HABITAT DISTRIBUTION AND IMPACTS OF HABITAT DISTURBANCE ON SOMATIC AND REPRODUCTIVE INVESTMENTS IN THE BLACK-CAPPED CHICKADEE

by

Harry van Oort

BSc., University of Victoria

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

NATURAL RESOURCES AND ENVIRONMENTAL STUDIES

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

May 2004

ABSTRACT

The objectives of this thesis were (1) to determine if more suitable habitats are more likely to be settled by high-quality birds, and (2) to study the impacts of local habitat heterogeneity on life-history traits of dominant and subordinate male black-capped chickadees (*Poecile atricapillus*). The studies took place in a landscape with two habitats that differ in suitability; an Undisturbed mixed-forest habitat, and a Disturbed habitat characterised by young conifer plantations. Most of my results suggested that food is less abundant in the Disturbed site, making it locally poor habitat relative to that in the Undisturbed site. Natal nutrition did not seem to influence the probability of males settling in either habitat. In contrast, females settled in the Undisturbed habitat were more likely to have a history of better natal nutrition compared with females settled in the Disturbed habitat. Recruits to the Disturbed habitat carried larger fat stores suggesting that food is less dependable in this habitat. During the breeding season, hematocrit levels were elevated among dominant males, and there was a near-significant tendency for males living in the Disturbed habitat to have greater hematocrits. Male body condition was not affected by habitat, however, there were adjustments made to reproductive behaviours. Dominant males in the Disturbed habitat reduced levels of sexual advertisement in early spring, but maintained levels of paternal care later in the season. The opposite was true for subordinates. My findings suggest that in locally poor habitats, although dominant males are particularly good mates, the reliability of sexual advertisement is compromised. These results also support current theories that males adjust the many competing life-history demands on their energy budgets when resources become limiting.

CO-AUTHORSHIP

The original research presented in this thesis could not have been accomplished without the help of several people, who will be recognized as junior authors in the resulting publications. Ken Otter was involved in the planning of each study, provided research funds, and helped collect data. For Chapter 3, Kevin T. Fort and Carmen I. Holschuh aided in collecting two years of dawn chorus data (2000/1); and for Chapter 4, Zoe McDonell and Kevin T. Fort collected one year of provisioning data (2001). Dave Gummeson was a collaborator in the feeder study (Appendix 1).

Authorship arising from this thesis

van Oort, H., and K.A. Otter. *in preparation*. Natal nutrition and habitat distribution among juvenile black-capped chickadees (Chapter 2)

van Oort, H., K.A. Otter, K.T. Fort, and C.I. Holschuh. *in preparation.* Habitat quality affects the reliability of a condition-dependent signal in black-capped chickadees (Chapter 3).

van Oort, H., K.A. Otter, K.T. Fort, and Z. McDonell. *in preparation*. Habitat quality has little effect on body condition of breeding male chickadees, but affects provisioning benefits associated with dominance. (Chapter 4).

van Oort, H., D. Gummeson, and K.A. Otter. *in preparation*. Can feeders be used to assess habitat quality? (Appendix 1).

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

First of all, I would like to express my love and appreciation for my better half - Mandy Kellner.

Secondly, I can not thank Ken Otter enough for giving me the opportunity to be his student. Ken has been an exceptional advisor throughout my thesis work, and has always gone beyond the call of duty to offer theoretical and technical advice, to help gather data, and to edit my writing. My committee – including Staffan Lindgren, Russ Dawson, and Mike Gillingham have been excellent and I greatly appreciate them agreeing to offer support in this way.

I appreciated the suggestions, comments and constructive criticisms made by all members of my committee, which greatly improved many aspects of this thesis. In addition, Mandy Kellner, Julie Michaux and Boudewyn van Oort all gave excellent editorial suggestions.

I would like to express my sincere thanks to everyone who willingly engaged in discussions relevant to my thesis (and other topics), especially: Ken Otter, Erin O'Brien, Carmen Holschuh, Kevin Fort, Tania Tripp, Pierre-Paul Bitton, Mandy Kellner, and Russ Dawson. I have greatly enjoyed the companionship of many people throughout this work including the spaghetti eaters, regulars of the bouldering cave, and many other people who enjoyed food, festivities and the outdoors with me.

I warmly thank Ken Otter, Mike Gillingham, Russ Dawson, and Lana Ciarniello for offering much appreciated statistical advice.

In the field I had help from a number of people including Ken Otter, Inge-Jean Hansen, Mandy Kellner, Kara Litwinow, Zoe McDonell, Dave Gummeson, in addition to several volunteers. In every case, I was impressed at the capabilities of these people, and I am grateful for their help. Many thanks to Kathy Parker, Mark Shrimpton and Russ Dawson who kindly let me use their equipment.

This research was funded by an NSERC grant to Ken Otter, in addition to the Canada Foundation for Innovation, BC Knowledge Development Foundation, and the Northern Land Use Institute. UNBC employed me as a Teaching Assistant throughout the program; I greatly appreciate the learning experience and employment. UNBC awarded me with various additional funds, which were greatly appreciated.

1. GENERAL INTRODUCTION

Reproductive success, and the resulting spread of genes, is governed by how well an individual performs within the environment in which it lives. Individuals who possess traits favourable to fitness within their environment will contribute disproportionately to the next generation, and their genes (and associated traits) should predominate in the region. Selective pressures may differ between regions, resulting in variation in morphology and/or behaviour among genetically separated populations.

Within populations, gene flow among habitats prevents the evolution of habitat-specific adaptations (Haldane 1956; Slatkin 1985). Consequently, individuals are likely to be adapted to habitats that have the greatest contribution to a population's gene pool, regardless of which habitat they settled in. As such, individuals that live within uncommon, or low-quality habitats may be poorly adapted to their environment and behave maladaptively (e.g., mistimed reproduction – Dias and Blondel 1996; maladaptive clutch size - Dhondt et al. 1990).

Local habitat heterogeneity may, therefore, have considerable impact on an individual's fitness. Individuals living in heterogeneous landscapes may use several strategies to deal with this problem. Avoidance of such 'locally poor' habitats may be one strategy. Once settled in a locally poor habitat, individuals could also make adjustments to costly investments which may, or may not, help them enhance their fitness in a habitat for which they are poorly adapted. This thesis explores habitat selection, and the effect of habitat on costly traits of phenotypic quality in a non-migratory, forest-generalist species, the black-capped chickadee (*Poecile atricapillus*).

1.1 Habitat selection

Habitat-selection theory attempts to understand how populations are partitioned among habitats. Traditionally, two models of habitat selection have been studied: the ideal free distribution and the ideal despotic distribution (Fretwell and Lucas 1970). The ideal free distribution suggests that densities among habitat patches are proportional to differences in relative habitat quality, effectively equalizing resource access among individuals and allowing them to achieve similar fitness, regardless of habitat quality in which they settle. This model does not explain settlement patterns in most territorial songbird species, because reproduction is correlated with habitat quality in free-living populations (e.g., Andrén 1990; Møller 1995; Riddington and Gosler 1995; Zanette et al. 2000; Suorsa et al. 2003). The ideal despotic distribution may be more applicable to explaining territorial settlement in songbirds. In this model, individuals may monopolize preferred habitats, thereby limiting densities in these habitats, and forcing other individuals to settle in less-suitable habitats (Fretwell and Lucas 1970). As such, the ideal despotic distribution predicts a positive relationship between reproductive success and habitat quality.

Habitat selection is especially well studied in migratory songbirds where breeding habitats are contested each season, and most studies support the ideal despotic distribution. For example, habitat settlement is assortative, whereby dominant individuals monopolize preferred habitats, gain an advantage in attracting mates and have greater reproductive success than subordinate males (Sherry and Holmes 1989; Holmes et al. 1996; Petit and Petit

1996; Huhta et al. 1998; Bayne and Hobson 2001). Consequently, productive habitats are sequestered by the most competitive phenotypes, and the high productivity in these habitats is probably a combination of *both* habitat quality and the phenotypic quality of the settling pair.

In non-migratory species, however, habitat selection is more ambiguous. In many resident songbird species, inexperienced juveniles disperse and select a permanent site of residence during the period of natal dispersal. Whether there is assortative settlement of habitats during natal dispersal in non-migratory songbirds is poorly understood. Natal dispersal begins shortly after independence, and lasts for only a couple of weeks (e.g., Wiese and Meyer 1979). In titmice (Paridae), observed patterns of dispersal behaviours have lead to the hypothesis that males disperse until they find a vacancy, whereas females disperse until they find a productive habitat (Greenwood et al. 1979; Nilsson 1989). Consequently, it is possible that among male Parids, habitat quality and individual quality are not coupled; high-quality males could settle in low-quality habitats, and fitness may be less biased towards productive habitats.

Once settled, individuals living in locally poor habitats may experience an array of challenges for which they are poorly adapted. In some traits, the ability to compensate in poor habitats may be genetically constrained. In Parids, individuals breeding in locally poor habitats produce maladaptive clutch sizes (Dhondt et al. 1990) and have mistimed reproduction relative to local peaks in prey abundance (Dias and Blondel 1996) suggesting that there is limited phenotypic plasticity in these traits. Nonetheless, individuals settled in locally poor habitats might be able to adjust other costly traits/behaviours that are regulated by resource availability.

1.2 Life-history traits and trade-offs

Life-history theory is concerned with the allocation of limited resources to traits and behaviours that promote fitness (Stearns 1992). *Somatic investments* such as growth and self-maintenance (for survival), and *reproductive investments* such as sexual advertisement and the provisioning of young, are costly and limited by resource supply (Gadgil and Bossert 1970; Stearns 1992). Because resources are limited, trade-offs exist in resource allocation among competing life-history investments; for example, between reproductive effort and self-maintenance (Ots and Hõrak 1996; Spencer and Bryant 2002), between sexual advertisement and reproductive effort (Gustafsson et al. 1995; Griffith 2000), and also between sexual advertisement and body condition (Blount et al. 2003b; Faivre et al. 2003; McGraw and Ardia 2003; Kilpimaa et al. 2004). Consequently, investments in life-history traits such as self-maintenance, sexual advertisement, and reproductive effort may be affected by differences in resource supply associated with habitat quality.

The manner in which life-history traits are impacted by habitat quality is likely to be dependent on: (1) strategies of priority, whereby one investment is favoured over another (Stearns 1992; Spencer and Bryant 2002); and (2) phenotypic differences in energy requirements and resource-holding potential (see section 1.3 below). First, the way in which life-history traits are prioritised is likely to depend on the life history of a species (Stearns 1992). In songbirds, it is probable that somatic investments are prioritised over reproductive investments as songbirds can typically reproduce over several breeding seasons (pending survival), and tend to improve their reproductive performance with age. Notably, Spencer and Bryant (2002) demonstrated that barn swallows (*Hirundo rustica*) prioritise somatic investments in this way, because parental effort was reduced when the cost of self-maintenance was experimentally increased. Likewise, Godfrey and Bryant (2000) found that European robins (*Erithacus rubicula*) decreased social behaviours, including song output, when their self-maintenance costs were increased, as the manipulated birds were preoccupied with foraging. These studies suggest that somatic investments are prioritised over both reproductive investments and sexual advertisement; however, this is not ubiquitous (Ots and Hõrak 1996). Nonetheless, it appears that resource allocation to life-history traits occurs in a prioritised fashion, where traits are not adjusted in parallel when food availability is lacking; rather, certain traits (such as sexual advertisement and parental care) can be abandoned to maintain adequate investments in other traits (such as body condition).

1.3 Individual differences - costs and benefits of social dominance

The fitness of individuals is probably related to their energetic efficiency, that is, their ability to invest resources towards reproduction without affecting their survivorship: consequently, fitness depends on both the environment and their phenotype. Those with larger energy requirements may be especially disadvantaged in habitats where food is scarce (Qvarnström and Forsgren 1998). Conversely, those that are more competitive may be able to buffer the effects of poor habitat because they are better able to compete for scarce resources (Carrascal et al. 1998). Both high competitive ability and high energy budgets are associated with socially dominant males, which gives contrasting predictions of the ability of such birds to deal with stressful environments. Thus, it is unclear as to whether dominant males will have less energy to invest in reproduction and sexual advertisement in non-productive habitats due to their elevated costs of self-maintenance (Qvarnström and Forsgren 1998), or whether their superior competitive ability will enable them to secure sufficient resources to not only offset their high energy costs, but to also invest in other life-history traits, even if resource availability is somewhat diminished (e.g., Carrascal et al. 1998).

Socially dominant males are generally thought to have high phenotypic quality (Hogstad 1989; Qvarnström and Forsgren 1998). Dominant males tend to be older (Hogstad 1989; Smith 1991; H.v.O. unpublished data), which suggests higher survival ability. Once dominance is achieved, such males have access to the best resources in their home range. Such resource benefits include access to preferred foraging niches (both natural and artificial food sources - Ekman and Askenmo 1984; Desrocher 1989; Hogstad 1989; Ekman 1990), and preferred territories (Pärt and Qvarnström 1997). Because dominant males apparently gain better access to food, it is not surprising that they often have better body condition than subordinates (Carrascal et al. 1998; Gosler and Carruthers 1999), which is reflected in their condition-dependent advertisement signals (e.g., Otter et al. 1997; Pärt and Qvarnström 1997).

The ability of dominants to achieve better condition, and allocate resources towards life-history traits, however, should be limited by the size of the resource benefits they acquire. In some bird species, the resource benefits achieved by dominant males are offset by greater energy requirements (Røskaft et al. 1986; Hogstad 1987; Bryant and Newton 1994). In Parids, for example, dominant males have resting metabolic rates that are as much as 25 % greater than subordinates (Hogstad 1989). Consequently, it is possible that dominant males suffer relatively poor nutritional status if they are not acquiring large enough resource benefits to offset their metabolic costs. Evidence that the cost of dominance impacts nutrition was seen in European starlings (*Sturnus vulgaris*) where dominant males were shown to have greater sensitivity to nutritional stress than subordinates (Swaddle and Witter 1994). Recently, Hay et al. (2004) presented evidence that social dominance was negatively correlated with nutritional status during the winter, a time when food availability is relatively low. Hence, because dominant and subordinate males have different access to food and different metabolic needs, they are likely to have different sensitivities to levels of environmental stress (e.g., Swaddle and Witter 1994), which could potentially result in a reversal of nutritional condition achieved by dominant and subordinate males occupying non-productive habitats.

If dominant and subordinate males have different sensitivities to habitat quality, local habitat heterogeneity could potentially have large consequences for the relative phenotypic quality of dominant males (Qvarnström and Forsgren 1998). The way in which habitat quality impacts the relative nutritional status of dominants is likely to vary with the time of year (due to seasonal changes to energy budgets and resource abundance) and with how they prioritise allocation of resources to life-history traits (Spencer and Bryant 2002).

The two primary objectives of this thesis are (1) to determine how habitats are selected during natal dispersal, and (2) to study the resulting impacts of local habitat heterogeneity on life-history traits (e.g., advertised and realized phenotypic quality) of dominant and subordinate males.

1.4 Study Species

I studied the black-capped chickadee in this research. The black-capped chickadee is the most widespread titmouse species in North America and has a geographical range extending from central Alaska to central Utah, and from the coast of British Columbia to the eastern shores of Newfoundland (Smith 1991). Black-capped chickadees are associated with deciduous or mixed forests, which in British Columbia includes alder (*Alnus* sp.), trembling aspen (*Populus tremuloides*), birch (*Betula* spp.), black cottonwood (*Populus balsamifera*), and willow (*Salix* spp.)(Campbell et al. 1997). This bird species is abundant throughout much of its range and can often be found occupying locally poor habitats (Smith 1991; Fort and Otter in press).

Black-capped chickadees are non-migratory throughout their range (Smith 1991). During winter, they forage in flocks comprised of two or more mated pairs. Their winter diet includes insects, animal fat, berries and seeds, and they rely heavily on hoarding food in many hidden caches (Smith 1991). In spring, they become territorial, and subdivide flock home-ranges among breeding pairs (Smith 1991). During the fertile period when females are laying, males partake in the dawn chorus, which is generally believed to function as a forum for sexual advertisement (Otter and Ratcliffe 1993; Otter et al. 1997). Although chickadees are socially monogamous, they have high rates of extra-pair paternity (Otter et al. 1998). Females apparently instigate extra-pair copulations (Smith 1988) and target males with higher phenotypic quality than their mate (Otter et al. 1998), which is partially ascertained by comparing their vocal signals (Mennill et al. 2002). While laying eggs, females continuously utter begging calls during the day to which their mates respond by bringing large arthropod food items (Smith 1991). Once the clutch is complete, females alone incubate the eggs and are provisioned with food delivered by males. Nestlings are fed by both members of the pair, but the male is responsible for most of the provisioning when nestlings are young and females spend considerable amounts of time brooding (Smith 1991; Chapter 4).

