PARENTAL CARE IN NORTHERN FLICKERS: SEX-RELATED PATTERNS OF

FORAGING, PROVISIONING, AND HABITAT USE

A Thesis Submitted to the College of Graduate Studies and Research in Partial

Fulfillment of the Requirements for the Degree of Doctor of Philosophy in the

Department of Biology,

University of Saskatchewan,

Saskatoon.

By

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ABSTRACT

The sexes have different life histories that can influence their parental care strategies. I studied northern flicker, *Colaptes auratus,* parents and simultaneously radio-tracked mates during the nestling and post-fledging periods. I tested hypotheses about sex differences in parental care strategies by examining foraging patterns, provisioning effort and habitat use. Males and females used the same microhabitats, but avoided overlap of their foraging areas on the home range consistent with the hypothesis that mates separate the home range to reduce competition. During temporary (i.e., 24 hr) brood size manipulations, both parents decreased provisioning to reduced broods, but did not increase provisioning to enlarged broods or alter their foraging pattern on the landscape. I suggest flickers were energy limited and were incapable or unwilling to respond to increased brood demands. During the post-fledging period, males spent more time near their fledglings, and cared for their fledglings longer than females (16 days versus 12 days, respectively). Approximately 36% of females abandoned their brood in the post-fledging period and females with high levels of feather corticosterone were more likely to abandon. Older males and those with high provisioning rates in the nestling period fed their fledglings longer. Nearly 45% of fledglings died within the first week after leaving the nest, but survival was higher for fledglings with intermediate body mass and those that occupied areas of dense cover. Families moved a greater distance from the nest during the first 4 days post-fledging when there was less tree cover within 250 m of the nest site. Parents brought fledglings to areas with dense vegetation within the first week post-fledging, but subsequently shifted to open grassland habitats. My results show that parents invest in their offspring indirectly by taking them to habitats that increase survival. This research stresses the importance of studying parental care during the post-fledging period to gain a more complete understanding of the total parental investment of males

versus females and how each sex may react differently to trade-offs between investing in the

current brood versus self-maintenance.

DEDICATION

On my last day collecting data for this thesis, a fledgling and adult Great Grey Owl flew in front

of me and sat on a branch, for several minutes, 15 m away. At this time I knew this work should

be dedicated to my late father, **A. Duncan Gow**. The Great Grey Owl alluded my father for 30+

years, and some of my fondest memories of him were searching and eventually finding his

'nemesis bird'. My father's enthusiasm for nature (and birds) and the encouragement he gave me

to pursue my passions are the best gifts a parent can ever give a child.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Life History and Parental care

Life history theory suggests that decisions about how much to invest in current reproduction are based on a tradeoff with adult survival (Williams 1966). Generally, for short-lived species there is higher selective pressure to invest heavily in the current reproductive attempt over future survival, whereas long-lived species are selected to invest more in self-maintenance over reproduction (Linden and Møller 1989; Martin 2004). These predictions assume reproduction is costly and that reproductive output is inversely related to survival (Linden and Møller 1989; Ricklefs 2000). Some animals invest in parental care that increases offspring survival, but most provide no care (Royle et al. 2012). The type of care given varies according to species and may include egg guarding in some amphibians, fish and invertebrates, to the more elaborate forms of care found in birds and mammals that often involve incubation, brooding, protection and feeding until offspring are capable of independence (reviewed in Balshine 2012; Trumbo 2012). Thus, understanding the costs and benefits of parental care can contribute to our understanding of life-history evolution, and can help explain the proximate and ultimate patterns of life history variation within a species (Martin 2004).

When the advantages and disadvantages of providing parental care differ between the sexes, sex differences in the amount of parental care given are expected (Kokko and Jennions 2008). In birds, biparental care occurs in 90% of species (including 9% that breed cooperatively), 1% have no parental care (i.e., brood parasitism, or geothermal heat), and 1% and 8% respectively, have male or female only care (Cockburn 2006). There are several hypotheses that offer an explanation for why male-only, female-only or biparental care may evolve. Early hypotheses suggested that females should invest more in parental care because they invested more heavily in gamete production (i.e., eggs are more expensive to produce than sperm; Trivers

1972). However, this idea is inaccurate because future investment is not determined by past investment but by future pay-offs (Dawkins and Carlisle 1976; Kokko and Jennions 2008). Several hypotheses explain how physiological or ecological differences between males and females influence the relative contribution of each sex. For instance, one sex may experience higher energy costs to providing care or be a more efficient and better parent (Clutton-Brock 1991). Another idea is that investment is related to expected parentage (Trivers 1972), which is usually greater for females compared to males (Queller 1997). Similarly, one sex may be less willing to invest in parental care if they have numerous alternative mating opportunities (Clutton-Brock 1991; Székely and Cuthill 2000). Parental care may be favoured as a sexually selected trait by one sex (Hoelzer 1989; Alonzo 2010) and competition for a partner that provides care may vary with the operational sex ratio in the population (Kokko and Jennions 2008).

1.2 Foraging and movement patterns during breeding

During breeding, parents need to acquire resources to both feed themselves and their offspring, so food can often limit reproductive success (Martin 1987). Thus, foraging behaviour such as the choice of foraging locations and lengths of foraging bouts likely affects productivity. Optimal foraging theory suggests that animals forage in ways to maximize their net energy gain while spending the least amount of time doing so (MacArthur and Pianka 1966). Birds during breeding face additional time and energy constraints because they must return food items to a central place (often the nest; Orians and Pearson 1979). Depending on the ecological context, parents can increase foraging efficiency by foraging with their mate or conspecifics, or alternatively by foraging alone. The preferred strategy presumably depends on the associated costs and benefits. For instance, foraging with others can reduce predation risk and help in

finding new resources (reviewed in Elgar 1989), while competition for resources at each

foraging site would select for solitary foraging (Krause and Ruxton 2002).

1.3 The post-fledging period

The period from fledging (leaving the nest) until departure for migration may be a critical stage

in the life history of birds because mortality of juveniles is often highest during the first few

weeks post-fledging and it can ultimately limit population size (Russell 2000; Naef-Daenzer et al.

2001). The post-fledging period is a critical time period for birds to learn life skills such as

flying, escaping predators, and foraging (e.g. Vega Rivera et al. 1998; Wheelwright et al. 2003)

and those that manage to survive the first days or weeks out of the nest often have a strong

likelihood of making it to adulthood and reproducing in the future (e.g. Anders et al. 1997; King

et al. 2006). The challenges of learning to fly make fledglings an 'easy' target for predators, thus

fledgling survival may be influenced by the habitat fledglings occupy on the landscape (Kershner

et al. 2004). Understanding how juveniles learn to use their environment, and quantifying

offspring survival is needed for accurate models of population dynamics and for targeting

conservation measures more efficiently (e.g. Lang et al. 2002).

A full accounting of the amount of parental investment must include the post-fledging

period (Evans Ogden and Stutchbury 1997; Lessells 2012) because parents can feed and defend

their offspring for weeks to months after they leave the nest (reviewed in: Russell et al. 2004).

Investing in fledglings presumably also entails trade-offs for the parents in terms of their own

survival and self maintenance. For instance, parents can face a strong trade-off between

continuing to provide parental care versus beginning moult, or migration, and the sexes may have

different costs and benefits to their choices (e.g. Stutchbury et al. 2011; Gow and Stutchbury

2013). Ultimately, the post-fledging period is likely a deciding factor in how much effort parents

provide to their young during the nestling period to developmentally prepare them for the post-fledging period (Dial 2003) and decisions about when to terminate care can shape life histories (Russell et al. 2004). In this thesis, I will study parental care during the nestling and post-fledging periods, and the survival and movements of juveniles during the post-fledging dependency period.

1.4 Study species

Northern flickers (*Colaptes auratus*) are a keystone, cavity nesting woodpecker (Martin et al. 2004) common to open forests and grasslands in North America. Flickers are a useful species for studies on parental care because their partially reversed sex roles lead to predictions about parental investment that are not typical for birds. Males gain their reproductive success with nearly 100% assurance of paternity within their brood (Wiebe and Kempenaers 2009). Females can increase their reproductive success by engaging in polyandry (up to 5% of females per year) or intraspecific brood parasitism (~17% of broods contain at least one parasitic egg; Wiebe and Kempenaers 2009). The amount of investment a female provides to her brood during incubation depends on the alternative mating opportunities she may have (Wiebe 2008). Both sexes contribute to the different stages of breeding but males do more of the nest excavation, incubation and brooding (Wiebe and Moore 2008) and feed the nestlings slightly more than females (Gow et al. 2013a). Males are also more competent than females at rearing offspring alone when they are widowed (Wiebe 2005).

Flickers are single brooded, but very rarely, <1%, may attempt double brooding/double clutching (Gow and Wiebe 2012). Clutch sizes range between 3–12 eggs (mean 7.6; Wiebe and Swift 2001) but the size of the eggs is one of the smallest relative to body size of any bird so egg production is probably not energetically limiting (Wiebe 2006). The incubation period lasts ~ 12

days and the nestling period ~ 27 days (Wiebe and Moore 2008; Chapter 4). Flickers have a 43% survival rate that is the same for both sexes and is lower than most woodpecker species so the relatively short lifespan suggests a fast or 'r-selected' life history and heavy investment in the current reproductive effort (Fisher and Wiebe 2006a). Unlike most other woodpeckers, flickers are migratory and leave the summer range following breeding. They forage mainly on the ground for ants (Gow et al. 2013b; Appendix A) within relatively large home ranges for a woodpecker (Elchuk and Wiebe 2003a). Flickers do not defend feeding territories, and their home range can change in size throughout the breeding season depending on food availability (Elchuk and Wiebe 2003b).

1.5 Thesis objectives and chapter synopses

The main objective of my thesis is to understand sex differences in parental care strategies, in particular how these may involve differences in habitat use and provisioning effort. To accomplish this, I determine how traits of parents such as their sex, age, and body condition determine the amount of parental care and foraging strategy in relation to brood demands and various life history trade-offs. Below, I outline the hypotheses and predictions in each of my four data chapters which focus on two main themes: 1) identifying potential differences between the sexes in foraging behaviour and provisioning rates to offspring (Chapters 2, 3, 4) during two time periods (nestling and post-fledging); and 2) how habitat use of two age classes (adult and juveniles) contributes to parental care strategies (Chapters 2, 5). Throughout, I investigate these themes using the methods of radio-telemetry and the monitoring of feeding rates at the nest.

In Chapter 2, I test whether mates forage together on the home range, which may indicate cooperative information-sharing about food patches or whether they forage apart, which may indicate niche segregation. If food is limited or quickly depleted in a patch, I predict that partners

will forage on the home range with less overlap than random. If niche segregation occurs, I further test the specialization and social dominance hypotheses by examining if members of a pair specialize on different prey types (Appendix A) or use different microhabitats and whether or not spatial segregation is enforced by aggressive interactions.

In Chapter 3, I conduct a temporary brood manipulation experiment to test the flexibility of parents to respond to proximate cues of brood demands both in terms of provisioning rates and foraging strategies. I also test the willingness and ability of parents to increase workload for the current brood. Because both sexes have similar energy constraints during nestling rearing, both parents probably face similar energetic trade-offs and so I predict they would react in a similar way to brood manipulations.

In Chapter 4, I followed flicker families in the post-fledging period and recorded the length of time males and females fed fledglings. Generally, I predict that because male flickers have a high assurance of paternity and females can increase their reproductive success through polyandry and conspecific brood parasitism that females may be more likely to take advantage of willing males and reduce or abandon parental care before males. Furthermore, individuals may differ in the resources they can, or are willing, to invest in parental care, so I predict that older birds or those in better physiological condition would allocate more care to offspring. I also examine correlates of fledgling mortality.

In Chapter 5, I modeled the survival of fledglings according to their habitat use because parents may increase survival of their fledglings by taking them to safer habitats. Assuming that dense vegetative cover is safer from predators, I predict that survivorship would be positively correlated with vegetation density at perching sites used by fledglings. Furthermore, I predict that parents with little cover around nest sites would take their fledglings farther from the nest during the first days post-fledging.

CHAPTER 2:

SEXUAL SEGREGATION DURING FORAGING ON HOME RANGES REVEALED BY SIMULTANEOUS RADIO-TRACKING OF BREEDING NORTHERN FLICKER PAIRS

2.1 ABSTRACT

Foraging with others can reduce predation risk but may increase competition for resources. Within species, sex or age classes may use different niches to reduce resource competition. Two main hypotheses have been proposed to explain niche segregation in birds, the specialization and dominance hypotheses. We tested these hypotheses and whether members of a breeding pair foraged closer or farther from each other than random. We recorded simultaneous foraging locations of radio-tagged male and female northern flickers (*Colaptes auratus*) to assess microhabitat differences and to detect patterns of space use on the home range. Mates used the same microhabitats for foraging but were more spatially segregated on the home range than random. Males foraged closer to the nest than females but both sexes avoided returning to the same foraging patch repeatedly, perhaps because of prey depletion. Members of a pair spent over 90% of the time > 50 m apart, but flew in the same direction from the nest to initiate a foraging bout more than expected. Use of the same microhabitats is counter to the ecological specialization hypothesis but neither did we see any aggressive behaviours which is counter to the dominance hypothesis. Flickers may benefit from niche separation on the home range by reducing depletion of food patches. We emphasize the importance of simultaneous tracking of mates to identify niche segregation at the home range scale and recommend this technique for other studies on niche separation.

2.2. INTRODUCTION

There are several proposed benefits and costs to foraging with other individuals. Animals that forage together increase the probability of detecting a predator while reducing their time spent in vigilance (reviewed in Elgar 1989) but may have increased competition for limited food resources (Krause and Ruxton 2002). Another benefit to group foraging is the use of social information to more efficiently detect patchy food sources (Krebs et al. 1972; Benkman 1988). When the benefits of foraging together outweigh the costs, social foraging would be selected and individuals should become synchronized in their foraging activities and forage together (Rands et al. 2003).

In contrast to hypotheses that predict that members of a pair should forage together is the idea of niche separation between the sexes. For example, the sexes may segregate socially as found in many terrestrial animals such as ungulates (reviewed in Ruckstuhl and Neuhaus 2005), and pinnipeds (reviewed in Staniland 2005), which may lead to the use of the same areas but at different times, 'temporal segregation', or the use of different areas or habitats, 'spatial and habitat segregation', which sometimes leads to diet segregation (reviewed in Conradt 2005). Studies on habitat segregation in terrestrial birds are common; however, the focus has been on differences in foraging techniques between the sexes (e.g. Kilham 1965; Selander 1966; Enoksson 1988) and the use of different microhabitats such as foraging heights in arboreal species (e.g. Radford and duPlessis 2003; Stenberg and Hogstad 2004; Franzreb 2010) especially during the non-breeding period (e.g. Temeles 1986; Ardia and Bildstein 1997). In comparison, there is sparse information about how mates may spatially divide the home range during breeding. Spatial segregation of home ranges may only be evident when the members of a pair are monitored simultaneously but this has rarely been attempted for terrestrial birds.

Factors that lead to niche separation are complex but there are two general hypotheses for birds, the specialization and the social dominance hypotheses (Catry et al. 2005). Differences in size or morphology may make each sex optimally suited to feed on different prey types (Radford and duPlessis 2003) or to use different habitats or foraging substrates (Selander 1966; Ginnett and Demment 1999; Levin et al. 2013). Birds may benefit by segregating foraging niches because they can better use the limited resources on the home range, and may increase reproductive success (Ligon 1968). Such habitat preferences may be innate (Morton 1990). Alternatively, the social dominance hypothesis suggests the dominant sex competitively excludes the other from its favoured foraging habitat (Peters and Grubb 1983).

Separate foraging niches for the sexes appear to be common in woodpeckers (Family Picidae) perhaps because trees are structurally complex and birds can specialize at specific heights, tree branch diameters, species and decay classes (Pasinelli 2000). Because the degree of sexual size dimorphism is not large for most woodpeckers, social dominance of males over females is thought to enforce the different feeding niches (Peters and Grubb 1983; Pasinelli 2000; Hogstad 2010). Studies on niche separation in woodpeckers have focused on arboreal foraging species but here we study a ground-foraging species, the northern flicker (*Colaptes auratus*), which specializes on ants (Wiebe and Moore 2008). Previously, we showed that the sexes of flickers do not differ in diet composition (Gow et al. 2013b; Appendix A), but here we were interested in testing whether members of a pair coordinated their activities in space and time in order to forage together or used separate foraging niches on the home range. Alternatively, males and females may simply forage independently of each other such that their distribution in relation to each other is random.

In order to detect niche segregation between members of a pair, it is important to monitor the use of foraging substrates (microhabitat scale) and the location of foraging patches within the

home range. Furthermore, partners must be monitored simultaneously because separation may occur in time but not necessarily space. If food patches are limited or easily depleted on the home ranges, we predicted sexual segregation of foraging patches with less overlap than random. However, if there is little competition for resources but benefits to social foraging, we predicted more overlap of foraging patches and closer distances between partners than random. For central place foragers, Ashmole (1963) suggested that foraging patches near the nest may become depleted first and so we also tested if the distance parents foraged from the nest increased with the age of the nestlings, and if the foraging overlap between partners decreased with nestling age.

2.3 METHODS

We studied northern flickers at Riske Creek in central British Columbia, Canada (51° 52'N, 122° 21'W), from 2010−2012. The study site covered an area of ~100 km^2 and was a patchy mosaic of open grasslands interspersed with small saline lakes, groves of trembling aspen (*Populus tremuloides*) and larger patches of mixed coniferous forest consisting of Douglas fir (*Pseudotsuga menziesii*), white spruce x Engelmann spruce hybrids (*Picea engelmannii x. glauca*) and lodgepole pine (*Pinus contorta*; Chapter 5; Gow and Wiebe 2014a). Flickers have large home ranges (3−112 ha; Elchuk and Wiebe 2003a) and forage on the ground exclusively for ants and ant larva (Elchuk and Wiebe 2002; Gow et al. 2013b; Appendix A). We trapped adults at the nest by plugging the cavity entrance and then flushing them into a net placed over the entrance. During capture, we weighed, measured (bill length and width, rectrix length, wing chord, and tarsus) and aged flickers up to four years according to moult (Pyle et al. 1997). We attached a 1.5 g radio-tag (Holohil Inc. Carp, Ontario, CAN) to the central rectrices with cyanoacrylate glue.

We radio-tracked the male and female of a pair simultaneously during four time periods, based on nestling age: 4 – 6 (early), 9 – 11 (middle), 13 – 15 (middle 2), and 19 – 22 (late) days old (N = 35, 32, 36, 28 tracking sessions, respectively). We walked in on birds to sight them using TRX-2000S receivers (Wildlife Materials Inc., Murphysboro, Illinois, USA) and Yagi 3-element antennae. We noted behaviours between mates such as aggressive (chasing or attacking) or cooperative (following each other) and recorded whether the male and female foraged in the same patch at the same time—within 50 m of each other. If both parents were at the nest at the same time to provision offspring, we recorded the general direction (i.e., NE, SE, NW, SW quadrants) the first bird flew to begin its next foraging bout and tested whether the second bird flew off in the same directional quadrant as the first more often than expected by chance with a Chi-squared Test.

2.3.1 Microhabitat Characteristics of Foraging Patches

During the 2−3 hr tracking sessions, we recorded the behaviour and locations of parents continuously and marked up to five independent foraging locations for each bird per tracking session. We ensured at least 30 min had elapsed between foraging points, or the bird had made a provisioning visit to the nest (see Elchuk and Wiebe 2002). Foraging locations were only recorded from locations were the bird was observed foraging. After the bird left the foraging location, we recorded the Universal Transverse Mercator (UTM) coordinates using a Global Positioning System (GPS) and the type of ground cover in 1 m quadrants (percent coverage of: rock, lichen/moss, bare ground, grass <10cm high, grass 11–20cm, grass >20cm, cow patties, and thatch). We also recorded the distance from the patch to escape cover (defined as woody vegetation high enough, > 1 m, to provide concealment to a flicker) and to forest edge (defined as

a cluster of trees spanning an area > 10 m). EAG estimated all ground cover within quadrants (N = 362) to remove observe bias.

We characterized foraging patches by reducing the dimensionality of the variables (% ground cover types, distance to edge and cover) using an unconstrained iterative multivariate ordination, nonmetric dimensional scaling (NMDS). We used standardized data and the Euclidean distance metric because it had the best fit compared to other distance metrics. We used conventional techniques to select the number of dimensions (axes) to retain, including scree plots and procrustes rotations that allowed us to visually assess differences between the dimensions (McCune and Grace 2002; Oksansen et al. 2012). We used the scores for each dimension (axis) derived from the ordination in subsequent analyses, and tested for differences between males and females within pairs using a Linear Mixed Effects Model (LME) with the random effects of individual, nest and stage to account for multiple observations of foraging patches per individual and within tracking sessions and pairs in the data set.

2.3.2 Spatial Use of the Home Range

We assessed if males and females foraged at different distances from the nest and whether foraging distance from the nest increased as the nestlings aged using a LME. We log-transformed the response variable of distance from the nest to achieve normality. We compared males and females on the same home range by nesting the pair within a tracking session as a random factor and included individual as a random factor to account for multiple observations across time and within tracking sessions. To see whether individuals used the same foraging patch repeatedly over time, we recorded the UTM coordinates of foraging points from the first tracking session and noted whether any foraging points from subsequent tracking sessions occurred within 50 m of any of the points from the first tracking session more often than expected by chance. The 50 m

radius areas divided by the total area of the home range represents the proportion of subsequent foraging points expected in the same place by chance. We used a paired t-test for males and females to assess if the observed number of foraging points in the 50 m radii differed from those expected.

To measure the degree of overlap of the foraging areas of mates on the home range within a given tracking session, we drew a 100% minimum convex polygon (MCP) around the foraging points from each individual (minimum sample of three foraging points; $N = 126$ male and 124 female tracking sessions) and calculated the area of overlap between the polygons. We performed a bootstrapped estimate of random overlap of foraging polygons, to determine if the degree of overlap was greater or less than expected based on random distribution of the foraging polygons. To calculate the bootstrapped estimates, we first drew a 100% MCP around the home range of the pair based on the pooled foraging points for both pair members. Within the home range area, we then generated two random locations per tracking session, using R 2.15.2 (R Core Development Team 2012). Next, we calculated the spatial size of the foraging area used by an individual during a tracking session and drew a circle of equivalent area around each random location and measured the area of overlap. This was repeated 100 times per tracking session to obtain a frequency distribution of amount of overlap expected by chance and the observed area of overlap was compared to the bootstrapped estimates with a Z-score test.

As members of a pair were tracked simultaneously, each observer kept a continuous record on a map of the bird's location, and we could determine roughly the distance between males and females during the tracking session. We calculated the proportion of time members of a pair spent within three distance categories from each other 50 m, 51−200m, and >201 m. Parents within 50 m of each other were interpreted as using the same foraging patch, those within 51−200 m may be able to detect alarm calls from the mate but were not using the same foraging

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patch and those > 201 m apart were unassociated with each other during foraging. We used

repeated measures ANOVA to test if parents increased their distance from each other as the

nestlings aged. To see whether the distribution of inter-pair distances within the three distance

categories was different than random, we used 100 bootstrap estimates of the distance between

two random generated points on the home range and compared it to the observed inter-pair

distances with a chi-squared test (χ^2).

All statistical analyses were conducted in R 2.15.2 (R Core Development Team 2012),

except for the χ^2 tests were conducted in JMP10 (SAS Institute Inc 2013), and were two tailed.

Variance is expressed as ± SE unless otherwise specified. Test statistics and *P*-values from LME

models are presented based on type III sums of squares approximation.

2.4 RESULTS

2.4.1 Microhabitat Characteristics of Foraging Patches

We used NMDS scores from three axes as dependent variables to characterize the ground

cover of foraging patches and their placement in relation to habitat edges. The three axes had a

stress value of 0.15, and an adjusted R^2 fit of 0.87, which is good for ecological data (McCune &

Grace 2002). Plots with high scores on the first axis (NMDS1) had a high percentage of bare

ground and a low percentage of thatch cover (Fig. 2.1a). High scores on the second axis

(NMDS2) were associated with grass cover 11–20 cm high but not with shorter grass, and were

relatively close to edge and cover (Fig. 2.1). High scores on NMDS3 indicated foraging patches

with tall grass > 21 cm high and with lots of rocks but with an absence of cow patties and lichen

(Fig. 2.1b). Males and females did not significantly differ in their use of microhabitat (LME:

NMDS1: $F_{1,311} = 0.02$, $P = 0.97$; NMDS2: $F_{1,311} = 0.02$, $P = 0.34$; NMDS3: $F_{1,311} = 1.6$, $P =$

0.83) and plot characteristics did not change with nestling age category (NMDS1: $F_{3,311} = 0.5$, P

= 0.15; NMDS2: $F_{3,311}$ = 0.01, P = 0.88; NMDS3: $F_{3,311}$ = 1.6, P = 0.19) and there were no

interaction effects (NMDS1: $F_{3,311}$ =2.24, P = 0.08; NMDS2: $F_{3,311}$ = 1.01, P = 0.39; NMDS3:

$F_{3,311}$ =1.69, P = 0.17).

a.

