

INTRABROOD DOMINANCE HIERARCHIES IN JUVENILE
RED-COCKADED WOODPECKERS:
THE ROLE OF EARLY SOCIAL ENVIRONMENT ON
POST-FLEDGING SURVIVAL AND NATAL DISPERSAL

Erin Lorraine Hewett Ragheb

Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in
partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Biological Sciences

Jeffrey R. Walters
Dana M. Hawley
James D. Fraser
John B. Phillips

6 September 2011
Blacksburg, Virginia

Keywords: benefits of philopatry, delayed dispersal, multistate mark-recapture, sibling rivalry

Copyright © Erin L. Hewett Ragheb 2011
This work may be copied provided credit is given and copies are not intended for sale

INTRABROOD DOMINANCE HIERARCHIES IN JUVENILE RED-COCKADED
WOODPECKERS: THE ROLE OF EARLY SOCIAL ENVIRONMENT ON POST-
FLEDGING SURVIVAL AND NATAL DISPERSAL

Erin L. Hewett Ragheb

ABSTRACT

Competition among individuals over shared resources reveals asymmetries in quality resulting in the formation of dominance hierarchies. These hierarchies act as a mechanism for social selection by partitioning resources among group-living animals. The following chapters describe my dissertation research which investigates the factors contributing to competitive asymmetries among broodmates as well as the short- and long-term consequences of the early social environment for the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*). My research revealed that fledgling red-cockaded woodpeckers form male-biased, linear dominance hierarchies. Among fledgling males, high relative nestling condition strongly predicted fledgling dominance, and this condition–rank relationship persisted through independence. Male nestlings are slightly larger and heavier than females; however, the sexual size dimorphism in mass is only present in mixed-sex broods, suggesting that the subtle structural size advantage gives males a competitive advantage over their sisters. Conflict rates among siblings increased with decreasing targeted feeding rates, and dominant fledglings were able to secure more food from provisioning adults through scramble competition. First-year survival favored males over females and dominant males over subordinates. Females were more dispersive overall than males, and subordinate males were more likely to disperse than

dominants. The social environment prior to fledging influenced male dispersal decisions and subordinates delayed dispersal in the spring in situations where all dominants died over the winter. The probability of delayed dispersal in females was higher for females raised without brood-mates in one of two populations included in a long-term demographic data analysis. The availability of breeding vacancies may explain the differences in female dispersal behavior according to social environment between these populations. This research contributes to a greater understanding of the relative contribution of intrinsic benefits versus extrinsic constraints as an influence on delayed dispersal decisions in red-cockaded woodpeckers. Inter- and intra-sexual social rank is correlated with individual access to natal food resources and the probability of first-year survival. The intrabrood variation in dispersal strategies driven by social rank is sufficient to regularly produce both dispersal strategies among males and provides additional support that delaying natal dispersal is the preferred strategy for males in this system.

ACKNOWLEDGMENTS

Funding for this project was provided by the U.S. Department of Defense, Marine Corps Base Camp Lejeune and Department of the Army, Fort Bragg to J.R.W.; the National Science Foundation (BSR-8307090) to J.R.W.; the Virginia Tech Bailey Fund to J.R.W., and the Virginia Tech Graduate Research Development Program to E.L.H.R.

This research would not be possible without the help of past and current field staff working with both the Sandhills and Camp Lejeune study populations. I am grateful for their long-hours in the field and their dedication in the collection of high-quality demographic data. I especially thank the staff and associates from the Sandhills Ecological Institute: K. Brust, S. Anchor, J. H. Carter III, V. Genovese, M. King and J. Maynard for welcoming me as a friend, training me in the field and extending their workload to assist with my data collection. I also thank the U.S. Army Fort Bragg Endangered Species Branch: J. Britcher and J. Schillaci for their permission to conduct research on the population of woodpeckers they have committed to protect. Many thanks to B. Beck from the North Carolina Sandhills Gamelands and Wildlife Resources Commission for his help painting nestling bills, sharing his photographs and towing my truck out of the sand. From the Camp Lejeune population, I thank K. Rose and K. Hudgins for conducting the winter censuses analyzed in Chapter 3 as well as the natural resource managers: C. Tenbrink, G. Haught, J. Townson and B. Rogers for their cooperation with the collection of the long-term demographic data.