Black-capped chickadees are synchronous breeders and are single-brooded. Nestlings fledge when approximately 16-days old, and fledglings become independent in two to four weeks (Smith 1991). Once independent, juveniles undergo natal dispersal, which lasts for only ‘a few weeks’ (Weise and Meyer 1979). Dispersal distances have been recorded to range from 0.4 to 11.2 km, with a median distance of 1.1 km; once settled, recruits develop strong site fidelity that usually lasts throughout the remainder of their lives (Weise and Meyer 1979; Smith 1991).

Newly recruited juveniles usually become subordinate members of a flock headed by an experienced dominant male (Hogstad 1989; Smith 1991; H.v.O. personal observation). Dominant males forage in the most profitable microhabitats, and offer protection from conspecific interference to their mates, who therefore also gain access to preferred foraging sites (Desrocher 1989; Ekman 1990; Hogstad 1992). Dominant males typically have greater survivorship (Welling et al. 1997), greater sexual advertisement (Otter et al. 1997), are selected as extra-pair sires (Otter et al. 1998), and have greater within-pair reproductive success (Otter et al. 1999; Fort and Otter in press). Hence, dominant males generally seem to have greater phenotypic quality in this species compared with subordinate males.

1.5 Study site

This research took place in the forests surrounding the University of Northern British Columbia at Prince George. The 200 ha study site (Figure 1.1) is situated on an elevated bench (Cranbrook Hill). Approximately half of the study site is comprised of mature mixed forest dominated by trembling aspen, paper birch (*B. papyrifera*), hybrid white spruce (*Picea glauca x engelmannii*) and lodgepole pine (*Pinus contorta* var *latifolia*), while subalpine fir

(*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*) and black cottonwood (*Populus balsamifera* var *latifolia*) are also common (canopy height ~25 m). Throughout this thesis, I refer to this mature, mixed-forest habitat as 'Undisturbed'. The habitat in the remaining portions of the study site has been highly altered: first by agricultural clearing, and then by managed forestry practices. This 'Disturbed' habitat was deforested during the 1960's and 1970's and today is a patchwork of various young regenerating forests including several lodgepole pine plantations (1.5 to 11.3 ha) interspersed among natural re-generation of alder and willow (canopy height 5-25 m). The Disturbed habitat includes several small fragments (<4 ha each) of mature forest that together comprise less than 10 % of the total area. In this thesis, the terms 'Undisturbed' and 'Disturbed' are used specifically to denote the habitat patches in the UNBC study site.

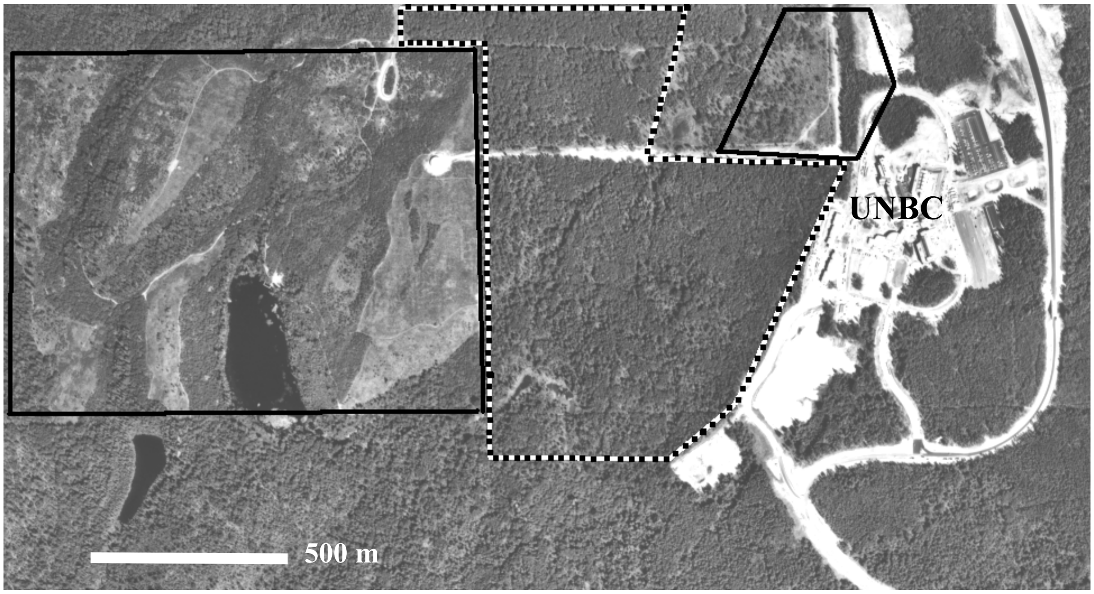

Figure 1.1 Aerial photograph of the UNBC study site (~ 200 ha) showing the distribution of habitats. Undisturbed habitat is outlined in alternating black/white; Disturbed habitat is outlined in black.

The chickadee population in the study site has been colour-banded and monitored since 2000. Population densities appear to be similar in both Disturbed and Undisturbed habitats (Fort 2002; personal observation). Early work at this study site found that nesting success was lower in the Disturbed habitat, especially among subordinate pairs (Fort and Otter in press). In that study, the leading cause of nest failure was nest abandonment early in the breeding season. Because canopy volume is reduced in the Disturbed habitat, it was suggested that food abundance might be lacking in this habitat. Recent research supports this idea: systematic observations during the winter found that chickadees living in the Disturbed habitat showed significantly greater use of temporary feeders upon discovery (Appendix 1). Winter food abundance may impact birds at other times of the year. First, winter food abundance is known to have downstream effects on reproductive behaviour (Smith et al. 1980). Second, winter food abundance may correlate with summer food abundance, as the primary food items (folivorous insects in the summer; and insects hibernating under bark, and seeds in the winter) are associated with tree volume (Smith 1991; Fort 2002), and the forest structure differs between habitats. Evidence that differences in food supply persist at least into the laying period come from studies monitoring female solicitation calls during the nesting period; females in the Disturbed habitat beg for food at different rates than those in the Undisturbed habitat (H.v.O. and K.A. Otter, unpublished data) a behaviour known to correlate with immediate hunger in other species (Tobias and Seddon 2002). Other lines of evidence suggesting low food abundance in the Disturbed habitat are given in the research articles included in this thesis.

1.6 Outline of thesis research articles

This thesis contains three original research articles. In the following section, I give a brief description of the specific problems tackled in these.

1.6.1 Natal nutrition and the habitat distribution of juvenile black-capped chickadees.

To compare how organisms respond in different environments in the field, it is necessary to assess how they select habitat. If there is assortative settlement among habitat types based on phenotypic quality, then comparisons of differences in reproductive and advertisement behaviours between habitats become complicated by associated differences in phenotypic quality. Habitat selection is known to conform to the ideal despotic distribution in migratory songbirds, however, in resident species such as chickadees, the primary habitat selection occurs during natal dispersal. It is unknown if juvenile chickadees compete for preferred habitats. In Chapter 2, I assess the importance of natal condition – an index of phenotypic quality *prior to* dispersal, in determining which individuals settle in Disturbed and Undisturbed habitats. In addition, I assess their physical attributes to look for habitat-induced changes to their body condition during their first winter in either habitat.

1.6.2 Habitat quality affects the reliability of a condition-dependent signal in black-capped chickadees.

Many species have evolved mate-choice signals that are costly to produce or maintain. As sexual advertisement is costly, expression of these signals is typically state-dependent. Optimal levels of costly advertisement may be controlled by the opposing pressures of natural and sexual selection. Levels of advertisement may be reduced in locally poor habitats where resources are scarce. Such habitat effects may impact the ‘normal’ functioning of sexual advertisement, especially if dominant and subordinate males show different sensitivities to habitat quality. In Chapter 3, I compare levels of sexual advertisement for dominant and subordinate male chickadees breeding in Disturbed and Undisturbed habitats.

1.6.3 Habitat quality has little effect on body condition of breeding male chickadees, but affects provisioning benefits associated with dominance.

In socially monogamous species with bi-parental care, males provide important direct fitness benefits by provisioning food to nestlings. Dominant males may be able to provide larger provisioning benefits to their mates because they have access to better resources, and are generally in better condition. The ability of socially dominant males to offer such benefits, however, may erode in locally poor habitats due to diminished resource benefits and the energetic costs associated with dominance. The way in which habitats affect male quality also depends on how the birds allocate resources to self-maintenance versus reproduction. In Chapter 4, I document the patterns of paternal care (provisioning trips to nestlings) and physiological state (body condition and hematocrit) during the nestling period, for dominant and subordinate male chickadees breeding in Disturbed and Undisturbed habitats.

2. NATAL NUTRITION AND THE HABITAT DISTRIBUTION OF JUVENILE BLACK-CAPPED CHICKADEES

ABSTRACT. Habitat selection is poorly understood in non-migratory birds who permanently settle following natal dispersal. In this study, I test a fundamental prediction of despotic habitat distribution in a non-migratory passerine bird: the tendency for superior phenotypes to settle in superior habitats. I compared the past natal nutrition of newly recruited black-capped chickadees settled among habitats that differ in suitability. Natal nutrition was measured by the size of the growth bars in tail feathers of birds in their first winter of life. There was a positive correlation between body condition of individuals at time of capture and width of growth bars, supporting the idea that natal nutrition impacts future phenotypic quality. I did not, however, find any indication that natal nutrition altered the probability of juvenile males settling in either of two adjacent habitats, despite evidence that suggests one to be of poorer quality than the other. Females, on the other hand, were more likely to settle in the Undisturbed habitat if they had a history of good natal nutrition. Once settled, recruits to the relatively poor Disturbed habitat carried larger fat stores suggesting that they perceived food to be less available compared with those recruited in the Undisturbed habitat. Body condition did not appear to be affected by habitat. Hence, females, but not males, tended to select local habitats where they perceived food to be more available. These findings are consistent with an untested hypothesis generated from studies of dispersal in Parids, that females are more selective than males.

2.1 Introduction

To maximize fitness, animals are expected to select the highest quality habitat among those available. There are two alternate models of habitat selection outlined by Fretwell and Lucas (1970). The ideal free distribution suggests that individuals are free to settle across habitats in a manner that results in equal distribution of resources, so that individuals' fitness levels are independent of habitat quality. By contrast, the ideal despotic distribution suggests that preferred habitats are secured by dominant individuals, preventing access by less competitive individuals who must instead settle in poor habitats.

The ideal despotic distribution appears to be a good model for predicting habitat selection in territorial songbirds because (1) individuals differ in resource-holding potential and restrict habitat settlement of competitors (e.g., Krebs 1971; Sherry and Holmes 1989), and (2) reproductive parameters, such as nestling nutrition or reproductive success, often differ among habitats (e.g., Andrén 1990; Riddington and Gosler 1995; Zanette et al. 2000; Suorsa et al. 2003). The coupling of phenotypic quality with habitat quality predicted by the ideal despotic distribution can be difficult to assess, however, because a similar association can arise if occupancy of a good quality habitat elevates an individual's condition (and apparent quality) post-settlement. This issue is less of a logistical problem when studying migrant songbirds because such species must simultaneously compete for breeding habitats each year and the sequential settlement of different-quality habitats can be tracked to the start of the breeding season. Many studies of migrant songbirds suggest that the most competitive individuals secure preferred habitats, exclude less competitive individuals, and therefore offer strong support for the ideal despotic distribution (e.g., Sherry and Holmes 1989; Holmes et al. 1996; Petit and Petit 1996; Huhta et al. 1998; Bayne and Hobson 2001).

It is less clear how habitat selection occurs in non-migratory songbird species, such as titmice (Paridae), that show strong site fidelity. In such species, habitat quality can impact reproductive success (e.g., Andrén 1990; Riddington and Gosler 1995; Fort and Otter in press), suggesting that habitat settlement may follow the despotic model (Andrén 1990); however, the principal selection of habitats by non-migratory species often occurs when yearlings undergo natal dispersal: a time when individuals possess low competitive abilities (Hogstad 1989). Furthermore, in many non-migratory species, there is a limited array of habitats to select from later in life (post-dispersal) because individuals do not move far from a location once settled (e.g., Weise and Meyer 1979); if so, initial habitat settlement at the time of natal dispersal might be highly relevant to their lifetime fitness. Consequently, there may be some level of competition among dispersing juveniles to settle in preferred habitats; yet, there is currently a lack of studies addressing how habitat selection occurs during natal dispersal (but see Verhulst et al. 1997; Ekman et al. 2001).

In addition to the competitive ability, habitat settlement may differ among sexes. In Parids, males and females show remarkably different dispersal behaviours. Females typically disperse farther than males (Greenwood et al. 1979; Robbins et al. 1986; Nilsson 1989; Matthysen et al. 2001). Furthermore, males increase dispersal distances when population densities are high, and when they are late dispersing; while the opposite is true on both accounts for females (Greenwood et al. 1979; Nilsson 1989). A hypothesized explanation for these observations is that males take the first vacancy that they find while females are more selective in their choice (Greenwood et al. 1979; Nilsson 1989). Consequently, in heterogeneous environments, females may compete for preferred local habitats, leading to despotic habitat distribution; whereas males compete to settle quickly into available openings with less regard for habitat quality. Whether these differences in dispersal behaviours between sexes have consequences for habitat settlement awaits confirmation.

In this study, I examined the relationship between pre-settlement phenotypic quality of male and female yearling black-capped chickadees, and their probability of settling in two habitats that differ in quality. As a measure of phenotypic quality prior to dispersal, I used an index of natal nutrition. Early nutrition has long-lasting effects on future phenotypic quality; for example, poor nutrition during early stages of growth can have impacts on survival (Merilä et al. 1999) and future levels of sexual advertisement (Nowicki et al. 2000; Ohlsson et al. 2002; Blount et al. 2003a; Buchanan et al. 2003; Spencer et al. 2003). Individuals that experience poor nutrition early in life are likely to be at a disadvantage during natal dispersal if competing for preferred habitats. I measured the natal nutritional status of recruits retroactively by measuring records of feather growth rate (Grubb 1995). I assessed whether natal nutrition is a relevant measure of phenotypic quality by looking at the relationship between natal growth-bars and post-settlement condition at the time of capture. I then examined whether pre-settlement nutrition influenced settlement patterns with respect to habitat quality.

2.2 Materials and Methods

2.2.1 Winter Captures

During January and February of 2002 and 2003, I captured chickadees at seven to nine seasonally permanent feeding stations located around the study site. Feeders were stocked with black-oil sunflower seeds during (and restricted to) the capture period. Capture sessions rotated around these feeding stations in a systematic order and took place between

0800 hrs and 1500 hrs. I trapped intensively until I had caught most of the birds living in the study site. This was confirmed in the breeding season when very few territories were occupied by unmarked birds (n = 4 out of 74 breeding birds 2002; n = 7 out of 94 in 2003). Upon capture, yearling recruits were identified by wear patterns on their tail feathers (Meigs et al. 1983). Individual birds were colour-marked with leg bands for future identification. Only data taken at first capture were used. The two outer tail feathers (L6 and R6) were removed and stored in coin envelopes. In addition, I measured several body measures including mass (to nearest 0.1 g), flattened wing chord (to nearest 0.5 mm), tail length (to nearest 0.5 mm), and tarsus length (to nearest 0.1 mm). To decrease measurement error, the average of three tarsus measurements was taken at first capture, which gave high repeatability (estimated using recapture records; $F_{12, 2} = 40.15$, repeatability = 0.95; Lessels and Boag 1987). The sex was determined by body measurements (approximately 90% accurate; Desrocher 1990); sex designations were also confirmed by behavioural observations during the breeding season. Furcular fat stores were visually scored using a six-point scale (after Gosler 1996) where no visible fat deposit in the furcular pit scores zero, and a full pit that is bulging with fat scores five. Supplemental food was administered in both habitats throughout all winter captures, making habitat comparisons of body condition conservative. All measurements were done by the same person.

2.2.2 Estimating pre- and post-settlement condition

Growth of tails in first-winter birds begins in the nest and is completed approximately at the time of independence – chickadees do not moult their tail feathers until after their first breeding season (Pyle 1997). This moult schedule was supported by the regular occurrence of fault bars (developmental defects seen in feather vanes; Bortolotti et al. 2002) extending across the entire suite of tail feathers in yearling recruits (H.v.O. personal observation), which suggests that their tail feathers grew simultaneously (as a nestling) unlike moulted tail feathers (Pyle 1997). Thus, size of the growth bars in tail feathers, which is positively associated with nutrition (Grubb 1995), should reflect nutritional status of the birds during time spent in the nest and during post-fledge dependence on parental feeding. As the width of the growth bars will be associated with nutrition of the young in their natal nests, I refer to this measure simply as "natal nutrition" from here on.

Tail feathers collected from recruits were mounted on black construction paper cards using a small strip of cellophane tape over the proximal portion of the vane. Growth bars were marked on the card by poking holes through the feather vane with a thin pin into the mounting card. Eight to ten growth bars, centred at two thirds along the feather from the proximal end, were measured with callipers off the marked mounting card to calculate an average growth bar size (after Grubb 1989). In nine cases, growth bar data could not be estimated due to indistinct growth bars or naturally missing tail feathers. Because I collected left and right tail feathers for most birds, I averaged the growth bar measures taken from each feather when two feathers were available.