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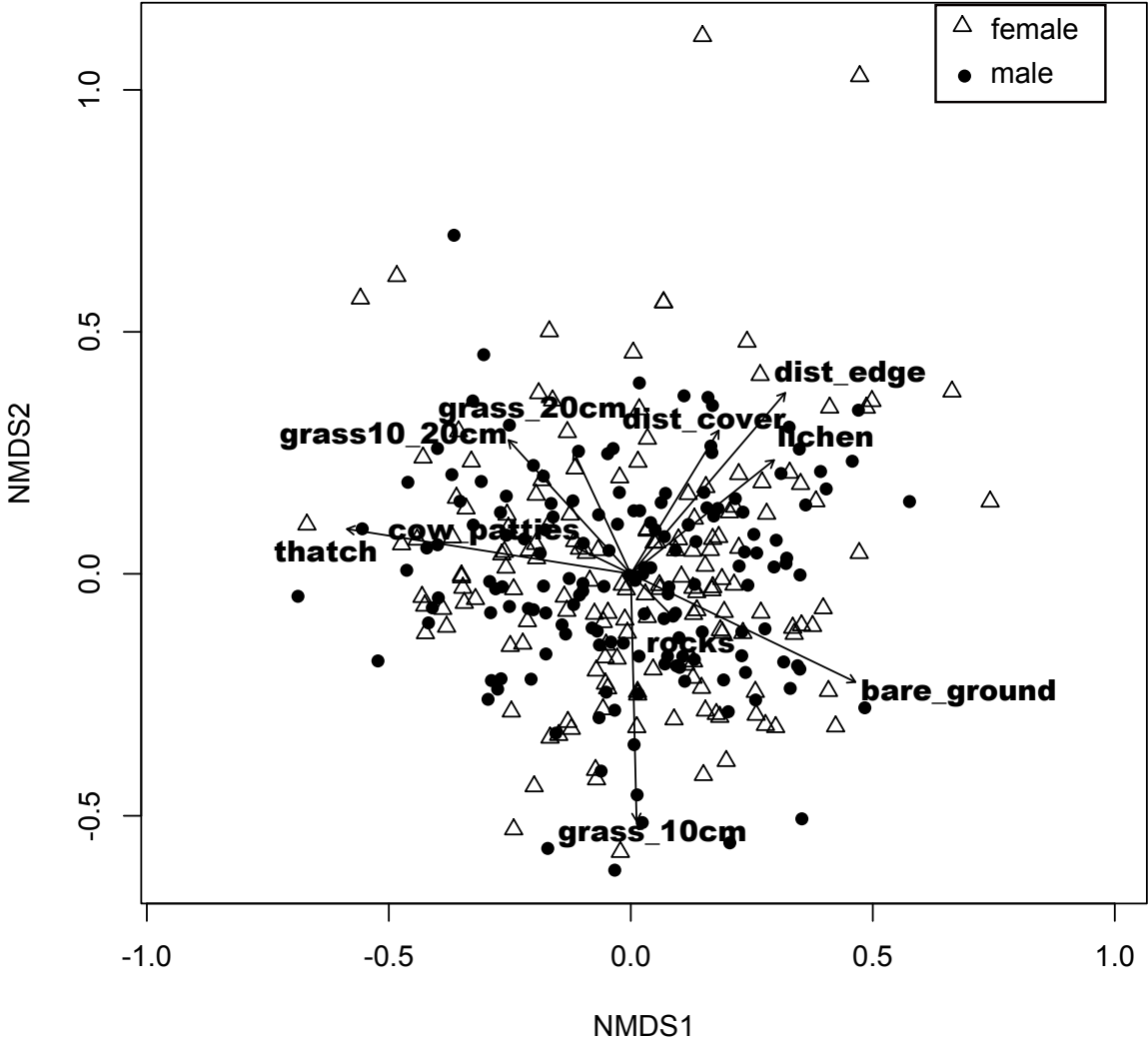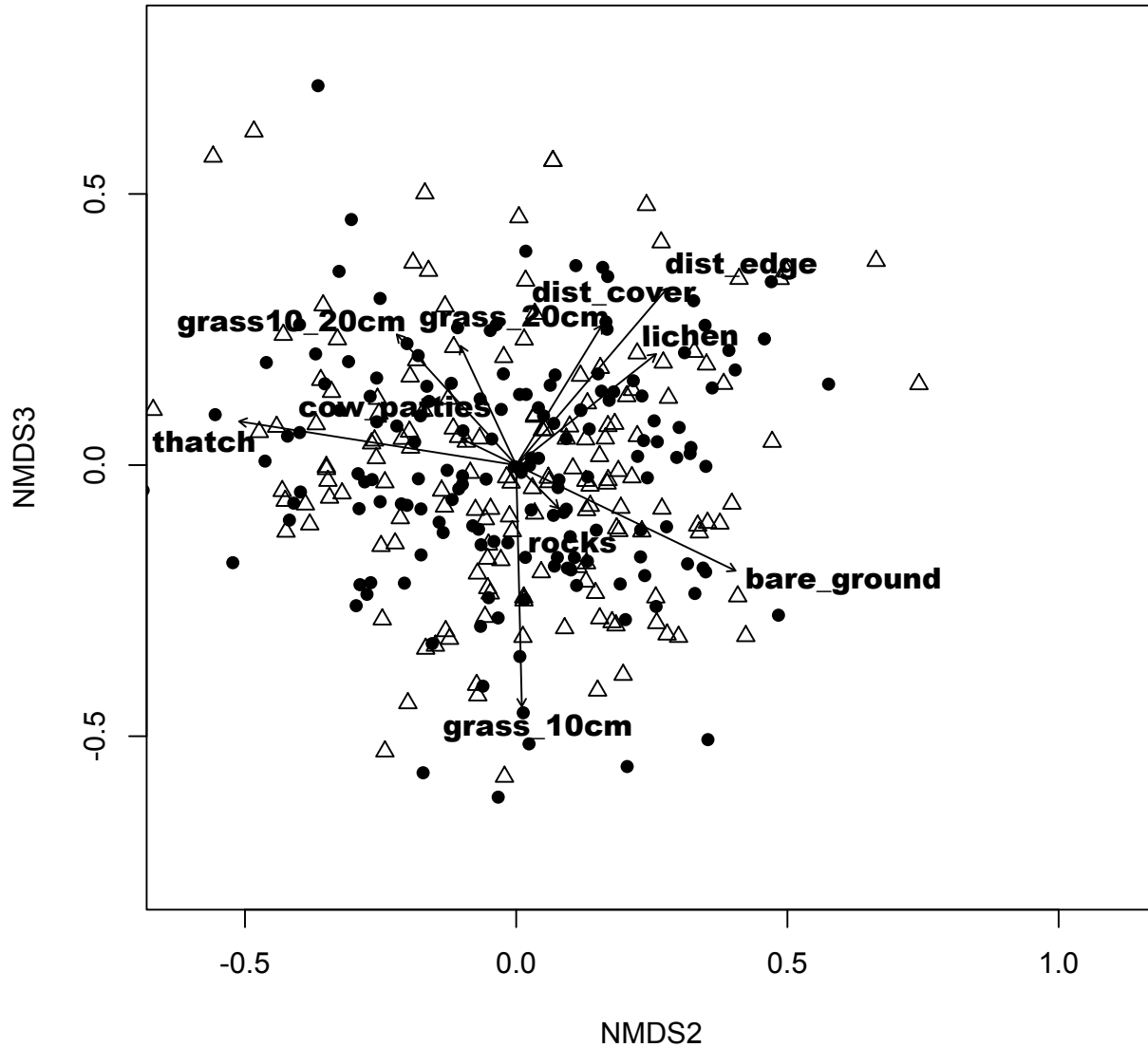
b.

Figure 2.1. Triplots showing the position of male (triangles; Δ) and female (circles; •) northern flicker, in central British Columbia, foraging locations ($N = 362$) in the microhabitat space represented by a) NMDS axis 1 versus NMDS axis 2, and b) NMDS axis 2 versus NMDS axes 3. The vectors represent the percent cover variables where the weaker predictors have shorter arrows than strong predictors. The angle of the vectors indicates which axis it is most strongly affecting and the direction indicates whether it is positive or negative. Plots with high NMDS1 scores had a high percentage of bare ground and low percentage of thatch cover. High scores on

NMDS2 were associated with grass cover 11–20 cm high but not with shorter grass, and were

relatively close to edge and cover. High scores on NMDS3 indicated foraging patches with tall

grass > 21 cm high and with lots of rocks but with an absence of cow patties and lichen.
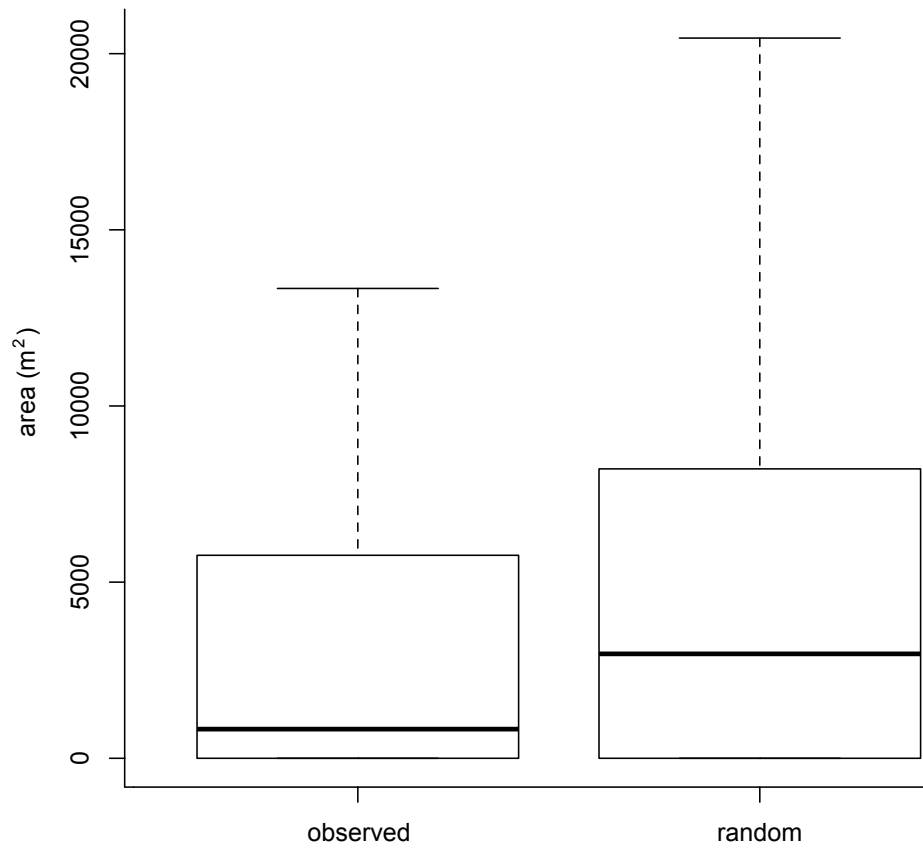
Figure 2.2. The observed spatial overlap during tracking sessions between foraging areas of male and female northern flickers in central British Columbia, Canada, was lower than expected by random. The area of random overlap was calculated by 100 bootstrap estimates.

2.4.2 Spatial Use of the Home Range

During tracking sessions, the average size of the foraging area used by males (mean: 35627 m^2 ± 3240, range: 15 – 178415 m^2) was smaller than the spatial area used by females (mean: 41185 m^2 ± 3746, range: 152 – 264490 m^2) but not significantly so (repeated measures ANOVA: sex effect: $F_{1,212}$ = 1.35, P = 0.25). During tracking sessions, 15 ± 2 % (range = 0–100 %, median = 4 %) of a female's foraging area overlapped with the male's foraging area and 18 ±2 % (range = 0 – 80 %, median = 4 %) of the male's foraging area overlapped with the female's foraging area. The total area of overlap averaged 5039 ± 782 m^2. The area of overlap between the foraging polygons of each member of the pair was less than expected by random (mean: 6906 ± 104 m^2, Z-test: Z = -45.64, P < 0.0001, Fig 2.2). Within a tracking session, after a nest visit, females and males returned to the same foraging patch (i.e., within 50 m of their previous location) in 32% of 307, and 29% of 310 foraging trips, respectively. Both sexes foraged repeatedly in the same foraging patches across tracking sessions less than expected by chance (paired t-test: female: t_{35} = -7.9, P < 0.001; male: t_{36} = -4.3, P < 0.001) and only returned to a foraging patch on average between tracking sessions 3.5 % of 462 foraging points for females and 6.4 % of 484 foraging points for males.

There were only six instances during the 261 hours of radio-tracking where a bird, usually the male (83%), followed its mate to a foraging location. We did not observe any aggressive interactions between mates, and no instances of vocalizations between partners while foraging. Within tracking sessions, males foraged within 50 m of a foraging location also used by the female 11% of 703 times, but in only 60% of these times was the pair occupying the same patch at the same time (7% of 703 together). Males foraged closer to the nest than females (LME: $F_{1,1221}$ = 3.4, P = 0.013; Fig. 2.3), but there was no effect of nestling stage on foraging distance for either sex (nestling stage: $F_{3,1221}$ = 0.23, P = 0.7; interaction: $F_{3,1221}$ = 2.2, P < 0.09; Fig 2.3).

When both males and females were at the nest together, they flew in the same direction for their subsequent foraging bout 52% of 69 times which was more frequently than expected by chance (Chi-squared test: $\chi^2_1 = 12.25$, $P < 0.001$). The direction of departure from the nest did not differ from random for both males and females suggesting that partners did not consistently prefer to leave the nest in a specific direction (Chi-squared test: $\chi^2_1 = 0.02$, $P = 0.89$).

Mates spent 89% of their foraging time > 50 m apart (Fig. 2.4). The distances of > 201 m and $50-200$ m were negatively correlated ($r = 0.81$, $N = 131$, $P < 0.0001$) and so only one variable was used in the repeated measures ANOVAs. The amount of time parents spent at each distance apart was not dependent on the nestling's age (ANOVA: >200 m: $F_{3,83} = 1.17$, $P = 0.33$; <50 m: $F_{3,83} = 0.96$, $P = 0.41$). Within tracking sessions, the distance between mates was non-random when compared to the bootstrap estimates (Chi-squared test: $\chi^2 = 22.1$, $P < 0.0001$). In particular, parents spent less time close together (<50m) than expected (Fig. 2.4).
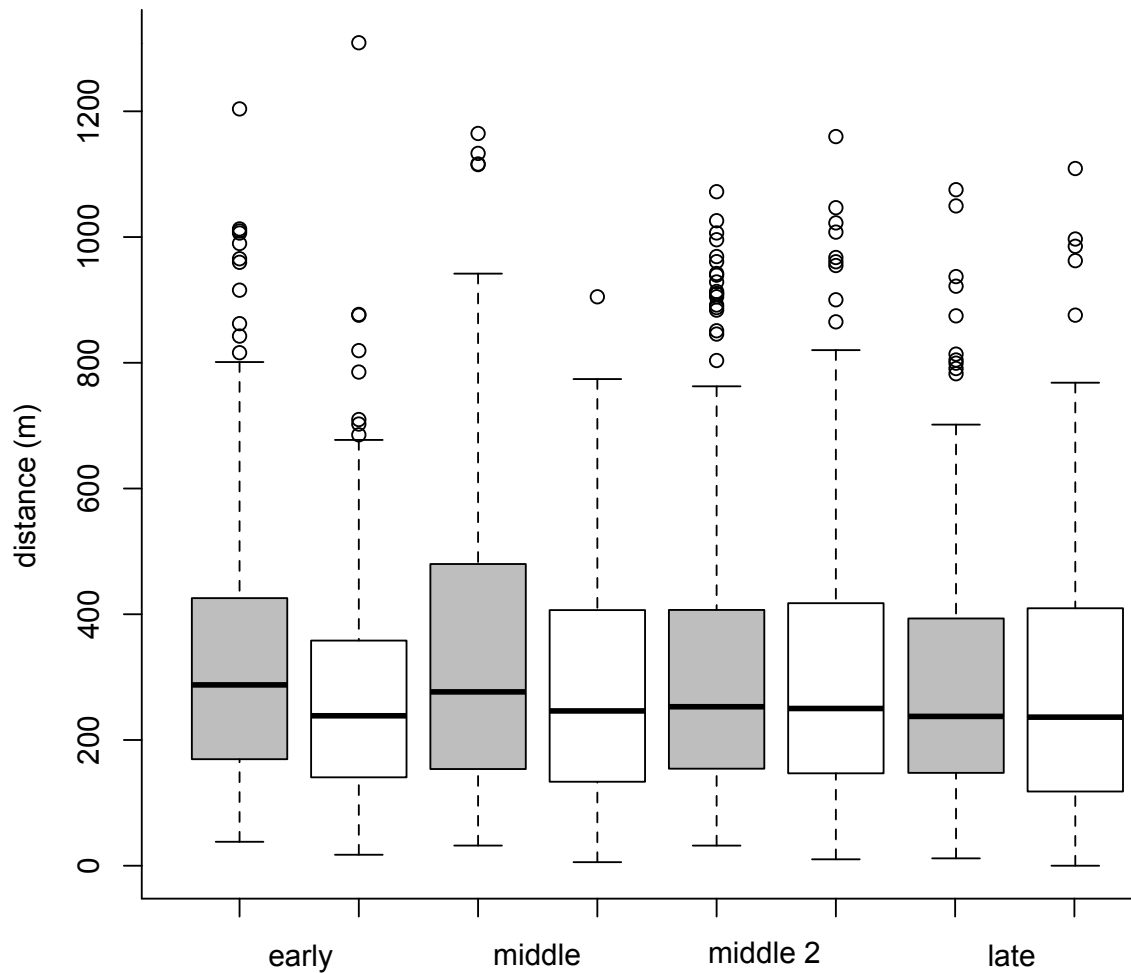
Figure 2.3. Males foraged closer to the nest than female northern flickers, in central British Columbia, as measured over the four nestling age categories (females are the grey boxes). The nestling age categories are: 'early' (4–6 days), 'middle' (9–10 days), 'middle2' (13–15 days), and 'late' (19–22 days). Distances are based on simultaneous radio-tracking of pairs during the breeding season (May–July) in 2010, 2011 and 2012. Outliers are represented by circles and are values greater than 1.5 times the interquartile range above the 75% quartile. Sample sizes are 619 foraging locations from 41 males and 605 foraging locations from 41 females.
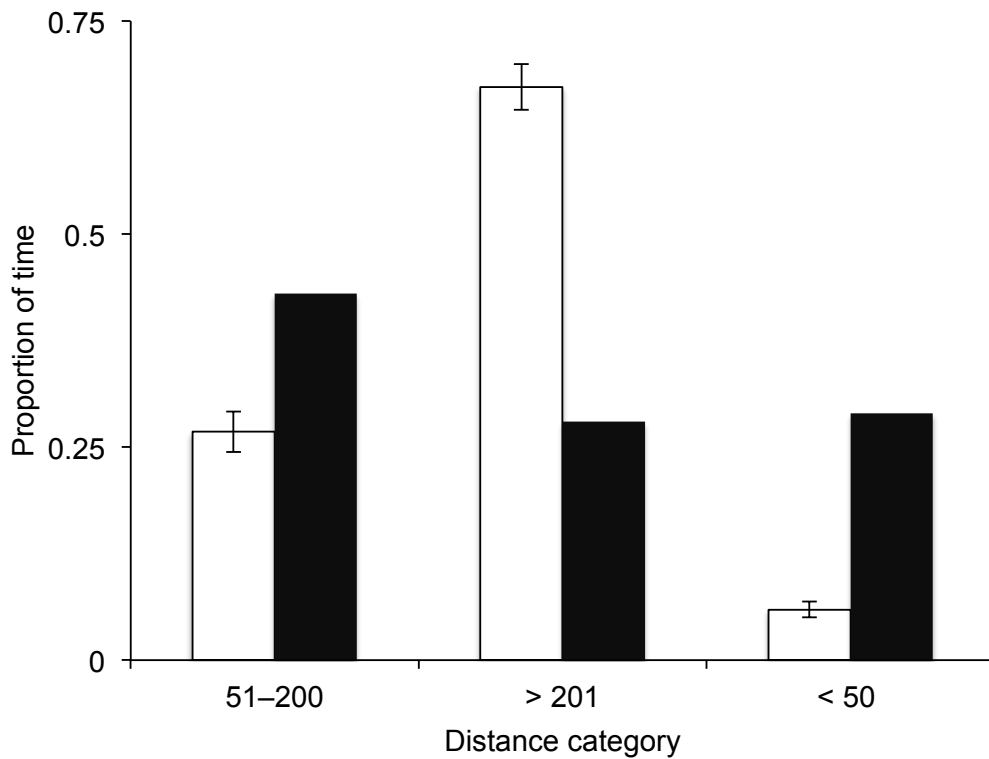
Figure 2.4. The proportion of total foraging time which male and female northern flickers, in central British Columbia, spent at each distance category, < 50 m, 51–200 m, and > 201 m, from each other during tracking sessions (open bars) versus that expected by random (black bars) based on a bootstrap analysis of 100 randomly placed locations on the home range. Distances and the proportion of time in each distance category are based on simultaneous radio-tracking of pairs during the breeding season (May–July) in 2010–2012.

2.5 DISCUSSION

Our observation that mates foraged together for only 7% of foraging points, and spent only 11% of their time foraging in the same patch suggests there were few benefits for social foraging in flickers. Instead our data support the hypothesis that mates reduced competition while foraging by avoiding overlap on home ranges. Another study on the same population reported that in 29% of cases, foraging flickers were near a conspecific and 8% of cases were within 50 m of their partner (Elchuk and Wiebe 2003b). Thus, the frequency at which pairs foraged together was consistent between the two studies. Flickers also sometimes foraged with other birds such as American robins (*Turdus migratorius*), and European starlings (*Sturnus vulgaris*; this study; Elchuk and Wiebe 2003b), which is consistent with the idea of benefits from increased vigilance and low competition in mixed-species flocks (Morse 1977). Nevertheless, most foraging by breeding flickers was done in isolation.

In contrast to flickers, insectivorous species in which mates occupy territories year round, especially in the tropics, may obtain greater benefits by foraging together because of higher levels of predation risk and less competition for food. For instance, dusky antbirds (*Cercomacra tyrannina*) foraged on average 5.6 m from their mate (Gorrell et al. 2005) and white breasted antbirds (*Myrmeciza longipes*) and checker-throated antbirds (*M. exsul*) spent 61% and 19% of their time, respectively, within 5 m of their mate, and 4% and 56% of their time > 20m from their mate (a similar resolution to our study when the smaller home range size of the antbirds are considered; Stutchbury et al. 2005). But tropical birds may differ in their foraging dynamics than temperate breeding species because of their needs to defend year-round stable territories that provide sufficient food resources (Gorrel et al. 2005).

Selander (1966) proposed that mates within a shared territory could achieve separation of foraging niches in three ways, by using: 1) the same foraging technique and microhabitat but

taking different types of prey items; 2) different foraging techniques but foraging in the same area or microhabitat, such as hairy woodpeckers (*Picoides villosus*; Kilham 1965), lesser spotted woodpeckers (*D. minor*; Hogstad 2010), and middle spotted woodpeckers (*Dendrocopos medius*; Pasinelli 2000); or 3) different areas or microhabitats. The first two scenarios do not apply to flickers that consume the same sizes and types of prey items (Gow et al. 2013b) and foraged in the same microhabitat, but our data support the third method. Among terrestrial bird species, all three methods are used to reduce intersexual niche competition for food and in many cases they are not mutually exclusive, with the use of different microhabitats being exploited by the different foraging techniques of the sexes. For instance, among woodpeckers, differences in foraging techniques between the sexes such as excavating versus bark-probing has been noted for downy woodpeckers (*P. pubescens*; Williams 1980), Nuttall's woodpeckers (*P. nuttallii*; Jenkins 1979), red-cockaded woodpeckers (*P. borealis*; Rudolph et al. 2007), and Eurasian three-toed woodpeckers (*P. tridactylus alpinus*; Pechacek 2006), and this same suite of species also shows niche separation in foraging height and/or the diameter of foraging substrates (branches).

Although flicker mates foraged in spatially segregated areas at any given time, each did not continuously use only a small section of the home range or "hotspot" over the nestling period. Thus, home ranges were not permanently divided between males and females in a fixed way over time. Furthermore, we never observed aggressive behaviours within pairs and so, counter to the social dominance hypothesis, aggression was not responsible for enforcing the different foraging areas. The specialization hypothesis for sexual niche separation can also be ruled out because both sexes used the same microhabitat, and consumed the same prey items. Instead, members of a pair must have achieved spatial segregation by more subtle mechanisms, perhaps by monitoring and avoiding the general foraging location of the partner in "real time", or by using general foraging rules such as distance from the nest.

Our study is one of the first to show how members of a pair distribute themselves on the home range in real time and we were able to see that they avoided foraging together when simultaneously tracked. What little comparative data exist for other species is mostly based on small sample sizes so the prevalence of spatial segregation as a foraging strategy is not clear. However, rufous hummingbirds (*Selasphorus rufus*) appear to subdivide the home range (Temeles and Roberts 1993) and Swihart and Johnson (1986) observed American robin (*Turdus migratorius*) mates split the home range by foraging in different directions. Similarly, Hogstad (2009) inferred mates used different parts of the home range because they returned to the nest from different directions. Male and female amakihis (*Loxops virens*) used different feeding stations placed on their home ranges but it is unknown whether this segregation of foraging areas is true in a natural context (Kamil and van Riper III 1982).

There are different mechanisms that may explain how mates stay apart while foraging. One explanation is that birds forage near their activity centers (Holmes 1986) and this may affect their use of space. For example, male Henslow's sparrows (*Ammospiza henslowii*) foraged closer to territory boundaries where they could more easily defend territories whereas females tended to stay close to their nest (Robins 1971). Female Eurasian treecreepers (*Geothlypis trichas*; Morimoto and Wasserman 1991) and common yellowthroats (*Certhia familiaris*; Aho et al. 1997) also foraged closer to the nest than males. Because flicker males devote more to nest construction and defense than females (Wiebe and Moore 2008) and feed the nestlings slightly more than females, it may be more beneficial for the males to stay close to the nest and this may result in some passive segregation of the home range. Another mechanism to avoid foraging overlap is the active monitoring of the location of the partner. Our finding that mates tended to fly in the same direction when they both happened to be at the nest together raises the question as to whether this was a use of social information to locate foraging patches, or whether individuals

were flying in the same general direction to pinpoint the mate's location and then avoid overlap. Alternatively, vegetation structure or habitat features around nest sites may have just funneled departing birds in a particular direction.

Foraging distance from the nest did not increase as nestlings aged counter to 'Ashmole's halo' hypothesis (Ashmole 1963) and the area of foraging overlap between partners did not decrease over time. Aside from one paper that found that birds travelled farther from the nest as with nestling age (Naef-Daenzer 2000), most support for Ashmole's hypothesis appears to be in seabirds for which prey are depleted near the colony forcing parents to search for food at farther distances (e.g. Gaston et al. 2007; Elliott et al. 2009). Evidence for a similar pattern of food depletion around the nests of terrestrial birds is lacking. For flickers, the ant prey is probably not uniformly depleted near the nest site because the abundance of the ants on the surface is related to daily and seasonal fluctuations in temperature and precipitation, and flickers move their foraging locations according to the degree of overhead shading in relation to ambient temperature (Elchuk and Wiebe 2003b; Wiebe and Gow 2013). Hence, the optimal habitat types for foraging on the landscape may be scattered quite widely on the home range and vary on an hourly or daily basis.

The idea that repeated foraging within a patch depletes ant prey for flickers was supported by a simulated foraging experiment in which the number of ants in quadrants declined when they were repeatedly removed from the ground surface (Elchuk and Wiebe 2003b). Apparently the reproductive rate within the ant colonies is not high enough to sustain repeated exploitation by flickers over several days. The relatively high (30%) return rate to foraging patches during tracking sessions suggests that flickers may benefit by returning to a known prey 'hotspot' in subsequent foraging bouts until the ants are locally depleted. Once depleted, however, they seem to avoid the same patch for days or weeks. Flickers do not defend foraging areas against conspecifics (Elchuk and Wiebe 2003a,b) probably because defending such sparse and ephemeral

prey over a large home range is unprofitable. Instead, flickers may try to avoid each other to reduce competition, or forage systematically to optimize time needed for resource replenishment (Davies 1980).

In sum, we present one of the first accounts of how mates forage in "real time" on the home range and demonstrated using simultaneous radio-tracking that the sexes foraged in different areas of the home range but used the same microhabitats. This is in contrast to many other terrestrial arboreal-foraging species in which the sexes specialize on different foraging substrates at the microhabitat scale (e.g. Ligon 1968; Desrochers 1989; Pasinelli 2000). Apparently, mates have some knowledge of where the partner is foraging at any given time and avoid each other to maximize prey gain. Thus, flickers may use social information from both their mate or other conspecifics to help determine where prey patches are abundant or depleted. Such a foraging strategy would have not been detected by tracking each sex at different times and so we encourage future studies to investigate niche segregation with simultaneous tracking of both members of the pair.

CHAPTER 3:

RESPONSES BY CENTRAL-PLACE FORAGERS TO MANIPULATIONS OF BROOD SIZE: PARENT FLICKERS RESPOND TO PROXIMATE CUES BUT DO NOT INCREASE WORK RATE

3.1 ABSTRACT

Manipulations of brood size measure the willingness or ability of parents to invest in offspring and different reproductive roles may lead to differences in feeding effort between the sexes. Parental investment in birds is usually assessed by quantifying feeding rates, but provide an incomplete picture of parental effort because it fails to account for how parents collect food on the landscape. We studied northern flickers (*Colaptes auratus*), a woodpecker with reversed sex roles, and used a repeated measures design and short-term (24h) brood enlargements ($N = 35$) and reductions ($N = 27$) to assess effects of treatment on feeding rates to nestlings and parental foraging behaviour. Parents of enlarged broods didn't significantly increase feeding rate, resulting in a decline in nestling mass. Parents of reduced broods decreased their feeding rates by 84%, but increased per capita feeding rates, resulting in nestling mass gain. Foraging pattern on the landscape remained the same during the enlarged treatment for both sexes. We conclude that flickers respond to proximate cues in brood demands, but aren't willing to increase effort to enlarged broods, at least in the short-term. A literature review suggested that this lack of response is atypical for short-lived species. We hypothesize that parents in species with large home ranges and long nestling periods face energy limitations which constrain their ability to respond to enlarged broods. We encourage future studies to assess foraging behaviour on the landscape to document important trade-offs for parents such as predation risk and energy expenditure while feeding offspring.

3.2. INTRODUCTION

Because parental care is energetically expensive (e.g. Drent and Daan 1980), parents must balance potential trade-offs between their current investment in a brood and their own survival and future reproduction (Stearns 1989). Numerous studies have experimentally manipulated brood size to test whether parents respond to proximate cues of nestling demand, such as number of gapes and begging rates, and the results indicate how willing, or able, parents are to increase effort. Feeding rates (i.e., rate of food deliveries to the nest) are usually quantified but provide an incomplete picture of parental effort because they do not necessarily account for how the food is collected (e.g. spatial foraging pattern on the landscape). Classical models of central place foraging can better encapsulate costs by taking into account the spatial location of foraging patches (reviewed in: Pulliam 1974; Charnov 1976). Foragers should minimize costly travel by foraging close to the central place or loading up with more food if they are travelling from distant patches, and should do so while minimizing predation risk by foraging close to escape cover. A few studies using radio-telemetry have monitored spatial patterns of foraging at the landscape scale in seabirds (e.g. Wanless et al. 1991; Adams and Navarro 2005), but to our knowledge, none has tracked foraging patterns of parents in response to experimentally increased brood demands.