I thank my academic advisor, Jeff Walters for his careful development and supervision of this elegant long-term research project. I will always treasure my experience as a PhD student at Virginia Tech because of his patient and generous academic advising style. My colleagues from the Avian Ecology Lab also played a critical role in making my graduate school experience so

enjoyable; I thank them for their instruction and friendship: L. Blanc, D. Bruggeman, R. Danner, V. Garcia, M. Johnson, M. Jusino, J. Kappes, D. Kesler, H. Lessig, A. Malueg, R. McGregor, O. Milenkaya, J. Moore, B. Olsen, J. Perkins and S. Zeigler. My committee members: J. Fraser, D. Hawley, J. Philips provided their kind academic support and guidance throughout my entire graduate career. C. Eikenaar read through many manuscript drafts and provided critical advice throughout the development of my research. I am also very grateful for V. Garcia, J. Cohen and D. Catlin for their patient assistance with mark-recapture analysis methods.

Lastly, I thank my husband Ragy, and my family and friends for their logistical support, verbal encouragement, and prayers over the last five years. I am grateful for their love and the perpetual reminder that my strength and inspiration comes from the Lord, who is the creator of every beautiful thing in science, nature and friendship.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGMENTS	iv
TABLE OF CONTENTS	vi
LIST OF FIGURES	ix
LIST OF TABLES	x
ATTRIBUTION.....	xi
CHAPTER I. AN INTRODUCTION TO SOCIAL DOMINANCE AND THE RED- COCKADED WOODPECKER	1
BACKGROUND	1
Group living and social dominance hierarchies	1
Asymmetries leading to hierarchy formation	2
Dominance within broods.....	3
Cooperatively breeding birds and the evolution of delayed dispersal.....	5
Intrabrood dominance and cooperative breeding.....	6
STUDY SPECIES: THE RED-COCKADED WOODPECKER	7
Description.....	8
Breeding Behavior.....	9
Social behavior.....	10
RESEARCH SUMMARY	11
CHAPTER II. FAVOURITISM OR INTRABROOD COMPETITION? ACCESS TO FOOD AND THE BENEFITS OF PHILOPATRY FOR RED-COCKADED WOODPECKERS.....	14
ABSTRACT.....	14
INTRODUCTION.....	15
Aims and Predictions.....	17
GENERAL METHODS	20
Study Population and Species Biology.....	20
Field Methods	22
PART 1: AGONISTIC BEHAVIOUR IN FLEDGLINGS	23
Methods	23
Results	25
PART 2: SIZE AND SOCIAL RANK.....	27
Methods	27
Results	29
PART 3: ALLOCATION OF FOOD.....	29
Methods	30
Results	31
PART 4: SOCIAL RANK AND DISPERSAL	32
Methods	32
Results	33
DISCUSSION.....	34
ACKNOWLEDGEMENTS.....	40

FIGURE CAPTIONS	41
CHAPTER III. THE ROLE OF INTRABROOD SOCIAL ENVIRONMENT ON POST-FLEDGING SURVIVAL AND NATAL DISPERSAL IN RED-COCKADED WOODPECKERS: A MULTISTATE MARK-RECAPTURE STUDY	50
ABSTRACT	50
INTRODUCTION.....	51
Aims and predictions	53
MATERIALS AND METHODS	56
Biology of study species	56
Study populations	57
General methods.....	58
PART 1: Intra brood social environment (males only)	59
PART 2: Intra brood social environment (both sexes)	65
RESULTS	69
PART 1: Intra brood social environment (males only)	69
PART 2: Intra brood social environment (both sexes)	72
DISCUSSION	74
Intra brood social rank and natal survival.....	75
Natal dispersal.....	77
Costs of dispersal	79
First-year reproductive roles	82
Conclusion	82
FUNDING	83
ACKNOWLEDGMENTS	84
FIGURE CAPTIONS	85
CHAPTER IV. NESTLING COMPETITIVE ENVIRONMENT INFLUENCES DEGREE OF SEXUAL SIZE DIMORPHISM AND FEMALE HELPING BEHAVIOR IN RED-COCKADED WOODPECKERS.....	102
ABSTRACT.....	102
INTRODUCTION.....	103
Aims and predictions	106
METHODS	108
Study population and species biology	109
Field Methods	111
Statistical analysis	112
RESULTS	116
Part 1: Sexual size dimorphism in nestlings	117
Part 2: Natal brood sex-ratio and individual fitness	120
Part 3: Female helping behavior	121
DISCUSSION	122
Sexual-size dimorphism and competitive environment	122
Early competitive environment and future life history traits	124
Female helping behavior.....	126
Conclusion	129