Because tail feathers were observed to occasionally be missing or in the process of re-growing, I was concerned that a proportion of the collected tail feathers were not grown as nestlings. Replacement feathers could be separated however, because they have smaller growth bars than those found on original feathers, as is normally the case with replacement feathers (e.g., Grubb 1989, 1991; Hogstad 1992). To screen for replacement feathers, I assumed that the true distribution of original growth bars is normally distributed, and I removed all data that fell below two standard deviations below the mean (with s.d. and mean calculated from the entire data set). While the removal of replacement feathers would improve the reliability of these tests by reducing measurement error, inadvertent removal of original feathers would decrease the power of the test. Consequently this screening should decrease measurement error, but possibly make the test more conservative.

I estimated body condition at the time of capture using residuals saved from a multiple regression that included body mass as a dependent variable, and with 'tarsus' and 'fat' as continuous predictors. Fat was included because it is generally associated with limited access to food resources in Parids, and can therefore make weight a less reliable measure of body condition (Gosler 1995). Although some of the residual scatter around the linear regression line results from measurement error, the residuals also contain variation resulting from individual differences in body condition (for details and discussion of this technique, see Merilä et al. 1999). As chickadees show a linear and continuous gradation of body sizes across sexes, I pooled all recruits for this regression, allowing for a larger sample size in estimating the morphometric relationship between mass, fat, and body size.

2.2.3 Determining habitat occupancy

To determine which habitat birds were settled in, I mapped out locations of individuals and their flocks over several observations. I relied on several sources of information including lists of birds found at feeders and systematic playback surveys using the 'chickadee' calls. By combining all locations where individuals/flocks were seen, I acquired a good knowledge of flock membership and distribution. Most individuals/flocks could easily be assigned to one habitat or another; however, 31 individuals were excluded from analysis, either because they were regularly seen in both habitats or, more commonly, because I had insufficient data to assess which habitat they had settled in. These missing cases probably do not bias the conclusions, as many of these birds were likely to be floaters (unsettled birds) or visiting birds settled outside the study site (Smith 1991).

2.2.4 Analysis

To assess the importance of natal nutrition as an index of initial (pre-settlement) phenotypic quality, I tested the relationship between this variable and body condition at the time of capture (residual mass). For this test, I used a general linear model, with ‘body condition’ as the dependent variable, ‘year’ and ‘sex’ as categorical predictors, and with ‘natal nutrition’ as a continuous predictor. Interaction terms were sequentially removed in order of non-significance, beginning with the highest order interaction term, and ending with main effects.

Logistic regression (Tabachnick and Fidell 2000) was used to test the probability of settling in either the Disturbed or Undisturbed sites based on the size of growth bars and structural body size. As with the previously discussed analysis, I sequentially removed terms from the model that were not significant. Because I had *a priori* reasons for suspecting different patterns of settlement among sexes, males and females were tested separately.

In other analyses, single factor analysis of variance (ANOVA; Zar 1999) were used to test for differences in means among levels of categorical factors (e.g., habitat), and linear regressions were used to test relationships between two continuous variables where the magnitude of one variable was thought to depend on the magnitude of another (Zar 1999). To control for a covariate (e.g., time), analysis of covariance was used (ANCOVA; Tabachnick and Fidell 2000). All probability values are two-tailed, and all statistical procedures were run with SYSTAT 9.0 (SPSS Inc. Chicago, IL).

2.3 Results

2.3.1 Pre-settlement condition

In 2002 and 2003, I captured a total of 67 and 51 recruits respectively. Growth bars had a skewed distribution ranging from 1.5 mm to 2.9 mm in size (mean = 2.45, s.d. = 0.242, n = 183, skewness = -1.52, Kolmogorov-Smirnov d = 0.154, $P < 0.01$), with 94.5 % of the measured growth bars being larger than 1.97 mm. The removed data had a similar range in growth bar widths (1.5 to <1.97) to a sample measured from 14 known replacement feathers grown after the original was collected (1.53 to 1.95). After, removing the probable replacement feathers and averaging the remaining paired data (within individuals), the distribution became normal (mean = 2.49, s.d. = 0.19, n = 103, skewness = -0.44, K-S d = 0.096, $P > 0.20$). Among recruits, growth-bar size was not significantly associated with tarsus length indicating that this measure of natal nutrition is relatively independent of skeletal size (linear regression: $r^2 = 0.004$, $F_{1,\,106} = 0.42$, $P = 0.52$).

To estimate body condition, residuals were saved from a multiple regression of mass on tarsus length that controlled for fat stores (multiple $R^2 = 0.48$, $F_{1,\,100} = 14.7$, $P < 0.0005$). The residuals (body condition) were analysed with a general linear model testing for the relationship between natal nutrition and body condition at the time of capture. All interaction terms, and year were removed from the model as they did not significantly explain variation in body condition. Males were in better condition than females ($F_{1,\,86} = 16.9$, $P < 0.0005$);

after controlling for sex, natal nutrition was a significant predictor of condition at the time of capture ($F_{1, 86} = 10.8$, $P = 0.001$).

Among males, there was no indication that their natal nutrition altered the probability of settling in either Disturbed or Undisturbed habitat. A logistic regression including tarsus length and natal nutrition did not significantly predict settlement of males among habitats ($\chi^2 = 0.23$, d.f. = 1, $P = 0.89$). This result did not change when either natal nutrition ($\chi^2 = 0.86$, d.f. = 1, $P = 0.35$), or tarsus ($\chi^2 = 0.064$, d.f. = 1, $P = 0.80$, Figure 2.1a) was removed from the equation. In the logistic regression for females, however, there was a trend for recruits with a history of poor natal nutrition to settle in the Disturbed habitat (n = 41, $\chi^2 = 4.53$, d.f. = 1, $P = 0.081$). Tarsus did not appear to be predictive in this model (t-ratio = 0.66, $P = 0.51$), while natal nutrition approached significance (t-ratio = 1.75, $P = 0.08$). Tarsus was removed, and the resulting model had a significantly better fit to the data compared with the constant-only model (n = 41, $\chi^2 = 4.09$, d.f. = 1, $P = 0.043$, Fig. 2.1b), although the strength of association was weak (McFadden's rho-squared = 0.074).

2.3.2 Post-settlement fattening strategies and body condition

Sex did not have an effect on fat stores (one-way ANOVA: $F_{1, 101} = 0.17$, $P = 0.68$). Likewise, fat stores were not different across years ($F_{1, 101} = 0.72$, $P = 0.40$), however, fat scores did increase during the day with capture time (linear regression; $r^2 = 0.18$, $F_{1, 99} = 22.3$, $P < 0.0001$). Consequently, when I analysed the effect of habitat on the size of fat stores carried by newly caught recruits, I controlled for time of capture statistically by including time of day as a covariate. To test the assumption of homogeneity of regression, I first ran an ANCOVA model that included a habitat by time interaction term (Tabachnick and Fidell 2001). The interaction term between time and habitat was not significant ($F_{1,73} =$

0.99, $P = 0.46$) and was dropped from the model. After controlling for time of capture, recruits that settled in the Disturbed habitat had significantly higher fat reserves than recruits that settled in the Undisturbed habitat ($F_{1,76} = 8.1$, $P = 0.006$, Figure 2.2). Recruits in either habitat did not show large differences in winter body condition. Only 'sex' was a significant predictor of body condition ($F_{1,79} = 24.3$; $P < 0.0001$), while 'year', 'habitat' and all interaction terms were not significant (all $P > 0.14$).

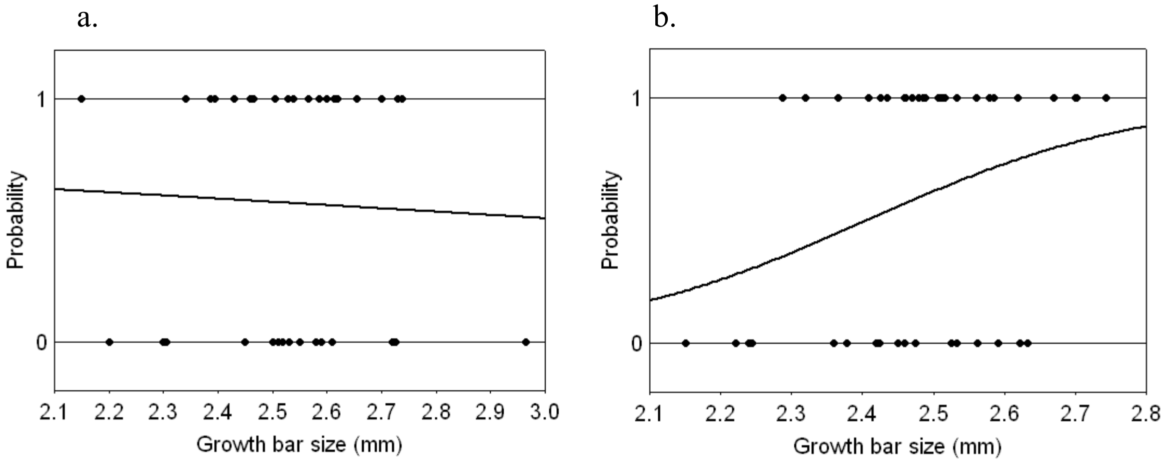

Figure 2.1 Results from two logistic regressions that test how growth bar size (natal nutrition) influences the probability of (a) male and (b) female recruits settling in Undisturbed habitat (1) versus Disturbed habitat (0). Data are plotted to show the distribution of growth bars sizes seen among recruits in either habitat. The non-significant probability curve in plot 'a' is shown for illustrative purposes.

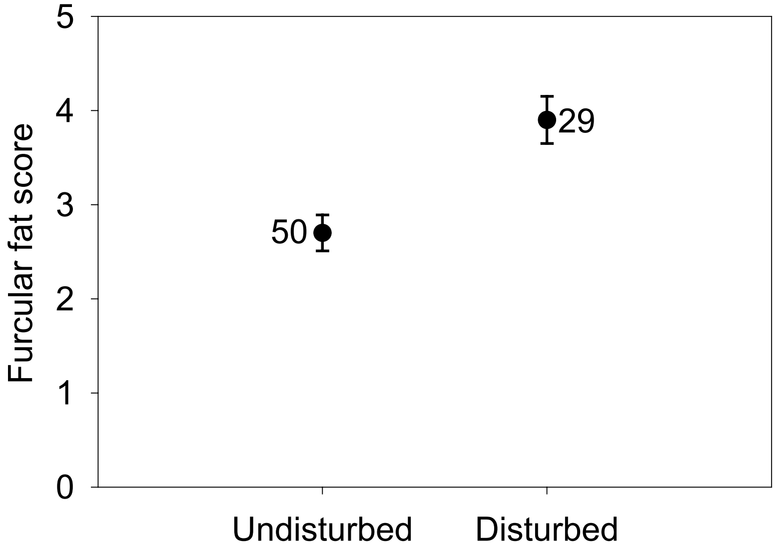

Figure 2.2 The effect of habitat on the size of fat stores carried by recruits during their first winter. Mean (± SE) furcular fat scores adjusted for the time of capture are shown.

2.4 Discussion

I demonstrated that natal nutrition was associated with future body condition during winter. The relationship between natal nutrition and first winter condition detected in this study suggests that natal nutrition has impacts on future phenotypic quality, as has been shown in several recent studies (Merilä et al. 1999; Nowicki et al. 2000; Ohlsson et al. 2002; Blount et al. 2003; Buchanan et al. 2003; Spencer et al. 2003). Consequently, it is probable that natal nutrition is a functional index of pre-settlement phenotypic quality, and is associated with the condition of individuals during natal dispersal.

There are few studies that address habitat selection during natal dispersal, yet for many species, the primary decisions of habitat settlement are made at this time. In black-capped chickadees, habitat quality has impacts to their reproduction (Fort and Otter in press), suggesting that habitat selection is more likely to conform to the ideal despotic distribution rather than the ideal free distribution (Fretwell and Lucas 1970). An important prediction of the ideal despotic distribution is that preferred habitats are occupied by individuals with superior phenotypic quality. Using growth bars as an index of natal nutrition, I found evidence that such assortative habitat settlement is more likely to occur among females than males.

The ability to search and compete for preferable habitats is probably affected by body condition. Individuals in good condition may have greater freedom to explore landscapes, and may also have greater resource-holding potential. Consequently, if habitat settlement is competitive among dispersing juveniles, high-quality habitat patches should contain recruits that were raised with relatively better nutrition. Accordingly, I found that for females, the probability of settling in the Undisturbed habitat depended on natal nutrition; however, there was no indication of such condition-dependent habitat selection seen among males.

Because natal nutrition can be affected by habitat quality (e.g., Riddington and Gosler 1995) high levels of local recruitment could lead to the pattern seen among females in this study. It is therefore possible, but unlikely, that local recruitment, where juveniles do not disperse outside of their natal habitats, might account for these results. In the UNBC study site, habitat patches are adjacent and relatively small compared with dispersal distances of chickadees (see Chapter 1). Consequently, emigration/immigration rates are probably high. This is suggested by banding records from the UNBC study site: after banding 375 nestlings over four years (2000-2003), only 15 banded recruits have been documented (H.v.O. and K.A. Otter, unpublished data as of March 2004). Hence, levels of recruitment from the study site appear to be low, which is consistent with reports from various other study sites (reviewed in Smith 1991). Moreover, female black-capped chickadees, like other Parids, are known to disperse farther than males (Robbins et al. 1986); consequently, if local recruitment had impacted my results, males would be more likely than females to show an association between natal nutrition and habitat quality. Hence it is unlikely that the results I obtained are an artefact of birds raised in the same habitat patch within which they settled.

It is more likely that the sex differences observed arise from different habitat selection strategies used by male and female chickadees during natal dispersal. Previous studies suggested that males Parids take the first available vacancy, while females, who cover more ground during natal dispersal, are more selective in their choice of where to settle (Greenwood et al. 1979; Nilsson 1989). As such, any evidence of juvenile competition for habitats differing in quality should occur between females, as males compete for early settlement rather than selecting among habitats. My results concur with this prediction because I found evidence of condition-dependent habitat settlement in females but not in males. Consequently, this study suggests that habitat settlement of dispersing females proceeds in an assortative way, as predicted by the ideal despotic distribution (Fretwell and Lucas 1970). In contrast, and counter to predictions of the ideal despotic distribution, there is no association between initial male quality and habitat quality. Males, however, are impacted by the habitats within which they settle (Fort and Otter in press; Chapters 3 and 4), which also contrasts with predictions from the Ideal Free Distribution (Fretwell and Lucas 1970). Therefore, male chickadees do not seem to fit either of the Fretwell-Lucas models in their settlement patterns during natal dispersal.

In theory, larger individuals could have a competitive advantage in fighting over resources, resulting in larger birds being more likely to settle in preferred habitats. Although habitat-size associations have been documented in Parids (Ulfstrand et al. 1981; Lemel 1989) this is not ubiquitous (e.g., Riddington and Gosler 1995). Furthermore Lemel (1989) found little evidence that dominance was linked to body size, making such habitat-size associations difficult to interpret. Dominance is not well associated with structural size in the UNBC population even though dominant males are heavier for their size (Chapter 4). Hence, the use of structural size is probably not a very powerful method for assessing despotic habitat settlement patterns among Parids. Consequently, it is not overly surprising that I found no indication that either males or females who settled in the Undisturbed habitat were larger than those who settled in the Disturbed habitat.

Once settled, new recruits may experience different living conditions depending on the habitat in which they have settled. In this study, tests of post-settlement habitat effects were conservative because supplemental food was supplied during capture sessions. Nonetheless, recruits in the Disturbed habitat were found to carry larger fat stores. Fat stores are not necessarily indicative of condition in Parids (Gosler 1996). In extreme cases, reduced fat can be seen among individuals in poor condition because individuals suffering from severe malnutrition are unlikely to carry large fat stores. As such, my results could potentially be explained by recruits in the Undisturbed habitat suffering from severe malnutrition; however, this is unlikely to be the case for several reasons: (1) it is unlikely that food is lacking in the Undisturbed habitat because this habitat is a better breeding environment for chickadees (Fort and Otter in press); (2) I found no difference in the body condition of birds settled in either habitat, suggesting that birds living in the Undisturbed habitat are not suffering from severe malnutrition; and (3) differences in feeder-use among habitats (Appendix 1) suggest that food is less abundant in the Disturbed habitat. Hence, it is unlikely that the differences in fat stores seen among recruits in either habitat are explained by low food abundance in the Undisturbed habitat.