Intrinsic factors such as the forager's body condition (Lifjeld 1988), or extrinsic factors such as the requirements of the brood may change the foraging strategy. For example, in response to increased brood demands, parents may: 1. alter the prey type (Moreno et al. 1995; Bańbura et al. 2004; García-Navas and Sanz 2010; Mänd et al. 2013); 2. alter foraging method or location (Mänd et al. 2013); 3. increase the rate of feeding visits either by increasing the total foraging time (Grieco 2002) and/or; 4. bring more food at each visit, e.g. by staying in a foraging patch longer or selecting larger prey (Grieco 2001). With extreme energy demands desperate parents

may make rapid feeding visits but with smaller or less palatable prey items (Lifjeld 1988). In addition, they may be forced to acquire more prey items by foraging farther distances from the nest which may lead to an increase in total distance travelled. We predict that increased demands may force parents to forage in lower quality patches e.g. those that are farther from the nest and increase predation risk by being farther from forest edges and escape cover. Additionally we predict that parents should increase the total time spent foraging, increase the length of foraging bouts and reduce their effort at nest defense.

In this study, our primary objective was to measure the flexibility of parents to respond to changes in brood demands in terms of altering their feeding rates as well as changing their foraging time budget and spatial pattern of foraging on the landscape. Additionally, we tested whether males and females differed in their response to brood demands by studying a species with partially reversed sex roles, the northern flicker (*Colaptes auratus*). The breeding diet of flickers consists of >99% 2–3mm long ants (Gow et al. 2013b; Appendix A) which are regurgitated to the nestlings and so parents would not be expected to change the size or type of prey. Instead, we focused on measuring foraging behaviours such as the length of foraging bouts, foraging locations on the home range and total distances as potential responses of parents.

In many bird species, feeding rates or foraging locations vary according to short-term changes in weather (Radford et al. 2001; Wiebe and Gow 2013), time of day (Cowie and Hinsley 1988), or effort by a mate (Wright and Cuthill 1990) and so we expected that flickers would be flexible and respond to short-term changes in brood demands. Other species feed broods at a fixed rate apparently deciding their investment at an early breeding stage by laying an optimal clutch size (Sæther et al. 1993). Furthermore, a review of the literature shows that in natural, but generally not in experimentally manipulated broods (Table 3.1), one sex of parent is often more responsive to brood demands than the other (e.g. Low et al. 2012), perhaps when energetic or

physical limitations imposed by breeding roles differ between the sexes. Flickers are an interesting study species because, in contrast to the pattern in most other birds, males invest more in parental care than females during nest building, incubation and brooding (Wiebe 2008) and females may be polyandrous (Wiebe 2002). The fact that 33% of females cease feeding fledglings before their partner does (Gow and Wiebe 2014b; Chapter 4) suggests males value the current brood more than females and would be more responsive to increased brood demands. However, both parents feed at similar rates during the mid-nestling period (Gow et al. 2013a) and if they experience similar energy constraints during that time may respond in a similar way to brood size.

To explain variation in parental responsiveness, we also investigated several intrinsic factors. Namely, we predicted that high levels of corticosterone (CORT, a 'stress hormone') would reduce investment in parental care (reviewed in Angelier and Chastel 2009). We also expected that older individuals and those in a better nutritional state (e.g. higher mass gain, higher feather regrowth rate (White 1991), or a higher body condition index) would respond more strongly to increased demands.

Table 3.1 Review of parental feeding rate responses to experimental manipulations of brood size. Responses are given as increased (+), decreased (-), or no change (0). The sex that responded to the manipulation is shown in parentheses as (m)ale, (f)emale, or (b)oth, or as NA if sexual differences were not tested.

Species	Enlarged brood	Reduced brood	Citation
Long-lived			
Red-tailed tropicbird (*Phaethon rubricauda*)	+ (NA)	NA	(Schreiber 1996)
Laughing gull (*Leucophaeus atricilla*) **	+ (NA)	NA	(González-Medina et al. 2010)
Razorbill (*Alca torda*)	+ (NA)	NA	(Llyod 1977)
Osprey (*Pandion haliaetus*)	0 (NA)	NA	(Green and Ydenberg 1994)
Tawny owl (*Strix aluco*)	0 (NA)	0 (NA)	(Sasvári and Hegyi 2010)
Barn owl (*Tyto alba*)*	0 (NA)	0 (NA)	(Roulin et al. 1999)
Short-lived			
American kestrel (*Falco sparverius*)	NA	- (f) 0 (m)	(Dawson and Bortolotti 2003)
Eurasian kestrel (*Falco tinnunculus*)	0 (b)	NA	(Tolonen and Korpimaki 1996)
African redbreasted sparrowhawk (*Accipiter	0 (NA)	NA	(Simmons 1986)

rufiventris)

Acorn woodpecker (*Melanerpes formicivorus*) ***	+ (b)	- (b)	(Koenig and Walters 2012)
House sparrow (*Passer domesticus*)	+ (b)	- (b)	(Hegner and Wingfield 1987)
Starling (*Sturnus vulgaris*)***	+ (b)	NA	(Wright and Cuthill 1990)
Starling	+ (b)	NA	(Wright et al. 1998)
Yellow warbler (*Dendroica petechia*)	+ (b)	- (b)	(Lozano and Lemon 1998)
Blue tit (*Cyanistes caeruleus*) ***	+ (b)	- (b)	(García-Navas and Sanz 2010)
Blue tit	+ (b)	- (b)	(Nur 1984)
Blue tit	+ (b)	- (b)	(Parejo and Danchin 2006)
Great tit (*Parus major*)	0 (b)	- (b)	(Smith et al. 1988)
Great tit	+ (b)	NA	(Hinde and Kilner 2007)
Great tit	NA	- (b)	(Verhulst and Tinbergen 1997)
Red winged blackbird (*Agelaius phoeniceus*)	+ (b)	- (b)	(Yasukawa et al. 1993)
Red-winged blackbird	+ (f)	NA	(Cronmiller and Thompson 1980)
Tree swallow (*Tachycineta*	+ (NA)	- (NA)	(Bortolotti et al. 2011)

bicolor)

Tree swallow	+ (b)	- (b), - (m)	(Ardia 2007)
Tree swallow	+ (b)	NA	(Shutler et al. 2006)
Fairy wren (*Hirundo ariel*)***	+ (b)	- (b)	(Magrath et al. 2007)
Pied flycatcher (*Ficedula hypoleuca*)	+ (m), 0 (f)	- (m), 0 (f)	(Moreno et al. 1995)
Pied flycatcher	+ (NA)	NA	(Wright et al. 2002)
Pied flycatcher	+ (b)	- (b)	(Sanz 1997)
Lesser elaenia (*Elaenia chriquensis*)	+ (NA)	- (NA)	(Sousa and Marini 2012)
Eastern phoebe (*Sayornis phoebe*)	+ (b)	- (b)	(Conrad and Robertson 1992)
White-rumped swiftlets (*Aerodramus spodiopygius*)	+ (NA)	0 (NA)	(Tarbuton 1986)
Common swift (*Apus apus*)	+ (b)	- (b)	(Martins and Wright 1993)

* Based on prey biomass
** Parents also handicapped to increase flight costs
*** Short-term brood manipulation

3.3. METHODS

We studied northern flickers at Riske Creek in central British Columbia, Canada (51° 52'N, 122° 21'W), from 2010−2012. The study site covered an area of ~100 km^2 and was a patchy mosaic of open grasslands used for foraging and was interspersed with small saline lakes and groves of trembling aspen (*Populus tremuloides*) used as nest trees (see Gow and Wiebe 2014a; Chapter 5 for more details). Fisher and Wiebe (2006b) found that nest predation by squirrels (the main nest predator) was higher in coniferous forest patches compared to the grassland/ trembling aspen habitat and so we only studied pairs in the grassland habitat to control the vegetation structure and level of predation risk across experimental pairs as much as possible. The home ranges of raptors, which were found on all parts of the study area and were the main predators of adults, encompassed numerous flicker ranges so it is unlikely that certain flicker pairs suffered much higher risk than others. Additionally, flickers do not defend feeding territories but instead forage for ants on large home ranges of 3−112 ha (Elchuk and Wiebe 2003a). Thus, food supply is more likely to be affected by precipitation (Elchuk and Wiebe 2003b) and temperature (Wiebe and Gow 2013) than by the exact location of the nest site within the grassland habitat. Flickers arrive on the study site after migration in spring and lay a clutch which varies in size from 4−13 and is incubated for about 12 days (Wiebe and Swift 2001). The nestling period lasts 25−29 days.

3.3.1 Brood Manipulation

　　We temporarily altered brood size when nestlings were between 12 and 14 days old, a time that coincides with the peak energy demands and feather growth rate of the nestlings (Gow et al. 2013a). We enlarged ($N = 35$) or reduced ($N = 27$) broods by transferring 2−4 ($N = 23/35$ nests with 3 nestlings added) nestlings between broods matched for hatching date. Nestlings were

added such that broods of 6, 7 and 8 received 3 nestlings (150, 140 and 138% of brood size), and broods of 5 received 2 nestlings (140%). Broods of 6,7, and 8 were reduced by 3 nestlings (50, 43 and 38% respectively), and broods of 4 and 5 by 2 nestlings (50 and 60% respectively). Brood size was maintained at 2−11 (average: enlarged = 8.9 nestlings; reduced = 3.4 nestlings) to stay within the natural brood sizes. Energy constraints may prohibit parents from responding to enlarged broods but such constraints would not prevent responses to reduced broods, and hence brood reductions are useful to examine whether or not parents are flexible and react to proximate cues of need from their offspring.

Prior to manipulation, we video-taped each nest for 3−4 hours, using Sony handycams placed about 5−10 m from the nest tree. Estimates of feeding rates remained the same after three hours of observation and another study (Wiebe 2005) found differences in provisioning rates using three hours of video, so this was a sufficient length of time to detect moderate changes. Filming of parental food transfers inside cavities in the context of other studies showed that a visit that occurred within five minutes of a previous feeding visit was associated only with removal of fecal sacs (KL Wiebe, unpublished data). Hence, when counting the number of feeding visits we excluded any trips that occurred within 5-min of a previous visit. Not including the fecal sac removals, filming inside cavities also showed that in the mid-nestling period, all visits to the cavity by adults were associated with feeding (KL Wiebe, unpublished data). After filming, we transferred nestlings and then filmed again for 3-hours the day after the transfer (i.e., at least 12-hours post-transfer) to allow the parents to acclimatize to the new brood size. Donour nestlings were then returned to their original nest. We weighed the nestlings before and after both video recordings as an index of food transfer and banded them with a USGS aluminum band for individual recognition. We calculated the average nestling mass per brood for comparisons (excluding the mass of any nestlings that died). Only 4 of 9 nestlings that died were transferred,

so these were just as likely to die as nestlings from the original brood and were not discriminated against by the parents. Zero nestlings died in reduced broods which is the typical for nestlings of this age. Nestlings died due to starvation or trampling and not by predators.

Adults were trapped at the nest by plugging the cavity entrance and then flushing them into a net placed over the entrance. At first capture, birds were weighed, measured (bill length and width, rectrix length, wing chord, and tarsus) and aged up to four years according to moult (Pyle et al. 1997). We then attached a 1.5 g radio-tag (Holohil Inc. Carp, ON, CAN) to the central rectrices with cyanoacrylate glue and plucked the second secondary (S2) feather from the parents in the enlarged treatment. We attempted to re-trap all adults with enlarged broods when the nestlings were 14−18 days old (2−3 weeks after first capture) in order to obtain a body mass and the re-grown S2 for analysis of corticosterone in the feather ($CORT_f$). We were able to re-trap 22 female parents of which 17 re-grew their feather, and 24 males of which 22 re-grew their feather.

3.3.2 Body Condition and $CORT_f$ Analysis

We tested whether physiological condition of parents affected their response to brood enlargement, we analyzed four measures of the parents: $CORT_f$, body condition during the nestling period, the change in mass between the incubation and nestling period, and the amount of secondary feather regrowth. Body condition was calculated as the residual of body mass (from the nestling period) regressed against a multivariate measure of size (Wiebe 2008). Relative feather growth was assessed by taking the residuals of feather length correlated to number of days of growth (i.e. days since feather was plucked) thus providing a measure of nutritional condition (White 1991).

For $CORT_f$ assays, we followed Bortolotti et al. (2008) where CORT was extracted from feathers using a methanol-based technique. Samples were measured in two assays with an intra-

40

assay coefficient of variation of 8.32%, an inter-assay coefficient of variation of 14.1%, and mean (±SD) limit of detection (ED80) of 10.99 ± 2.33 pg $CORT_f$/assay tube. Data values are expressed as pg CORT per mm of feather (pg/mm), which gives a valid estimate of $CORT_f$ per unit time of feather growth (Bortolotti et al. 2008). $CORT_f$ assays were performed at the University of Saskatchewan, Canada.

3.3.3 Radio-telemetry

We walked in on birds to sight them using TRX-2000S receivers (Wildlife Materials Inc., Murphysboro, Illinois) and Yagi 3-element antennae. We radio-tracked each pair for 2−3 hours during the control day prior to brood manipulations and again on the day following the manipulation. Tracking for this length of time revealed changes in the location of foraging points associated with nestling age (Chapter 2) so we believe the sampling period was long enough to detect changes in foraging behaviour. During each tracking session, we recorded five independent foraging locations by ensuring at least 30 min had elapsed between foraging points, or the bird had made a feeding visit to the nest (see Elchuk and Wiebe 2002). Foraging locations were only recorded from locations were the bird was seen foraging. At each foraging location, the Universal Transverse Mercator (UTM) coordinates using a Global Positioning System (GPS) we recorded the distance to escape cover (defined as woody vegetation high enough, > 1 m, to provide some concealment for a flicker), and the distance to forest edge (defined as a cluster of trees spanning an area > 10 m). Any differences in habitat such that flickers had to forage further from the nest because of a poor foraging substrate (Elchuk and Wiebe 2003a) would be accounted for because of our repeated measures analysis.

During tracking sessions, we marked visual sightings of birds on a large-scale map of the home range (generated from Google maps) and recorded their behaviour continuously during

tracking sessions so we could calculate travel distances. Both members of a pair were tracked at the same time. We calculated a time-activity budget based on the activities of foraging, sitting (or perching), and direct parental care (in the cavity with nestling or feeding at the hole), and a time-distance budget based on the time spent at three distances from the nest (<10m, 11−200 m, and > 200 m). We interpreted parents spending time within 10 m from the nest as providing the greatest nest defense (e.g. they could react to a squirrel predator on the nest tree by quickly entering the cavity), those 11−200 m from the nest as providing an intermediate level of vigilance (not always in direct sight of the nest but could react to auditory cues) and those > 200 m as investing in the least vigilance because they were less likely to hear calls of the mate or nestlings and return quickly. Time budgets were estimated based on visual observations and assumptions of activity based on the radio-telemetry signals. We calculated the average distance of up to five foraging locations from the nest site during each tracking session and the total distance flown by the birds to and from the nest (recorded as m/hr). We also recorded the length of each foraging bout, which we defined as the time foraging between subsequent nest visits.

3.3.4 Statistical Analysis

A preliminary analysis found that feeding rates were not influenced by time of day (regression: males: $r = 0.03$, $P = 0.20$; females: $r = 0.01$, $P = 0.45$), or temperature (males: $r = 0.003$, $P = 0.70$; females: $r = 0.03$, $P = 0.22$), similarly there were no curvilinear relationships, so we increased power by excluding these variables in subsequent models.

We tested differences between males and females in the way they responded to changes in brood demands and treatment effects using paired t-tests and repeated measures ANOVAs. This was a powerful design because it controlled for the spatial configuration of the home range and external factors such as weather. Analysis of data from control broods ($N = 61$) collected during a

different study (Gow et al. 2013a) showed that natural feeding rates of parents did not vary during the nestling ages of 11–15 days (Linear Mixed Effects: male: male: $F_{4,60} = 1.86$, $P = 0.11$; female: $F_{4,60} = 1.64$, $P = 0.16$). Hence, although 'treatment' sessions occurred one day after "control" monitoring, there should be no underlying time-associated bias related to estimates of feeding rates during the experiment. For repeated measures ANOVAs, we included the factors of treatment (control or enlarged), sex, and original brood size as a continuous variable to account for possible differences in individual quality. To assess what predictor variables ($CORT_f$, body condition, adult age, mass change, and feather regrowth rate) accounted for the change in feeding rates (response variable) we used Linear Mixed Effects (LME) models.

Test statistics and P-values from LME models are presented based on type III sums of squares approximation and variance is ± SE. All analyses were conducted in R 2.15.2 (R Core Development Team 2012) with two-tailed tests and significance set at $P \leq 0.05$. We conducted post-hoc analyses to assess significant differences between factors when $P \leq 0.05$.

3.4 RESULTS

During the control periods, feeding rates by males averaged 1.59 ± 0.07 trips/ hr and by females 1.49 ± 0.06 trips/ hr and rates did not differ between members of a pair (paired t-test: $t_{61} = 1.12$, $P = 0.27$). Neither were feeding rates of males and females within pairs negatively correlated ($r < 0.001$, $P = 0.96$), suggesting that partners did not compensate for each other.

3.4.1 Feeding Rates to Experimental Broods

There was no overall difference in provisioning rates between the sexes and both responded in the same way to enlarged or reduced broods (non-significant interaction term, Table 3.2; Figure 3.1a). The original brood size of the parents prior to manipulation also did not predict feeding

rates. The feeding rate response differed strongly between treatments (treatment*time, Table 3.2) and so we analyzed each treatment individually and found that parents significantly reduced feeding rates to reduced broods (paired t-test: $P = 0.007$), but did not change their feeding rate to enlarged broods ($P = 0.26$; Figure 3.1a). There was, however, considerable variation in responses to enlarged broods with 37 % of females and 43% of males increasing their feeding rates by at least 25%, but 26% of females and 34% of male decreased their feeding rates by at least 25%. For reduced broods, only 11% of females and 26% of males did not decrease their feeding rates. The degree that parents altered feeding rates to enlarged broods was not influenced by the level of $CORT_f$ (LME: $F = 1.03$, $P = 0.46$), body condition during the nestling period ($F = 0.11$, $P = 0.85$), age ($F = 0.55$, $P = 0.64$), mass change ($F = 0.74$, $P = 0.68$), or relative feather growth ($F = 0.57$, $P = 0.87$). There were also no interactions effects between sex and any of the physiological variables ($CORT_f$: $F = 1.03$, $P = 0.46$; body condition: $F = 0.003$, $P = 0.89$; age: $F = 1.18$, $P = 0.25$; mass change: $F = 0.17$, $P = 0.68$; feather growth: $F = 0.24$, $P = 0.52$).

There was a significant difference in the change in per capita provisioning rates between treatments (treatment*time, Table 3.2). Post-hoc tests showed that parents reduced their per capita feeding rates to enlarged broods (paired t-test: $P < 0.001$), and increased per capita feeding rates to reduced broods ($P < 0.001$; Figure 3.1b). In response, nestling mass decreased in enlarged broods on average by 5.09 g ± 0.75 (paired t-test: $t_{32} = 6.77$, $P < 0.0001$; Figure 3.2) and one or two nestlings died in 6 of 35 nests. In reduced broods, nestlings gained on average 8.9 g ± 1.25 ($t_{31} = -6.94$, $P < 0.001$; Figure 3.2) and no nestlings died.

Table 3.2. Results from repeated measure ANOVA models for brood manipulations, for the response variables of feeding rate (trips/hr), per capita feeding rate (trips/hr/nestling), and fecal sac removal rate (removal/hr). Treatment refers to enlarged or reduced, and time as pre or post treatment.

Variables	Feeding rate		Per capita feeding rate	
	F	P	F	P
Sex	3.66	0.057	2.71	0.10
Treatment	1.62	0.20	4.91	0.027*
Time	1.14	0.29	5.12	0.025*
Brood size	3.37	0.068	0.19	0.66
Treatment*time	9.62	0.002	87.47	<0.001*
Sex*treatment*time	0.18	0.91	0.25	0.86
Treatment*time*brood size	1.66	0.19	0.09	0.91

*P <0.05
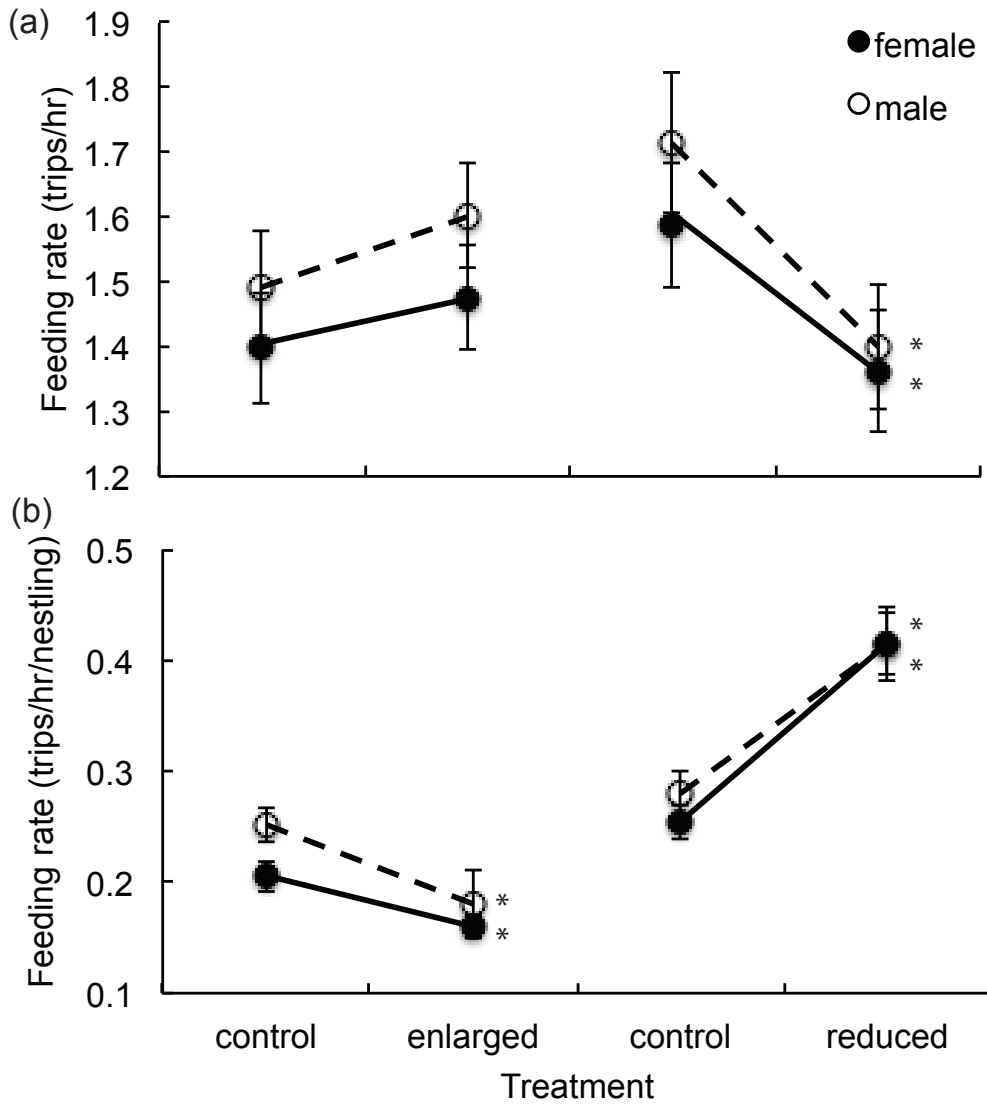
Figure 3.1. (a) Feeding rates (trips/ hr) of male and female northern flickers, in central British Columbia, between control (before manipulation) and enlarged (after manipulation; $N = 35$ pairs), and control and reduced broods ($N = 27$ pairs). (b) Per capita feeding rates (trips/ hr /nestling) of male and female northern flickers between control (before manipulation) and enlarged (after manipulation), and between control and reduced broods. Error bars are ± SE. Significant difference between control and treatment days are indicated (*). Temporary (24 hr) brood manipulations were conducted when nestlings were between 12 and 14 days old in 2010–2012.
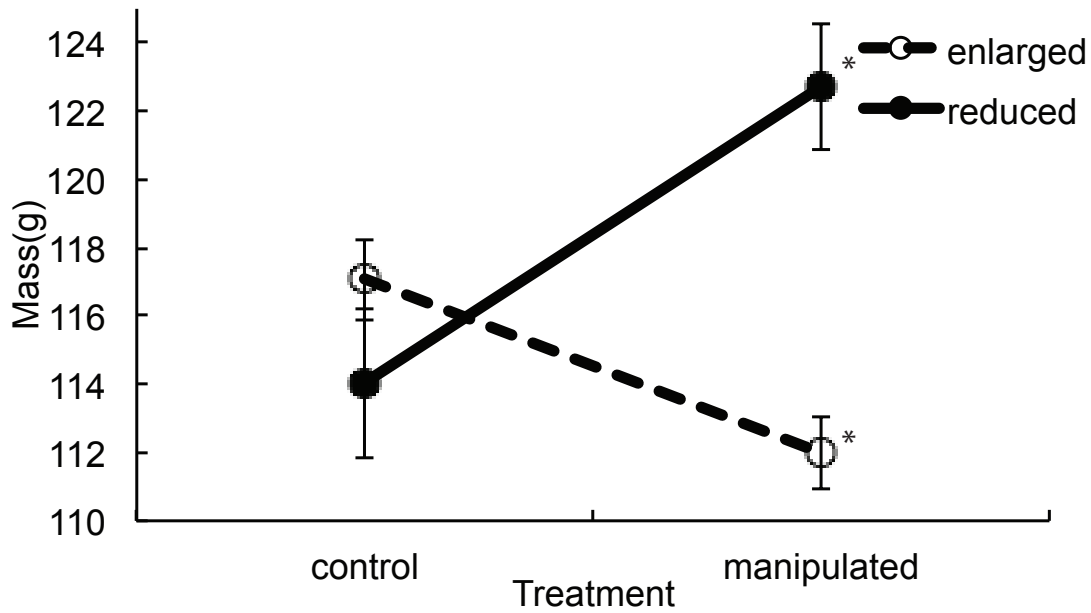
Figure 3.2. Average nestling mass, from northern flickers in central British Columbia, within control broods and the associated mass change in response to the experimental manipulation of brood size. Any dead nestlings were excluded. Error bars are ± SE. Sample sizes are 33 enlarged and 32 reduced nests. Significant differences between control and treatment days are indicated (*). Temporary (24 hr) brood manipulations were conducted when nestlings were between 12 and 14 days old in 2010–2012.

3.4.2 Foraging Patterns

Spatial patterns of foraging varied between individuals during the control tracking sessions. For example, 17% of the birds foraged during the entire tracking session within 200 m from the nest, 9% foraged consistently far (>600 m) from the nest, 19% foraged exclusively at intermediate distances (201 – 599 m from the nest) and the rest (57%) combined a mixture of trip lengths. The average foraging distance from the nest during control sessions was 311 ± 34 m for males and 314 ± 32 m for females and did not differ significantly between partners (paired t-test: t_{34} = -0.063, $P = 0.95$). Both females (86% of trips) and males (86% of trips) foraged more frequently within 600 m of the nest than at farther distances.

In concurrence with the lack of feeding response to increased brood demands, neither sex foraged farther from the nest when brood demands increased (repeated measures ANOVA: interaction: $F_{1,102} = 0.035$, $P = 0.85$; sex: $F_{1,102} = 0.079$, $P = 0.78$; time: $F_{1,102} = 1.06$, $P = 0.31$). There were no differences between the sexes in the average distance travelled (interaction: $F_{1,97} = 0.092$, $P = 0.76$, time: $F_{1,97} = 0.007$, $P = 0.93$; sex: $F_{1,97} = 0.69$, $P = 0.41$), although the average distance travelled by males during the enlarged treatment day, 740 ± 76 m/ hr, was slightly less than during the control tracking session, 769 ± 67 m/ hr. Females travelled on average 812 ± 82 m/ hr during the control session and those with enlarged broods travelled 829 ± 95 m/ hr. Foraging bouts during control tracking sessions averaged 23 ± 2 min for males and 26 ± 4 min for females and did not differ between partners (paired t-test: t_{32} = -0.68, $P = 0.5$). During control tracking sessions, females that foraged farther from the nest stayed longer consistent with ideas of central place foraging ($r = 0.67$, $P < 0.0001$), but the relationship between foraging bout length and distance from the nest was weaker for males ($r = 0.09$, $P = 0.085$). There was no interaction between the sexes in the response of foraging bout length to brood enlargement (interaction: $F_{1,99}$ = 0.04, $P = 0.84$), no time effect ($F_{1,99} = 2.82$, $P = 0.1$) or sex effect ($F_{1,99} = 0.79$, $P = 0.38$). When

forced to provision for a large brood, parents did not trade-off their own safety by foraging farther from edges (interaction: $F_{1,100} = 0.43$, $P = 0.52$; time: $F_{1,100} = 0.037$, $P = 0.85$; sex: $F_{1,100} = 0.4$, $P = 0.53$) or escape cover (interaction: $F_{1,100} = 0.32$, $P = 0.57$; time: $F_{1,100} = 0.12$, $P = 0.73$; sex: $F_{1,100} = 0.61$, $P = 0.44$).