ACKNOWLEDGEMENTS.....	130
FIGURE CAPTIONS	131
CHAPTER V. CONCLUSIONS	150
SUMMARY	155
LITERATURE CITED	156
APPENDIX A.....	172
APPENDIX B.....	176

LIST OF FIGURES

Figure 2. 1 Conflict rates among dyads with differing social distances	43
Figure 2. 2 Predicted cumulative probability of becoming the socially dominant fledgling.	44
Figure 2. 3 Two measures of relative condition for independent juvenile males.	45
Figure 2. 4 Shift in feeding type with increasing postfledging development	46
Figure 2. 5 Targeted- (a) and approach-feeding (b) rates.....	47
Figure 2. 6 Postfledging juvenile survival.....	48
Figure 2. 7 Breeding season settlement locations of juvenile males.	49
Figure 3. 1 Fledgling dispersal paths.	88
Figure 3. 2 Apparent monthly survival for juvenile males.....	89
Figure 3. 3 Monthly dispersal probability for juvenile males.	90
Figure 3. 4 Monthly survival for juvenile males and females.	91
Figure 3. 5 Monthly dispersal probability for juvenile males and females.	92
Figure 3. 6 Predicted probability of dispersal path by mass.....	93
Figure 4. 1 Distribution of social recruitment ages.....	134
Figure 4. 2 Nestling mass growth models.	135
Figure 4. 3 Nestling leg length growth models.	136
Figure 4. 4 Predicted nestling mass	137
Figure 4. 5 Predicted nestling leg length.	138
Figure 4. 6 Distribution of brood sex-ratio types.....	139
Figure 4. 7 Natal helping behavior in female fledglings.....	140

LIST OF TABLES

Table 3. 1: Predictions of hypotheses for adaptive significance of delayed dispersal behavior ...	94
Table 3. 2 Number of juvenile male natal and disperser resightings for the North Carolina Sandhills population (2007-2009).....	95
Table 3. 3 Selected multistate mark-recapture models for natal survival and dispersal for juvenile males with known intrabrood social rank from CS1-CS3.....	96
Table 3. 4 Binary logistic regression models for the probability of first-year survival.....	98
Table 3. 5 Binary logistic regression models for the probability of natal dispersal.	99
Table 3. 6 Multinomial logistic regression models for the probability that a juvenile will belong to the fall disperser, spring disperser or natal resident ‘dispersal path states.’.....	100
Table 3. 7 Coefficient estimates from the highest ranking multinomial logistic regression model of dispersal path state (shown in bold in Table 6)	101
Table 4. 1 Select linear mixed models for nestling red-cockaded woodpecker mass from broods containing only single-sex nestlings (1994-2009).....	141
Table 4. 2 Select linear mixed models for nestling red-cockaded woodpecker mass from broods containing mixed-sex nestlings (1994-2009).	142
Table 4. 3 Results from linear mixed models for nestling mass with model weights greater than 0.01 from single-sex and mixed-sex broods.....	143
Table 4. 4 Select linear mixed models for nestling red-cockaded woodpecker leg length from broods containing only single-sex nestlings (1994-2009).....	145
Table 4. 5 Select linear mixed models for nestling red-cockaded woodpecker leg length from broods containing mixed-sex nestlings (1994-2009).....	147
Table 4. 6 Results from linear mixed models for nestling leg length.	149
Appendix A. 1 Multistate mark-recapture models for natal survival and dispersal for juvenile males with known intrabrood social rank from CS1-CS3.....	172
Appendix B. 1 Mass for single-sex scenario	176
Appendix B. 2 Mass for mixed-sex scenario.....	178
Appendix B. 3 Leg length for single-sex scenario.....	180
Appendix B. 4 Leg length for mixed-sex scenario	182