It is more likely that the observed differences reflect different fat storage strategies employed by recruits in either habitat. Although carrying fat stores may reduce the risk of starvation; in birds, it is also costly to carry fat since the additional weight interferes with their flight performance (Krams 2002). Consequently, there is a trade-off between the risk of starvation and the risk of predation (Lima 1986). Hence, birds that have unpredictable or scarce food supplies tend to carry larger fat stores than those with better access to food (Ekman and Lilliendahl 1993; Bednekoff and Krebs 1995; Witter and Swaddle 1995; Gosler 1996). Also, birds living under greater predator pressure carry reduced fat stores (Krams 2000). The difference in fat stores seen between habitats is most likely a reflection of differences in either food abundance or predator pressure among habitats. Although there has been no systematic survey of predator abundance in either habitat, incidental observations of avian predators (e.g., northern pygmy owls, *Glaucidium gnoma*, Merlins, *Falco columbarius*, and forest hawks, *Accipiter* sp.) have been equally distributed across both habitats (H.v.O. and K.A. Otter personal observations). In contrast, the differences in feeder-use which suggest that food is lacking in the Disturbed habitat are consistent with these observed patterns of fat stores seen among recruits in either habitat (Appendix 1). Hence, these results are most likely to reflect differences in the perception of food availability.

Because feeders were present throughout the capture periods in this study, the true extent to which habitats impose impacts to body condition may be masked. Although I found that recruits in either habitat had similar body condition, further studies in the absence of food supplementation would be beneficial.

The results of this study, that males are not selective while females are, suggest that most differences in male performance found between habitats are probably the direct influence of the habitat in which males are settled, and less likely to be the result of selective recruitment. When assessing habitat related differences among females however, my results suggest that a portion of the differences observed can probably be attributed to differences in female phenotypes prior to their dispersal.

3. HABITAT QUALITY AFFECTS THE RELIABILITY OF A CONDITION-DEPENDENT SIGNAL IN BLACK-CAPPED CHICKADEES

ABSTRACT. Conditional handicap models of sexual selection predict that the expression of mate-choice signals honestly reveal information about the signaller’s state, indicating the potential of the signaller to provide fitness benefits as a mate. Habitat quality, however, will also affect state-dependent behaviours. As such, different habitats may alter the absolute expression of condition-dependent signals, with reduced expression in locally poor habitats. Yet it is not clear whether this also affects the reliability of the signals; i.e., whether high-quality males still have relatively higher trait expression in poor environments. Using black-capped chickadees (*Poecile atricapillus*) as a model species, I examined the expression of a condition-dependent signal, song output in the dawn chorus, among dominant and subordinate males across two habitats that differ in suitability. Song output was lower in Disturbed habitat; however, this divergence was driven largely by dominant birds in each habitat. Very little habitat effect was seen among subordinate males. This suggests that dominant males may be more sensitive to differences in habitat quality in their signals, which contrasts with patterns of nesting success, causing the reliability of condition-dependent signals to be questionable in poor habitats.

3.1 Introduction

Conditional handicap models of sexual selection predict that the expression of mate-choice signals honestly reveal information about the signaller's physical state (Zahavi 1975; Kodric-Brown and Brown 1984; Nur and Hasson 1984; Grafen 1990). If increased signal expression is costly, only individuals that readily meet the energetic requirements of self-maintenance can afford large investments in the expression of the signal (Zahavi 1975). In populations that use condition-dependent signals in mate choice, greater expression of such traits is expected to indicate the intrinsic quality of the signaller, a point that continues to be well supported by many empirical studies (see review in Kotiaho 2000).

In addition to the intrinsic quality of the signaller, the expression of condition-dependent signals is also influenced by extrinsic factors such as habitat quality (Hill 1995). Among songbirds, food availability can strongly affect song output (Reid 1987; Alatalo et al. 1990; Thomas 1999), and alter plumage ornamentation (Hill 2000). As such, variation in resource availability among habitats that differ in quality is likely to influence the ability of males to express condition-dependent signals at a regional scale. Hill (1995) suggested that condition-dependent traits could be used as indicators of environmental quality and reviewed evidence of this process at a time when very little information was available; since then, several studies have found further support for habitat-induced signal expression. Most notably, Eeva et al. (1998) showed that the expression of carotenoid-dependent plumage signals is depressed when great tit (*Parus major*) nestlings were raised in close proximity to an industrial source of pollution associated with low food abundance. Hõrak et al. (2000, 2001) also found that the expression of carotenoid plumage ornaments showed regional variation according to differences in habitat quality. Hence, habitat quality appears to create different contexts of signal expression; males living within poor habitats may have low signal expression, while those living in more favourable habitats have greater expression. Consequently, variation in signal expression can be attributed to differences in environmental quality (among habitats), as well as phenotypic quality of individuals (within habitats) suggested above.

It is poorly understood, however, how the effects of habitat and phenotypic quality interact in free-living populations. Specifically, it is unclear how the extrinsic effect of habitat quality alters the reliability of condition-dependent signals as indicators of male phenotypic quality. It is important to determine whether relative signal expression among males who differ in phenotypic quality is conserved within habitats, even if overall expression of the trait within the population is depressed, as lost reliability will diminish the strength of selection on female preferences. Badyaev and Hill (2002) found that carotenoid ornamentation in experienced male house finches (*Carpodacus mexicanus*) was not an honest indicator of parental quality in a Montana population with highly variable signals, which contrasted with findings from relatively bright eastern populations. Such regional variation in honest advertisement has a great potential to alter patterns of sexual selection, yet, there is very little understanding of such processes.

The issue of how signal reliability is affected by habitat quality is especially pertinent in species where social dominance is equated with phenotypic quality, as there are good reasons to suspect that dominant and subordinate males have different sensitivities to habitat quality. Predictions of how dominant and subordinate phenotypes respond in different habitats are difficult to make for natural populations, however, as many factors may affect the energetic costs and benefits associated with achieving dominant status. Dominant males have access to better foraging sites and therefore receive some level of resource benefit (Desrocher 1989). Yet this is balanced by increased metabolic costs associated with being dominant in social hierarchies (Røskaft et al. 1986; Hogstad 1987). This energetic cost has been demonstrated in a captive study, where dominant starlings (*Sturnus vulgaris*) showed greater sensitivity to nutritional stress when housed separately (Swaddle and Witter 1994). In high-quality habitat, the costs associated with dominance appear to be offset by the ability to access resources, but this cost-benefit ratio may change if habitat quality varies. In habitats that are sufficiently poor, dominants may pay high individual costs to secure access to the best resources in an impoverished environment (Qvarnström and Forsgren 1998), and their reduced condition may become evident in the expression of condition-dependent signals relative to subordinate males in the same habitat. Yet if dominant individuals still provide greater reproductive benefits to their mates in these habitats by either securing the best available territories or providing more parental effort, signal expression becomes unreliable, because the signal value does not accurately advertise the direct benefits that they can offer females. Alternately, dominants may eliminate subordinate access to the remaining pockets of adequate forage, leaving subordinates with disproportionately poor nutrition (e.g., Carascal et al. 1998). Consequently, signal reliability in this context could potentially be enhanced in poor environments where dominants are easily discerned from subordinates.

As a first step towards understanding regional variation in signal reliability, I looked at signalling of dominant and subordinate male black-capped chickadees in two habitats that differ in suitability (see Chapters 1 and 2). By studying a labile signal, song output during the dawn chorus, I was able to assess levels of advertisement generated during the fertile period, when female mating decisions are influence by singing activity (Mennill et al. 2002).

Previously work has suggested that the dawn chorus in black-capped chickadees serves as a forum for male advertisement (Otter and Ratcliffe 1993; Otter et al. 1997). During this period, breeding males sing long bouts of continuous ‘fee bee’ songs close to the nest site at dawn (Otter et al. 1997). This dawn chorus signal often lasts over 45 minutes. Song output at dawn is associated with paternal care and survival in the willow tit (*Parus montanus*; Welling et al. 1997), and social rank in the black-capped chickadee (Otter et al. 1997). Accordingly, chorus output peaks during the fertile period (Welling et al. 1995). Song production in the Carolina chickadee (*Poecile carolinensis*) is positively associated with male body mass at dawn indicating that this activity is state-dependent (Lucas et al. 1999). Consequently it is thought that the dawn chorus is an intersexual, condition-dependent signal of male quality that can be used by females to compare male quality in a communication network (Otter and Ratcliffe 1993).

In the Disturbed habitat (Chapter 1), chickadees appear to perceive reduced food availability in the Disturbed habitat (Chapter 2; Appendix 1) which should register in their state-dependent signals. Furthermore, females mated to dominant males have disproportionately greater reproductive success relative to those mated to subordinates in the Disturbed habitat (Fort and Otter in press). Therefore, if signals are to remain honest indicators of phenotypic quality, a larger disparity in signal expression between social ranks will be seen in the Disturbed habitat, with a greater effect of habitat quality seen among subordinates.

3.2 Methods

This study took place over three years (2000-2002) at the UNBC study site. Each year, individuals were captured and marked as described in section 2.2.1. As flocks broke up in April, territories were mapped out daily by following pairs, and noting locations of nest excavation and territorial disputes with neighbouring males. In most cases, territories were clearly in one habitat or another. For each breeding pair, I classified territories as occurring in either Undisturbed or Disturbed habitat if at least 80% of the territory fell into one of the two habitats. Territories for which such a distinction could not be made were omitted from this study.

3.2.1 Dominance Observations

Within-flock dominance relationships were determined each winter (January to March) by observing dyadic interactions at feeding stations supplied with black-oil sunflower seeds. Aggressive interactions were recorded, tallied, and used to determine the relative dominance between flock members (see Otter et al. 1997). Flocks were typically composed of only two pairs and males could usually be classified simply as 'dominant' or 'subordinate'. Intermediate ranks from larger flocks, or individuals without dominance information, were not included in this study.

3.2.3 Dawn chorus recordings

Feeders were removed in early March leaving at least a month of winter conditions prior to the start of breeding activity; thus any effects of supplemental feeding on singing performance were likely to be minimized. I began recording dawn song bouts between 26

April and 3 May each year, during the later stages of nest excavation. No recordings were made after clutch completion. Thus the data reflect male advertisement levels during the period of female fertility. They also reflects a period of probable limited resource availability to males, as the female fertile period in the UNBC study population occurs several weeks prior to bud-burst, when Lepidopteran insect prey become abundant (Hunter and Elkinton 2000).

A total of two to four birds were recorded each morning, distributed among each habitat and rank class where possible. Recordings of individual males during the dawn chorus were made using Marantz PMD430 audiocassette recorders in conjunction with one of the following directional microphones: a Sennheiser ME 67 with a K6 power supply, a Sennheiser MKH 70 with a MZA14 power supply, or an Audiotechnica ATB-815a. Recordings began from the first song of the day and continued until the chorus finished; the chorus was deemed to have ended when males did not sing for at least five consecutive minutes (after Otter et al. 1997).

I digitised and analysed recordings with Avisoft SASlab Pro, version 3.8 (R. Specht, Germany). Once digitised, the entire dawn chorus recording was subdivided into consecutive one-minute intervals. Three output variables were extracted: average song rate (average number of songs per minute), maximum rate (greatest number of songs in a minute during the chorus), and total number of songs in the chorus. Birds that did not sing, or with incomplete recordings, and recordings of birds of uncertain identity were excluded from analysis. For seven subjects, more than one recording was available across years; for these cases I randomly selected one recording for inclusion in the analysis.

3.2.4 Analysis

Thirty-one males were included in the analysis (11, 7, and 13, respectively from 2000, 2001 and 2003), and these were distributed evenly across factor cells (Undisturbed/Dominant, n = 9; Undisturbed/Subordinate, n = 7; Disturbed/Dominant n = 8; Disturbed/Subordinate n = 7). The range of sample dates was similar for all groups of males. Using this data set, I collapsed the three dawn chorus output variables into a single output variable (PC 1 scores) using a principal components analysis (Tabachnick and Fidell 2001). The PC 1 scores were analysed using SYSTAT analysis of covariance (ANCOVA; SPSS Inc. 1998): PC 1 scores were entered as the dependent variable, ‘year’, ‘rank’ and ‘habitat’ were entered as categorical predictors, with Julian date entered as a continuous predictor, and this initial model included all possible interaction terms. Non-significant interaction terms and main effects were sequentially deleted (see Chapter 2 for details).

3.3 Results

Mean song output was lower in the Disturbed habitat compared with those in the Undisturbed habitat in all three measures: number of songs sung, maximum song rate, and average song rate (Table 3.1). On average, dominant males in the Undisturbed habitat sang the greatest number of songs, sang at greatest average rate, and also sang at the greatest maximum rate compared with all other groups of males; in contrast, dominant males in the Disturbed habitat produced the lowest average number of songs, and had the lowest maximum song rate average. Only minor differences were seen among subordinates across habitats, which sang at intermediate levels (Table 3.1). Thus it appeared that dominant males showed excessive sensitivity to habitat disturbance in their advertisement signals. This pattern was tested by analysing PC 1 scores.

Table 3.1 Means (± SE) of three song output variables (number of songs, average song rate, maximum song rate) between dominant (Dom.) and subordinate (Sub.) males living in the Undisturbed and Disturbed habitats. Rates are given in songs per minute.

	Undisturbed habitat			Disturbed habitat		
	Dom.	Sub.	Total	Dom.	Sub.	Total
n	9	7	16	8	7	15
Number	457±44	375±50	421±34	287±47	370±50	326±35
Average	13.8±0.92	12.6±1.1	13.3±0.68	11.2±0.98	10.9±0.1	11.0±0.70
Maximum	20.4±0.99	18.9±1.1	19.8±0.76	17.5±1.1	19.6±1.1	18.5±0.78

Average song rate, maximum rate, and total number of songs, all loaded strongly and positively into the first component (+0.85, +0.85, and +0.73 respectively; Eigenvalue = 1.98), which explained 66 % of the total variation in chorus output. Therefore, the first component (PC 1) was a reliable index of song output (Jackson 1993), where high scores indicate large output. The final model was a two-factor ANCOVA (Tabachnick and Fidell 2001) that included ‘habitat’, ‘rank’, and a ‘habitat by rank’ interaction term, in addition to date as a covariate ($F_{4,26} = 11.47$, $P = 0.01$; Table 3.2). When considering all males, song output (PC1) was significantly reduced among birds that were settled in the Disturbed habitat (date-adjusted mean PC1 scores ± SE: Undisturbed 0.37 ± 0.21; Disturbed –0.42 ± 0.22), and a significant interaction between habitat and rank was interpreted as high-ranking males having greater sensitivity to differences in habitat quality (Table 3.2; Figure 3.1).

Table 3.2 Results from an ANCOVA used to assess the effects of two factors, habitat quality and social rank, while controlling for date (covariate), on song output (PC1) during the dawn chorus.

Source	d.f.	SS	*F*	*P*
Habitat	1	4.773	6.697	0.016
Rank	1	0.056	0.078	0.782
Habitat-rank interaction	1	3.71	5.201	0.031
Date	1	4.67	6.549	0.017
Error	26	18.5		

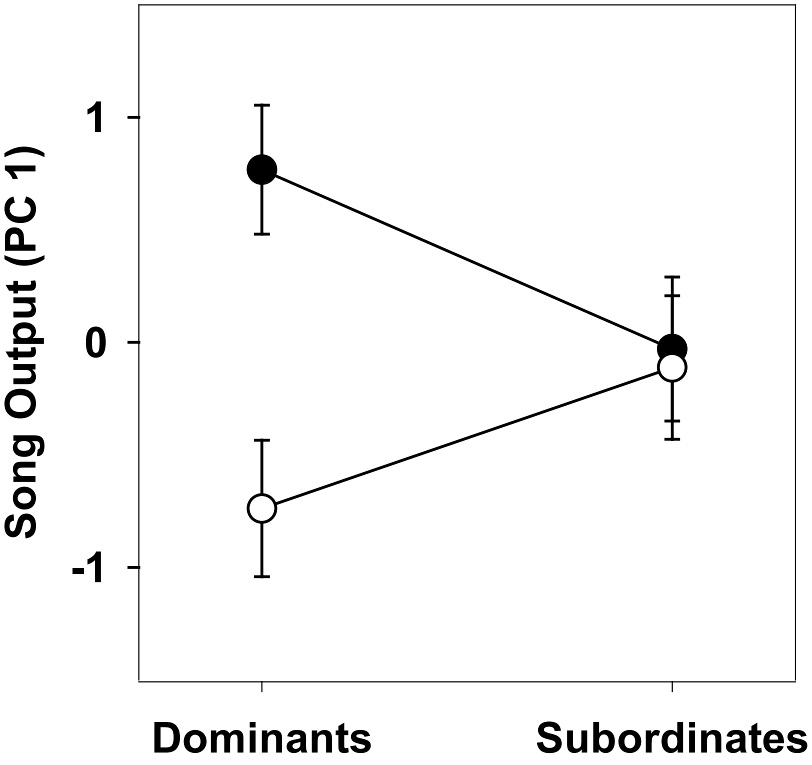

Figure 3.1 The interactive effects of habitat (● Undisturbed; ○ Disturbed) and dominance on mean (± SE) song output (PC1) factor scores after controlling for date. Large PC1 scores indicate greater song output.

3.4 Discussion

Conditional-handicap models suggest that signals of phenotypic quality should be costly to produce or maintain, making the expression of such signals state-dependent (Zahavi 1975). As the energetic state of individuals may be affected by habitat quality, the expression of such signals should be depressed in poor environments (Hill 1995); however, it is poorly known how such habitat effects alters the ability of females to compare male quality. In this study, I compared the signals of dominant and subordinate males among two habitats thought to differ in quality, and show that dominant males were more sensitive to habitat quality, suggesting that signal reliability can be lost in locally poor habitats.