During control tracking sessions, the average percent time spent foraging by males (67 % ± 0.034 of their time budget) did not differ from that spent by females (64 % ± 0.030; $F_{1,98} = 0.54$, $P = 0.46$) and neither sex altered the amount of time foraging to enlarged broods (sex*time interaction: $F_{1,98} = 0.45$, $P = 0.5$; time: $F_{1,97} = 4.24$, $P = 0.42$). The sexes also did not differ in the amount of time providing direct parental care ($F_{1,98} = 3.13$, $P = 0.8$) and such care by both parents did not change between days (interaction: $F_{1,97} = 0.25$, $P = 0.64$; time: $F_{1,97} = 2.44$, P = 0.12; Figure 3.3). There were no sex, time or sex*time differences in the amount of time males and females spent at each distance category (<10 m, 11−200 m, and >201m) from the nest (MANOVA: interaction: $F_{3,73} = 0.59$, $P = 0.62$; sex: $F_{3,73} = 0.66$, $P = 0.58$; time: $F_{3,73} = 1.17$, $P = 0.33$; Figure 3.3).

3.5 DISCUSSION

3.5.1 Energy Limitation and Feeding Responses

Contrary to our prediction and in contrast to results from most other species (Table 3.1), northern flickers did not increase their feeding rates or change their foraging strategy when brood size was experimentally increased in the short term. Generally, short-lived species are expected to be more willing to invest in the current brood and less in self maintenance and survival than longer-lived species (Stearns 1989), a pattern that was supported by the literature review (Table 3.1). In particular, 50% of 6 studies on long-lived species (> 80 % survival rate per year), and 90% of 29 studies on short-lived species found that parents increased feeding rates to enlarged broods.
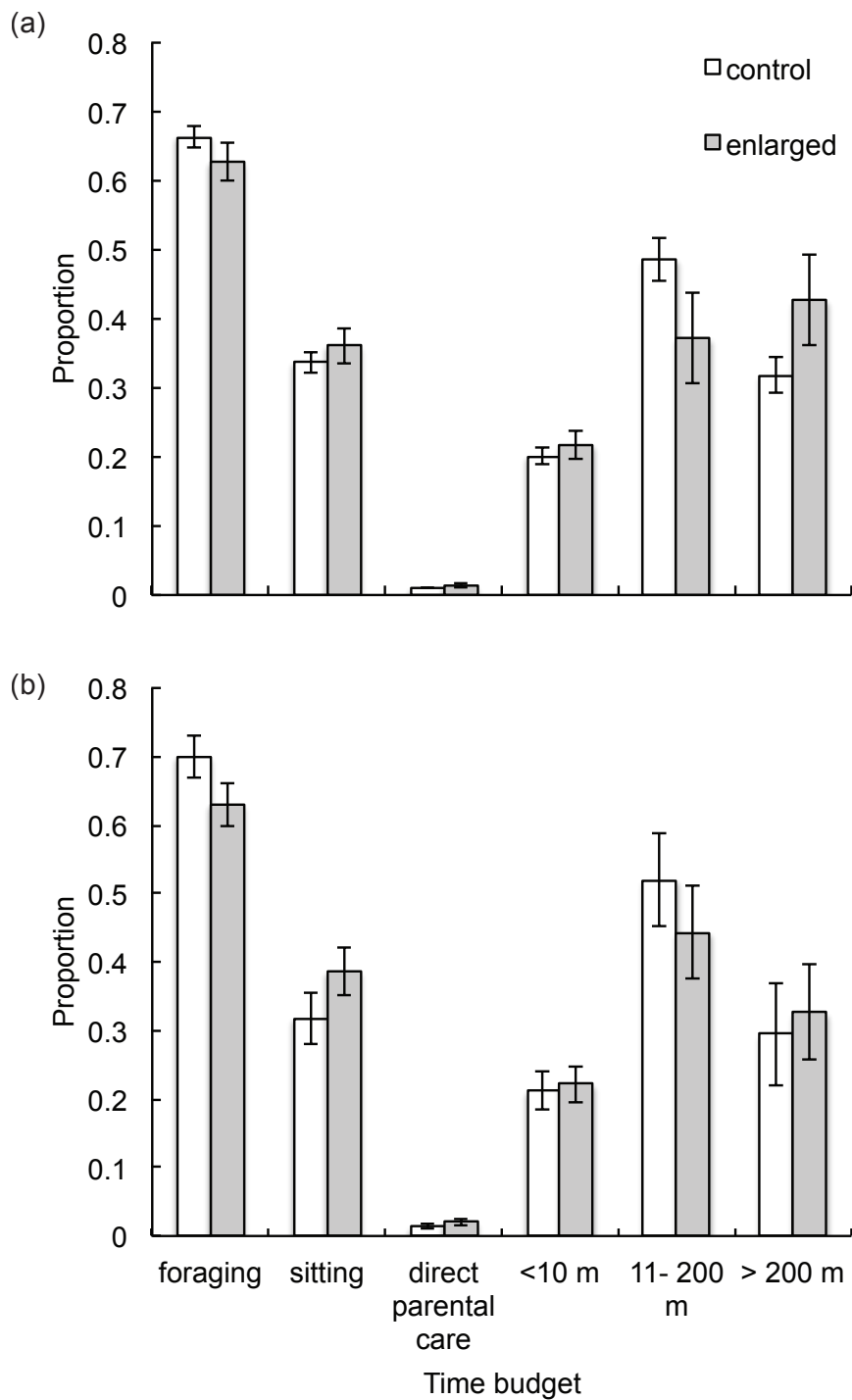
Figure 3.3 Activity and distance time budgets of northern flicker females (a) and males (b), in

central British Columbia, in control and enlarged broods. The proportion of the time spent at

various activities and at various distances from the nest is shown based on 132 hours of

observation from 34 males and 130 hours from 34 females. Direct parental care refers to parents being in the cavity, in close physical contact with the nestlings. Sitting refers to birds on the ground or perched in a tree. Temporary (24 hr) brood manipulations were conducted when nestlings were between 12 and 14 days old in 2010–2012. Males and females spent similar amounts of time at each distance category and engaged in each activity between the control and enlarged treatment days.

Flickers have relatively short lifespans compared to most birds (40% annual adult apparent survival rate; Fisher and Wiebe 2006a), and so they are atypical for a short-lived species by maintaining their feeding rates when given more young. However, flickers responded similarly to other species by reducing feeding rates when broods were reduced (Table 3.1).

We can exclude some potential explanations for why parent flickers did not respond to brood enlargements. The degree of brood enlargement was certainly sufficient to place extra demands on parents because nestlings in enlarged broods lost mass and a few died. It also appears that parents could respond to proximate cues from the brood and did not have a fixed feeding strategy because they decreased feeding rates to reduced broods. Therefore, flickers maybe unwilling or unable to increase their work rate. Some parents do not respond if they are energetically constrained and are simply incapable of increasing their effort because they are already working near their maximum, although they may perceive different levels of begging from offspring (Winkler 1987).

Although we did not measure energy expenditure of flicker parents directly with doubly-labeled water, a number of ecological and life history traits suggest they may be working near capacity during the nestling period. The caloric content of the main prey of flickers, ants (Gow et al. 2013b; Appendix A), is relatively high compared to other invertebrates (Rumpold and Schlüter 2013) but the size of prey is so small the limiting factor may relate to the patchy and ephemeral distribution of ants on the landscape (Elchuk and Wiebe 2003a) and the additional energy needed to travel the long distances to and from the nest. Secondly, flickers, and woodpeckers in general, may have a low energy reserve buffer because they must provision offspring during a nestling period which is unusually long for an altricial bird its size (Yom-Tov and Ar 1993). The general importance of foraging distances on the landscape and the length of

investment in nestlings in determining responsiveness of parents to extra demands is highlighted in Table 3.3. In particular, 83% of 6 species which did not respond to increased brood demands had large (>25 ha) feeding ranges and longer nestling periods compared to the 81% of 16 species that responded.

The lack of a strong feeding response to enlarged broods was unexpected because a previous experiment on the same population found that widowed parents provisioned at a rate of 1.61 (male) and 1.80 (female) times higher than at biparental nests (Wiebe 2005), suggesting parents could increase feeding rates. However, the extra feeding visits did not prevent high mortality in broods of widowed parents suggesting the amount of extra food the parents could actually deliver was limited, i.e., they probably delivered less food per visit. The current study showed that a short-term (24 hour) spike in nestling demands was not enough to motivate extra effort whereas a more chronic stressor caused by a missing partner increased the rate of feeding visits. Hence, during the short-term, there may be some sexual conflict in that parents may expect their partner to contribute to the extra workload (Houston and Davies 1985) but when this does not happen, nestlings may soon suffer mass loss. Thus, if brood manipulations were conducted long-term parents may either allow brood reduction to occur to match a set (fixed) feeding rate or eventually increase feeding rates.

Table 3.3. Life history traits of species presented in Table 3.1 (plus northern flicker) according to whether parents responded or not to experimentally enlarged broods. Citations are for home range sizes which are presented as the range if known and the (mean). Species are ordered according to decreasing home range size.

Species	Mean brood size	Number of broods	Nestling period (days)	Home range (ha)	Feeding response	Source
Red-tailed tropic bird	1	1	73+	13600[a]	Y	(Le Corre *et al.* 2003)
Razorbill	1	1	19	500−2900[a]	Y	(Lavers, Hipfner & Chapdelaine 2009)
Osprey	3	1	50+	2955[a]	N	(Peery 2000)
Barn owl	5	2	50+	20−3174 (511)	N	(Taylor 1994)
Laughing gull	3	1	35+	113−523[a]	Y	(Dosch 2003)
Eurasian kestrel	5	1	30	386	N	(Peery 2000)
African redbreasted sparrowhawk	2	2	30	NA	N	NA
Tawny owl	5	2	60+	0.6−148	N	(Sunde & Redpath 2006)
American	4	1	28	142	NA	(Schoener 1968)

kestrel

Northern flicker	8	1	27	2−112 (25)	N	(Elchuk & Wiebe 2003a)
Tree swallow	5	1	20	19[a]	Y	(Quinney & Ankney 1985)
European starling	5	2+	21	12[a]	Y	(Feare 1984)
Lesser elaenia	2	1	NA	5−15	Y	(Stutchbury & Morton 2001)
Acorn woodpecker	5	1	31	6	Y	(MacRoberts & MacRoberts 1976)
Pied flycatcher	6	2+	16	1.4	Y	(Dale & Slagsvold 1990)
Great tit	8	2+	19	1.18−1.34	Y/N	(Krebs 1971)
Blue tit	9	2+	19	0.95−1.47 (1.1)	Y	(Both & Visser 2000)
House sparrow	5	2+	14	0.08−1.0[a]	Y	(Peach *et al.* 2008; Shaw 2009)
Yellow warbler	4	1	9	0.2−0.45	Y	(Lowther *et al.* 1999)
Eastern phoebe	5	2+	16	0.03−1.8[a]	Y	(Weeks 2011)
Red-winged	2	2+	12	0.05−0.47	Y	(Hurly & Robertson

blackbird				$(0.22)^{b}$		1984)
Fairy martin	3	2+	15	NA	Y	NA
White-rumped swiftlets	2	1	40+	NA	Y	NA
Common swift	2	1	25	NA	Y	NA

[a] Home range calculated as a circular area based on the average foraging distance from the nest.

[b] Home range of females calculated from a map of territories.

3.5.2 Individual Traits and Feeding Effort

The considerable variation in the degree to which parents altered their feeding rates to enlarged broods was not explained by measures of physiological condition or age. This is in contrast to a study of parental care in the post-fledging period in which female flickers with high $CORT_f$ levels abandoned their broods, and older males cared for offspring longer (Gow and Wiebe 2014b; Chapter 4). During the nestling period, parents still have a long period of care ahead of them and hence they may be reluctant to increase work effort above a certain threshold and thereby deplete energy reserves too quickly and risk the whole nesting attempt. Nearer to the end of parental investment, during the post-fledging period, parents may be in a better position to judge their own physiological condition and reserves relative to the needs of offspring and adjust their investment accordingly. In some species, the energy trade-off may be strong enough that individuals may gain a fitness advantage by reducing parental effort during the late breeding stages in order to minimize breeding-moult overlap (Hemborg and Merila 1998; Helm and Gwinner 2006). In flickers, perhaps it is not so much feeding rate which is adjusted but the total length of parental care.

Consistent with our observation that the sexes had similar roles during the mid-nestling period, both sexes responded in a similar way to the brood manipulations. Likewise, most previous studies found no differences between the sexes in their response to manipulated broods (Table 3.1), namely in 86 % of 21 studies, both sexes responded to changes in brood demands. However, with unmanipulated broods, feeding rates by males is often more fixed than in females and is dependent on male quality and additional mating opportunities, whereas females often respond more flexibly to environmental factors such as food supply (e.g. Grundel 1987; Schwagmeyer and Mock 2003; Nakagawa et al. 2007; Low et al. 2012).

3.5.3 Foraging

We are apparently the first to study spatial patterns of foraging on the landscape in response to increased brood demands but found that parents changed neither their foraging pattern nor rate of feeding when brood demands increased. In particular, parents did not forage farther from edges, escape cover, or the nest. The type of habitat used for foraging by flickers depends on short-term changes in temperature that affect ant abundances (Wiebe and Gow 2013) showing that parents can shift foraging locations rapidly and on a small spatial scale in a way which maximizes prey capture. If parents are already using the habitat patches, which maximize encounters with patchy prey, it may not be possible for them to increase capture rates when brood demands increase by shifting to different foraging patches. However, parents also did not increase the length of foraging bouts within patches suggesting they did not bring larger food loads to the nest. Other studies of avian parents did not observe foraging locations or bout lengths but monitored the type of prey brought to the nest. For instance, blue tits (*Cyanistes caeruleus*) brought larger prey items, indicative of better quality prey, when brood demands were temporarily decreased, but did not change prey size when broods were enlarged (García-Navas and Sanz 2010). Pied flycatcher (*Ficedula hypoleuca*) parents brought more caterpillars, fewer adult lepidopterans (Mänd et al. 2013), and heavier prey loads (Siikamäki et al. 1998) to larger broods.

In sum, flicker parents seem able to respond to proximate cues of demand from the brood, but in the short term readily reduce their work rate but do not increase it. We suggest that the need to forage over a relatively large spatial area and during a relatively long nestling period are factors which constrain work rate in flickers and birds generally. It is important to conduct both reduced and enlarged treatments to identify if parents respond to proximate cues of brood demands and a long-term brood size manipulation may reveal whether a more chronic demand on

parents eventually elicits any increased effort. Given that feeding rates did not increase in our study, it is perhaps not surprising that spatial patterns of foraging on the landscape also did not change. However, we encourage other researchers conducting brood manipulation experiments to record spatial patterns of foraging because it may reveal important trade-offs linked to predation risk and travel costs which otherwise go undetected in central place foragers.

CHAPTER 4:

DETERMINANTS OF PARENTAL CARE AND OFFSPRING SURVIVAL

DURING THE POST-FLEDGING PERIOD: MALES CARE MORE IN A SPECIES

WITH PARTIALLY REVERSED SEX ROLES

4.1 ABSTRACT

Sexual conflict is magnified during the post-fledging period of birds when the sexes face different trade-offs between continuing parental care or investing in self maintenance or other mating opportunities. Species with reversed sex roles provide a unique opportunity to study the relationship between mating systems and investment in parental care. Here, we provide the first detailed study of the length of care by males versus females ($n = 24$ pairs) during the post-fledging period, assessing factors that may promote care within and between the sexes. In the northern flicker *Colaptes auratus*, a species with partly reversed sex roles, males cared longer than females (average 16 versus 12 days, respectively). Overall, 36% of females but no males deserted the brood prior to fledgling independence. Parents that provisioned nestlings at a high rate also spent more days feeding fledglings. Among males, age and nestling feeding rates were positively associated with the length of care. Among females, a low level of feather corticosterone ($CORT_f$) was associated with a longer length of care. About 45% of fledglings died within the first week, but fledglings with intermediate body mass had the highest survival suggesting stabilizing selection on mass. Fledgling survival was also higher in individuals with larger broods and lower levels of $CORT_f$. We demonstrate that because females can be polyandrous they often desert the brood before males, and that the sexes respond to different cues relating to their energy balance when deciding the length of care given to their offspring.

4.2 INTRODUCTION

Parental care promotes the survival and fitness of offspring but males and females often differ in their evolutionary interests surrounding reproduction which leads to sexual conflict (Chapman et al. 2003). Life history theory predicts that when biparental care is required (e.g. birds with altricial young) sexual conflict over brood desertion will be low (Olson et al. 2008). However, brood desertion may occur if an individual benefits more from additional reproductive opportunities than any loss of offspring from the current brood (Kokko and Jennions 2008; Olson et al. 2008). Among the key factors promoting desertion by one partner are low offspring quality (Erikstad et al. 1997), small brood size (Beissinger and Snyder 1987), low perceived paternity (reviewed in Olson et al. 2008), high probability of re-mating (Székely et al. 1999), and good body condition or intrinsic quality of the parent (Hõrak 2003). Furthermore, if an individual perceives that its mate has a good ability to care for the offspring, it may desert, leading to an evolutionary game of mutual assessment (Griggio et al. 2005). In some cases, mainly in species with precocial young, brood desertion is normal and one sex always wins (Székely et al. 2007). In other species, the sex that has the possibility of attracting additional mates may cease caring for offspring in order to pursue new partnerships.

In birds, offspring desertion can occur during the incubation stage (Székely et al. 2007), nestling rearing (Beissinger and Snyder 1987; Griggio et al. 2005) or immediately after fledging (Morton et al. 2010). Usually it is the male that deserts but in some species it may be either sex, or rarely the female (e.g. Eldegard and Sonerud 2009; Morton et al. 2010). Brood desertion may be more frequent than previously thought because most studies do not quantify care after the young leave the nest, due to the logistical difficulties in following families on the landscape. Factors that contribute to the length of care are important because the post-fledging period may be a time of high energy demands for the parents when each may face different trade-offs involving parental

care, self maintenance, or other mating opportunities. Although parents may increase the survival of their young by continuing to provide care after they leave the nest (Grüebler and Naef-Daenzer 2010), extended parental care may negatively affect parental survival or delay moult or migration (Stutchbury et al. 2011). The later in the season the offspring fledge, the more severe the potential time and energy conflict for parents.

One way parents may reduce the amount of investment needed in the post-fledging period is to invest strongly at the nestling stage to fledge large and healthy offspring that may become independent sooner. If the body condition of nestlings at the time of fledging determines the length of subsequent investment, we predict that the amount of care given in the nestling period and the fledging mass of nestlings will be inversely correlated with care during the post-fledging period. Conversely, if parents differ in quality or the amount of resources, parents in good body condition may invest more both at the nestling and post-fledging stages (van Noordwijk and de Jong 1986). Other studies show that a parent may reduce parental care if it has a poor body condition (Angelier and Chastel 2009) so we predict that parents with high corticosterone (CORT) levels or relatively low mass will stop caring sooner. Environmental factors are unlikely to explain sex differences in care when both parents use the same habitat on the same home range and are equally susceptible to predation risk, weather events and food shortages.

Here, we study sexual conflict and brood desertion in a woodpecker, the northern flicker *Colaptes auratus*, a species with partly reversed sex roles in which males contribute more care than females (Wiebe 2005, 2008; Gow et al. 2013a) and females may be polyandrous (Wiebe and Kempenaers 2009). This allows for a unique opportunity to study how mating systems and sex roles influence the amount of care. Furthermore, male flickers (Wiebe and Kempenaers 2009) and woodpeckers generally (Michalek and Winkler 2001) have a high assurance of paternity. These traits suggest that brood desertion by females would be favoured in woodpeckers and this was

confirmed in mate-removal experiments in the northern flicker (Wiebe 2005). In the wild, 11% of female lesser-spotted woodpeckers *Dendrocopos minor* apparently stopped feeding nestlings but were later observed feeding fledglings (Wiktander et al. 2000) so it is uncertain whether brood desertion occurs in woodpeckers as a general pattern.

Woodpeckers may provide a model system to understand how brood desertion evolves in species with biparental care and we tested hypotheses relating the length of post-fledging care to 1) prior investment in the brood (nestling feeding rates), 2) adult body condition, 3) seasonal time of breeding, 4) parent age, and 5) sex. Because female flickers are usually single brooded (but see Gow and Wiebe 2012) they would be unlikely to re-pair and begin a second breeding attempt in the current year. However, females which abandon care early may gain a fitness advantage by scouting out future males for polyandry, or searching for additional nest cavities in which to lay parasitic eggs (Wiebe and Kempenaers 2009). The rate of juvenile survival may indicate for how long biparental care is beneficial for offspring and so we also modelled juvenile survival based on the covariates of fledgling mass, fledgling physiological condition (feather corticosterone; $CORT_f$), brood size, and nestling sex.

4.3 METHODS

4.3.1 Study Site and Species

We studied northern flickers at Riske Creek, British Columbia, Canada (51° 52'N, 122° 21'W), from 2010−2012. Female flickers are facultatively polyandrous, where up to 5% of females annually have two nests with two different males. In addition, intraspecific brood parasitism occurs in 17% of broods and <1% of young are extra-pair (Wiebe and Kempenaers 2009). Northern populations are migratory, imposing constraints on individuals to breed within a fixed time window. Incubation of clutches ranging from 3−13 eggs lasts about 12 days and the nestling

period lasts from 25−28 days (Wiebe and Moore 2008). In this study, mean brood size at fledging was 5.9 ± 1.3 SD (range 3−8, *n* = 28 nests).

4.3.2 Radio-tag Deployment

We accessed flickers by cutting small, replaceable doors in the tree trunk near the base of the nest cavity (Wiebe 2008). Adults were captured at the cavity by plugging the entrance and then flushing the bird into a net over the entrance. Captured adults were weighed, measured (length of wing, bill, tail, tarsus, 9th primary, and bill depth), aged up to four years based on moult (Pyle et al. 1997) and banded with a unique colour combination. We monitored parental movements during the post-fledgling period using radio-telemetry and 10-week, 1.5 g radio-tags (Holohil Inc. Carp, Ontario, CAN) attached with cyanoacrylate glue to the central rectrices, of the male and female of a pair. We walked in on birds to sight them directly using TRX-2000S receivers (Wildlife materials, Murphysboro, Illinois, USA) with Yagi 3-element antennae. Signals could be detected up to 5 km from high points on the study site. In 2010, we radio-tracked 11 pairs during the post-fledging period and in 2011 and 2012 we followed 8 and 10 pairs respectively. However, two females (one in 2012 and one in 2010) dropped their tail feathers and tag prior to their young fledging. We tracked only those pairs in which both the male and female were alive at the time their nestlings fledged (*n* = 27 females and 28 males). Because some adults moved off of the study site to private property or disappeared (i.e., may have died) we could confirm the number of days of care for 24 females, and 24 males.

4.3.3 Measurements on Fledglings

Nestlings were weighed when 20 days old and colour banded with unique combinations and the wing chord was measured. The mass of flicker nestlings plateaus after 18 days old (Gow et al.

2013a), and so we assumed mass at day 20 was a reliable indicator of condition at fledging which occurred about five days later. To maintain statistical independence we chose randomly one fledgling per nest to receive a 0.5−0.6 g radio-tag which represented about 0.4% of its body mass. Sample sizes of radio-tagged nestlings were 13 in 2011 and 25 in 2012. From these tagged nestlings we measured the amount of CORT deposited in feathers ($CORT_f$) by cutting the tip of a secondary feather (S2 or S3). CORT is a glucocorticoid hormone that is secreted in high levels during periods of food limitation and $CORT_f$ is an integrative measure of hormone levels deposited in the feather over the period of its growth (Bortolotti et al. 2008). Therefore, the collected feather reflected CORT secreted during day 6 to 20 of the nestling period. We calculated nestling condition on day 20 by using the residual body mass versus wing chord and averaged the condition of nestlings in a brood to obtain "brood condition", which was used in the analysis of length of care by the parents. Finally, we determined date of fledging by visually checking nests or radio signals every day after nestlings were 20 days old.

Previous studies have found that several factors increase fledgling survival including early date of fledging, high body mass (Naef-Daenzer et al. 2001), higher values of the 'stress hormone' CORT (Rivers et al. 2012), and having few siblings (Styrsky et al. 2005). The relationship between some of these variables and fledgling survival may not be linear but instead an intermediate value (e.g. of body mass or CORT level) may be optimal and so we entered quadratic terms into the statistical models.

4.3.4 Monitoring Parental Care

For a measure of parental effort prior to the post-fledging period, we quantified parental feeding rates (trips/hr) at each nest during the nestling period at two stages: middle (nestlings 10−15 days old) and late (days 19−21). The feeding trips were videotaped with analog Sony handycams placed

about 5 m from the nest tree for 3−4 hr sessions on days it was not raining. Preliminary analysis showed that estimates of feeding rates remained the same after three hours of observation and did not vary throughout the day or with temperature (EA Gow unpublished). To see how long parents fed their young, we began radio-tracking each pair within two days of fledging and every second day thereafter. The tracking sessions lasted 1 hr and occurred between 0700−1900 hr. Parental care was assumed to have ended after two consecutive sessions in which parents never fed fledglings. We defined a parent as abandoning the brood when it was seen alive for two sequential tracking sessions and never fed nestlings although its partner was feeding them. Our accuracy in determining when parents stopped feeding was strong because parents were observed not feeding fledglings in 3% of 162 tracking sessions (males) and 6% of 126 tracking sessions (females) but then feeding during the next tracking session. The radio-tracking and vocalizations given by young meant that we almost always detected feeding visits if they occurred during the session, but we were sometimes unable to see the duration of the food transfer or specific identify of the fledging being fed when tree branches blocked our view. Thus, assessing how much food each fledgling received was impossible.

The mobility of fledglings also made it difficult to record precisely the instantaneous locations of both fledglings and parents, and so we calculated the distance between parents and offspring based on four categories: <50 m, where parents were in visual contact with fledglings and could quickly react to predators by alarm calling or mobbing; 50–300 m, where parents could return to fledglings relatively quickly; 300−700 m, a typical foraging distance from the nest during the nestling period; and >700 m. We eliminated tracking sessions and times during a tracking session when the location of the parents or fledglings were unknown (142 hr) and thus report the proportion of time at each distance based on a total of 256 hr of tracking (female 112 hr, male 144 hr). We assumed parents investing more in the protection of their fledglings stayed closer to them.

We used a MANOVA to investigate factors that were associated with the proportion of time parents spent at the four distance categories from at least one of their fledglings as the dependent variable. For some analyses, we divided the tracking data into two time periods based on the age (and hence mobility) of the fledglings: early (1−7 days post-fledging) when fledglings were less mobile and typically did not follow parents and late (8 days to independence) when fledglings flew > 100m during tracking sessions, and often followed parents.

4.3.5 Body Condition and $CORT_f$ Analysis

We used two measures to assess physiological condition of adults trapped during the nestling period; $CORT_f$ and a body condition index calculated as the residual of body mass regressed against a multivariate measure of body size (see Wiebe 2008). We plucked a secondary (S2) feather when the adult was first captured during incubation. During recapture, 2−4 weeks later (nestlings were 14−18 days old), we re-weighed the adult and cut the regrown secondary.

For $CORT_f$ assays we followed Bortolotti et al. (2008) where CORT was extracted from feathers using a methanol based technique. Samples were measured in two assays with an intra-assay coefficient of variation of 8.32%, an inter-assay coefficient of variation of 14.1%, and mean (±SD) limit of detection (ED80) of 10.99 ± 2.33 pg $CORT_f$/assay tube. Data values are expressed as pg CORT per mm of feather, which gives a valid estimate of $CORT_f$ per unit time of feather growth (Bortolotti et al. 2008). $CORT_f$ assays were performed at the University of Saskatchewan, Canada.

4.3.6 Statistical Analysis

The tagged fledglings were tracked every-other day, weather permitting, to determine whether they were alive or dead. If a fledgling's signal disappeared from the study area and it was not re-

sighted with the family group for two consecutive tracking sessions it was assumed dead. We

estimated individual survival of 33 fledgling flickers using known-fate models in Program MARK

(White and Burnham 1999). These models use the Kaplan-Meier product-limit estimator which is

advantageous because it allows biological covariates to be evaluated and multiple models to be

compared (White and Burnham 1999). We examined whether juvenile survival during the post-

fledging dependency period varied over the first 16 days post-fledging by using the biologically

meaningful covariates: year, fledging date, fledging mass, fledgling $CORT_f$, brood size at fledging,

and fledgling sex. We ranked models using Akaike's information criterion corrected for small

sample sizes (AIC_c). We considered all models with $\Delta AIC_c \leq 2$ to show substantial support, while

$\Delta AIC_c \leq 4$ showed some support (Burnham and Anderson 2002). We considered parameter

estimates with 95% confidence intervals that overlapped zero to be insignificant. We used model

averaged weights to identify the most important models and variables (Burnham and Anderson

2002). We increased the power of our analysis by using a base model with two time intervals. To

assess model validity (all models with $\Delta < 2$) we conducted a bootstrap test with 1000 simulations

(White et al. 2001).

