds in disturbed habitat are still territorial to some extent, in that they respond aggressively to playback simulations of aggressively intruding neighbours (H. Van Oort unpubl. data). This suggests that birds in sub-optimal habitats may lower territorial defence costs by tolerating non-aggressive intruders. If this response is insufficient to compensate for poor habitat quality, birds may abandon a breeding attempt entirely to increase their chances of survival until the next breeding season.

Territory quality may be lower in disturbed habitats as a result of substantially reduced food availability. Although I did not measure food availability directly in the present study, canopy height combined with territory area could serve as a rough measure of the volume of feeding area available to breeding pairs in gleaning feeders such as chickadees. As disturbed habitat types are characterized by low canopy height or decreased canopy cover (chapter 4), birds breeding in areas featuring these habitat types may compensate by expanding their territory area. In chapter 4, I found that territories in the disturbed site were larger than those in the undisturbed site. In addition, I found that pairs in disturbed habitats were far more likely to forage into neighbouring territories in my disturbed than in my undisturbed sites (chapter 3). This would suggest that resources may be scarce, forcing birds outside their own territories to secure resources necessary for breeding. Indeed, as intraspecific competition may limit the extent to which territory expansion is possible, intrusions may be a consequence of this constraint.

There will be an upper bound on territory size beyond which the energetic costs associated with transporting food items to and from the nest site will exceed the physiological capabilities of the organism (Bovet and Benhamou 1991). Additionally, the feeding rate may fall below the threshold level required to sustain the brood or the incubating female. Thus, although birds may potentially compensate if food availability is lower in disturbed habitats by expanding territory size and foraging outside their defended territories, they are likely to be under considerably greater energetic strain than birds breeding in undisturbed habitats.

The greater rate of breeding attempt abandonment in disturbed habitats (chapter 2) is consistent with this hypothesis, as is the reduction in expenditure of energy in territorial defence (chapter 3).

Future work will need to focus on direct measures of food availability between habitats, and how this impacts the birds settling in either site. Possible mechanisms of achieving this would be to utilize frass traps to quantify lepidopteran abundance among the various areas of the study site to determine the level of the prey base during breeding (Bańbura et al. 1994, Dias and Blondel 1996). By also monitoring signals known to be limited by resources (such as male song rate in the dawn chorus), one could also assess whether differences lead to decreased condition in birds occupying the disturbed sites.

5.2. Settlement Bias and Patterns of Nest Success

Nest success in disturbed habitat is lower overall, and is heavily biased towards high-ranking birds (chapter 2). I have argued in this thesis that these results can best be explained with reference to the direct effects of differences in habitat quality between disturbed and undisturbed areas. However, a similar pattern of results would be generated if low-quality individuals were forced by intraspecific competition from undisturbed habitats, settling instead in disturbed habitats. Decreased reproductive success in disturbed habitats would thus be a direct consequence of bird quality prior to settlement, and only indirectly an effect of sub-optimal habitat. As my methodology for determining relative rank primarily

involves intra-habitat comparisons (chapter 2), it is difficult to discount entirely the possibility that birds in disturbed habitat are lower-quality birds overall.

However, a number of lines of evidence suggest that birds do not differ between habitats with respect to initial quality. First, high-ranking birds display behavioural similarities in both habitats. High-rankers are equally bold and aggressive at winter feeders with respect to their competitive interactions with lower-ranking birds. If high-ranking birds were truly of relatively poor quality in disturbed habitat, they would likely limit the extent to which they engage in such energetically costly activities. Second, recent studies have shown that chickadees disperse randomly in our region with respect to body condition (H. Van Oort unpubl. data), in that a measure of juvenile body condition (daily growth rate of feathers) had no relationship to subsequent choice of breeding habitat type. Body condition is thought to correlate positively with phenotypic quality (of which rank is a measure) under normal circumstances. However, the relationship between condition and quality is not straightforward, so this line evidence for random dispersal with respect to rank is only suggestive at this time. Third, I occasionally had the opportunity to record interactions between birds that ultimately settled in different treatments (n=32). High-ranking birds in disturbed habitat were consistently dominant to low-ranking birds in undisturbed habitat in these instances (K. Fort unpubl. data). Finally, birds within the disturbed habitat showed no differences in territory composition with respect to rank, indicating that high-rankers did not exclude low-rankers from better quality patches in disturbed habitat (chapter 4). As there is no

evidence for intra-habitat settlement biases based on rank, I believe that inter-habitat biases are unlikely.

Studies examining the interrelationships between phenotypic quality and condition for birds breeding in different habitats are currently being conducted. However, future work would benefit from explicit examination of dominance interactions between birds settling in different habitats. This could be accomplished by means of artificial confrontations by disturbed and undisturbed birds of known rank in an aviary setting.

5.3. The Effect of Year on Reproductive Success

In chapter 2, I determined that fledging success did not differ between years. However, only 22 of 39 (~56%) of nests successfully fledged young in 2000, while 22 of 29 (~75%) of nests were successful in the second year. Patterns of fledge success both within and between habitats were similar across both years of the study (chapter 2). Although not statistically significant, the magnitude of the difference in overall reproductive success between years suggests that annual variability might be a significant factor driving reproductive success in my study area. Additionally, in 2002, a mild year, there was no difference in fledge success, although reproductive output was significantly lower in the disturbed site (H. Van Oort unpubl. data).