In the UNBC study site, habitat disturbance is associated with reduced nesting success, suggesting that the Disturbed habitat is inferior to the Undisturbed habitat (Fort and Otter in press). Furthermore, birds wintering in the Disturbed habitats carry larger fat reserves than birds wintering in Undisturbed habitats (Chapter 2), and fat deposition is known to increase in Parids when they *perceive* unpredictable access to food (Ekman and Lilliendahl 1993; Gosler 1996), which is also reflected in their response to feeders (Appendix 1). Consequently, nutrition appears to be less dependable in the Disturbed habitat, which should be reflected in the expression of condition-dependent signals (Hill 1995; McGregor et al. 2000).

As predicted, an overall reduction in dawn chorus output was found in chickadees inhabiting the Disturbed habitat. Thus, my data support the idea that the expression of condition-dependent signals is indicative of habitat quality (Hill 1995; McGregor et al. 2000). This effect has been reported before in traits such as plumage ornaments (Hill 1995; Eeva et al. 1989; Hõrak et al. 2001); however, the effect of habitat-induced shifts to overall signalling on signal honesty has been largely unexplored.

I used social dominance in winter as a measure of phenotypic quality, which is apparently valid in both habitats. Only subordinate males show reduced nesting success as a result of habitat disturbance (Fort and Otter in press) suggesting that in terms of productivity, subordinates are more sensitive to habitat quality in the UNBC study site. Hence, dominant males would appear to be the superior phenotype in the Disturbed habitat, which, according to conditional handicap models, should be advertised honestly through costly signals (Zahavi 1975). In contrast, I found that dominant males in the Disturbed habitat signalled at levels that tended to be lower than their neighbouring subordinates. As the pattern of song output in the Disturbed habitat does not appear to mirror overall reproductive success between males of different social rank, signalling in the chorus appears to be unreliable in this habitat. This suggests that the ability of females to use such signals for mate assessment, and thus the potential strength of sexual selection, may change among environments differing in quality.

Signal reliability may be lost in resource-poor environments for several reasons. First, dominant males may have different sensitivities to habitat quality compared with subordinates simply because their greater resource-holding potential comes with larger energy requirements, as outlined in the Introduction. Assuming that patterns of signal expression are strictly a reflection of condition, my results suggest that the cost/benefit of social dominance is greatly altered by habitat quality in early spring.

Resource benefits accrued through social dominance appear to exceed the energetic costs of dominance in the (species-typical) Undisturbed habitat, as high-ranking males in these habitats generally sing at higher rates than subordinates. This trend agrees with the pattern in song output observed in another study that also took place in mature woodlands (Otter et al. 1997), and fits well with models of sexual selection (e.g., Zahavi 1975). In Disturbed habitat, however, song output by dominant males was depressed to unusually low levels suggesting that during the fertile period, these males were not obtaining resource benefits large enough to offset the cost of their dominant status. My findings fit with those from a study on European starlings where dominant birds showed greater sensitivity to food stress as measured by levels of fluctuating asymmetry (Swaddle and Witter 1994). Other processes, however, may contribute to the large reduction of signals by dominants in the Disturbed habitat.

The pattern I observed could also be explained by mechanisms that do not imply dominants in the Disturbed habitat are relatively stressed. One possibility is that in resource-poor environments, natural selection selects against males who are predisposed to allocating resources to costly advertisement. As a consequence of this process, males who tend to reduce advertisement in the Disturbed habitat may have enhanced survivorship making them more likely to achieve a position of social dominance. In large tracts of poor habitat, this would lead to a population with reduced dawn chorus signals in both dominants and subordinates. In the UNBC study site, however, the areas of habitat disturbance are small relative to dispersal distances (Chapter 2), facilitating genetic mixing between habitats. Thus, given the lack of isolation, it is possible that new, low-ranking recruits settle in the Disturbed habitat, some of which are genetically predisposed to chorusing at high levels compared with the resident dominant males, which have survived as a result of their low advertisement levels.

Alternately, dominants in poor habitats might reduce signalling as a strategy to save resources for within-pair reproduction (Badyaev and Hill 2002). Chickadees are socially monogamous, and males are heavily involved with within-pair reproductive activities (Smith 1991). Several reasons *might* promote a low signalling strategy in a resource-poor environment. Dominants, being older and more experienced (Hogstad 1989), may have learned to reduce signalling effort in order to maintain adequate effort towards within-pair reproduction (i.e., to aid in egg production by provisioning females with food during the remainder of the day). It is also possible that the benefits of advertisement are absent in poor habitats causing dominant males to forgo advertisement as a strategy to improve fitness. This may seem likely, as low-ranking females have reduced probability of successful reproduction in disturbed habitats (Fort and Otter in press), and tend to be of lower quality than females recruited in the Undisturbed habitat (Chapter 2); therefore, females mated to low-ranking males may not be worth advertising to as extra-pair partners. The above explanations involving a male strategy are difficult to accept, however. The dawn chorus is a signalling network and evidence suggests that females may use the output of males during the chorus in mate choice decisions (Otter and Ratcliffe 1996). Dominant males who opt to reduce song output may lose paternity if their vocal signals are perceived as low quality compared with their neighbours (Mennill et al. 2002). Although densities appear to be slightly reduced in the Disturbed habitat, multiple males are usually audible (Hansen 2003). Therefore, low signalling effort would not make a viable strategy for improving fitness for dominant males unless subordinates are signalling at lower rates as well. A strategic decision to reduce output would be adaptive if (1) females abort extra-pair matings in locally poor habitats, or (2) males increase levels of (effective) mate guarding.

Either way, my data suggest that signalling may be constrained in poor habitats, such that it no longer reliably reflects the intrinsic status of males. Song output during the dawn chorus was depressed in a locally poor habitat where reproductive success is reduced, and where birds maintain larger fat stores. This finding supports conditional handicap models of sexual selection, and illustrates how signalling contexts differ among environments. More importantly, dominant and subordinate males differed in their sensitivity to habitat quality. Interestingly, dominant males were more sensitive to reduced habitat quality, suggesting that honesty of dawn chorus signalling is less reliable in poor quality environments. Future studies should establish how the energetic cost/benefit of dominance is altered by changing conditions during the fertile period. Also, studies are needed to address the idea that natural selection operates on the predisposition to advertise with costly signals. The idea that dominant males strategically reduce advertisement in favour of within-pair reproductive investments would be worthwhile to investigate; in particular, it would be necessary to determine how dominant males avoid being cuckolded. Finally, because the reliability of signals is dependent on habitat quality, I expect that habitat has impacts on the behaviour of receivers. Such impacts of lost signal reliability may include maladaptive extra-pair matings or a reduction in the frequency of extra-pair paternity.

4. HABITAT QUALITY HAS LITTLE EFFECT ON BODY CONDITION OF BREEDING MALE CHICKADEES, BUT AFFECTS PROVISIONING BENEFITS ASSOCIATED WITH DOMINANCE

ABSTRACT. Paternal-care behaviours, such as provisioning food to nestlings, are limited by energy budgets. Consequently, the provisioning effort of males may vary with phenotypic differences in both resource-holding potential and cost of self-maintenance, in addition to the availability of resources in the environment. Socially dominant males have larger costs of self-maintenance, but also acquire resource benefits. The relative provisioning benefit associated with being mated to socially dominant males is likely to differ among habitats causing potentially large differences to their relative quality as mates. I assessed patterns of body condition and provisioning quality of dominant and subordinate male black-capped chickadees breeding in two habitats differing in quality. Although not quite significant, males breeding in the poor habitat tended to have raised hematocrits suggesting that they experienced larger workloads. Males were of similar body size and condition in both habitats. A habitat-rank interaction showed that there were larger provisioning benefits associated with dominant males in the locally poor habitat, where only subordinates tended to reduce provisioning rates in the poor habitat. These results suggest that dominant males are particularly good mates in locally poor habitats.

4.1 Introduction

Females birds often receive direct fitness benefits by selecting males who provide superior paternal care (e.g., Badyaev and Hill 2002; Voltura et al. 2002). The ability of males to provide such benefits is constrained by their energy budgets (Gadgil and Bossert 1970; Stearns 1992). Consequently, variation in the quality of paternal care delivered by social mates can partially be explained by phenotypic differences in both resource holding potential and cost of self-maintenance, in addition to the availability of resources in their environment. In songbirds, the resource-holding potential (competitive ability) of males may affect their ability to provision young. Socially dominant males have better access to resources including winter foraging sites and better territories (Desrocher 1989; Sherry and Holmes 1989; Ficken et al. 1990; Pärt 2001). Social dominance tends to be sexually selected, and has been associated with reproductive benefits, including enhanced paternal care and reproductive success (Otter et al. 1998, 1999; Qvarnström et al. 2000; Pärt 2001; Voltura et al. 2002). As such, male contribution in species with bi-parental care may be greater among dominant males (e.g., Qvarnström et al. 2000), simply because they have access to more resources and are in better condition (e.g., Pärt 2001). However, the ubiquity of this idea has recently been challenged as several studies have shown reduced paternal care associated with social dominance (Qvarnström and Forsgren 1998). One possible reason for such discrepancies is that the phenotypic quality of dominant males is disproportionately impacted by habitat quality compared with subordinates.

The direct benefits associated with being a dominant male are likely to vary when they receive different energetic profits for their social status, which in turn, is likely to vary with habitat quality. Dominant males have higher costs associated with self-maintenance than subordinate males, largely as a result of higher metabolism (Hogstad 1987; Røskaft et al. 1986). Oxygen consumption by dominant male Parids is known to be as much as 25% greater that that of subordinates (Hogstad 1989), and due to increased metabolism, dominant males may require larger food intake in the course of a day. This latter idea is supported by a negative relationship between social dominance and sensitivity to nutritional stress (Swaddle and Witter 1994). Providing resources are generally available in the habitat, dominant individuals will have a selective advantage, but if habitat quality is poor and resources are limiting, the energy gained from priority access to resources may not offset the high metabolic costs of dominance.

If dominant males suffer disproportionately in poor environments compared to subordinates, then they may have relatively poor phenotypic quality (as mates) in these situations. Qvarnström and Forsgren (1998) suggested that dominant males might be more susceptible to starvation in resource-poor habitats due to their increased energy demands. Depending on how they allocate resources (Spencer and Bryant 2002), however, dominant males may instead provide fewer provisioning benefits if they need to spend relatively more time foraging for self-maintenance compared with subordinates. Hence, the physiological cost of dominance could impact either their body condition or their reproductive investments, either of which could render them undesirable as mates.

Alternately, it is possible that the resources monopolized by dominant males, have disproportionate impacts compared to subordinates in poor habitats. In poor habitats, dominant males may acquire larger territories containing rare pockets of preferred habitat, causing an increase to the relative cost of subordination. In this case, dominant males may be better able to buffer the impact of a poor habitat compared to subordinates who obtain the poorest territories in an already resource-depauperate landscape. Hence, it is also possible that dominants are better suited to living in resource-poor environments (e.g., Carascal et al. 1998).

It is, therefore, possible that both the cost of subordination (low resource availability), and the cost of dominance (high resource requirements) vary with habitat quality, with resulting impacts on the relative benefit of being mated to dominant males. The primary aim of this study was to assess how the provisioning benefits associated with dominance are affected by habitat quality. I investigated the patterns of reproductive effort and body condition among breeding dominant and subordinate black-capped chickadees nesting in Disturbed or Undisturbed habitat. Several lines of evidence suggest that the Disturbed habitat has low food availability (Chapter 1); we can now add to these differences in fattening strategies (Chapter 2) and differences in the expression of condition-dependent signals (Chapter 3). In the present study, provisioning effort was indexed by counting male feeding trips to the cavity during the first six days of nestling care, when the proportion of provisioning trips made by males is greatest (Smith 1991). Body condition was assessed by measuring their relative mass (corrected for size) during the nestling period. I also measured hematocrit levels to compare the metabolic workloads (Carpenter 1973; Saino et al. 1997a, 1997b).

4.2 Methods

For this study, males were initially trapped and marked as described in Section 2.2.1, and the classification of male rank and territory habitat proceeded as described in Section 3.2.

4.2.1 Male provisioning effort

Male provisioning observations were made in the breeding seasons of 2001 and 2003. Nests were typically located during the period of nest excavation, and the progression through the nesting cycle was monitored. When females are laying, pairs are highly conspicuous as females beg for food continuously during the day (Smith 1991). As the laying period progressed, territories were checked every second day to get an estimate of when females initiated incubation. Chickadee incubation period is approximately 12-13 days (Smith 1991). Nest monitoring commenced two days prior to the predicted hatch day. Nests were checked every second day until evidence of hatching was documented, occasionally through direct observation into the nest cavity, but primarily by noting behavioural changes in the parents. Prior to hatching, males typically deliver food items to females at low rates of one to three trips per hour. Behavioural evidence of hatching was determined by (1) male delivery rates increasing to more than three food deliveries per hour, (2) males entering the cavity with food, or (3) either parent removing fecal sacs. The reliability of hatch day estimates appeared to be acceptable, as judged by nestling development when the nests were accessed for banding nestlings six to ten days later.

To investigate male provisioning rates, nests were observed for two one-hour observation periods. Observations were limited to two hours in order to maximize the number of territories that could be visited. Chickadees are relatively synchronous in their breeding activities, so it was logistically difficult to conduct more extensive observations throughout the nesting period without sacrificing sample size. All observers were experienced at reading leg bands. During nest watches, the observer was positioned far enough from the cavity to avoid disrupting chickadee behaviour (>10m). The first one-hour observation took place when nestlings were three days old and the second took place when they were six days old. During nest observations, all feeding trips made by the male, and all the trips by the female were counted. Chickadees often build nest cavities well above the ground in the upper canopy, which can occasionally make nest observations difficult. However, parent identification could readily be determined, and in most cases it was possible to see whether food items were delivered to the nest. Males were never observed entering the cavity without food, and it was assumed that all male visits to the cavity were feeding events. Trips were also noted for females, however, these data are less reliable as females were often seen returning to the cavity without food items. Hence, I did not directly analyse female provisioning rates in this study; despite this, the number of feeding trips made by the male were compared with the total number of visits made by the female (regardless of whether she had food or not) as a conservative estimate of the relative contribution of male provisioning in this species. For the main analysis of provisioning rates, I summed day 3 and day 6 data for a total of two hours of observation per territory.

Several additional predictor variables were considered in the design of the data collection or for controlling statistically: time of day, temperature, date, and brood size. Because I aimed to pool the two hours of observation, time of day was primarily controlled for by conducting all observations between 7:30 am and 11:30 am. The start time was noted in order to statistically control for this effect in separate analyses if necessary. The start time for day 3 and day 6 observations was alternated between early (7:30 – 8:30) and late (9:30-10:30) where possible, so that cases would not be biased by time of day. In addition, start times were balanced between social ranks and habitats where possible. Hourly temperature data were obtained from an Environment Canada weather station located at the Prince George airport (elevation 690m), ~10.5 km east of the study site and the importance of daily differences in temperature was tested. The effect of brood size could be assessed for a sub-sample of nests accessed after the provisioning trials were completed (n = 22). I controlled for date statistically by including this variable as a covariate in the main analysis of pooled data.

4.2.2 Male captures

During the breeding seasons of 2002 and 2003, males were caught at the nest cavity during the nestling period when nestlings were four to eight days old. Upon capture, males were weighed using a Pesola (Pesola AG, Baar, Switzerland) spring balance (to 0.1 g), and their tarsus length was measured with vernier calipers (to 0.1 mm). Furcular fat stores were scored from 0 to 5 after Gosler (1996). To measure hematocrit levels, a ~ 50 µl blood sample was drawn with a heperinized capillary tube from a puncture in the brachial vein and stored in a cooler until the sample could be processed later in the day. Blood samples were centrifuged for 11 minutes at 11, 500 rpm. Hematocrits were measured as the total packed cell volume (not including the buffy coat layer) divided by the total volume of blood. Male body condition was estimated as the residuals from a regression of body mass on tarsus length. For territories where I sampled both male body condition and provisioning rates (in

2003), male captures always took place after male provisioning observations were completed. All captures and measurements were performed by the same person. All procedures were approved by the Animal Care and Use Committee of the university in compliance with Canadian Council on Animal Care guidelines.

4.2.3 Analysis

Two-factor analysis of variance (ANOVA; Zar 1999) was used to assess the effects of habitat and rank on the male capture data. To control for continuous ‘nuisance’ variables that could impact male provisioning rates (e.g., date), I used analysis of covariance (ANCOVA; Tabachnick and Fidell 2001). Because sample sizes were small, I avoided using complicated models with many covariates (Tabachnick and Fidell 2001); consequently, only one covariate was included in provisioning ANCOVA model. To select a covariate, I ran simple linear regressions and selected the covariate, which showed the most significant relationship with male provisioning rates. Type III sums of squares were used in all analyses (Tabachnick and Fidell 2001). All statistical procedures were run with Statistica 6.1 (StatSoft Inc 1998). Males that were included in more than one field season were treated as independent samples (n = 4 in the condition data set; n = 6 in the provisioning data set). I report means and the standard error of the means, except for ANCOVA results, where adjusted means are shown.