We used linear mixed effects models (lme) to analyze influences on the length of parental

care for males and females during the post-fledging period, with length of time each parent fed

their fledglings as the dependent variable and year as a random factor. Because only a subset of

birds were re-trapped, we ran one analysis with a reduced data set of the re-trapped parents which

included the variables of $CORT_f$ and body condition during the nestling period and one analysis

with the larger sample of parents without those variables. Because of a small sample size in the

reduced dataset ($n = 13$ females, 12 males), we limited the number of independent variables to

four: parent age, body condition, date of fledging and $CORT_f$. To meet the assumptions of

normality $CORT_f$ was log transformed. For the full dataset the independent variables were: brood

size at fledging, the condition of the brood at fledgling, parent age, feeding rate during the nestling period, and the date of fledging.

For the lme models, we confirmed model validity by using likelihood ratio tests to compare the fixed effects models to null models with only the random effects using ANOVA (Zuur et al. 2010). We present *P*-values estimated from Markov Chain Monte Carlo methods (MCMC) with statistical significance set at $\alpha = 0.05$. All other statistical analyses were run in R 2.14.2 (R Core Development Team 2012), were two-tailed, and met the assumptions of normality.

4.4 RESULTS

4.4.1. Fledgling Behaviour and Survival

Flicker fledglings could fly when leaving the nest and one first flight from the cavity was about 200 m across an open field. During the first week after their young fledged, parents left them at a certain location (often clinging to the side of a tree) and periodically returned to feed them. To initiate feeding, parents gave a soft series of 'wicka' calls that signalled fledglings to move towards the parent to receive the regurgitated meal. Between 7−10 days post-fledging, offspring followed their parents to foraging sites and either foraged themselves or watched their parents. A few fledglings attempted to forage as soon as two days post-fledging, by hopping and pecking at the ground. Parents did not usually split the brood, but in 3 of 25 cases certain young were only seen with one of the parents.

Fledgling mortality was high within the first eight days after fledging with 45% (17/38) of radio-tagged fledglings dying and the daily survival calculated by program MARK was 0.866 ± 0.032. In comparison, daily survival was 0.984 ± 0.015 between 9 to 16 days post-fledging (Fig. 4.1). The location and nature of the dead fledgling remains, either in raptor nests or as plucked piles of feather and bones suggested avian predators were responsible for most of the mortality.

We observed an American kestrel *Falco sparverius* catch and consume a recently fledged flicker. One tag was located in a red-tailed hawk *Buteo jamaicensis* nest, and on several occasions Cooper's hawks *Accipiter cooperii* chased the flicker fledglings. A chewed radio-tag was also observed in black bear *Ursus americanus* scat and two others were cached in, or buried under logs suggesting mammalian predators.

The program MARK analysis resulted in three models with ΔAIC values ≤ 2; these contained four covariates (mass, mass^2, CORT, and brood size at fledging) and accounted for 61.8 of the AIC$_c$ weight (Table 4.1). Mass^2 and mass occurred in all six of the top models with ΔAIC values ≤ 4, suggesting these variables were important for predicting fledgling survival and cumulatively had an AIC$_c$ weight of 0.87. The AIC$_c$ weights for the variables of brood size and CORT were 0.70 and 0.45, respectively. Fledglings with high and low mass had lower survival probabilities than those with intermediate mass (Fig. 4.2), those fledglings from larger broods had higher survival than those from small broods and survival was negatively correlated with the amount of CORT$_f$. The quadratic relationship with fledgling mass was not driven by the two extreme values because it remained in the top models with these two data points removed. The bootstrap goodness of fit test showed that the data fit the top three models ($P = 0.24$, 0.001, and 0.001).

Table 4.1. Model selection using Akaike's information criterion (AIC_c) from Program MARK's known fate model of fledgling survival. Only models with a $\Delta AIC_c \leq 7$ are shown. The base model (time only) had an AIC_c value of 102.641. K refers to the number of parameters, w_i to the AIC_c weight of each model. Models are based on samples from 32 fledgling northern flickers.

model	K	AICc	ΔAIC_c	w_i
Φ+mass+mass^2+broodsize+CORT	5	86.38	0	0.27
Φ+mass+mass^2+mass*broodsize	4	87.25	0.87	0.18
Φ+mass+mass^2+broodsize	4	87.33	0.95	0.17
Φ+mass+mass^2+broodsize+CORT+mass*broodsize	6	88.79	2.41	0.082
Φ+mass+mass^2+CORT	4	89.38	3.01	0.061
Φ+mass+mass^2+mass*CORT	4	89.49	3.11	0.057
Φ+mass+mass^2	3	90.46	3.35	0.051
Φ+mass+mass^2+broodsize+CORT+CORT*broodsize+mass*broodsize	7	90.53	4.08	0.035
Φ+mass+mass^2+year	4	91.78	4.15	0.034
Φ+mass+mass^2+sex	4	93.21	5.4	0.018
Φ+mass*CORT	2	93.78	6.83	0.009
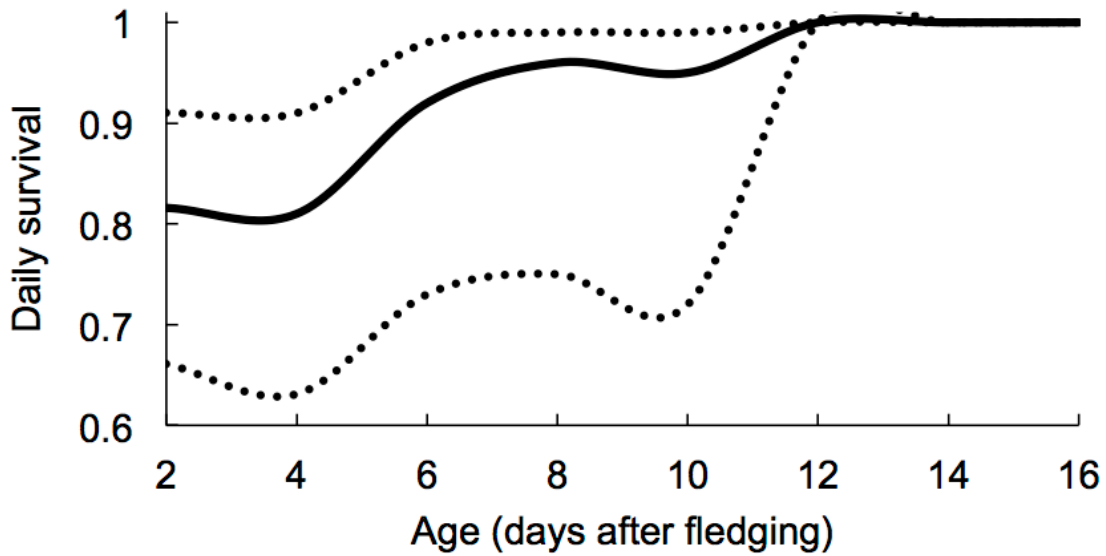
Figure. 4.1. Daily survival of radio-tagged northern flicker fledglings, in central British Columbia, during the first sixteen days after leaving the nest calculated using Program MARK's known fate model. Sample size is 28 fledglings for 2011 and 2012. The dotted lines indicate the 95% CI.
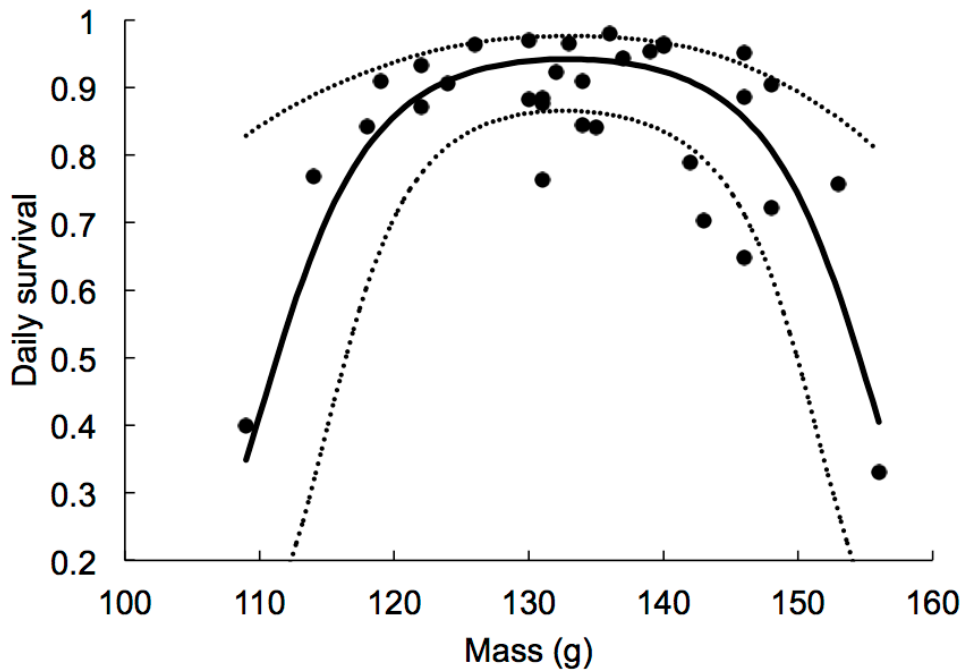
Figure. 4.2. Survival of northern flicker fledglings, in central British Columbia, according to their body mass. Actual values are plotted along with the derived daily survival (solid line) from the top model Φ + CORT + broodsize + mass + mass^2. The dotted lines represent the upper and lower 95% CI.

4.4.2 Length of Post-fledging Parental Care

After the first week, fledglings often acted aggressively towards their parents once the adults began to rebuff their begging attempts, by pecking and flying at the parent, sometimes knocking it off a branch. Likewise, parents sometimes attacked begging offspring aggressively, or flew away or ignored solicitation attempts from their young. After about 5 − 30 minutes of begging, the fledglings usually stopped and began to forage on their own. On average, fledglings received food from at least one parent for 16.6 ± 0.7SE days. Males fed their fledglings on average for 16.6 ± 0.7SE days (range 11−22 days), which was longer than the care period of females, which fed fledglings for 12.3 ± 1.1SE days (range: 0 − 21 days; paired t-test: t_{23} = -2.93, P = 0.0076). The length of care was not correlated between members of a pair (r = 0.13, n = 25, P = 0.082; Fig. 4.3) suggesting that an adult did not compensate for the amount of care given by its mate.

Only one male stopped caring for his young before his partner, and this was in a pair that appeared to have split the brood. However, 9 of 25 females (36%) deserted the brood while the male was still feeding the fledglings. These deserting females typically spent several days either on the nesting home range or at another location, sometimes 1−2 km away. During this time, females were always at least several hundred meters from the family and were observed 'wica dancing' (displaying) with neighbouring males, prospecting for new cavities, or engaging in self maintenance such as preening or foraging. Five of the nine females that deserted the brood soon disappeared from radio-range (i.e., > 3km away), and were not relocated again on our study site despite extensive searching. In two cases, females paired-up the following year with the neighbouring males they were observed displaying with after they abandoned their broods.
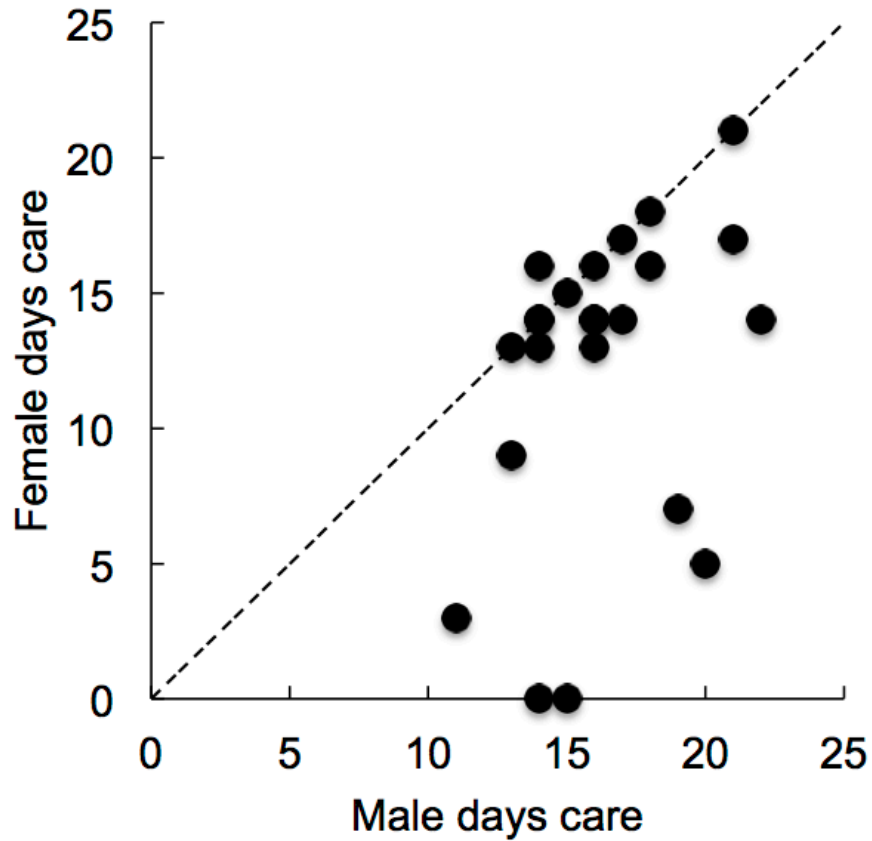
Figure. 4.3. The relationship between the number of days the male and female of each northern flicker, pair fed their fledglings, in central British Columbia. The dashed line indicates an equal number of days feeding by the male and female in a pair.

4.4.3 Factors Influencing the Length of Post-fledging Parental Care

We re-trapped 17 female parents of which 15 re-grew their feather, and 19 males of which 15 re-grew their feather. Among these recaptured adults for which we obtained $CORT_f$, older males ($t = -2.76$, $P = 0.011$) fed fledglings for significantly longer. The mean duration of care for yearling males was 14.5 ± 0.82 (SE) days and that for older males was 17.2 ± 0.67 (SE) days. Male body condition ($t = 1.3$, $P = 0.23$), the date of fledging ($t = 0.25$, $P = 0.81$), and $CORT_f$ ($t = 0.87$, $P = 0.40$) were not significant predictors of the length of care. For females, $CORT_f$ was negatively related to the length of post-fledging care ($t = -2.71$, $P = 0.03$; Fig. 4.4), but age ($t = -1.49$, $P = 0.18$), date of fledging ($t = 0.94$, $P = 0.38$), and body condition ($t = 1.82$, $P = 0.11$) were not significant.

In the full dataset containing all parents, males that had provisioned more frequently during the nestling period also fed their fledglings longer in the post-fledging period ($t = 2.74$, $P = 0.012$) (Fig. 4.5a) and similar to the reduced dataset, older males also fed their fledglings longer ($t = -2.2$, $P = 0.039$). The brood size at fledging ($t = 0.3$, $P = 0.76$), the mean offspring body condition ($t = -0.97$, $P = 0.34$), and the date of fledging ($t = 0.3$, $P = 0.76$) did not significantly influence how long males cared for their offspring. Females that had high feeding rates during the nestling period also cared for their fledglings longer ($t = 2.8$, $P = 0.012$, Fig. 4.5b). Brood size at fledging ($t = -1.41$, $P = 0.17$), brood condition at fledging ($t = 0.38$, $P = 0.71$), the age of the female ($t = -0.45$, $P = 0.66$) and date of fledging ($t = -0.78$, $P = 0.44$) did not affect the duration of female parental care.
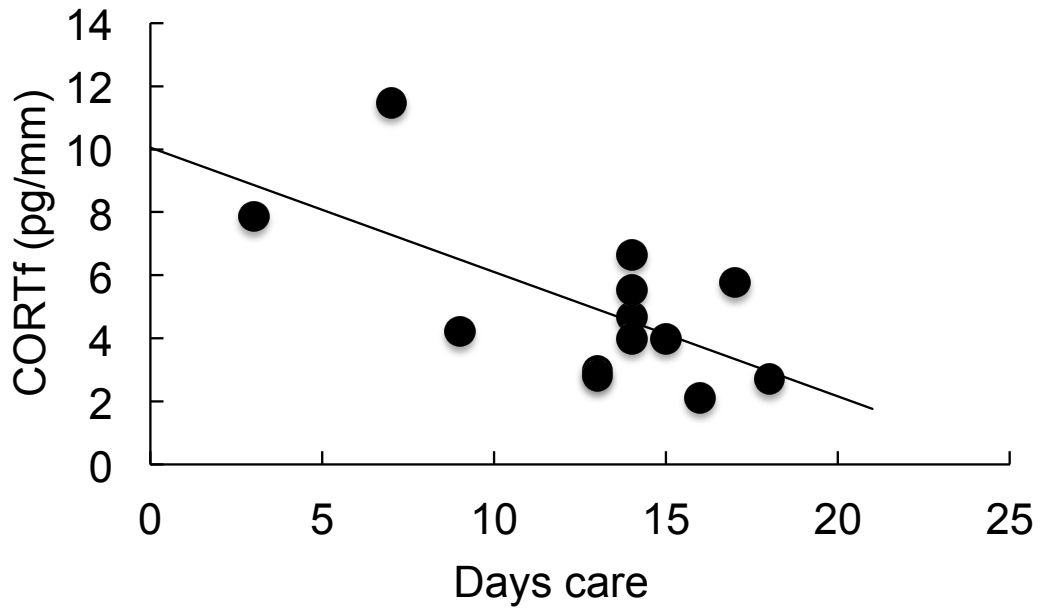
Figure. 4.4. The number of days female northern flickers, in central British Columbia, spent caring for their fledglings was negatively related to $CORT_f$ ($t = -2.71$, $P = 0.03$) from feathers grown during the nestling period. Samples are from 2010, 2011, and 2012.
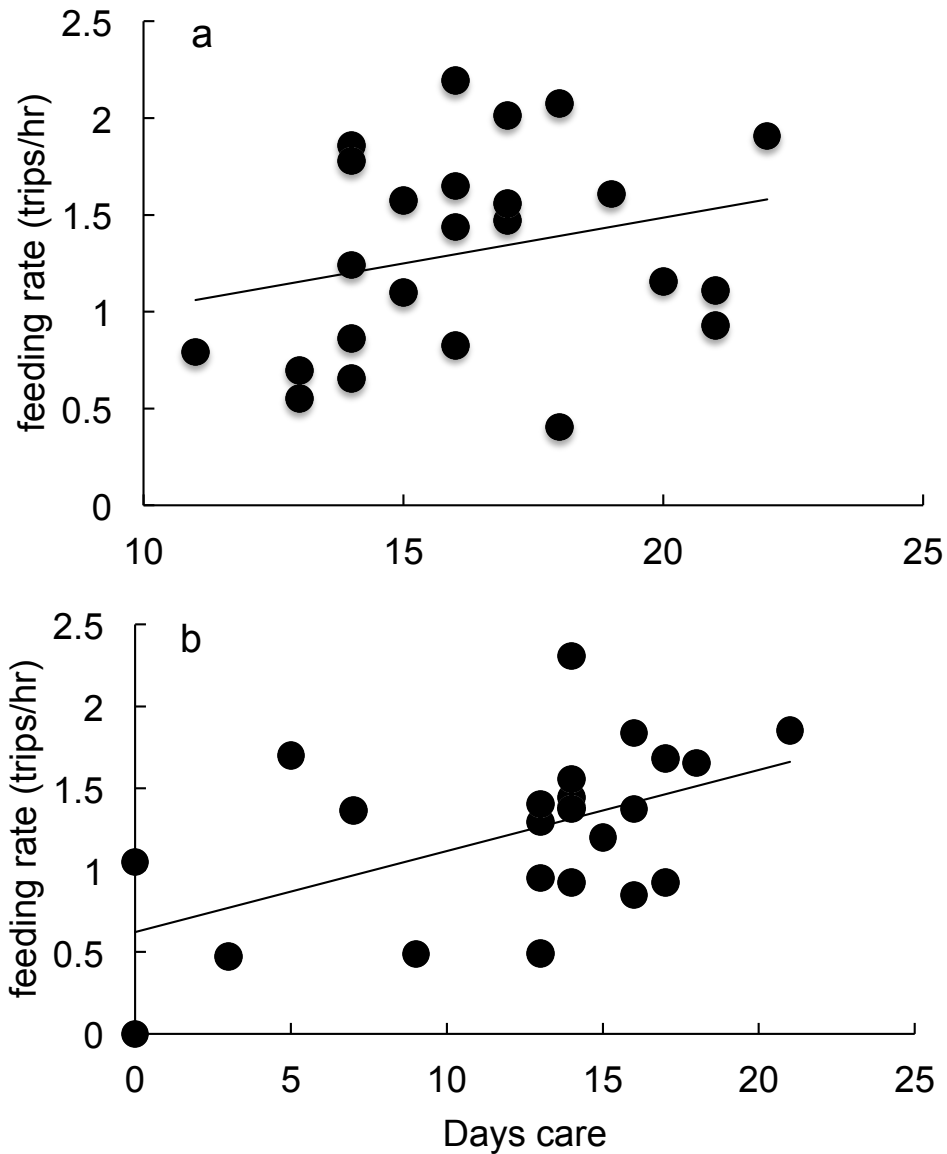
Fig. 4.5. The number of days that northern flicker males (a) and females (b), in central British Columbia, spent caring for fledglings and the relationship to the feeding rate (trips/hr) during the nestling period. Both males ($t = 2.74$, $P = 0.012$), and females ($t = 2.8$, $P = 0.71$) with higher feeding rates during the nestling period fed their fledglings for more days.

4.4.4 Distance Between Parents and Fledglings

There were significant differences between males and females in the time they spent at various distances from fledglings ($F_{4,85} = 6.05$, $P = 0.0002$), and a strong suggestion that these distances differed between the early versus late time periods ($F_{4,85} = 2.45$, $P = 0.052$). Despite the effect of sex and time period on parental proximity to their young, there was no interaction between the two variables ($F_{4,85} = 0.032$, $P = 0.58$), and older parents did not spend more time close to their fledglings ($F_{4,85} = 0.048$, $P = 0.38$). A post-hoc ANOVA revealed that males spent more time close to fledglings (< 50 m) than females and they tended to remain closer to the fledglings as the offspring aged (Table 4.2, Fig. 4.6). In comparison, the distance between females and their offspring tended to increase as the fledglings aged and females spent more time far from juveniles, regardless of the fledglings' age.

4.5 DISCUSSION

4.5.1 Sex-biased Brood Desertion

Overall, 36% of females deserted their brood and 18% did so within 10 days after their offspring left the nest. We did not observe any desertion by males. Our results suggest that a female's propensity to desert depends on her physiological state in relation to how she responded to stressors as revealed by high $CORT_f$ levels, and that some females reach a point at which they are unwilling to trade-off increased offspring care with increased 'stress'. A previous mate-removal experiment conducted during the nestling period showed that male flickers were about twice as effective as single parents than females (Wiebe 2005). Females do not naturally desert during the nestling period, apparently because a lack of unpaired males and an even population sex ratio (Wiebe 2005), would mean little chance of initiating a new brood with a second partner.

Table 4.2. Results from a post-hoc ANOVA with the proportion of time adults spent at the four distance categories from their fledglings as the dependent variables, and sex, stage and age as the independent variables. Stage refers to two stages, <1 week, and >1week. Sample sizes are 23 females and 27 males during the early stage, and 18 females and 25 during the late stage.

	< 50 m		50−300 m		300−700 m		> 700 m	
Model	F	P	F	P	F	P	F	P
Sex	4.69	0.033*	2.65	0.11	11.88	0.00087*	5.95	0.017*
Stage	9.92	0.0022*	5.05	0.027*	1.79	0.18	0.015	0.9
Age	2.61	0.11	1.72	0.19	1.72	0.63	1.61	0.21
Sex*stage	2.00	0.16	0.21	0.65	1.72	0.19	0.15	0.7

* ≤ 0.05
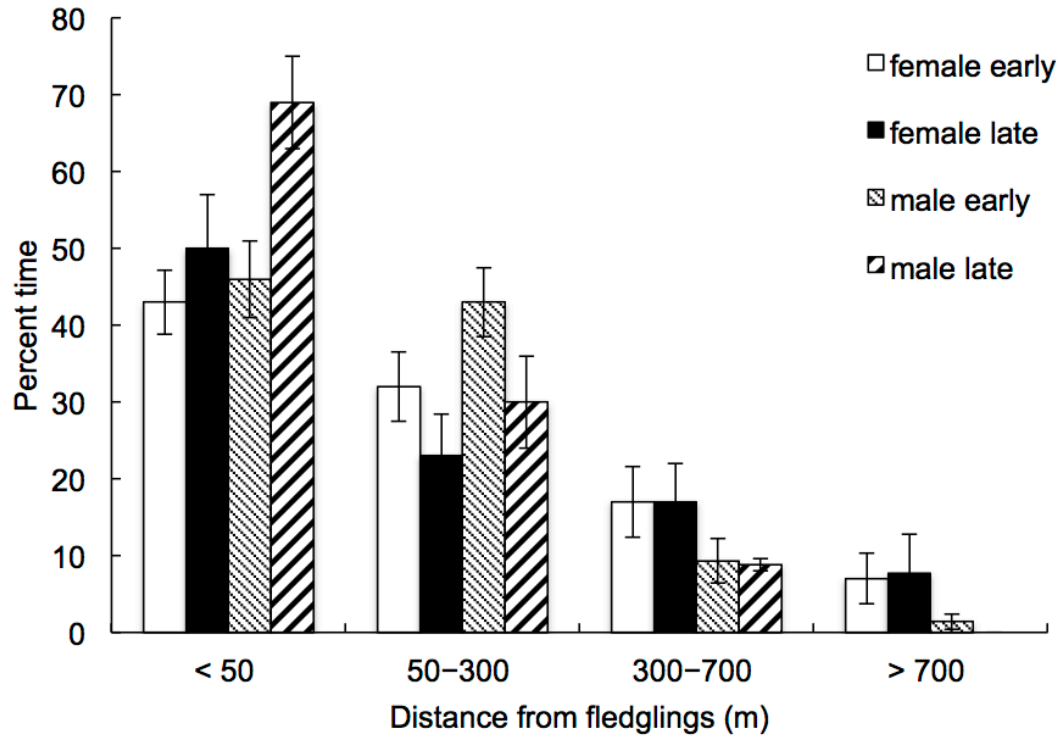
Figure. 4.6. The amount (percent) of time male (144 hr) and female (112 hr) northern flicker parents, in central British Columbia, spent at certain distances from their fledglings over two time periods, early (<1 week old young), and late (>1 week old young). Males spent more time close to their fledglings than females ($F_{4,85} = 6.05$, $P = 0.0002$).

During the late part of the breeding season, the trade-off parents face between continuing to invest in parental care and initiating moult or migration are particularly strong because heavy investment can negatively affect post-breeding physiological condition (Done et al. 2011) or the scheduling of moult and migration (Stutchbury et al. 2011). Although both sexes of flickers presumably benefit by reducing the length of care to fledglings, male flickers may be more willing to invest than males of many other species because they have a high assurance of paternity (Wiebe and Kempenaers 2009). In addition, the potential for polyandry in flickers may cause higher intrasexual competition among females compared to males. High intrasexual competition may make females less willing than males to undergo moult when energetically stressed and more willing to trade-off parental care with the courting of potential future mates.

Brood desertion during the post-fledging period has not been recorded, to our knowledge, in other single-brooded altricial species but records of the length of male and female contributions to parental care are lacking. Both sexes appear to care for fledglings among woodpeckers, (e.g. middle spotted woodpeckers *Dendrocopos medius*, and great spotted woodpeckers *Dendrocopos major*; Michalek and Winkler 2001), but the length of care was not documented. In another study, "temporary female desertion" was observed during the nestling period of middle-spotted woodpeckers, but all females returned to care for fledglings during the post-fledging period (Wiktander et al. 2000). Clearly, more studies of the post-fledging care period are needed not only among woodpeckers, but among all birds to understand the length of investment by each sex.