Stochastic events such as insect outbreaks and severe weather conditions may potentially interact with habitat disturbance to exacerbate reproductive deficits. For instance, if breeding birds make the decision to abandon breeding attempts based on a threshold response to current resource levels or current condition, birds breeding in

sub-optimal habitat will likely reach that threshold before those breeding in undisturbed habitats. If most birds in undisturbed habitats fail to fall below the threshold, the gap in reproductive output between habitats may widen.

An outbreak of tent caterpillars (*Malacosoma disstria*) occurred in 2000. Due to their protective hairs and noxious taste, these insects are not a favoured food item for most songbirds (Heinrich & Collins 1983, Smith 1991). Additionally, defoliation caused by tent caterpillars is likely to negatively impact the abundance of other phyllophagous insects (predominantly other lepidopteran larvae) in the canopy (Pellech & Hannon 1995), and thus has the potential to lower reproductive success of songbird species, such as chickadees, reliant on this food source. Thus, the insect outbreak may have contributed to the lower overall fledge success in 2000. However, the reproductive gap between habitats did not widen in this year, so there is currently no evidence of an interaction effect.

5.4. Source-Sink Dynamics

In this study I have determined that fledge success is much lower in disturbed than undisturbed habitats. Also, average reproductive output (fledglings/ female) is lower, but not significantly so, and habitat productivity (fledglings/ ha) in disturbed habitat is nearly half that of the undisturbed site (chapter 2). Thus, there is substantial evidence that the disturbed habitat may function as a population sink, in that fledgling productivity may not match the local mortality rate. If this were the case, the population of birds breeding within the disturbed site would require the

influx of immigrants from potential sources such as the undisturbed site for continued existence.

However, a number of other demographic parameters are required to validate this claim. Habitat-specific rates of adult survivorship and post-fledge juvenile survivorship must be determined, as these parameters may differ between sub-populations (Pulliam 1988; Pulliam & Danielson 1991; Murphy 2001). For example, rates of breeding attempt abandonment were higher in disturbed than undisturbed sites (chapter 2). As reproductive effort is negatively related to adult survival (Gustafsson et al. 1995, Gustafsson and Sutherland 1988), annual adult survival rates may be higher in disturbed habitats. Conversely if, as I have hypothesized, food resource levels are lower in the disturbed habitat, fledglings produced in these areas may be nutritionally stressed during the nestling and post-fledging periods (Magrath 1991). As a result, over-winter survival of juveniles born in disturbed habitat may be lower than those of undisturbed juveniles, as these birds enter their first winter in poorer condition.

Disturbed and undisturbed habitats likely function as true sub-populations, as birds tend to remain within the same breeding area for their entire life after juvenile dispersal (Smith 1991, personal observations). Adult dispersal between disturbed and undisturbed sites is limited, although it does occasionally occur (personal observations). Source-sink dynamics also require an exchange of genetic information between sub-populations. It is very likely that this is the case with respect to disturbed and undisturbed sites in this study. Recapture data indicate that

juveniles fledged from one habitat within the study site occasionally settle in the other habitat. Dispersal distances in this species are not accurately known, but juveniles are thought to disperse from 6–10 km in random directions from the nest site (Smith 1991). As this will entail dispersal out of the study area, the relative rarity of juvenile resettlement within the study site should not be considered evidence of a lack of genetic exchange between sub-populations. Furthermore, current research in the study area suggests that there is no relationship between winter condition of HY birds, and their subsequent settlement in either disturbed or undisturbed habitats (H. Van Oort unpublished data). Thus, although recapture information is scarce, knowledge of chickadee dispersal mechanisms and the lack of evidence for habitat settlement biases provide strong evidence that there is no barrier to genetic flow between populations breeding in disturbed and undisturbed habitats in our region.

In chapter 4, I argued that chickadee habitat preferences were maladaptive, as birds failed to avoid habitats associated with low reproductive success. Additionally, constant exchange of genetic information between disturbed and undisturbed habitat types will render behavioural adaptations to sink habitats unlikely (Holt 1996). If juvenile dispersal is indeed random with respect to habitat quality, initially equivalent birds settling in disturbed habitats will suffer negative impacts to their body condition relative to birds in undisturbed habitat, as they struggle to cope with the sub-optimal environment. In order to offset energetic deficits, they may relax territorial defence (chapter 3), allowing neighbours to forage

within their territory, further depleting already scarce resources. Ultimately, birds may abandon breeding attempts altogether, trading off immediate reproductive failure for increased overwinter survival prospects and a better of chance of breeding in the following year.

Lowered reproductive success is but one potential consequence of breeding in sub-optimal habitat. Future work, some of which is currently underway, should focus on the extent to which birds differ between habitats with respect to various measures of condition, such as heterophil:lymphocyte ratios and parasite loads (Mazerolle and Hobson 2002, Ruiz et al. 2002). Future studies also need to address the issue of the relative costs and benefits of differing reproductive strategies in terms of lifetime fitness. For example, does breeding postponement have a measurable impact on survival to the next breeding season in this population? Also, low-ranking birds in disturbed site may be saving up their reproductive effort for one good year, whereas similar birds in undisturbed habitats may breed in their first year and have an opportunity to breed in subsequent years. How does the lifetime reproductive output compare between these two groups? Answers to these questions will help to further our understanding of the mechanisms underlying reproductive decisions in birds, as well as provide realistic estimate of population parameters critical for predictions of population persistence.

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