4.3 Results

A two factor ANOVA suggested a weak tendency for dominant males to have larger tarsi than subordinate males (dominants: 19.1 mm ± 0.13; subordinates: 18.8 mm ± 0.13; $F_{1, 30} = 2.9$, $P = 0.10$), but there was no relationship between tarsus size and habitat type

(Undisturbed: 19.0 mm ± 0.12; Disturbed: 18.9 mm ± 0.15; $F_{1, 31} = 0.22$, $P = 0.65$). Dominant males were significantly heavier than subordinates (dominants: 11.4 g ± 0.12; subordinates: 10.9 g ± 0.08; $F_{1, 31} = 13$, $P = 0.001$), but the absolute mass of males in either habitat did not differ (Undisturbed: 11.2 g ± 0.13; Disturbed: 11.1 g ± 0.10; $F_{1, 31} = 0.035$, $P = 0.85$). There was a significant relationship between mass and tarsus length (linear regression: $F_{1, 35} = 10$, $r^2 = 0.23$, $P = 0.003$) and the residuals were saved for analysis. In a factorial ANOVA, there was no indication of a habitat-rank interaction on residual mass ($P = 0.28$), so this term was dropped from the model. Residual mass (body condition) was significantly greater among dominant males compared with subordinates ($F_{1, 30} = 7.2$, $P = 0.012$), but habitat did not contribute to variation in residual mass ($F_{1, 30} = 0.069$, $P = 0.80$; Figure 4.1a).

Hematocrit levels varied with habitat and rank (Figure 4.1b), and there was no evidence of a habitat-rank interaction ($P = 0.85$), which was removed from the model. The two-factor ANOVA showed that dominant males had larger hematocrits than subordinates (dominants: 0.51 ± 0.007; subordinates: 0.49 ± .006; $F_{1, 27} = 7.0$, $P = 0.013$), and males living in the Disturbed habitat tended to have larger hematocrits than their counterparts living in the Undisturbed habitat, although this result was not quite statistically significant (Undisturbed: 0.49 ± 0.006; Disturbed: 0.51 ± 0.007; $F_{1, 27} = 4.2$, $P = 0.051$). Furcular fat stores were low in all breeding males (ranging from 0 to 1) and were not analysed.

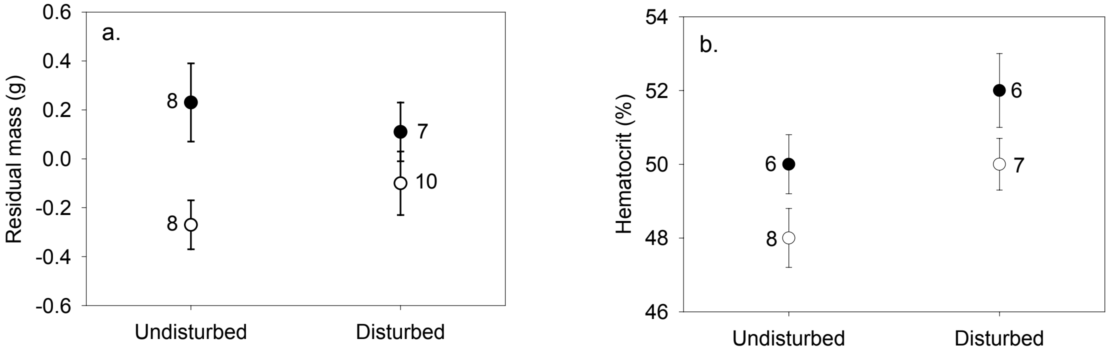

Figure 4.1 The effects of habitat on (a) residual mass and (b) hematocrits, of breeding dominant (●) and subordinate (○) male chickadees. Means (± SE) and sample sizes are shown.

During the observation periods, females spent a large portion of their time brooding (35 ± 1.9 min/hour on day three and 25 ± 2.2 min/hour on day six). Among all trials, males made the majority (65%) of the total trips to the nest. Because many of the trips made by females were not food delivery trips, the average male contribution is undoubtedly greater than 65% during the first six days of nestling provisioning.

After combining the data from three-day and six-day observations, the total number of male provisioning trips varied from six to 23 trips in two hours. The number of provisioning trips was not significantly related to brood size (Linear Regression; $F_{1, 20} = 2.1$, $r^2 = 0.05$, $P= 0.17$), but there was a linear decrease in provisioning associated with date (Linear Regression; $F_{1, 38} = 4.6$, $r^2 = 0.12$, $P = 0.039$). To further investigate whether brood size was having considerable effects on the provisioning rates, I first analysed the overall number of provisioning trips made by males in relation to habitat and rank using a model that tested both factors of interest (habitat and rank) while controlling for both covariates (date and brood size; n = 21). Brood size was not a significant predictor of male provisioning in this model ($F_{1,15} = 1.8$, $P = 0.20$), although date was ($F_{1,15} = 8.9$, $P = 0.0053$). I dropped brood size from the model, which allowed me to include the full sample of males in an ANCOVA model controlling for date only (n = 37); conclusions were not altered by doing so. I checked for homogeneity of regression by first including covariate-factor interaction terms. Interaction terms between the covariate (date) and either rank or habitat were not significant (both $P > 0.7$) and were dropped. In the final model, total number of provisioning trips did not show a significant relationship with either habitat or rank, however there was a strong habitat-rank interaction (Table 4.1; Figure 4.2). The interaction showed a large effect of rank in the Disturbed habitat, where dominant males made more trips in two hours than subordinate males, whereas, there was no indication of a rank effect in the Undisturbed habitat.

Table 4.1 Results from ANCOVA model controlling for date, showing the effect of habitat and dominance on the number of male food deliveries in two hours of observation.

Source	d.f.	SS	*F*	*P*
Habitat	1	11.8	0.82	0.37
Rank	1	18.5	1.3	0.26
Habitat-rank interaction	1	131	9.1	0.005
Date	1	129	8.9	0.005
Error	32	460		

I also considered analysing the provisioning data separately for day-three and day-six observations as this allowed me to control for two other potential covariates (temperature and time of day), which I could not consider when data were pooled. Only one univariate regression significantly predicted provisioning rate: time of day on day 3 observations ($F_{1,44} = 5.3$, $r^2 = 0.11$, $P = 0.027$). An ANCOVA model that controlled for time of day (n = 44) found significantly lower values in day 3 food deliveries in the Disturbed habitat ($F_{1,39} = 4.2$, $P = 0.046$) in addition to a significant habitat-rank interaction ($F_{1,39} = 5.7$, $P = 0.021$). Like the previous analysis, the interaction term suggested a large rank effect in the Disturbed habitat due to low provisioning rates of subordinates.

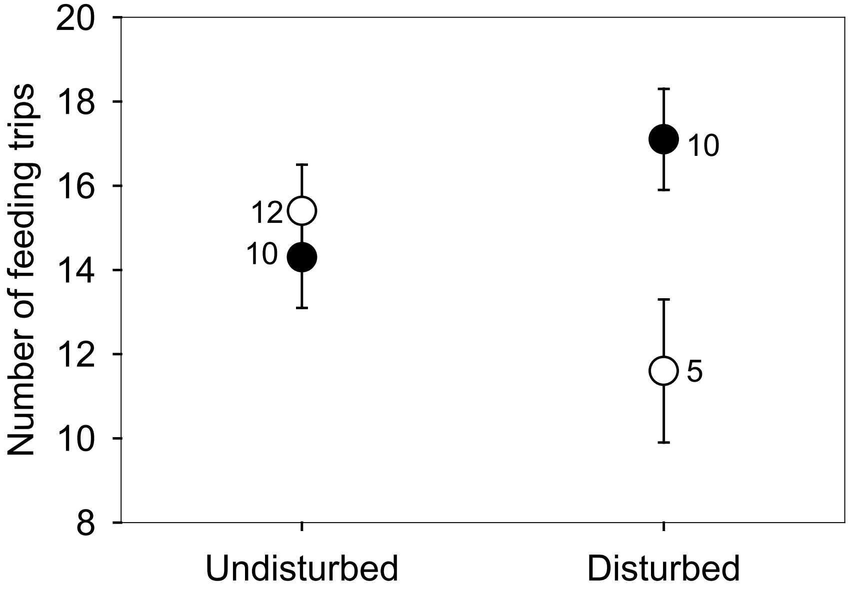

Figure 4.2 Mean (± SE) number of provisioning trips in 2 hours of observation for dominant (●) and subordinate (○) males living in Undisturbed and Disturbed habitats after controlling for date. Sample sizes are noted.

4.4 Discussion

It has been proposed that the energetic costs of dominance may cause dominant males to perform poorly as social mates in locally poor environments (Qvarnström and Forsgren 1998). Life-history theory predicts that low resource supply could impact either somatic or reproductive investments (Stearns 1992); hence, if dominant males make relatively poor mates in poor environments, then this could occur through impacts to either their body condition or their ability to provision young. In this study, I found little evidence that habitat altered somatic investments, however, the provisioning benefit associated with social dominance was affected. In contrast to the predictions of Qvarnström and Forsgren (1998), I found that dominant males offered relatively larger provisioning benefits in a locally poor habitat.

At the UNBC study site, Disturbed habitat is relatively poor compared to the Undisturbed habitat apparently due to a reduction in food availability (Chapter 5). If food supply is low, then males will have to work harder to find adequate food for self-maintenance and reproduction (Godfrey 2003). I found that hematocrit levels were generally higher among dominant males, and, although not quite significant, among males living in the Disturbed habitat, with the effects of habitat and rank being additive.

Hematocrits represent the oxygen-carrying capacity of the blood, and larger hematocrit levels are thought to indicate higher workloads or faster metabolisms rather than overall condition. Hematocrits are poor indicators of body condition in nestlings and adults (Dawson and Bortolotti 1997a, 1997b), however, they have often been found to be elevated in association with factors that increase metabolic workloads; for example birds species that are strong flyers may have elevated hematocrits compared with those that are week flyers

(Carpenter 1975). Likewise, elevated hematocrits are associated with degree of tail ornamentation thought to impede flight performance (Saino et al. 1997a, 1997b).

In the present study, I found evidence for both habitat and rank effects on hematocrit levels. Socially dominant males probably have raised hematocrits simply because they have higher metabolic rates; dominant individuals have larger oxygen consumption rates (Hogstad 1987; Røskaft et al. 1986), which may lead to greater erythrocyte production. Dominant males may also have elevated hematocrits if they have higher levels of circulating androgens (Sturkie 1976). Importantly, I found that hematocrits also tended to be raised among all males breeding in the Disturbed habitat. Although, this result is not quite statistically significant, the magnitude of the effect might be biologically important. Hematocrit values had a total range of 10%; hence the 2% difference seen between habitats is relatively large. Furthermore, this trend fits well with theories of how energy expenditure relate to habitat quality. It is possible that elevated hematocrits indicate a greater workload incurred through reduced foraging efficiency in the Disturbed habitat; males need to work harder to find adequate amounts of food (Stearns 1992). Previous work has shown an association between habitat and hematocrit (Ots et al. 1988), however habitat-hematocrit associations are generally elusive in the scientific literature (Dawson and Bortolotti 1997a and references therein). The direction of the potential habitat-hematocrit association detected in this study is consistent with the idea that daily energy expenditure can be used to index habitat quality (Godfrey 2003).

Individuals with poor access to resources should be less able to simultaneously invest in both self-maintenance and reproduction; as such, I expected a reduction in body condition and/or provisioning effort among birds living in the Disturbed habitat. Previous work has suggested that birds opt to reduce reproductive investments when energy budgets are strained (Spencer and Bryant 2002). I found large effects of social status on body condition of breeding males (with higher condition associated with higher rank), but there was little indication that body condition was affected by habitat quality. This suggests that males living in the Disturbed habitat are still maintaining relatively normal levels of self-maintenance even though they may be working harder to find food. In contrast to body condition, I found evidence that investments into reproduction are reduced in the Disturbed habitat. The reduction in provisioning associated with habitat quality was not dramatic, however, because dominant males in the Disturbed habitat managed to maintain adequate provisioning rates. Nonetheless, this study supports the general idea that reproductive investments are reduced in order to maintain adequate somatic investments (Spencer and Bryant 2001).

The primary issue that I intended to resolve in this study was to distinguish between two contrasting hypotheses concerning the phenotypic quality of dominant males in good and poor environments. Dominant males have raised metabolic rates (Hogstad 1987; Røskraft et al. 1986), which may make their cost of self-maintenance relatively high (e.g., Swaddle and Witter 1994). My data are consistent with the idea that dominants have raised energy expenditures because they had elevated hematocrits compared with subordinates. Because dominance comes with the cost of increased energy demands, it has been suggested that dominants may make poor mates in unfavourable environments (Qvarnström and Forsgren 1998). Alternately, dominant males may be better able to buffer the effects of habitat quality in the breeding season as they have access to the best resources within an environment (e.g., Carascal et al. 1998).

In this study, I found no evidence that dominants were handicapped in a poor environment because they maintained adequate body condition, and still provisioned at high rates. Contrary to the idea dominants are poor mates in low-quality environments (Qvarnström and Forsgren 1998), I found that provisioning benefits associated with mating with a dominant male were proportionately greater in the relatively poor Disturbed habitat. It is possible, but unlikely, that using food delivery rate as an index of male provisioning is flawed, because I could not control for the amount of food delivered by males in each visit to the nest. In another songbird species, the house finch (*Carpodacus mexicanus*), food delivery rates are known to be predictive of total prey biomass delivered (Nolan et al. 2001). Furthermore, the validity of these results is reinforced by the fact that these results parallel findings in another study from this banded population, which compared levels of nesting success among dominant and subordinate pairs living in either habitat (Fort and Otter in press). In that study, nest abandonment was the leading cause of nest failure, and was particularly common among subordinate males in the Disturbed habitat, leading to a large rank effect in the Disturbed habitat (Fort and Otter in press). The similarity between these results suggest that subordinate males suffer disproportionate losses to their reproductive success in the Disturbed habitat.

Although I found no indication that dominant males suffered low body condition in the Disturbed habitat, it is possible that they show greater sensitivity to habitat quality at other times of the year. Why, and especially when, metabolic rates differ most between dominants and subordinates is poorly understood. Not surprisingly, metabolic rate has been experimentally linked to levels of testosterone (Buchanan et al. 2001). If larger testosterone titre is the primarily reason why dominant males have raised metabolic rates, it is likely that this cost is minimal (although still present based on my hematocrit results) during the nestling period when testosterone levels are close to baseline (Foerster et al. 2002). In this case, greater impacts of habitat quality on dominant male energy budgets would exist earlier in the year during the period of intense sexual advertisement, territory establishment and courtship feeding, when testosterone titres are elevated to maximal levels. At this time of year, costs to females may include a low level of mate provisioning during the laying period or an increased chance of being widowed (Qvarnström and Forsgren 1998). I found evidence that dominants are at a disadvantage during early stages of reproduction because dominant males advertised in the dawn chorus at unusually low levels in the Disturbed habitat, compared with subordinate males who were apparently unaffected by habitat quality (Chapter 3). I do not know if courtship-provisioning effort is reduced at this time of year, although preliminary studies show that females in the Disturbed habitat have higher food solicitation call rates (H.v.O. and K.A. Otter, unpublished data), which has been associated with increased hunger levels in other species (Tobias and Sneddon 2002).

I conclude that dominant males can provide greater provisioning benefits than subordinates in poor environments while still maintaining adequate levels of somatic investment during the nestling period. With chickadees, the dominant phenotype is sexually selected (Otter and Ratcliffe 1996; Otter et al. 1998), and appears to be superior in other facets of phenotypic quality (Otter et al. 1997; Otter et al. 1999). The provisioning pattern found in this study is very similar to the patterns found for reproductive success (Fort and Otter in press) and taken together, these studies strongly suggest that the dominant phenotype will be particularly favoured in locally poor habitats where competitive phenotypes gain a larger relative advantage in the breeding season. I suggest that future studies assessing habitat-related costs associated with social dominance should target the early spring when testosterone levels are elevated, and food is still scarce.