Unisexual care and female brood desertion occurs much more frequently in other taxa, such as fish. Male only care is found in 61% of fish families (Gross and Shine 1981) and male parental care is typically associated with territorial behaviour of a spawning site (Gross and Sargent 1985). For male fish, defending a spawning area increases reproductive success, because females are choosy about where to attach their eggs (Gross and Sargent 1985). In this way males

do not reduce the number of matings because defending a territory allows them to care for their fry and also acquire future matings (Gross and Sargent 1985). In our study, although male flickers are non-territorial they may have more to gain by staying with their offspring longer. If males that stay are better equipped (by occupying the home range longer) to defend a nest site the following year, or if females base future mating decisions on the past investment by a male (e.g. parental care is a sexually selected trait), males may gain more in the future by staying and investing in a current reproductive attempt.

4.5.2 Factors Influencing the Length of Post-fledging Care

A parent's willingness to desert offspring is related to their value and the parent's perception of the capability of their partner to raise the brood without help (Olson et al. 2008). Although larger broods are expected to be more valuable and to need more care, brood size did not influence the length of care for either parent. Brood size may still have influenced the amount of food delivered by parents but we could not measure it. In our study, 45% of fledglings died within the first eight days post-fledging so presumably the energy demand on parents declined rapidly after the first week. In addition, the good flying ability of young flickers at fledging and the relative ease with which they can learn to collect their main prey (ants) from the ground may reduce the need for prolonged care compared to many other altricial species.

The prediction that parents which invested heavily during the nestling period would be those that also invested heavily during post-fledging was supported. This suggests that differences in quality between individuals masked a trade-off between high parental effort in the nestling period and high effort in the fledging period and that high quality parents could provide substantial care throughout the reproductive cycle (Nakagawa et al. 2007). Females were more sensitive than males to their 'stress level' (i.e. high $CORT_f$), which was perhaps linked to their physiological

condition when deciding levels of investment, but care was not related to any measure of condition in males. Instead, care increased with age of the male. Terminal investment may explain high effort at older ages if the likelihood of future reproduction is low (Clutton-Brock 1984) as seems to be the case in flickers (annual mortality rate around 60%; Fisher and Wiebe 2006a). Another explanation is that males may invest more heavily in their first year to find, excavate, and defend a cavity tree whereas in subsequent years, the energy saved by returning to the same nest may be invested in offspring care.

CORT may mediate the survival-reproduction trade-off in birds (Ricklefs and Wikelski 2002). Increases in CORT in adult birds have been linked to increased foraging behaviour (apparently to improve the individual's energy balance) at the cost of parental behaviour and in other studies there is a negative relationship between the levels of prolactin , 'the parental care hormone', and CORT (reviewed in Angelier and Chastel 2009). In contrast to plasma CORT, which is a single snapshot, $CORT_f$ is a summation of CORT levels over the time of feather growth and hence is an integrated measure of the response to stressors over a longer time (Bortolotti et al. 2008; Fairhurst et al. 2013). Therefore, flicker females with high $CORT_f$ likely experienced more chronic activation of the hypothalamic-pituitary-adrenal axis from response to various stressors (e.g. food deprivation, predators, etc.) during the nestling period. In a proximate sense, flicker females apparently reacted to a certain $CORT_f$ threshold after which they were not willing or capable of continuing parental care. It is intriguing that average $CORT_f$ levels did not differ for males and females (EAG unpubl. data); thus, males seem to be more tolerant of high $CORT_f$ than females. The negative relationship between $CORT_f$ and days care may need to be interpreted cautiously, because the relationship was driven by two data points. Aside from higher levels of $CORT_f$ those two females did not appear to differ from other females in any way. In contrast to our finding that the more 'stressed' female flickers abandoned broods it was the females with more

fat reserves which abandoned offspring in Tengmalm's owls *Aegolius funereus*. Apparently female owls which abandoned their offspring often initiated a second brood with a new mate and needed high energy reserves to do so (Eldegard and Sonerud 2009).

Males and females differed not only in their length of parental care but also in their proximity to fledglings, suggesting that the sexes valued the brood differently. Males spent more time within 50 m of their young at all fledgling ages, perhaps as a result of two (not mutually exclusive) mechanisms. First, fledglings may opt to follow the male rather than the female if he provides food frequently. Second, males may be more attentive to the needs of fledglings and more willing to invest in vigilance and offspring defense compared to females. Females seemed to have more interest in prospecting for future mates or nest sites than in spending time near family. If females select future mates (the following season) in part based on the male's ability to provide parental care, the post-fledging period may be a good time to assess future males because females can use social information to judge his production and care of offspring near the end of the breeding season (Betts et al. 2008).

4.5.3 Fledgling Survival and Parental Care

Fledglings with higher mass have higher survival in some species such as great tits *Parus major* and coal tits (*Periparus ater*; Naef-Daenzer et al. 2001), but stabilizing selection on fledgling mass occurs in juvenile and adult blue tits (*Cyanistes caeruleus*) in the presence of sparrowhawks (*Accipiter nisus*; Adriaensen et al. 1998). We found stabilizing selection on mass of fledgling flickers during the first two weeks after they left the nest. Heavier birds may experience higher predation risk because body mass reduces flight manoeuverability (reviewed by Lind et al. 2010). Relatively lightweight fledglings may benefit if predation risk is high (Adriaensen et al. 1998) but face a higher risk of starvation if foraging success is unpredictable (Lima 1986). We did not find

any fledglings that died of starvation as a proximate cause but our results suggest that lightweight fledglings were also susceptible to predators, perhaps because they were less energetic fliers. Low body mass may also be reflective of other conditions that may affect survival such as disease, high parasite loads or a reduced immune response (Møller et al. 1998).

Although sibling competition and food shortages can explain lightweight fledglings in a brood, the presence of heavy fledglings with apparently low survival is more difficult to explain. Perhaps an unpredictable food supply leads the more competitive fledglings in a brood to continue begging and gaining weight past the optimal level as a buffer against starvation? A second explanation is that we measured survival in the first 2-weeks post-fledging when predation risk was the main proximate cause of mortality. Over the longer term as the young become independent from parental feeding, starvation as a mortality factor may have increased in importance such that a relatively heavy body mass may become more advantageous (e.g. Witter and Cuthill 1993). In sociable weavers *Philetairus socius*, there was stabilizing selection on juvenile mass that carried over into future years, such that birds with an average fledgling mass had the highest survival over the seven-year study period (Covas et al. 2002). Unfortunately, flicker juvenile recruitment is less than 1% per year at our study site and so the longer-term effects of fledging mass on survival could not be determined. A final explanation is that predation risk on our study area was unusually high, and a heavy fledgling mass may be advantageous in other populations with fewer predators.

Our results that the survival of flicker fledglings was negatively related to their levels of $CORT_f$ is in contrast to Rivers et al. (2012) who found a positive relationship between baseline plasma CORT and juvenile survival in Swainson's thrushes *Catharus ustulatus*; but agree with two other studies relating handling induced plasma CORT (Blas et al. 2007) and experimentally elevated CORT levels (Goutte et al. 2010) to reduced juvenile and adult survival respectively.

In conclusion, the shorter duration of parental care by female compared to male flickers may be explained by a high assurance of paternity and by partly reversed sex roles where females appear to have more to gain than males by prospecting for future breeding sites and partners. At the proximate level, for females length of care is mediated by $CORT_f$ levels, whereas males are not as sensitive to their own condition when deciding levels of care. However, further test on the effects of CORT on the length of parental care using larger samples are needed to substantiate this result. Our study provides an example of how reversed sex roles can contribute to a reduction in care by females and we encourage others to study parental contributions at the post-fledging stage for a more complete understanding of investment by the sexes.

CHAPTER 5:
SURVIVAL AND HABITAT USE BY FLEDGLING NORTHERN FLICKERS IN A FRAGMENTED FOREST LANDSCAPE

5.1 ABSTRACT

The post-fledging dependency period of birds is often characterized by high juvenile mortality, but fledglings in specific habitats may have increased survivorship. We describe habitat use by fledgling northern flickers (*Colaptes auratus*) in relation to the availability of patchy forest and prairie habitat in central British Columbia, Canada. We used radiotelemetry to monitor survival of fledglings according to their use of habitats during the dependency period. The fledglings occupied habitats with a higher density of trees than either random locations or nest sites and they switched from forested areas to more open grasslands after 7−10 days post-fledging. Some moved >1 km from the nest within 4 days post-fledging. Fledglings from nests in small tree clusters with little forest cover within 250 m moved farther from their nest within the first 4 days post-fledging than fledglings from nests in larger forest patches. Fledgling survival was positively correlated with the amount of canopy cover and negatively correlated with the amount of forest cover at the larger landscape scale. Young flickers moved among habitat types, which may occur as a result of trade-offs between predation risk and food abundance between habitats. We conclude that fledgling flickers at younger ages used dense forested areas and grassland habitat and forest at older ages to maximize survival and to access food sources. Maintaining patches of dense cover and the amount of forest cover on less than 35% of the landscape may improve fledgling survival of flickers.

5.2 INTRODUCTION

The post-fledging period of altricial birds is often characterized as having low survival with an average of around 50−55% of young surviving to 2 months of age (Anders et al. 1997; Suedkamp Wells et al. 2007; Eng et al. 2011; Cox and Kesler 2012a). For short-lived species, demographic models often show that the juvenile age class is the most elastic stage, because it contributes proportionally more to population growth than other age classes (Wisdom et al. 2000). Nevertheless, the survival of fledgling birds has received little attention because juveniles are often cryptic or immobile and difficult to re-sight. Even so, several studies have established that survival rates of juvenile birds can improve as they age and that survival can vary among habitat types (Krementz et al. 1989; Anders et al. 1997; Vega Rivera et al. 1998). In contrast, other studies have not found an effect of habitat on fledgling survival (Rush and Stutchbury 2008; Moore et al. 2010; Cox and Kesler 2012a). The discrepancy may be a result of species life histories or particular uses of habitats by the young. Detailed knowledge about the movements and habitat selection of juveniles during the post-fledging dependency period may improve our understanding of juvenile survival particularly in fragmented environments.

For many birds, habitat fragmentation can increase mortality of eggs or nestlings (Donovan et al. 1995; Sekercioglu 2007). Cavity nesters may be somewhat buffered from nest predation (Lampila et al. 2005), but the impacts may be felt later by the fledglings, which must contend with the abundance of predators that occupy fragmented landscapes. Gaps between forest fragments, or open areas, may be risky because juveniles and adults are more likely to be detected by predators (Rodríguez et al. 2001); thus, fragmented landscapes may restrict bird movements. Alternatively, fledglings may increase the risk of predation by attempting to cross gaps within the first few days after fledging to find safer habitat some distance away from the nest. The juveniles of many species do not move far from the nest during the first few days post-

fledging (e.g. Moore et al. 2010; Streby and Anderson 2013), so testing hypotheses relating habitat use to subsequent survival is difficult. Several studies have examined fledgling survival in fragmented landscapes. For instance, Rush and Stutchbury (2008) found that fragment size did not influence the distance hooded warbler (*Setophaga citrina*) fledglings moved from the nest and did not find an effect of fragment size on fledgling survival. Conversely, Eng et al. (2011) found that hooded warblers on heavily logged sites had higher fledgling survival compared to those on older more mature forest reference sites. For spotted owls (*Strix occidentalis*), continuous older growth forest was associated with higher juvenile survival (Miller et al. 1997).

Several studies have supported the hypothesis that parents move their young during the fledgling stage to the closest available brood-rearing habitat and do not travel farther than necessary (Cohen and Lindell 2004; Berkeley et al. 2007; White and Faaborg 2008; Streby and Anderson 2013). As fledglings grow and become stronger fliers, they also move to safer habitats (Moore et al. 2010), and we predict they should do so as soon as they are capable. This hypothesis, however, has been investigated only in altricial species with relatively limited flight capabilities within the first week after leaving the nest (e.g. Rush and Stutchbury 2008; Wightman 2009).

In woodpeckers, Cox and Kesler (2012a) modeled habitat effects on juvenile survival of red-bellied woodpeckers (*Melanerpes carolinus*), over the 5-month juvenile dispersal period after fledging and found no effects of habitat on survival. Although they found that young fledglings had lower survival than older birds, their assessment did not address habitat selection during the period when the young are dependent on parental feeding. Fledgling survival is generally low during the first 1 to 2 weeks post-fledging (e.g. Anders et al. 1997; Suedkamp Wells et al. 2007) thus the types of habitat fledglings use may play a large role in fledgling survival.

We provide one of the first accounts of fledgling survival in relation to habitat use for a woodpecker during the parental feeding dependency period. Northern flickers (*Colaptes auratus*) are habitat generalists that occupy grasslands, a variety of open temperate and riparian forests, and continuous tracts of boreal forests throughout North America (Wiebe and Moore 2008). We studied post-fledging survival in a landscape characterized by patchy grassland and forest fragments. We assessed 3 hypotheses. First, we assessed whether flicker fledglings used habitats different from those surrounding nest sites and random areas on the landscape. Second, because young flickers can fly considerable distances after leaving the nest, we tested the prediction that the distance traveled within the first few days post-fledging would be negatively associated with forest cover. Finally, we evaluated whether the types of habitats used and forest cover on the landscape influenced fledgling survivorship.

5.3 STUDY AREA

We studied fledgling northern flickers at Riske Creek in central British Columbia, Canada (51° 52'N, 122° 21'W), from 2010−2012. The study site covered an area of approximately 100 km^2 and was a patchy mosaic of open grasslands, interspaced with small saline lakes and groves of trembling aspen (*Populus tremuloides*), with the remaining areas consisting of larger tracts of continuous forest dominated by Douglas fir (*Pseudotsuga menziesii*) and white spruce (*Picea glauca*). Grasslands covered about 60−70% of the area, saline lakes accounted for approximately 5−10%, aspen clumps covered roughly 5−10%, and the remaining 10−30% of the area was continuous forest. A considerable lodgepole pine (*Pinus contorta*) component of the forest was nearly completely decimated by the mountain pine beetle (*Dendroctonus ponderosae*) with many standing dead pines on the landscape (Martin et al. 2004). The forest tracts had become more fragmented as a result of mortality from pine beetles beginning in 2004 and from a series of

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wildfires including an extensive fire in 2010 that affected nearly 50% of the study area. Because most home ranges of flickers are relatively large (i.e., between 5–109 ha; Elchuk and Wiebe 2003b), breeding pairs regularly use and travel between several types of habitats. Flickers arrive on the site after migration in spring and their clutch size averages from 4−13 with an incubation period of about 11 days (Wiebe and Moore 2008). During this study, the nestling period lasted 23−29 days and the post-fledging parental dependency period lasted on average 16 days (Chapter 4).

5.4 METHODS

We used radio-tags to monitor the locations of both adults and fledglings. To aid in the capture of adults and to access the nest we cut small, replaceable doors in the tree trunk near the base of the cavity (Wiebe 2008). We captured adult flickers during incubation by plugging the cavity entrance and then flushing them into a net over the hole. We attached 1.5-g radio-tags (BD-2; Holohil Inc., Carp, Ontario, Canada) to adults' central rectrices with cyanoacrylate glue (Kenward 1987) and 0.5–0.7-g radio-tags to fledglings using a leg-loop harness (Rappole and Tipton 1991). To maintain statistical independence, we randomly chose 1 nestling per brood to tag at approximately 20 days old (to avoid premature fledging). In 2010, we followed 11 families in the post-fledging period and in 2011 and 2012, the sample size was 8 and 10 families, respectively. We sampled different families each year and tagged both the male and female. In most cases, we tagged parents of radio-tagged nestling ($n = 18$), which allowed us to continue following the brood even if the fledgling with the radio-tag died.

Every second day (or sometimes third day depending on the weather), we used hand-held Yagi 3-element antennae and TRX-2000S receivers (Wildlife Materials Inc., Murphysboro, IL) to track families and to determine visually whether a tagged fledgling was alive or dead. We tracked

birds for 1-hr sessions and avoided tracking during rain, hail or impending thunderstorms. We recorded the geographic coordinates (Universal Transverse Mercator, UTM coordinates) where we first sighted the fledging with a global positioning system (GPS). For families without a tagged fledgling, we followed the tagged parents until we saw them attending a fledgling and recorded this location immediately after the family moved. After locating the fledglings, we minimized disturbance by staying 10–100 m away depending on vegetation cover. We monitored family groups until approximately 20 days after fledging or until we failed to locate any family members for 3 consecutive tracking sessions (mean 13.6 days $\pm$ 3.88). In the rare cases that parents split the brood ($n = 3$ of 28 cases), we used only locations from the radio-tagged fledgling because they followed only the female or only the male parent. We conducted this study under Animal Care Permit number 20010113 from the University of Saskatchewan and complied with the current laws of Canada.

5.4.1 Habitat Use

We quantified vegetation in 5-m radius circular plots, and used methods modified from James and Shugart (1970), around the points where we first located fledglings ($n = 292$) during each tracking session, hereafter referred to as "fledgling plots". We split the circular radius plots into 4 quadrants (using ropes as quadrant lines), to help in counting vegetation. We randomly chose the placement of the quadrant lines, within the circular plot, by spinning a pencil. Because the effectiveness of trees as perching or gripping surfaces for fledglings and cover from predators may depend on the density and size of trees within the vegetation plot, we measured the diameter at breast height (dbh) of each tree, the number of alive and dead trees, and recorded the species. We also counted the number of dead fallen trees, and the number of shrubs (woody stems <3 cm dbh). Ground cover influences concealment of fledglings when they hop on the ground; therefore

we measured the percent ground cover using a 4.5-cm diameter tube held at waist height for 20 points within the circular plots (along the quadrant lines). Ground cover was defined as any green forbs taller than 5-cm, which we considered was sufficient to conceal flickers on the ground. Tree canopy may reduce attacks by aerial predators such as prairie falcons (*Falco mexicanus*); therefore we also measured live canopy cover using a 4.5-cm diameter tube held straight up to record the presence or absence of live canopy at 20 locations within the circular plots (along the quadrant lines).

We measured the same vegetation data close to the nest sites of each family and at random points across the study area. At nest sites, we measured a 5-m radius area plot centered at the nest and 4 other locations placed at a distance of 25-m from the nest tree in 4 directions (90°, 180°, 270°, 360°; $n = 44$ nests and 225 plots). For the random locations, we measured habitat at 7 points within a 1,000-m radius of the nest for each tagged fledgling (except those that died within the first day). We generated the random points ($n = 174$) using the Randbetween function in Microsoft Excel (Microsoft Corporation, Redmond, WA) to obtain random distances and directions from the nest. We reduced the dimensionality of our 11 habitat variables (688 plots) by using non-metric dimensional scaling (NMDS), an iterative multivariate ordination technique (McCune and Grace 2002) and tested—using the NMDS scores—whether the habitat used by fledglings differed from that surrounding nest sites and from random habitat. We included the proportion of coniferous trees, the number of dead snags, and the number of living trees classified into 1 of 5 dbh categories (3−15 cm, 15.1−27 cm, 27.1−39 cm, 39.1−51 cm, and >51.1 cm) in the NMDS analysis. We also included the percentages of canopy cover and ground cover (out of 20 points), the number of shrubs, and the number of fallen trees. Because we measured the variables on different scales (i.e., counts and percentages), we standardized the data between 0 and 1 to give all variables equal weighting while retaining ranking (a range standardization).

Many values of the vegetation variables were zero because locations in open grassland lacked trees. We then used the Bray-Curtis distance metric, which is commonly used in ordination and robust for datasets with many zeros (Faith et al. 1987; McCune and Grace 2002). We created a scree plot to determine stress as a function of dimensionality (McCune and Grace 2002) and procrustes plots were to visually assess differences between dimensions (Oksansen et al. 2012). We then used the NMDS scores for each axis in subsequent analyses. We conducted the NMDS analysis using package vegan in R 2.14.2 (Oksansen et al. 2012; R Core Development Team 2012; www.R-project.org, accessed 25 Apr 2013).

To determine whether the vegetation characteristics differed between the fledgling, nest, and random points, we compared the scores generated by the NMDS as dependent variables in linear mixed effects models (lme), using the packages lme4 (Bates et al. 2011) and languageR in R (Baayen 2011). We used an lme with age (number of days post-fledging) as the independent variable and NMDS scores as the dependent variables to determine if habitat use by fledglings changed with number of days post-fledging. We also used an lme to test if age (independent variable) influenced if fledglings used specific fragment sizes more frequently (small clump <1 ha, large clump >1ha, continuous forest >10 ha, or grassland). For all lme analyses, we included the individual as a random factor because of multiple habitat measures on the same individual over time. Prior to conducting the lme models, we first checked that each response variable met all assumptions of the models. We assessed models using likelihood ratio tests to compare models with only fixed effects to null models with only the random effects using analysis of variance (ANOVA; Zuur et al. 2010). We estimated P-values from Markov Chain Monte Carlo methods with statistical significance set at $\alpha = 0.05$.

5.4.2 Fledgling Movements

We tested whether older fledglings moved farther from the nest than younger fledglings using a lme, with fledgling age as the response variable and distance from the nest as the predictor variable with nest as the random factor to account for repeated measures. We assessed movements of fledglings using 2 methods. First, because a lack of suitable vegetative cover surrounding the nest may cause parents to move fledglings farther distances, we, tested for a correlation between the distance the offspring traveled from the nest during the first 4 days and the density of trees in the nest site plots using a Pearson's regression. The distance travelled and density of trees was log transformed to meet the assumptions of normality in parametric tests. Second, we used Google Earth Pro (Google, Mountain View, CA) to measure the area of forest cover within 4 buffer zones of increasing radii from the nest: 250 m, 500 m, 750 m, and 1,000 m. Because the amount of forest cover around flicker nests varied greatly and because habitat use can differ between fragmented habitats versus larger forest tracts (Rush and Stutchbury 2008), we predicted that flickers nesting in small clumps with little available forest cover within 250 m of the nest would move farther distances. We thus assessed the influence of forest cover on the distance fledglings traveled from the nest using a subset of our data. We used only nests with forest cover, in the 250 m radii, below the 50% quartile (<16.4 % forest cover, $n = 26$). We log transformed the distance traveled to meet the assumptions of normality in parametric tests. We used a general linear model (glm) with the maximum distance parents moved their fledglings within the first 4 days post fledging as the dependent variable and the proportion of habitat at the 4 radii (250 m, 500 m, 750 m, 1,000 m) surrounding the nest as the independent variables.

All statistical analyses were 2-tailed and we set significance at $\alpha = 0.05$. Values are presented as means ± (SE), unless noted otherwise.

5.4.3 Fledgling Survival

We calculated fledgling survival using Program MARK's "young survival from marked adults" analysis which estimates individual fledgling survival, not overall brood survival (Lukas and Dreitz 2010). We conducted 2 analyses. The first investigated effects of microhabitat around the fledgling plots detected within the first 6 days post-fledging. We averaged (from plots within the first 6-days) the microhabitat covariates percent canopy cover, the number of trees, and the number of conifers, measured in the 5-m radius plots as described above. We focused on habitat used in the first 6 days because this was the period of highest fledgling mortality (Chapter 4). Our second analysis focused on the amount of landscape-scale forest cover surrounding the nest in the 4 radii as covariates (250 m, 500 m, 750 m, and 1,000 m).

The MARK model contains 2 parameters, apparent survival (ϕ) and detection probability (p) and requires that both parents are easily relocated and identified without error and the offspring with them can be counted (Lukas and Dreitz 2010). Thus, the young do not need to be marked, but their parents must be identifiable (Lukas and Dreitz 2010). This was possible in our study because flicker fledglings remained in family groups and parents frequently interacted and fed multiple fledglings within 1-hour tracking sessions. We monitored 29 families of flickers with marked adults during the post-fledging period but only included 26 in the analysis because in 1 case a parent died and in 2 cases the families moved to inaccessible private land.

We recorded survival over 22 days, based on tracking sessions normally conducted every 2 days except when inclement weather prevented it (i.e., rain or thunderstorms). Lukas and Dreitz (2010) recommend against using time-dependent survival when the intervals between observations are short, when re-sighting probabilities vary greatly, and when offspring are mobile. Therefore, we used a base model of constant survival $\phi(.)$ and time-dependent detection $p(t)$. We ranked models using Akaike's information criterion corrected for sample size (AIC_c; Burnham and Anderson 2002). We considered all models with $\Delta AIC_c \leq 2$ to show substantial

support, while $\Delta AIC_c \leq 4$ showed some support (Burnham and Anderson 2002). We considered parameter estimates with 95% confidence intervals that overlapped zero to be insignificant. We used the derived daily survival estimates from the covariates in the top models to investigate the nature of the relationship between fledgling daily survival and each covariate in the model. To assess model validity (all models with $\Delta < 2$) we conducted a bootstrap test with 1000 simulations (White et al. 2001).

5.5 RESULTS

5.5.1 Fledgling Movements

Flicker fledglings tended to stay in family groups and were often within 50 m of each other. The fledglings were relatively strong fliers and within the first 4 days after leaving the nest, they were located on average 50 ± 232 m (SD; median:145 m; range: 26−1,074 m) from the nest site. During the 1-hour tracking sessions, young within the first 4 days of fledging rarely moved more than 150 m from their initial point at the start of the tracking session and did not follow their parents. In contrast, after about 7 days post-fledging, the young often traveled several hundred meters, usually following their parents during a tracking session. Most families appeared to occupy specific home ranges for several days in a row. At 18 days post-fledging, the young had moved an average of 592 ± 353 m (SD; range: 64−1325 m) from the nest.

Based on nest site plots, the density of trees surrounding the nest and the distance moved over the first 4 days post-fledgling were not correlated ($r = 0.02$, $P = 0.46$). For flickers that nested in sparsely treed areas with <16.4% forest cover within 250 m of their nests, movement distance was negatively correlated with proportion of forest within 250 m of their nesting cavity during the first 4 days after fledging (GLM: $t = -2.37$, $P = 0.03$; Fig. 5.1). We did not find a relationship between the distance moved and the available forest cover at 500 m ($t = -1.46$, $P =$

0.16), 750 m ($t = 1.34$, $P = 0.19$), or at 1,000 m from the nest ($t = -1.99$, $P = 0.06$). For nests with >16.4% forested cover within 250 m, we did not find a relationship between the amount of forested cover available within 250 m of the nest and the distance fledglings moved in the first 4 days after fledging ($r < 0.01$, $P = 0.99$, $n = 23$).

5.5.2 Habitat Use

The NMDS analysis generated 2 vegetative axes with a stress of 0.157, and an adjusted R^2 fit of 0.90. The first axis had negative significant loadings for trees in each of the dbh categories, canopy cover, and total tree density, and a positive loading for ground cover. This means that plots with negative values on the NMDS1 axis had high tree densities, whereas positive scores had fewer trees and greater ground cover (Fig. 5.2a). The NMDS2 axis was positively associated with the number of snags, the number of fallen trees, and number of shrubs, and negatively related to the proportion of coniferous trees (Fig. 5.2a). Thus, locations with positive NMDS2 scores likely were in burned areas characterized by many dead and fallen trees and re-growing shrubs.

The NMDS1 scores of fledgling habitat plots were more negative (mean $= -0.083 \pm$ 0.008) than either the nest site plots (mean $= 0.02 \pm 0.01$; $t = 5.97$, $P < 0.01$) or the random locations (mean $= 0.11 \pm 0.01$; $t = 9.14$, $P < 0.01$; Fig 5.2b). Thus, fledgling plots tended to have a greater density of trees than nest plots, which tended to be in sparse forests or on forest edges, and random plots, which encompassed more open grassland. The NMDS2 scores differed between fledgling habitat (mean $= -0.01 \pm 0.01$) and nest habitat (mean $= 0.02 \pm 0.01$; $t = 2.31$, $P = 0.02$), with nest sites occurring in areas with more snags. The number of snags or shrubs did not differ between fledgling and random plots (mean $= -0.01 \pm 0.01$; $t = -0.11$, $P = 0.91$; Fig 5.2b).
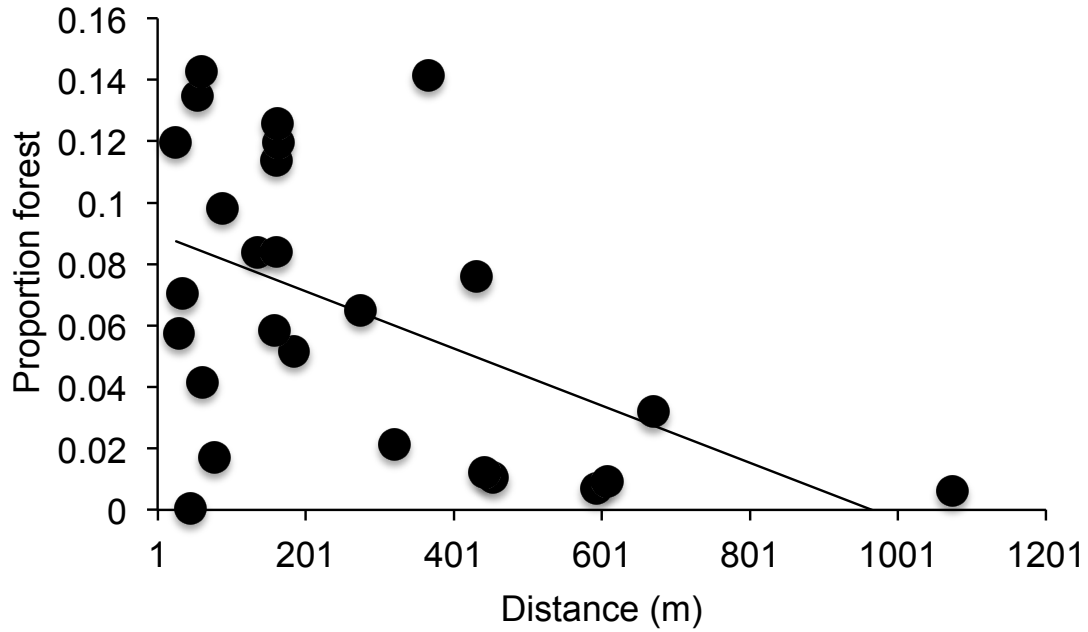
Figure 5.1. The proportion of forest within 250 m of the nest, for nests located in sparsely treed fragments with less than <16.4% forest cover within 250 m of the nest, was negatively associated with the distance northern flicker fledglings moved from the nest within the first 4 days post-fledging in central British Columbia, Canada, 2010–2012.
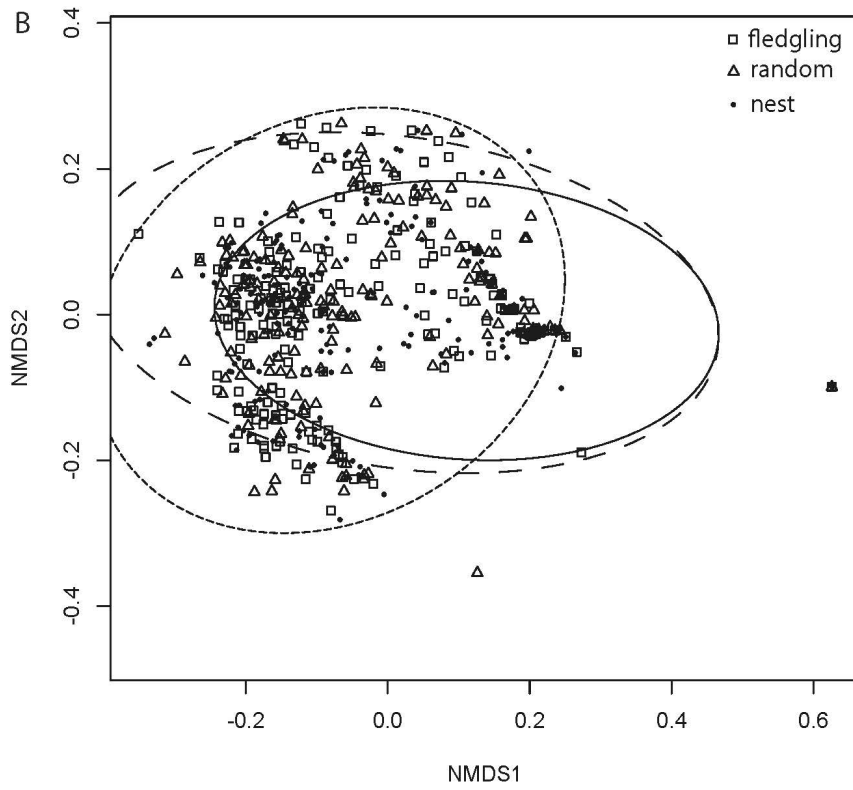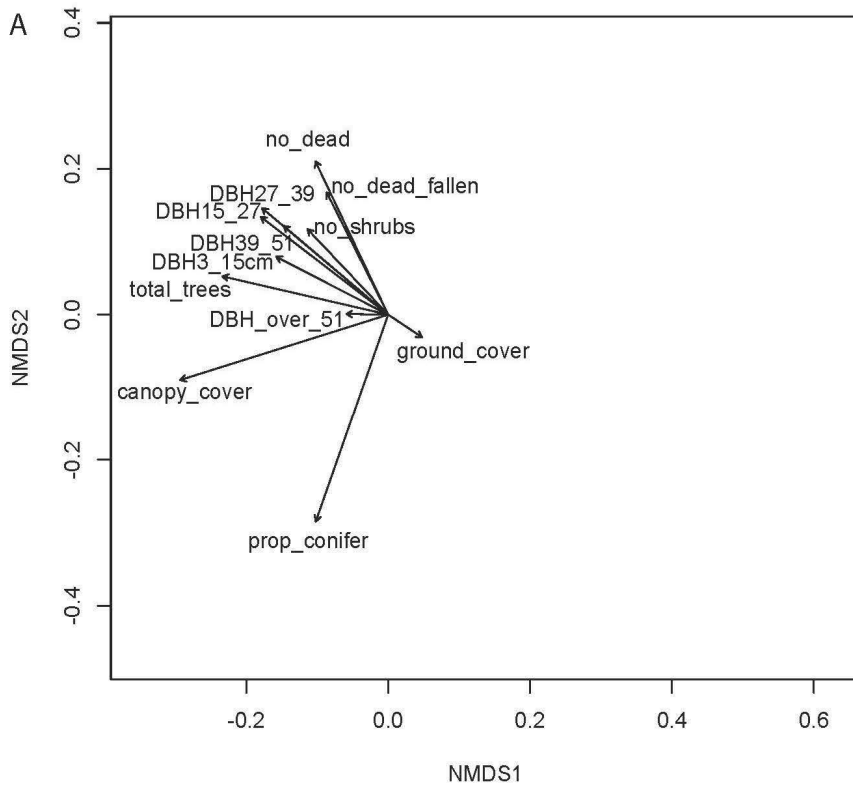
Figure 5.2. Non-metric dimensional scaling (NMDS) ordination biplots showing northern flicker fledgling habitat use, nest site characteristics, and random locations in central British Columbia, Canada 2010–2012. (A) The length of the vectors, representing the habitat variables, indicate the strength of the variable (i.e., weak predictors have short arrows and strong predictors have long arrows). The angle of the vector indicates which axis it is most strongly affecting and the direction indicates whether it is positive or negative. NMDS1 was positively associated with tree size (dbh), canopy cover, and total number of trees, and negatively associated with ground cover. NMDS2 was positively influenced by the number of dead standing trees, the number of shrubs, and the number of fallen trees, and negatively associated with the proportion of conifers. (B) The position of fledgling, random, and nest vegetation plots in the vegetation composition space represented by NMDS1 and NMDS2. The dispersion ellipses represent the 95% confidence intervals based on standard deviation for each of the groups: fledgling (short dash), random (solid), and nest (long dash). Fledgling locations were characterized with a high density of trees, compared to both nest plots and random locations.

As fledglings aged, they moved farther from the nest (lme: $t = 8.78$, $P < 0.01$; Fig. 5.3). Older fledglings were located in more open areas with low canopy cover, and fewer trees compared to younger fledglings (glm: NMDS1: $t = 5.36$, $P < 0.01$; NMDS2: $t = -1.53$, $P = 0.13$). The size of forest fragment that fledglings occupied was not correlated with age ($t = 1.08$, $P = 0.28$; Fig. 5.4), but a greater proportion of observations were in grasslands after fledglings were >12 days old ($\chi^2 = 31.83$, $P < 0.01$; Fig. 5.4).

5.5.3 Fledgling Survival

Fledgling survival was related to some characteristics of the habitat fledglings used. The top model, ϕ(canopy cover + no. conifers)p(t)), was 41 times better than the base model, ϕ p(t) (Table 5.1). Two covariates (canopy cover and no. conifers) appeared in the top 2 models with ΔAIC_c values ≤ 2, and all 3 covariates (canopy cover, no. conifers, and no. trees) appeared in the top 4 models with ΔAIC_c values ≤ 4, suggesting that each vegetation co-variate affected daily survival of fledglings. The confidence intervals for all variables did not overlap zero indicating they represented biological effects. Fledglings occupying habitats with more canopy cover had higher survival (Fig. 5.5a). According to the top model, estimated daily survival was 0.994 ± 0.004 over the 22-day time period. Re-sighting probability varied (mean $= 0.458 \pm 0.159$) with a range from 0.313 to 0.73 over the 22-day period and tended to increase as the fledglings aged. The observed deviance of the top 2 models was reasonably likely to occur based on a bootstrap analysis ($P = 0.38$, 0.39). Correlation coefficients between variables were 0.014, 0.49, 0.018 (canopy cover by conifers, canopy cover by trees, and conifers by trees, respectively).
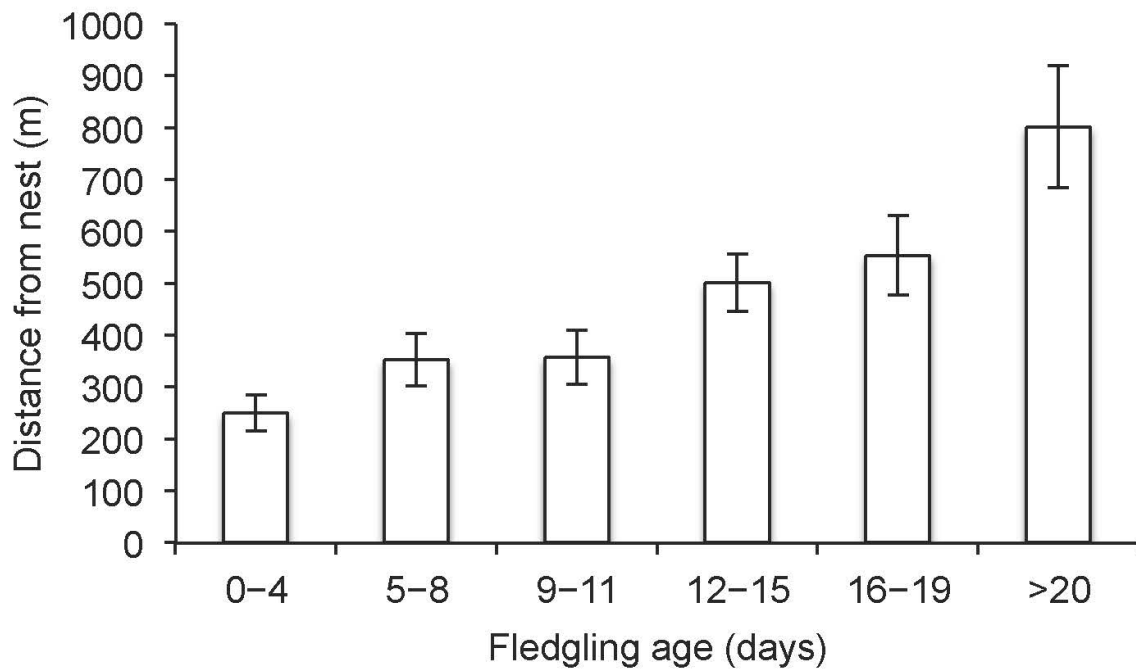
Figure 5.3. Northern flicker fledglings move farther from the nest as they age (days post-fledging) in central British Columbia, Canada, 2010–2012. Columns indicate the average distance and the error bars are ±SE. The max <20 category indicates the average maximum distance a fledgling moved from the nest within the first 20 days post-fledging.
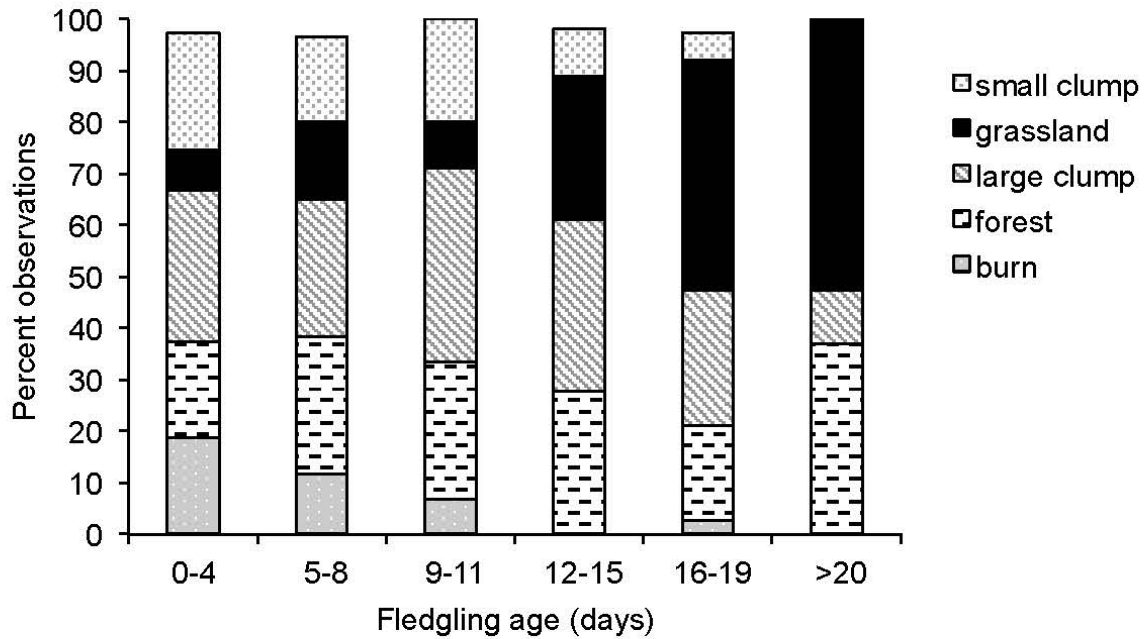
Figure 5.4. A bar plot describing the percentage of northern flicker fledgling locations that occurred in each vegetation type over 6 fledgling age categories (number of days post-fledging) in central British Columbia, Canada, 2010–2012. Fledglings were observed more frequently in forested areas when they were <12 days after fledging. Small clumps consist of a cluster of trees <1 ha, a large clump is >1 ha, forest is a >10 ha, grassland are open areas with no trees or sparse trees, and burn are areas with recent burn activity (<3 years).

The second survival analysis, which investigated effects of forest cover at various landscape-scales, found that all models, were better than the base model, $\phi p(t)$, with the top model, $\phi(750\text{ m}) p(t)$ being 38 times better than the base model (Table 5.2) indicating that the effects of forest cover on fledgling survival are greatest in the area 750 m around the nest. Three covariates (radii 250 m, 500 m, 750 m,) appeared in the top 4 models with ΔAIC_c values ≤ 2, and the 1,000 m radius appeared in a model with ΔAIC_c values ≤ 4, indicating good support. This suggests that the effects of forest cover on the daily survival of fledglings were apparent at all scales. All 4 scales indicated that fledgling survival decreased with increasing forest cover and the greatest declines occurred around 35% (Fig. 5.5b). The top model estimated daily survival at 0.996 ± 0.004 over the 22-day period. The mean re-sighting probability was 0.449 ± 0.161 (range: $0.307-0.762$) over the 22-day period. The observed deviance of the top 3 models were reasonably likely to occur based on a bootstrap ($P = 0.41$, 0.4, 0.38). Correlation coefficients between variables were 0.4, 0.65, 0.14, 0.49, and 0.07 (250 by 500 m, 500 by 750m, 250 by 750, 500 by 1,000 m, and 250 m by 1,000 m, respectively). We removed the models that contained both 750 m and 1,000 m because they were highly correlated, 0.89).

Table 5.1. The results of model selection in which northern flicker fledgling survival in British Columbia, Canada, 2010–2012, was analyzed with habitat covariates measured at fledgling locations. The models are in ascending order of ΔAIC_c which indicates the difference in corrected Akaike's Information Criterion (AIC_c) from the model with the lowest AIC_c value. K is the number of parameters and w_i is the Akaike weight. Apparent survival (Φ), was kept constant over time but included the effects of the average canopy cover (canopy), the number of trees (trees), and the number of conifers (conifers) from 5 x 5-m vegetation plots from the first 6 days post-fledging. We compared models including effects of microhabitat variables on apparent survival (Φ) and include a model of constant survival (Φ) as a comparison. The re-sighting probability (p) was time dependent (t) and did not include any covariates.

Model	ΔAIC_c	w_i	K
Φ (canopy + conifers) p(t)	0[a]	0.45	13
Φ (canopy) p(t)	1.07	0.26	12
Φ (canopy + trees + conifers) p(t)	2.31	0.14	14
Φ (canopy + trees) p(t)	3.29	0.09	13
Φ (conifers) p(t)	5.79	0.03	12
Φ (trees + conifers) p(t)	7.10	0.01	13
Φ p(t)	7.42	0.01	11
Φ (trees) p(t)	9.41	0.00	12

[a] $AIC_c = 818.77$

Table 5.2. The results of model selection in which survival of northern flicker fledglings in British Columbia, Canada, 2010–2012 was analyzed with forest cover at the landscape scale, using 4 radii from the nest (250 m, 500 m, 750 m, and 1,000 m). The models are in ascending order of ΔAIC_c, which indicates the difference in corrected Akaike's Information Criterion (AIC_c) from the model with the lowest AIC_c value. K is the number of parameters and w_i is the Akaike weight. We compared models including effects of forest cover at different scales on apparent survival (Φ) and include a model of constant survival (Φ) as a comparison. The re-sighting probability (p) was time dependent (t) and did not include any covariates.

Model	ΔAIC_c	w_i	K
Φ(750 m) p(t)	0[a]	0.23	12
Φ(500 m + 750 m) p(t)	0.23	0.20	13
Φ(250 m + 750 m) p(t)	1.48	0.11	13
Φ(500 m) p(t)	1.81	0.09	12
Φ(250 m + 500 m + 750 m) p(t)	2.00	0.08	14
Φ(1000 m) p(t)	2.25	0.07	11
Φ(500 m + 1,000 m) p(t)	2.62	0.06	13
Φ(250 m + 1,000 m) p(t)	2.84	0.06	13
Φ(250 m + 500 m) p(t)	3.11	0.04	13
Φ(250 m + 500 m + 1,000 m) p(t)	4.07	0.03	14
Φ(250 m) p(t)	5.91	0.01	12
Φ p(t)	7.27	0.01	11

[a] $AIC_c = 821.24$
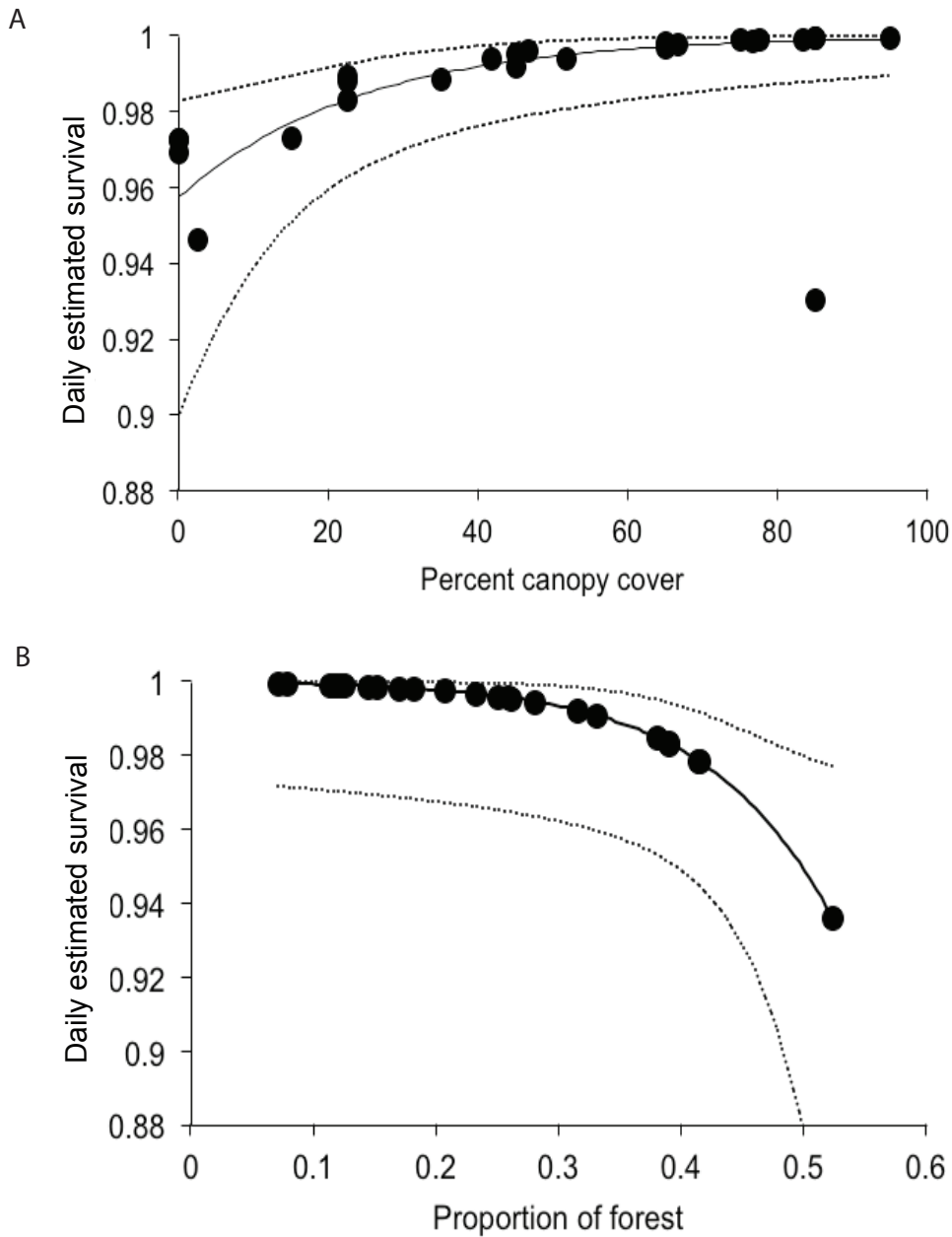
Figure 5.5. Daily survival estimates for fledgling northern flickers in central British Columbia, Canada, 2010–2012, from Program MARK's young survival from marked adults analysis. (A) Derived daily survival estimates for the covariate canopy cover from the analysis investigating survival based on fledgling locations. Estimates are derived from the top model, which included effects of canopy cover and number of conifers on survival and a time-dependent detection

probability. (B) Derived daily survival estimates from the covariate proportion of forest cover at a radius 750 m from the nest, from the analysis investigating survival based on forest cover at the landscape scale. Forest cover at all radii (250 m, 500 m, 750 m, and 1,000 m) from the nest showed the same relationship with survival as the covariate 750 m presented here. For both (A) and (B) the solid line indicates the predicted estimated daily survival, the individual circles indicate estimated daily survival of individuals and the dotted lines show the upper and lower 95% confidence intervals.

5.6 DISCUSSION

We documented habitat use by juvenile woodpeckers during the post-fledging, parental dependency period. We found that northern flicker fledglings occupied habitat non-randomly and used areas with different vegetative characteristics compared to nest sites. In particular, fledglings occupied areas with a high density of trees, but the size of trees (dbh) did not influence habitat selection. Parents also brought fledglings to areas with conifers although >95% of the nest trees were aspen (Wiebe 2001). Several studies of other altricial species also have found that the habitat used during the post-fledging period contains denser vegetation compared to the area around the nest site (Anders et al. 1998; Vega Rivera et al. 1998; King et al. 2006). In rose-breasted grosbeaks (*Pheucticus ludovicianus*), fledglings after 1 week moved higher into the canopy (Moore et al. 2010), but no studies on birds have documented a shift such as we observed where fledglings moved from more forested areas to more open areas as they aged. However, shifts from dense to open areas are common among other animals, particularly fish (Grubb 2010).

Although dense tree cover, as suggested from our MARK models, improved the survival of young fledglings, adults mainly forage in grasslands or clearings near small trees or fallen trees, where ground-dwelling ants are more abundant or accessible than in dense coniferous forests (Elchuk and Wiebe 2002; Wiebe and Gow 2013). Hence, young flickers may shift habitats as they age to increase their access to food, an explanation that has also been proposed to explain habitat shifts in wood thrushes (*Hylocichla mustelina*; Anders et al. 1998).

Young flickers are occasionally fed up to 22-days after they fledge, but parents began to rebuff food-begging attempts around 7−12 days post-fledging (Chapter 4) indicating that fledglings soon had to forage themselves to supplement food received from parents. In summary, a trade-off may exist between the use of forests versus grasslands if habitat patches with dense conifers are safer from predators but contain less prey. As fledglings grow, they become more

agile and the predation risk may decrease at the same time the need for food increases. This could explain the shift in habitat we observed.

5.6.1 Movements of Fledglings in Relation to Habitat and Age

Fledglings from nest trees with little surrounding forest cover moved farther from the nest within the first 4 days post-fledging. Fisher and Wiebe (2006b) found that the risk of nest predation by red squirrels (*Tamiasciurus hudsonicus*) was greater in larger forest fragments and closer to coniferous forest. Thus, parents may be trading off a safe nest site for eggs and nestlings, which are vulnerable to squirrel predation, with denser forest cover, which is safer for young fledglings. Although gap-crossing between forest patches may increase risk of exposure to some predators, flickers may use forested corridors when moving between fragments, as shown in juvenile red-bellied woodpeckers (Cox and Kesler 2012b) and ovenbirds (*Seiurus aurocapillus*; Desrochers and Hannon 1997). We observed 3 long distance movements of fledglings during the first week post-fledging; in all cases fledglings moved through forested areas instead of making direct flights across open grasslands. Even when fledglings grew and became strong fliers (approx. 2 weeks post-fledging) and moved hundreds of meters within 1-hour tracking sessions, they avoided making long-distance flights of >200 m over open terrain and instead flew between forest fragments. Therefore, flicker parents may be able to mitigate the potential negative effects of nesting in small, isolated tree clumps by using the forest patches as stepping stones when moving their fledglings farther distances to safer patches of more continuous and dense forest. Compared to many altricial passerine birds with poorer flying ability in the first week post-fledging, flicker fledglings can move greater distances soon after leaving the nest, which may explain why passerines are more constrained than flickers to choose a nest close to good post-fledging habitat (e.g. Refsnider and Janzen 2010; Streby and Anderson 2013).

5.6.2 Survivorship of Fledglings

The estimated daily survival rates of flicker fledglings were about average compared to those of 9 species summarized by Cox and Kesler (2012a). With survival rates standardized to a 2-month period, the survival of flicker fledglings was 0.64, about midway between that of red-bellied woodpeckers (Cox and Kesler 2012a) at the high end (0.92) and the wood thrush (Anders et al. 1997) at the low end (0.40).

Consistent with the hypothesis that fledglings occupy areas with more complex vegetation structure to reduce predation risk, especially at younger ages when they may be more vulnerable, flicker fledglings that used areas with a greater percent canopy cover during the first 6 days after leaving the nest had higher survival than those in more open areas. This indicates that high visual concealment at a small spatial scale surrounding fledgling perches improves juvenile survival. At the larger scale, survival of fledglings declined with increasing forest cover on the landscape, especially above a threshold around 30−35% (Fig. 5.5b). In contrast, juvenile spotted owls, an old-growth specialist, had reduced mortality when the proportion of forest cover increased on the landscape (Miller et al. 1997). At the landscape scale, forest cover may affect the abundances of predators (Schmidt et al. 2008), which may influence survivorship of fledglings. We did not document the landscape preferences of all predators on our study site, but some common predators such as accipiter hawks (*Accipiter spp.*), black bears (*Ursus americanus*), and weasels (*Mustela spp.*) were probably more abundant in areas with greater forest cover.

5.7 MANAGEMENT IMPLICATIONS

Flickers are not currently a species of conservation concern, but they are keystone cavity excavators (Martin et al. 2004), and their abundance influences the diversity and density of many

other species in the cavity-nesting community. Thus, maintaining the viability of flicker

populations should be considered in management decisions of grasslands and forests. Our

research indicates that management is needed at 2 spatial scales to benefit flickers. Flicker

fledglings need concealment cover especially during the first week after leaving the nest, but the

patch of dense forest cover need not be large. Indeed, larger forest patches may be detrimental as

the survivorship model suggested that forest cover on the landscape > 30–35% was linked to

poorer fledgling survival. Thus, efforts should be made to maintain grasslands with smaller

clusters of multi-aged trees including conifers that do not make up more than 35% of the

landscape. Such forested fragments would provide both nesting sites (snags) and protective cover

for fledglings. The young flickers did not appear to avoid burned areas, or areas with many

beetle-killed trees, but such habitat probably lacks good concealment. Therefore, we recommend

that any controlled burning should leave dense forest clusters on the grasslands that fledglings

can use while traveling over the landscape.