5. GENERAL DISCUSSION

Habitat heterogeneity can lead to regional differences in reproductive performance within populations. Previous research has demonstrated that the breeding performance of chickadees in this banded population was affected by the habitat in which they bred, with high rates of nest abandonment observed in the Disturbed habitat (Fort and Otter in press). Low food abundance in the Disturbed habitat was thought to be responsible for this pattern. All results produced by the present research are consistent with the hypothesis that nutritional resources are lacking in the Disturbed habitat compared with the Undisturbed habitat: (1) in winter, chickadees living in the Disturbed site carried larger fat stores (Chapter 2), a strategy that Parids and other bird species use when food availability is perceived to be less certain (Ekman and Lilliendahl 1993; Bednekoff and Krebs 1995; Witter and Swaddle 1995; Gosler 1996); (2) chickadees in the Disturbed habitat generally had reduced song output in the dawn chorus (Chapter 3) as expected when habitats are lacking in food abundance (Hill 1995; McGregor et al. 2000); (3) hematocrits were generally elevated in breeding males in the Disturbed habitat (Chapter 4), which matches predictions of increased daily energy expenditures being elevated in resource-poor environments (Godfrey 2003); and, (4) levels of paternal care tended to be reduced among subordinate males in the Disturbed habitat (Chapter 4), which also indicates low food resources (e.g., Zanette et al. 2001). Further evidence for the apparent lack of food in Disturbed habitat was demonstrated by a study that found differences in feeder-use during winter (Appendix 1), and another which found differences in the begging demands of females in either habitat (H.v.O. and

K.A. Otter unpublished data). Together, these observations consistently suggest that food abundance is greater in the Undisturbed habitat compared with the Disturbed habitat.

5.1 Habitat distribution

Before addressing the impact of habitat on chickadees, it was necessary to investigate habitat settlement during natal dispersal to determine whether chickadees with high-quality phenotypes are more likely to settle in favourable habitats as predicted by the ideal despotic distribution (Fretwell and Lucas 1970), making inferences about habitat impacts more complex. Previous attempts to unravel this issue in Parids have been inconclusive (Lemel 1989) and habitat selection during natal dispersal is poorly understood. I examined this issue by determining whether recruitment into either habitat depended on natal nutrition, a measure of pre-settlement quality (Chapter 2).

I found evidence for assortative habitat distributions among female but not male recruits, which is consistent with the sex-differences in dispersal behaviour previously described in Parids (Greenwood et al. 1979; Nilsson 1989). Regardless of the mechanism, the findings in Chapter 2 suggest that there is no difference in the pre-settlement quality of males settling in either habitat; consequently any differences in life-history traits appear to be caused by habitats *post*-settlement.

These results raise one potential complication with regards to the impacts of habitat on male behaviour. Females settled in the Disturbed habitat may provide poor maternal care because they are of lower quality. Therefore, males in the Disturbed habitat may have to compensate for low levels of maternal contribution, which could potentially explain some of the resulting impacts of habitat quality seen in males during the breeding season.

Consequently, low quality females essentially add to the difference in ‘resources’ available in either habitat, thereby amplifying difference in ‘habitat’ quality.

5.2 Life history investments in locally poor habitats

Males that settle in a poor habitat may find themselves faced with challenges and be forced to make selective compensations in their life history investments. It is unlikely that males in resource-poor habitats simply reduce all life-history traits in a parallel fashion (Stearns 1992); rather, resources are probably shunted towards prioritised investments at the expense of competing investments (e.g., Spencer and Bryant 2002). As such, the impacts of reduced resource availability are likely to result in diminished investments in low-priority life-history traits in order to maintain adequate investments in high-priority traits.

Somatic investments are probably prioritised over reproductive investments in songbirds (e.g., Spencer and Bryant 2002) because higher body condition helps assure future survival, and therefore fitness (e.g., Takaki et al. 2001). No impacts of local habitat quality were detected on the body condition of chickadees in winter or during the late breeding season. In contrast to somatic traits, differences were seen in reproductive investments; for example in levels of sexual advertisement and paternal care (Chapters 3 and 4). The combined results in this thesis generally support the idea that somatic investments are prioritised over reproductive investments in breeding songbirds.

To best understand how investments are prioritised, comparisons should be made on multiple traits during the same time period (e.g., Chapter 4). Unfortunately, comparisons of the impacts of habitat to multiple life-history traits during the fertile period could not be made in this thesis (Chapter 3) when some of the most interesting tradeoffs may exist. The fertile period may be one of the most energetically stressful periods for males. At this time of year, chickadees are only just beginning to enjoy greater food abundance after a winter of limited food supply. Concurrently, male chickadees are subjected to a number of new stressors to their energy budgets including (1) territory acquisition and defence, (2) nest excavation, (3) providing laying females with food, (4) maximal testosterone titres, and (5) sexual advertisement. Hence male chickadees allocate resources to several life-history traits at this time. I found that males reduced costly sexual advertisement in the Disturbed habitat, suggesting the levels of advertisement are sensitive to habitat quality. How other investments are impacted at this time remains unknown, as logistic constraints prevented catching sufficient males during this time period in a manner that would not influence somatic measurements (e.g., catching without the use of supplemental feeding – cage traps - or inducing elevated metabolism – mistnetting via playback). An experimental study of life history trade-offs at this time of year would promise to be especially interesting as males must balance somatic investments against investments to within-pair reproduction and among-pair sexual advertisement.

5.3 Habitat-rank interactions

In their review of costs associated with being mated to dominant males, Qvarnström and Forsgren (1998) pointed out that dominant males have raised metabolic rates, which potentially disadvantages them in poor habitats by reducing their survivorship. Essentially, this idea predicts a habitat-rank interaction in phenotypic quality whereby the quality of dominant males is relatively high in typical habitats, and relatively low in poor habitats. Although these authors specifically predicted that raised energy budgets would affect survivorship, it is reasonable to suggest that impacts could be seen in other life history investments, including parental care or sexual advertisement, if these traits are differentially lowered to preserve somatic investment necessary for survival.

I did not specifically assess whether or not dominant males suffer reduced survivorship in the Disturbed habitat; however, incidental observations suggest that they do not. Only four dominant males disappeared during the breeding season in the course of this thesis fieldwork: two in Disturbed, and two in Undisturbed habitats (H.v.O. unpublished data). Although these observations are few, they illustrate that the risk of starvation of dominant males is low, and therefore not overly important. Furthermore, no evidence was uncovered to suggest that dominants are sacrificing somatic investments in this habitat (discussed above). This suggests that there is no reason to suspect that dominant males risk either immediate starvation or future survivorship. Instead, they seem to reduce reproductive investments (extra-pair advertisement) when resources are limited. Even if females mated to dominant males are widowed, they have the best chances of rapidly acquiring replacement mates from subordinates when their mates are lost during the fertile period (Otter and Ratcliffe 1996; H.v.O personal observation). Consequently, the habitat-rank interaction implied by Qvarnström and Forsgren (1998) is more likely to occur in reproductive investments, which are likely to be of consequence to females.

Habitat impacts on two costly reproductive investments were assessed: sexual advertisement and paternal care. As expected, I found habitat-rank interactions in both of these traits, but the nature of these interactions were very different. In the study of sexual advertisement (Chapter 3), dominant males were more sensitive to local habitat quality than subordinates. Dominants had relatively high levels of advertisement in the Undisturbed habitat and relatively low levels of advertisement in the Disturbed habitat. This pattern fits nicely with predictions of Qvarnström and Forsgren (1998). In contrast, the study of paternal care (Chapter 4) found that later in the breeding season, subordinates were more sensitive to habitat quality, with dominant males providing relatively greater provisioning benefits in the Disturbed habitat. These latter results paralleled another study showing a similar pattern in nesting success in the same study population (Fort and Otter in press), which suggests a link between male quality and reproductive success.

The opposing nature of these findings could be explained by several hypotheses (see Chapter 3), including seasonal changes to energy budgets. In terms of energy budgets, these findings suggest that the absolute resource benefit attained by dominant males fluctuates seasonally. As such, the energetic profit of dominance may be insufficient to overcome the energetic costs of dominance in the Disturbed habitat in early spring. Later in the season, the resource benefit attained by dominant males grows as food abundance increases, possibly resulting from delayed differences in territory quality. Alternate explanations outlined in Chapter 3 could also explain why dominant males show such large sensitivity to habitat quality in their level of advertisement. Because of the puzzling nature of these findings, these hypotheses warrant study. Regardless of the mechanism, these results suggest that the reliability of condition-dependent signals may diminish in locally poor habitats.

A potential consequence of the lost reliability of advertisement signals in the Disturbed habitat could be maladaptive mate choice decisions. Dominant males normally have low levels of extra-pair young in their own nests (Otter et al. 1998). By dropping their level of sexual advertisement to minimal levels, dominant males living in the Disturbed habitat may lose their assurance of paternity. Females in this species regularly seek extra-pair copulations (Smith 1988), but the assurance of paternity held by dominants (Otter et al. 1998) is subject to change when vocal signals are manipulated (Mennill et al. 2002). Therefore, because the dawn chorus is thought to be the forum when females compare male quality (Otter and Ratcliffe 1993), I suspect that local habitat heterogeneity may have impacts on mate choice. Females mated to dominant males may second-guess the quality of their mates and seek extra-pair copulations. Alternately, if females detect that signals are unreliable, they may stop seeking extra-pair copulations altogether as they can no longer reliably compare males. The impact of habitat quality on extra-pair behaviours awaits assessment.

To conclude, the findings of this thesis demonstrate that local habitat heterogeneity can affect state-dependent life history investments. Only reproductive investments appeared to be reduced in the relatively poor local habitats, while somatic investments were maintained at normal levels. Interestingly, males from different social ranks appeared to make these reproductive adjustments in different traits. Dominant males reduced costly sexual advertisement, while subordinate males reduced parental effort. Therefore, dominant males potentially stand to lose their assurance of paternity, while subordinate males may have low offspring survivorship. Future work should investigate whether these findings result from seasonal rank-dependent differences in energetic states, or whether they reflect different strategies used by dominant and subordinate males.

REFERENCES

Alatalo, R. V., C. Glynn, and A. Lundberg. 1990. Singing rate and female attraction in the pied flycatcher: an experiment. *Animal Behaviour* 39: 601-603.

Andrén, H. 1990. Despotic distribution, unequal reproductive success, and population regulation in the Jay *Garrulus glandarius* L. *Ecology* 71: 1796-1803.

Badyaev, A. V., and G. E. Hill. 2002. Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. *Behavioral Ecology* 13: 591-597.

Bayne, E. M., and K. A. Hobson. 2001. Effects of habitat fragmentation on pairing success of ovenbirds: the importance of male age and floater behavior. *Auk* 118: 380-388.

Bednekoff, P. A., and J. R. Krebs. 1995. Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology* 9: 457-462.

Blount, J. D., N. B. Metcalfe, K. E. Arnold, P. F. Surai, G. L. Devevey, and P. Monaghan. 2003a. Neonatal nutrition, adult antioxidant defences and sexual advertisement in the zebra finch. *Proceedings of the Royal Society of London B* 270: 1691-1696.

Blount, J. D., N. B. Metcalfe, T. R. Birkhead, and P. F. Surai. 2003b. Carotenoid modulation of immune function and sexual attractiveness in zebra finches. *Science* 300: 125-127.

Bortolotti, G. R., R. D. Dawson, and G. L. Murza. 2002. Stress during feather development predicts fitness potential. *Journal of Animal Ecology* 71: 333-342.

Bryant, D. M., and A. V. Newton. 1994. Metabolic costs of dominance in dippers, *Cinclus cinclus*. *Animal Behaviour* 48: 447-445.

Buchanan, K. L., M. R. Evans, A. R. Goldsmith, D. M. Bryant, and L. V. Rowe. 2001. Testosterone influences basal metabolic rate in male house sparrows: a new cost of dominance signalling? *Proceedings of the Royal Society of London B* 268: 1337-1344.

Buchanan, K. L., K. A. Spencer, A. R. Goldsmith, and C. K. Catchpole. 2003. Song as an honest signal of past developmental stress in the European starling (*Sturnus vulgaris*). *Proceedings of the Royal Society of London B* 270: 1149-1156.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, M. C. E. McNall, and G. E. J. Smith. 1997. *Birds of British Columbia volume 3*. UBC Press, Vancouver.

Carrascal, L. M., J. C. Senar, I. Mozetich, F. Uribe, and J. Domenech. 1998. Interactions among environmental stress, body condition, nutritional status, and dominance in great tits. *Auk* 115: 727-738.

Carpenter, F. L. 1975. Bird hematocrits: effects of high altitude and strength of flight. *Comparative Biochemical Physiology A* 50: 415-417.

Dawson, R. D., and G. R. Bortolotti. 1997a. Are avian hematocrits indicative of condition? American kestrels as a model. *Journal of Wildlife Management* 61: 1297-1305.

Dawson, R., and G. Bortolotti. 1997b. Variation in hematocrit and total plasm proteins of nestling American kestrels (*Falco sparverius*) in the wild. *Comparative Biochemistry and Physiology* 117: 383-390.

Desrochers, A. 1989. Sex, dominance, and microhabitat use in wintering black-capped chickadees: a field experiment. *Ecology* 70: 636-645.

Dhondt, A. A., F. Adriaensen, E. Matthysen, and B. Kempenaers. 1990. Nonadaptive clutch sizes in tits. *Nature* 348: 723-725.

Dias, P. C., and J. Blondel. 1996. Local specialization and maladaptation in the mediterranean blue tit (*Parus caeruleus*). *Oecologia* 107: 79-86.

Eeva, T., E. Lehikoinen, and M. Rönkä. 1998. Air pollution fades the plumage of the great tit. *Functional Ecology* 12: 607-612.

Ekman, J. 1990. Alliances in winter flocks of willow tits; effects of rank on survival and reproductive success in male-female associations. *Behavioral Ecology and Sociobiology* 26: 239-245.

Ekman, J., and C. E. H. Askenmo. 1984. Social rank and habitat use in willow tit groups. *Animal Behaviour* 32: 508-514.

Ekman, J., S. Eggers, M. Griesser, and H. Tegelström. 2001. Queuing for preferred territories: delayed dispersal of Siberian jays. *Journal of Animal Ecology* 70: 317-324.

Ekman, J. B., and K. Lilliendahl. 1993. Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. *Behavioral Ecology* 4: 232-238.

Faivre, B., A. Grègoire, M. Préault, F. Cézilly, and G. Sorci. 2003. Immune activation rapidly mirrored in a secondary sexual trait. *Science* 300: 103.

Ficken, M. S., C. M. Weise, and J. W. Popp. 1990. Dominance rank and resource access in winter flocks of black-capped chickadees. *Wilson Bulletin* 102: 623-633.

Foerster, K., A. Poesel, H. Kunc, and B. Kempenaers. 2002. The natural plasma testosterone profile of male blue tits during the breeding season and its relation to song output. *Journal of Avian Biology* 33: 269-275.

Fort, K. T. 2002. The effects of habitat disturbance on the reproductive behaviour of the black-capped chickadee (*Poecile atricapilla*). Pages 111. University of Northern British Columbia, Prince George.

Fort, K. T., and K. A. Otter. in press. The impact of habitat disturbance on reproduction of chickadees. *Auk* .

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16-36.

Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection. *American Naturalist* 104: 1-24.

Godfrey, J. D. 2003. Potential use of energy expenditure of individual birds to assess quality of their habitats. *Science for Conservation* 214: 11-24.

Godfrey, J. D., and D. M. Bryant. 2000. State-dependent behaviour and energy expenditure: an experimental study of European robins on winter territories. *Journal of Animal Ecology* 2000: 301-313.

Gosler, A. G. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. *Journal of Animal Ecology* 65: 1-17.

Gosler, A. G., and T. Carruthers. 1999. Body reserves and social dominance in the great tit *Parus major* in relation to weather in southwest Ireland. *Journal of Avian Biology* 30: 447-459.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144: 517-546.

Greenwood, P. J., P. H. Harvey, and C. M. Perrins. 1979. The role of dispersal in the great tit (*Parus major*): causes, consequences and heritability of natal dispersal. *Journal of Animal Ecology* 48: 123-142.

Griffith, S. C. 2000. A trade-off between reproduction and a condition-dependent sexually selected ornament in the house sparrow *Passer domesticus*. *Proceedings of the Royal Society of London B* 267: 1115-1119.

Grubb, T. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* 106: 314-320.

Grubb, T. C. 1995. Ptilochronology: a review and prospectus. *Current Ornithology* 12: 89-114.

Grubb, T. 1991. A deficient diet narrows growth bars on induced feathers. *Auk* 108: 725-727.

Gustafsson, L., A. Qvarnström, and B. C. Sheldon. 1995. Trade-offs between life history traits and a secondary sexual character in male collared flycatchers. *Nature* 375: 311-313.

Haldane, J. B. S. 1956. The relation between density regulation and natural selection. *Proceedings of the Royal Society of London B* 145: 306-308.

Hansen, I. J. 2003. Communication breakdown: habitat influences on the communication networks and transmission of song in the black-capped chickadee (*Poecile atricapillus*). Pages 33. University of Northern British Columbia, Prince George.

Hay, J. M., P. R. Evans, R. M. Ward, and K. C. Hamer. 2004. Poor nutritional condition as a consequence of high dominance status in the coal tit *Parus ater*. *Ibis* 146: 103-107.

Hill, G. E. 1995. Ornamental traits as indicators of environmental health. *BioScience* 45: 25-31.

Hill, G. E. 2000. Energetic constraints on expression of carotenoid-based plumage coloration. *Journal of Avian Biology* 31: 559-566.