CHAPTER 6:
GENERAL DISCUSSION

6.1 Synthesis

The goal of this research was to understand sex differences in parental care strategies in terms of habitat use and provisioning effort. I achieved my primary goal by exploring sex differences in the use of habitat while foraging and its effects on diet (Chapter 2; Appendix A), provisioning responses to increased brood demands (Chapter 3), the length of post-fledging parental care (Chapter 4), and the use of habitat by families in the post-fledging period (Chapter 5). I examined parental care from a number of perspectives, which spanned the fields of ecology, behaviour, ecophysiology and landscape ecology. These varied perspectives allowed me to provide a composite picture of how life history and individual traits influence the habitat use and amount of care given by each sex.

One of my main findings was that mates reduced competition for the same prey (Appendix A) by avoiding temporal overlap of foraging areas on their home range, which presumably increases the amount of prey they can bring to their offspring (Chapter 2). This finding is unique among terrestrial birds, because studies have focused on differences in microhabitat or substrate use (e.g. Selander 1966; Pasinelli 2000; Hogstad 2010) rather than how and where mates forage on the home range. Thus, my results, from Chapter 2, add to our understanding of how mates coordinate foraging effort and provide a basis for future studies to directly link parental care to how mates partition their home range to optimize the amount of food each parent can obtain.

Both sexes responded to proximate cues of brood demands by decreasing their feeding rate to reduced broods, but they were incapable or unwilling to increase effort to enlarged broods, at least in the short-term (Chapter 3). Unpublished data show that when brood size is increased over the entire nestling period, parent flickers increase provisioning rates and raise more offspring (A Musgrove, unpublished), suggesting that parents do respond to increased brood

demands that are increased in the long-term throughout the nestling period. This does not negate the idea that parents lay the clutch size they are normally able to rear because nestlings from enlarged broods fledge with lower mass (A Musgrove, unpublished), and there may be costs to parental survival if they increase effort to enlarged broods.

The unresponsiveness of parent flickers to short-term increases in brood demands was in contrast to most other species (reviewed in Table 3.1), which suggests that flickers may be energy limited and working near their maximum capacity. Although one sex, typically the female, has more variable provisioning rates (e.g. Low et al. 2012) this was not the case for flickers. However, for natural (unmanipulated) broods, the provisioning rate of males was associated with a different set of predictors (nestling age and brood size) than the provisioning by females that was only predicted by brood size (Gow et al. 2013a). This suggests, that the sexes may respond to different cues when they decide how much to provision.

In Chapters 3, and 4, I tested whether variation in parental care could be explained by intrinsic, physiological measures. Feeding rates by both parents during the nestling period were not associated with body condition or $CORT_f$ level. In contrast, the length of female but not male parental care was negatively influenced by the 'stress' response ($CORT_f$; Chapter 4). Interestingly, the body condition of males is positively related to his contribution to incubation effort (Wiebe 2008) and negatively to feeding rates of nestlings (Gow et al. 2013a). Perhaps males tend to adjust their levels of care on a short-term basis according to their nutrient reserves whereas females tend to adjust the overall length of time they care for offspring according to their level of "stress" as averaged over the breeding cycle.

During the post-fledging period parents took their fledglings to habitat patches with dense cover that increased the survival of offspring (Chapter 5). Several other studies have also documented that denser vegetation increases survival of juveniles (King et al. 2006; Streby

2013), but this is not always the case (e.g. Moore et al. 2010). My findings go beyond most other studies of habitat use because they relate parental care to habitat use by fledglings and show a shift in habitat types as offspring age related to changing patterns of predation risk and foraging behaviour.

My work on flickers helps to complete the picture of how the sexes contribute to parental care in a bird with a facultatively polyandrous mating strategy. My thesis builds on previous research conducted during the incubation and nestling periods, which suggests male flickers contribute more care than females. Because male-biased care extends into the post-fledging period, I can conclude that males invest more heavily in parental care than females over the duration of the parental care period. The same pattern of sex-biased care may apply to other woodpecker species with similar life histories, such as three-toed woodpeckers (Pechacek 2006) and lesser-spotted woodpeckers (Wiktander et al. 2000), but there is little comparative data. Studies on parental care in facultatively and classical polyandrous species are rare. Thus, this thesis contributes to our understanding of reproductive decisions of females when females may have more to gain than males by searching for additional partners.

6.2 Future Research, Directions, and Considerations

I tested several hypotheses about parental care and laid a foundation for future work, both within flickers and in other species. Although many hypotheses about parental care allude to energetic costs, I did not measure such costs directly (e.g. with doubly-labelled water) because of the logistical challenge of trapping parents repeatedly. Such direct measures of energy expenditure by parents would help to explain investment decisions but such data is generally lacking for birds because of the logistical challenges of measuring energy expenditure in the field.

My finding that the investment by female parents was negatively related to $CORT_f$ levels is intriguing but needs to be confirmed with larger samples and tested in more species to see whether this relationship is common. It would be interesting to investigate the relationship between CORT and animal "personalities" (Cockrem 2007) to see whether levels of parental care can be linked to personality types in populations via a proximate link of CORT levels. Additionally, flickers would be a good species in which to test hypotheses about the link between CORT, prolactin and testosterone to parental care because of the partially reversed sex roles. Particularly in facultatively polyandrous species such as flickers, it would be intriguing to measure the levels of prolactin, the 'parental care hormone' (reviewed in Angelier and Chastel 2009) and the levels of testosterone in males versus females to see if the amounts differ compared to other species of birds in which males do not contribute as much to offspring care. For instance, studies on the relationship between testosterone and parental care have mainly been limited to species with biparental care and typical sex roles (e.g. Cain and Ketterson 2013, Rosvall 2013), and thus studying these hormones in flickers may provide novel insight into the functions of testosterone and prolactin in parental care.

My thesis documented differences in the length of parental care between males and females but it did not test whether partners compensated for each other or whether there were consequences to the offspring of abandonment by females. These questions can be investigated further by experimentally removing or handicapping male or female parents at different stages of the post-fledging or nestling periods. Similarly, it would be interesting to measure the survival and productivity of flicker parents in relation to whether or not they abandoned offspring the previous year. When male collared flycatchers (*Ficedula albicollis*) reduced parental care to moult early, their mate experienced reduced future fecundity (Hemborg and Merila 1998). Thus, female abandonment in flickers may reduce male condition if he must work harder to compensate

for the female. Knowing how mates negotiate care would further refine our understanding of how parental investment decisions influence the recruitment of juveniles.

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APPENDIX A

LACK OF DIET SEGREGATION DURING BREEDING BY MALE AND FEMALE

NORTHERN FLICKERS FORAGING ON ANTS

A.1. ABSTRACT

Sexual size dimorphism can result in reduced competition if it leads males and females to use different foraging techniques or consume different prey items. Among woodpeckers, differences between males and females in bill lengths are common and may explain why foraging differences in this family of birds. Northern Flickers (*Colaptes auratus*) are ground-foraging woodpeckers that specialize on ants. The overall contribution of ants to their diet and the proportions of particular ant genera in their diet are not well known. To understand the relationship between bill morphology and the consumption of prey items, we compared the bill length and bill width of male and female flickers. We then collected and analyzed fecal samples from breeding flickers (*N* = 40 males, 33 females) at a study site in central British Columbia, Canada. Bills of male flickers were significantly longer (4%) and wider (5%) than those of females. Of 11 prey types identified, ants made up over 99% of their diet, and the abundance and composition of ant taxa in the diet did not differ between the sexes. We found significant year and time of season effects, with the abundance of *Tapinoma sessile and Lasius* spp. increasing from May to the end of June and differing between years. This difference in diet composition between years may have been due to changes in the abundance or accessibility of certain ant taxa related to differences in vegetation structure or weather. Nine ant taxa were consumed by flickers of which the four most common were *Tapinoma sessile, Lasius* spp*., Myrmica* spp*.,* and the *Formica fusca* species group. The degree of dimorphism in bill size of male and female Northern Flickers in our study was smaller than reported for several species of arboreal-foraging woodpeckers, suggesting that bill size of ground-foraging woodpeckers may not be strongly linked to niche separation at the level of prey selection.

A.2. INTRODUCTION

One possible function of size dimorphism in birds is to reduce competition for food between the sexes by facilitating different foraging behaviour or techniques (Radford and du Plessis 2003, Temeles et al. 2010), and hence selection of different prey (Radford and du Plessis 2003, Lee and Severinghaus 2010). For some species, differences in bill size have been linked to dietary differences, with the sex with the larger bill eating larger prey items (Herrera 1978, Chazarretta and Ojeda 2011). Alternatively, sexual differences in bill size can be driven not by foraging, but by other activities such as reproduction (e.g., cavity excavation by males; Aulen and Lundberg 1991) or simply body size.

In most (~55%) species of arboreal North American woodpeckers, males have significantly longer bills than females (~2 mm; Short 1982), but differences between the sexes in bill length can be <1 mm as in downy woodpeckers (*Picoides pubescens*; Jackson et al. 2002) or as much as 23% in ladder-backed woodpeckers (*Picoides scalaris*; Lowther 2001). Differences in bill length may explain why males of some species typically forage on tree trunks and large branches and females forage on small branches (Austin 1976, Jenkins 1979, Aulen and Lundberg 1991). Alternatively, differences between males and females in use of foraging substrates may result from social dominance (Peters and Grubb 1983) rather than differences in the strength or size of bills. Although investigators have measured bill sizes in several species of arboreal woodpeckers and noted differences between the sexes in foraging substrates, no one to date has, to our knowledge, directly linked differences in bill size to differences in prey consumed by each sex.

Because arboreal woodpeckers use their bills as chisels and picks to excavate insects and larvae that are often buried several centimeters under hard layers of bark and wood (Short 1971), bill size (length) could influence the depth of excavation or the hardness of the substrate that each

sex could exploit. However, unlike arboreal woodpeckers, ground-foraging woodpeckers use their bills for probing and digging in softer dirt substrates (Short 1971). Ground-foraging woodpeckers may therefore be less limited by bill size and strength and so any differences between the sexes in bill length may be less likely to influence the type of prey consumed than might be the case for arboreal species. However, the possible effect of sexual dimorphism in bill size on diet has not been examined for any species of ground-foraging woodpecker.

Northern flickers (*Colaptes auratus*) are the only woodpecker in North American that forage primarily on the ground (Wiebe and Moore 2008). However, green woodpeckers in Europe (*Picus viridis*; Rolstad et al. 2000), ground woodpeckers (*Geocolaptes olivaceus*; Short 1971) in Africa, and other South American flickers in the genus *Colaptes* also forage on the ground (Short 1971, 1972). Beal (1911) examined the stomach contents of 684 Northern Flickers and reported that ants made up 50% of their diet, but did not examine seasonal variation in their diet or possible differences in the diets of males and females. When foraging on ants, Northern Flickers typically use their bills and tongues to probe the ground, lapping up adults and larvae from small colonies under rocks and just below the ground surface (Kilham 1983, Elchuk and Wiebe 2003).

The bills of male Northern Flickers average ~ 1 mm (4%) longer than in females (Wiebe and Moore 2008) and, given this minimal difference, we predicted that males and females would take similar-sized prey. We used fecal samples to analyze the diets of male and female Northern Flickers, a technique more reliable for determining the diet of insectivorous species than observation alone (Lee and Severinghaus 2010).

A.3. METHODS

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We studied Northern flickers at Bechers Prairie in central British Columbia, Canada (51° 52'N, 122° 21'W), in a study area covering ~100 km^2. Our study site was dominated by grazed grasslands interspersed with clumps of trembling aspen (*Populus tremuloides*). The prairie is surrounded by coniferous forests dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and white spruce (*Picea glauca*). Flickers typically nested in the aspen clumps and foraged on the prairie and along forest edges (Elchuk and Wiebe 2002).

We trapped adult flickers in nest cavities by plugging cavity entrances when birds were inside and then climbing up with a ladder and placing a modified fishing net over the cavity entrance (Wiebe 2008). After capture, we measured bill length from the anterior of the nares to the tip along the upper mandible and bill width at the anterior of the nares using digital calipers (± 0.01 mm). To compare differences in bill morphology, we used data collected from 1007 females and 1000 males captured from 1997 − 2010. All birds were measured by KLW.

Ant heads remain intact and undigested in flicker feces, and can be identified to genus and sometimes species level. Fecal samples were collected opportunistically when flickers defecated during capture; most flickers either did not defecate when captured or defecated when they hit the net so samples could not be located. We collected samples from 16 males and 14 females in 2011, and from 24 males and 19 females in 2012. One fecal sample was collected from each individual. Samples were collected from 12 May to 14 June 2011 and 18 May to 19 June 2012.

After drying fecal samples under a fume hood, we broke them apart and used a reference collection and key for the ants of the area compiled by RJH to aid in identification. We modified a technique described by Beckwith and Bull (1985) and analyzed a 100-mg subsample of feces using a top-illuminating dissecting microscope with 10−63 x magnification that allowed us to more easily count small prey items (heads <1 mm long). The number of prey items per

subsample averaged 83 ± 58 (SD) and the weight of the original fecal samples averaged 0.53 ± 0.36 g.

We assessed abundance of items in fecal samples using non-metric dimensional scaling (NMDS), an iterative multivariate ordination technique that has advantages over principal components analysis because non-normal and non-linear data can be used, as can any distance measure or transformation (McCune and Grace 2002). Although we eliminated rare prey items found in <3% of samples (e.g., *Leptothorax* spp. and *Aphaenogaster occidentalis*), the structure of the species abundance data in our fecal samples (*N* = 73) was uneven and many samples were negatively skewed by zeros. Therefore, we used the Bray-Curtis distance metric that is considered robust for datasets with many zeros (Faith et al. 1987). We followed conventional techniques in NMDS analysis by creating a scree plot and identifying the number of dimensions (axes) by looking for the elbow in the scree plot (McCune and Grace 2002). Procrustes rotation plots were used to visually assess differences between dimensions (McCune and Grace 2002, Oksanen et al. 2012). We subsequently used the NMDS scores from axes 1, 2, and 3 derived from the ordination using the 'scores' command in the package vegan for each axis in subsequent analyses.

We used general linear models (GLM) with the NMDS scores as the dependent variables to determine if the diets of males and females differed, if there were year or time of season effects, and if there was a significant interaction between year and time of season. We measured diversity of ant taxa in the sample using the Shannon Weaver diversity index (H') and the Simpson's diversity index (1-D) and tested for sex differences in the diversity index using a *t*-test. All statistical analyses were conducted using R 2.14.2 (R Development Core Team 2012). For the NMDS we used the package vegan and the function metaMDS (Oksansen et al. 2012). We used the diversity function in the package vegan to calculate the diversity of ant taxa in the

samples. All analyses are two-tailed, with significance set at α = 0.05. Values are presented as means ± SE, unless otherwise indicated.

A.4. RESULTS

A.4.1 Bill Size

Male northern flickers had significantly longer bills (30.4 ± 0.05 mm) than females (29.4 ± 0.05 mm; t_{2002} = 16.2, P < 0.0001), but the mean difference was < 4%. Males also had wider bills than females (7.3 ± 0.02 for females and 7.7 ± 0.02 for males; t_{2002} = 17.2, P < 0.0001), a difference of < 5%.

A.4.2 Frequency and Abundance of Ant Taxa in Fecal Samples

We identified nine ant taxa in flicker fecal samples (Table A.1), plus one beetle elytrum and one set of spider chelicerae. All ant taxa were found in fecal samples of both males and females except *Aphaenogaster occidentalis* was only found in the fecal sample of one male. Most samples contained three or four ant taxa (range = 1−7). Ants detected most often (>50% of samples) were *Tapinoma sessile*, *Lasius* spp*., Myrmica* spp*.,* and the *Formica fusca* species group. The least common ants (<15% of samples) were *Leptothorax* spp*., Aphaenogaster occidentalis,* and *Camponotus* spp. In general, ant taxa found most often in fecal samples were also the most abundant (Table A.1). Based on the Shannon Diversity Index, female Northern Flickers had a slightly more diverse diet than males (males: 0.85 ± 0.48, females: 1.05 ± 0.33; t_{69} = -2.1, P = 0.04), but this was not true with the Simpson Diversity Index (males: 0.55 ± 0.033, females: 0.53 ± 0.035; t_{70} = 0.5, P = 0.65).

A.4.3. Sex, Year, and Time of Year

To assess the effects of sex, year, and date on diet, we used the NMDS scores on three axes as dependent variables. The three axes had a stress value of 12.3, and an adjusted R^2 fit of 0.90 which is good for ecological data (McCune and Grace 2002, Zuur et al. 2007). The first axis (NMDS1) had significant negative loadings for the two taxa with the smallest ants (*Tapinoma sessile* and *Lasius* spp.), indicating that high scores along NMDS1 were lacking those ant taxa. NMDS2 was positively associated with *Myrmica* spp. and the *Formica sanguinea* species group and had a weak negative association with *Camponotus* spp., whereas NMDS3 had weak loadings and was negatively associated with the *Formica rufa* species group and positively with the *Formica fusca* species group (Fig. A.1).

Our initial GLM models on the NMDS axes scores contained first-order interaction terms, but none were significant so they were deleted. NMDS scores did not differ between the sexes on any of the axes (Table A.2, Fig. A.1). There were, however, significant year and date effects for NMDS1 scores, a significant date effect on NMDS2 scores, and a significant year effect on NMDS3 scores. Samples from 2011 had lower NMDS1 scores than those from 2012 ($mean_{2011}$ = -0.1 ± 0.037, $mean_{2012}$ = 0.073 ± 0.024) and higher NMDS3 scores ($mean_{2011}$ = 0.055 ± 0.019, $mean_{2012}$ = -0.038 ± 0.022, Table A.2). Hence, year effects were primarily driven by the ant taxa associated with NMDS1 and NMDS3, i.e., higher numbers of *Tapinoma sessile* and lower numbers of *Lasius* spp. and *Myrmica* spp. in fecal samples from 2011 than in 2012. The significant date effect indicated that birds caught later in the year had lower NMDS1 scores and higher NMDS2 scores, indicating there were more *Lasius* spp., *Tapinoma sessile*, and *Myrmica* spp. in their diets (Table A.2).

Table A.1. The proportion of fecal samples of northern flickers (N = 40 males, 33 females) containing each prey species, and the mean percentage (± SD) of those species among prey identified in each 100-mg subsample of feces. Fecal samples were collected from breeding adults at Riske Creek, British Columbia, in 2011 and 2012. Data for both years are combined. Species are ordered in decreasing proportions. The notation sg. is short for species group.

	Proportion of samples			Percent within sample		
Ant Taxa	Male	Female	Total	Male	Female	Total
Formica fusca sg.	0.74	0.87	0.79	18 ± 2.3	19 ± 26	18 ± 25
Tapinoma sessile	0.65	0.75	0.69	19 ± 23	29 ± 32	24 ± 28
Lasius spp.	0.72	0.57	0.65	35 ± 34	24 ± 30	30 ± 33
Myrmica spp.	0.69	0.57	0.64	17 ± 20	16 ± 23	16 ± 21
F. rufa sg.	0.34	0.57	0.44	2.8 ± 6	4.7 ± 8	3.7 ± 7
F. sanguinea sg.	0.34	0.39	0.36	4.8 ± 10	6.5 ± 2.1	5.6 ± 16
Camponotus spp.	0.12	0.15	0.13	3.0 ± 14	0.48 ± 1.4	2.0 ± 11
Leptothorax spp.	0.02	0.15	0.08	0.08 ± 4.4	0.02 ± 0.06	0.56 ± 0.32
Aphenogaster occidentalis	0.02	0	0.01	trace	0	trace
Other (spider/ beetle)	0.02	0.03	0.03	trace	0	trace

Table A.2. The effect of sex, year, and time during the season on the diet of breeding northern flickers. Three GLMs were conducted, with the dependent variables as the scores from each NMDS axis. NMDS1 was positively loaded with abundance of *Tapinoma sessile*. NMDS2 was positively associated with *Myrmica* spp. and *Formica sanguinea* species group, and a weak negative association with *Camponotus spp.* NMDS3 had negative loadings for the *Formica rufa* species group and *Formica fusca* species group.

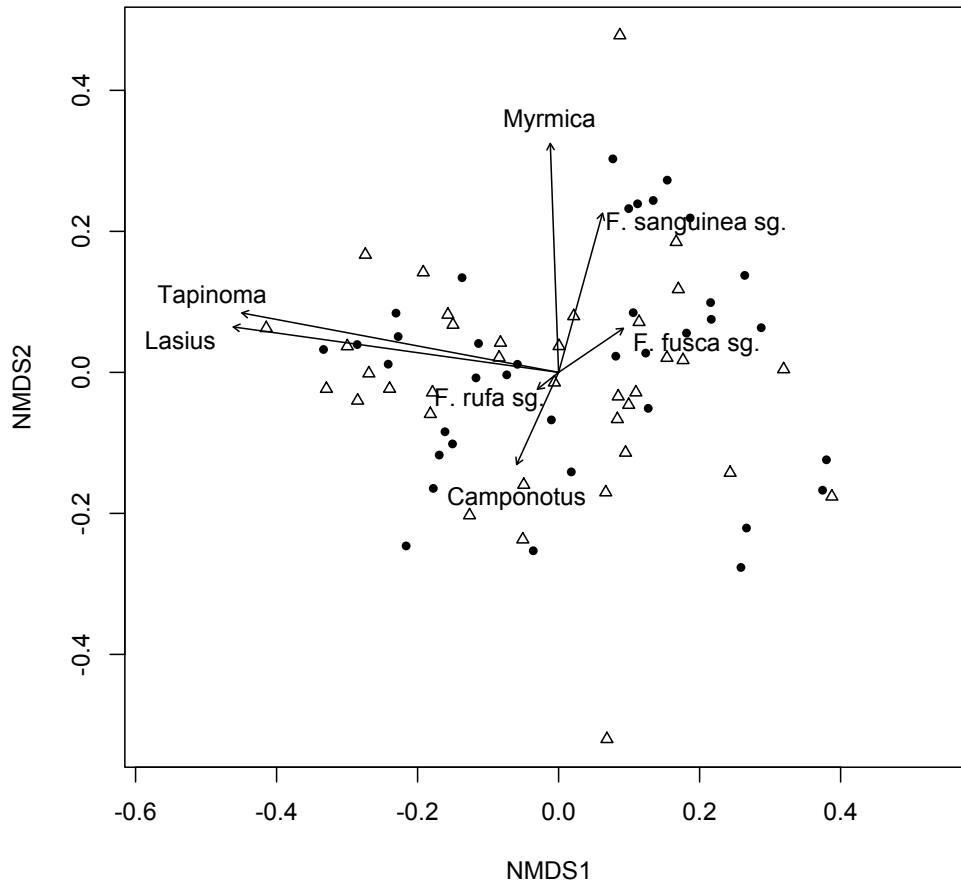| Ordination axis	Variable	Estimate	SE	*t*	*P*
NMDS1	Date	-0.0056	0.0024	-2.5	0.0013
	Sex	0.028	0.04	0.7	0.48
	Year	0.14	0.043	3.4	0.0012
NMDS2	Date	0.0042	0.0021	2.0	0.05
	Sex	0.028	0.035	0.8	0.43
	Year	0.052	0.038	1.4	0.17
NMDS3	Date	-0.0023	0.0018	-1.3	0.18
	Sex	-0.038	0.03	-1.3	0.21
	Year	-0.11	0.032	-3.3	0.0017

Figure A.1. A triplot showing the position of northern flicker males (filled circles) and females (open triangles) in the diet composition space represented by NMDS axis 1 versus NMDS axis 2. The vectors represent the ant (prey) taxa variables where the weaker predictors have shorter arrows than strong predictors. The angle of the vectors indicates which axis it is most strongly affecting and the direction indicates whether it is positive or negative. Ant taxa comprising <1% of the prey items in fecal samples were excluded. The notation sg. is short for species group. NMDS1 was positively loaded with abundance of *Tapinoma sessile*. NMDS2 was positively associated with *Myrmica spp.* and *Formica sanguinea* species group, and a weak negative association with *Camponotus spp.* Fecal samples located close to ant taxa vectors indicate they contain an abundance of that ant taxa. All samples were collected in central British Columbia in 2011 and 2012.

A.5 DISCUSSION

Male and female northern flickers did not differ in the taxa, and hence in the average size, of ants consumed. Although differences in the bill size of males and females were significant, the magnitude of the differences (4−5%) was smaller than reported for many arboreal woodpecker species. For example, bill length of males and females differed by 15 – 21% for insular (island-dwelling) woodpeckers in the genus *Melanerpes* and by ~10% for continental *Melanerpes* (Selander 1966). Bill lengths of male and female magellanic woodpeckers (*Campephilus magellanicus*) differed by ~12% (Chazzarta and Ojeda 2011), similar to the difference of ~12.3% for three-toed woodpeckers (*Picoides dorsalis*; Pechacek and Krisitin 2004). Differences in bill length of ~10% have been reported for several other species such as white-backed woodpeckers (*Dendrocopos leucotos*; Aulen and Lundberg 1991) and red-cockaded woodpeckers (*Picoides borealis*; Mengel and Jackson 1977). Although males have larger bills than females in several species of woodpeckers, little is known about the possible effects of such dimorphism on prey selection. Most researchers have documented that the sexes use different substrates for foraging, but have not quantified diets (e.g., Ligon 1968, Wallace 1974, Austin 1976, Hogstad 1976, Morrison and With 1987, Pasinelli 2000). The limited data available suggest that differences in substrate use do not always translate to differences in diet. For example, male magellanic woodpeckers (Chazzarata and Ojeda 2011), male three-toed woodpeckers (Hogstad 1976), and male white-backed woodpeckers (Aulen and Lundberg 1991) foraged on larger-diameter substrates (trunks and tree branches) than females, but male magellanic woodpeckers took larger prey than females whereas the three-toed woodpeckers did not (Pechacek and Kristin 2004). Aulen and Lundberg (1991) suggested that the larger bills of male white-backed woodpeckers (~12% or 1 mm) may have evolved to improve the efficiency of nest excavation (Aulen and Lundberg 1991), and not to enable the sexes to use different foraging niches. However, data

concerning the contributions of males and females to nest excavation are needed to more broadly test this hypothesis and are lacking for most species of woodpeckers. Clearly, more information about excavation behaviour and the diets of the male and female woodpeckers is needed before drawing general conclusions about the adaptive significance of bill-size dimorphism. Our results suggest that differences in the bill length of male and female flickers did not influence the ant taxa accessed when foraging on the ground.

We found that the diet of breeding northern flickers consisted almost entirely of ants, consistent with anecdotal reports of foraging behaviour of flickers in other North American populations (Wiebe and Moore 2008). Flickers in our study were reliant primarily on *Lasius* spp. and *Tapinoma sessile*. However, these ants are relatively small (~3−7 mm) and make up a smaller proportion of the diet in terms of biomass than their numbers suggest. Occasionally, during capture of adults feeding nestlings, parents expelled some of their crop contents, which frequently contained a mix of adult ants, eggs and larvae (EAG, pers observ.), and it is likely that adult flickers were also consuming these items. However, soft-bodied invertebrates cannot be identified in fecal samples and so we were unable to determine if males and females differed in their consumption of eggs and larvae. Our results suggest that the diet of northern flickers is similar to that of ecologically equivalent ground-foraging woodpeckers; green woodpeckers in Europe forage on similar ant taxa as northern flickers, with the *Serviformica* group and *Lasius niger* group comprising 62% and 18% of the prey biomass in their diet, respectively (Rolstad et al. 2000). The diet of green-barred woodpeckers (*Colaptes melanchloros*) in South America, based on stomach contents, consisted almost exclusively of ants in such genera as *Crematogaster, Camponotus, Paracrytocerus, Myrmobrachys,* and *Paracryptocerus* (Short 1972). These authors did not, however, compare the diets of males and females.

We were unable to determine if the diet of northern flickers reflects active preferences for certain ant taxa or opportunistic feeding based on temporal and spatial availability. Accessibility of ants may depend on whether they are subterranean or epigaeic and whether they are concealed by vegetation. Flickers in our study area preferred foraging in grasslands with relatively short grass and bare ground (Elchuk and Wiebe 2002), and adult flickers changed the type of microhabitat used for foraging depending on ambient temperature and ant activity (Wiebe and Gow 2013). Therefore, the difference in diet composition between years in our study may have been due to changes in the abundance or accessibility of certain ant taxa related to differences in vegetation structure or weather.

Our results confirm that Northern Flickers are highly reliant on ants during the breeding season and that both sexes consume the same types of prey. Although northern flickers exhibited significant bill size dimorphism, the magnitude of that difference was relatively small and our results did not support the hypothesis that differences in bill size relate to diet differences between the sexes. Additional research is needed to determine if male and female Northern Flickers maintain spatially segregated foraging areas within their home range to minimize competition. If so, however, our results suggest that such segregation apparently does not lead to the exploitation of different prey.

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