Hogstad, O. 1987. It is expensive to be dominant. *Auk* 104: 333-336.

Hogstad, O. 1989. Social Organization and dominance behavior in some *Parus* species. *Wilson Bulletin* 101: 254-262.

Hogstad, O. 1992. Mate protection in alpha pairs of wintering willow tits, *Parus montanus*. *Animal Behaviour* 43: 323-328.

Holmes, R., P. Marra, and T. Sherry. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): Implications for population dynamics. *Journal of Animal Ecology* 65: 183-195.

Hõrak, P., I. Ots, H. Vellau, C. Spottiswoode, and A. P. Møller. 2001. Carotenoid-based plumage coloration reflects hemoparasite infection and local survival in breeding great tits. *Oecologia* 126: 166-173.

Hõrak, P., H. Vellau, I. Ots, and A. P. Møller. 2000. Growth conditions affect carotenoid-based plumage coloration of great tit nestlings. *Naturwissenschaften* 87: 460-464.

Huhta, E., J. Jokimaki, and P. Rahko. 1998. Distribution and reproductive success of the pied flycatcher *Ficedula hypoleuca* in relation to forest patch size and vegetation characteristics; the effect of scale. *Ibis* 140: 214-222.

Hunter, A. F., and J. S. Elkinton. 2000. Effects of synchrony with host plant on populations of a spring-feeding lepidopteran. *Ecology* 81: 1248-1261.

Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology* 74: 2204-2214.

Kilpimaa, J., R. V. Alatalo, and H. Siitari. 2003. Trade-offs between sexual advertisement and immune function in the pied flycatcher (*Ficedula hypoleuca*). *Proceedings of the Royal Society of London B* 271: 245-250.

Kodric-Brown, A., and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist* 124: 309-323.

Kotiaho, J. S. 2000. Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behavioral Ecology and Sociobiology* 48: 188-194.

Krams, I. 2000. Length of feeding day and body weight of great tits in a single- and two-predator environment. *Behavioral Ecology and Sociobiology* 48: 147-153.

Krams, I. 2002. Mass-dependent take-off ability in wintering great tits (*Parus major*): comparison of top-ranked males and subordinate juvenile females. *Behavioral Ecology and Sociobiology* 51: 345-349.

Krebs, J. R. 1971. Territory and breeding density in the great tit *Parus major*. *Ecology* 52: 2-22.

Lemel, J. 1989. Habitat distribution of the great tit *Parus major* in relation to reproductive success, dominance, and biometry. *Ornis Scandinavica* 20: 226-233.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104: 116-121.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants in body mass in birds. *Ecology* 67: 377-385.

Lucas, J. R., A. Schraeder, and C. Jackson. 1999. Carolina chickadee (Aves, Paridae, *Poecile carolinensis*) vocalization rates: effects of body mass and food availability under aviary conditions. *Ethology* 105: 503-520.

Matthysen, E., F. Adriaensen, and A. A. Dhondt. 2001. Local recruitment of great and blue tits (*Parus major, P. caeruleus*) in relation to study plot size and degrees of isolation. *Ecography* 24: 33-42.

McGraw, K. J., and D. R. Ardia. 2003. Carotenoids, immunocompetence, and the information content of sexual colors: and experimental test. *American Naturalist* 162: 704-712.

McGregor, P. K., T. M. Peake, and G. Gilbert. 2000. Communication behaviour and conservation. Pages 261-280 in L. M. Gosling and W. J. Sutherland, eds. *Behaviour and Conservation*. Cambridge University Press, Cambridge.

Meigs, J. B., D. C. Smith, and J. Van Buskirk. 1983. Age determination of black-capped chickadees. *Journal Field Ornithology* 54: 283-286.

Mennill, D. J., L. M. Ratcliffe, and P. T. Boag. 2002. Female eavesdropping on male song contests in songbirds. *Science* 296: 873.

Merilä, J., R. Przybylo, and B. C. Sheldon. 1999. Genetic variation and natural selection on blue tit body condition in different environments. *Genetical Research* 73: 165-176.

Møller, A. P. 1995. Developmental stability and ideal despotic distribution of blackbirds in a patchy environment. *Oikos* 72: 228-234.

Nilsson, J. A. 1989. Causes and conseqences of natal dispersal in the marsh tit, *Parus palustris*. *Journal of Animal Ecology* 58: 619-636.

Nowicki, S., D. Hasselquist, S. Bensch, and S. Peters. 2000. Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. *Proceedings of the Royal Society of London B* 267: 2419-2424.

Nur, N., and O. Hasson. 1984. Phenotypic plasticity and the handicap principle. *Journal Theoretical Biology* 110: 275-297.

Ohlsson, T., H. G. Smith, L. Råberg, and D. Hasselquist. 2002. Pheasant sexual ornaments reflect nutritional conditions during early growth. *Proceedings of the Royal Society of London B* 269: 21-27.

Ots, I., and P. Hõrak. 1996. Great tits *Parus major* trade health for reproduction. *Proceedings of the Royal Society of London B* 263: 1443-1447.

Ots, I., A. Murumägi, and P. Hõrak. 1998. Haematological health state indices of reproducing great tits: methodology and sources of natural variation. *Functional Ecology* 12: 700-707.

Otter, K., B. Chruszcz, and L. Ratcliffe. 1997. Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behavioral Ecology* 8: 167-173.

Otter, K., S. M. Ramsay, and L. Ratcliffe. 1999. Enhanced reproductive success of female black-capped chickadees mated to high-ranking males. *Auk* 116: 345-354.

Otter, K., and L. Ratcliffe. 1993. Changes in singing behavior of male black-capped chickadees (*Parus atricapillus*) following mate removal. *Behavioral Ecology and Sociobiology* 33: 409-414.

Otter, K., and L. Ratcliffe. 1996. Female initiated divorce in a monogamous songbird: abandoning mates for males of higher quality. *Proceedings of the Royal Society of London B* 263: 351-354.

Otter, K., L. Ratcliffe, D. Michaud, and P. T. Boag. 1998. Do female black-capped chickadees prefer high-ranking males as extra-pair partners? *Behavioral Ecology and Sociobiology* 43: 25-36.

Pärt, T. 2001. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. *Proceedings of the Royal Society of London B* 268: 2267-2271.

Pärt, T., and A. Qvarnström. 1997. Badge size in collared flycatchers predicts outcome of male competition over territories. *Animal Behaviour* 54: 893-899.

Petit, J. L., and D. R. Petit. 1996. Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell-Lucas models. *Ecological Monographs* 66: 367-387.

Pyle, P. 1997. *Identification guide to North American birds, part I.* Slate Creek Press, Bolinas, CA.

Qvarnström, A., and E. Forsgren. 1998. Should females prefer dominant males? *Trends in Ecology and Evolution* 13: 498-501.

Qvarnström, A., S. C. Griffith, and L. Gustafsson. 2000. Male-male competition and parental care in collared flycatchers (*Ficedula albicollis*): an experiment controlling for differences in territory quality. *Proceedings of the Royal Society of London B* 267: 2547-2552.

Qvarnström, A., T. Pärt, and B. C. Sheldon. 2000. Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature* 405: 344.

Reid, M. L. 1987. Costliness and reliability in the singing vigour of Ipswich sparrows. *Animal Behaviour* 35: 1735-1743.

Riddington, R., and A. G. Gosler. 1995. Differences in reproductive success and parental qualities between habitats in the Great tit *Parus major*. *Ibis* 137: 371-378.

Robbins, M. B., M. J. Braun, and E. A. Tobey. 1986. Morphological and vocal variation across a contact zone between the chickadees *Parus atricapillus* and *P. carolinensis*. *Auk* 103: 655-666.

Røskaft, E., T. Järvi, M. Bakken, C. Bech, and R. E. Reinertsen. 1986. The relationship between social status and resting metabolic rate in great tits (*Parus major*) and pied flycatchers (*Fecidula hypoleuca*). *Animal Behaviour* 34: 838-842.

Saino, N., J. Cuervo, M. Krivacek, F. D. Lope, and A. P. Møller. 1997. Experimental manipulation of tail ornament size affects the hematocrit of male barn swallows (*Hirundo rustica*). *Oecologia* 110: 189-190.

Saino, N., J. Cuervo, P. Ninni, F. DeLope, and A. P. Møller. 1997. Haematocrit correlates with tail ornament size in three populations of the barn swallow (*Hirundo rustica*). *Functional Ecology* 11: 604-610.

Sherry, T. W., and R. T. Holmes. 1989. Age-specific social dominance affects habitat use by breeding American redstarts (*Setophaga ruticilla*): a removal experiment. *Behavioral Ecology and Sociobiology* 25: 327-333.

Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16: 393-430.

Smith, J. N. M., R. D. Montgomerie, M. J. Taitt, and Y. Yom-Tov. 1980. A winter feeding experiment on an island song sparrow population. *Oecologia* 47: 164-170.

Smith, S. M. 1988. Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour* 107: 15-23.

Smith, S. M. 1991. *The black-capped chickadee: behavioral ecology and natural history*. Comstock Publishing Associates, Ithica.

Spencer, K. A., and D. M. Bryant. 2002. State-dependent behaviour in breeding barn swallows (*Hirundo rustica*): consequences for reproductive effort. *Proceedings of the Royal Society of London B* 269: 403-410.

Spencer, K. A., K. L. Buchanan, A. R. Goldsmith, and C. K. Catchpole. 2003. Song as an honest signal of developmental stress in the zebra finch (*Taeniopygia guttata*). *Hormones Behavior* 44: 132-139.

Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press.

Suorsa, P., E. Huhta, A. Nikula, M. Nikinmaa, A. Jäntti, H. Helle, and H. Hakkarainen. 2003. Forest management is associated with physiological stress in an old-growth forest passerine. *Proceedings of the Royal Society of London B* 270: 963-969.

Sturkie, P. D. 1976. *Avian Physiology*. Springer-Verlag, New York.

Swaddle, J. P., and M. S. Witter. 1994. Food, feathers and fluctuating asymmetries. *Proceedings of the Royal Society of London B* 255: 147-152.

Tabachnick, B., and L. S. Fidell. 2001. *Using multivariate statistics*. Allyn and Bacon, Needham Heights, MA.

Takaki, Y., K. Eguchi, and H. Nagata. 2001. The growth bars on tail feathers in the male Styan's Grasshopper Warbler may indicate quality. *Journal of Avian Biology* 32: 319-325.

Thomas, R. J., and I. C. Cuthill. 1999. Two tests of a stochastic dynamic programming model of daily singing routines in birds. *Animal Behaviour* 57: 277-284.

Tobias, J. A., and N. Sneddon. 2002. Female begging in European robins: do neighbors eavesdrop for extrapair copulations? *Behavioral Ecology* 13: 637-642.

Ulfstrand, S., R. V. Alatalo, A. Carlson, and A. Lundberg. 1981. Habitat distribution and body size of the great tit *Parus major*. *Ibis* 123: 494-499.

Verhulst, S., C. M. Perrins, and R. Riddington. 1997. Natal dispersal of great tits in a patchy environment. *Ecology* 78: 864-872.

Voltura, K. M., P. L. Schwagmeyer, and D. W. Mock. 2002. Parental feeding rates in the house sparrow, *Passer domesticus*: are larger-badged males better fathers? *Ethology* 108: 1011-1022.

Weise, C. M., and J. R. Meyer. 1979. Juvenile dispersal and development of site-fidelity in the black-capped chickadee. *Auk* 96: 40-55.

Welling, P., K. Koivula, and K. Lahti. 1995. The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. *Journal of Avian Biology* 26: 241-246.

Welling, P. P., S. O. Rytkönen, K. T. Koivula, and M. I. Orell. 1997. Song rate correlates with paternal care and survival in willow tits: advertisement of male quality? *Behaviour* 134: 891-904.

Witter, M. S., and J. P. Swaddle. 1995. Dominance, competition and energetic reserves in the European starling *Sturnus vulgaris*. *Behavioral Ecology* 6: 343-348.

Zar, J. H. 1999. *Biostatistical analysis*. Simon and Schuster, Upper Saddle River, NJ.

Zahavi, A. 1975. Mate selection-a selection for a handicap. *Journal of Theoretical Biology* 53: 205-214.

Zanette, L., P. Doyle, and S. M. Tremont. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81: 1654-1666.

APPENDIX 1: HABITAT-DEPENDENT FEEDER USE BY MALES - PRELIMINARY RESULTS

If food availability differs between Disturbed and Undisturbed habitats, then chickadees living in these habitats may respond differently to artificial food sources. Specifically, birds within locally poor habitats may more readily utilize a novel food source than do birds in good quality habitats. In this study, I compared how male chickadees respond to feeders in new locations.

Methods. Habitats were sampled in a balanced manner during the winter of 2003, with the intent of sampling most individuals within the study site. Multiple trials were made along survey routes. All regions of the study site were sampled (i.e., most territories from previous breeding season), however, trials were never closer than 100 m from edges bordering each habitat. All trials took place on calm days without precipitation. At each station, a feeder was suspended from a branch (3 to 4 m above the ground) in a highly visible location allowing easy viewing by the observer and by birds. Observers were positioned at least 10 m away so that their presence did not interfere with feeder use. The feeder was a hanging bottle-type feeder equipped with a plastic collar to prevent access to the seed tray from all sides with the exception of a single entrance location where seeds could be accessed. Whole black-oil sunflower seeds were used. Once the feeder was in place, I broadcast playbacks of ‘chickadee’ call recordings to attract any nearby flock to the feeder. Trials were occasionally unsuccessful as chickadees were not attracted by the call playback. Call playbacks were ceased when a flock flew in to the feeder area.

Chickadees do not eat seeds at feeders, but instead remove a single seed to peck at the shell in a protected location. Successful trials began when the first seed was withdrawn from the feeder by a chickadee and lasted for the following ten minutes. All members of the flock were identified by coloured leg bands, and it was assumed that all members of the flock were aware of the feeder, even if they did not use it. The number of seeds taken by each individual was noted during the trial by recording voice notes into a tape recorder. Only the first observation period witnessed for an individual male was included in the analysis (total n = 58 males: 15 from Disturbed, 43 from Undisturbed).

Results and Discussion. The number of seeds taken by males during their first trial was greater in Disturbed habitat (ANOVA: $F_{1,56} = 17.3$, $P = 0.0001$), however, there were also fewer total numbers of birds in trials in this habitat (ANOVA: $F_{1,56} = 28.3$, $P < 0.0001$). There was a negative relationship between the group size and the number of seeds taken (linear regression: $r^2 = 0.10$, $F_{1,56} = 7.3$, $P = 0.009$). When group size was controlled for statistically, males in the Disturbed habitat still took more seeds than those in Undisturbed habitat (ANCOVA: $F_{1,55} = 9.1$, $P = 0.004$. Figure A1.1).

Previously a difference in feeder-use associated with food abundance has been documented (Carascal et al. 1998). Likewise, my preliminary results show that males living in the Disturbed habitat make greater use artificial food supplies. The direction of change in feeder-use seen among habitats is consistent with the direction of changes associated with habitat seen in fattening strategies (Chapter 2), and song rate (Chapter 4), both of which are known to vary with food abundance. The present finding suggests that food is less available, or of lower quality in the Disturbed site.

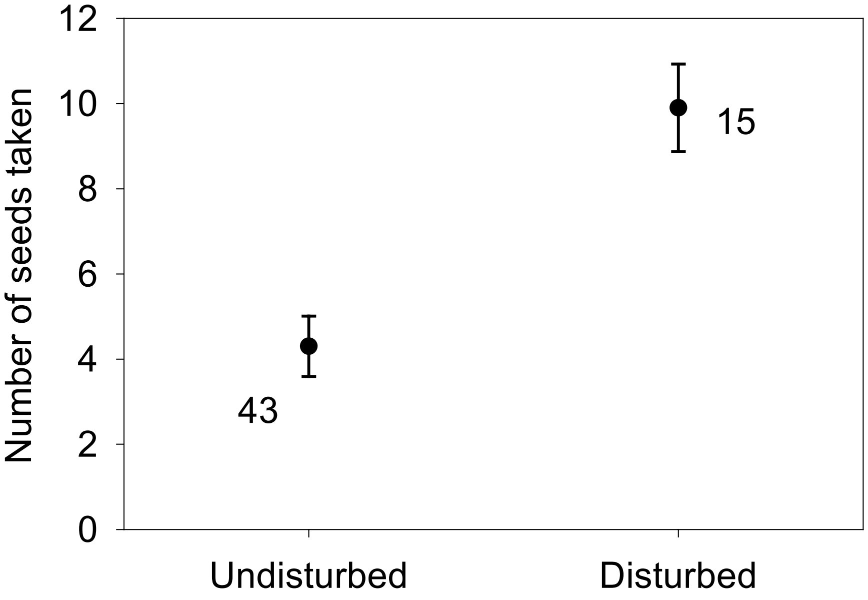

Figure A1.1 The effect of habitat on the average number of seeds taken by male chickadees during the first ten minutes after a flock discovers a new feeder. Mean number of seeds taken (± SE.) are shown after controlling for flock size. Samples sizes are shown.