ATTRIBUTION

Dr. Jeffrey R. Walters

Harold Bailey Professor, Department of Biological Sciences, 2119 Derring Hall, Virginia
Polytechnic Institute and State University, Blacksburg, Virginia 24061

Dr. Jeffrey R. Walters was my advisor throughout my dissertation research and chair of my dissertation committee. He was the co-author of all manuscripts included in this dissertation that were prepared for publication, including data chapters, II, III and IV.

CHAPTER I. AN INTRODUCTION TO SOCIAL DOMINANCE AND THE RED-COCKADED WOODPECKER

Erin L. Hewett Ragheb

BACKGROUND

Group living and social dominance hierarchies

Social interactions among individuals of the same species often occur in situations where shared resources are limited or when direct benefits for survival or reproduction are available through group living. Social groups are often organized by the formation of social dominance hierarchies that are the result of the outcomes of aggressive interactions. Consequently, dominant individuals have preferential, and sometimes unchallenged access to resources such as food, shelter or mates (Wilson 1975). In blue tits (*Parus caeruleus*), high ranking individuals take fewer risks after predator sightings and emerge from hiding later than subordinate individuals because they have guaranteed access to food resources during safer periods (Hegner 1985). Despite their low rank, subordinate individuals may profit from the general benefits of group-associations such as increased detection of food and predators (Sridhar et al. 2009) or benefits associated with nepotism (Ekman et al. 2000). Also, opportunities for subordinates to attain higher rank may occur due to aging, or through the death of more dominant individuals (Wilson 1975). Once a dominance hierarchy is established, there is often a significant reduction in the number of costly aggressive interactions between group members.

Dominance hierarchies can be either linear (unidirectional) or bidirectional. In linear hierarchies, a single individual is superiorly dominant to all other individuals in the group. Linear hierarchies are transitive; if animal A dominates B, and B dominates C, then A will also dominate C. This “pecking order” is a commonly observed behavior in domestic fowl (*Gallus gallus*), and once the hierarchy is established it can remain stable for a long period (Guhl 1968). If group composition changes frequently, stability will decrease, aggressive interactions will increase and the overall condition of individuals will decrease (Guhl 1968). Linear hierarchies rely on advanced memory and an ability to recognize individuals, even in large flocks (Guhl and Ortman 1953). In bidirectional hierarchies, social dominance is obtained as a result of conflict frequency and continual shifts in social rank among individuals causes such hierarchies to be less stable than linear hierarchies.

Asymmetries leading to hierarchy formation

There are many ways social status is determined, and often dominance is awarded to the winner of a physical aggressive encounter between two individuals. Dyadic encounters of this type are repeated until a hierarchy is formed. The probability of winning a contest may depend on physical asymmetries in individual resource holding potential (RHP, Parker 1974). These asymmetries are intrinsic attributes and may include age, sex, body size, overall physical condition, strength, or aggressiveness. In birds, dominance is often predicted by age and sex, with males generally dominating females, and older individuals dominating juveniles (Woolfenden and Fitzpatrick 1977; Carlisle and Zahavi 1986; Ligon and Ligon 1990; Gill 2003).

In some cases, the outcome of aggressive interactions is determined not only by an individual's RHP but also by extrinsic social experiences or relative energetic investment in the contested resource. Whether or not an individual achieves high social rank may be an artifact of the outcome of their own previous conflicts (reviewed in Chase et al. 1994; Van Doorn et al. 2003), or their observation of aggressive interactions among others (Oliveira et al. 1998). These winner, loser, and bystander effects may be independent of body size, or other intrinsic measures of RHP and reinforce the theory that in naturally occurring situations, RHP alone may not be enough to support stable social hierarchies (Chase et al. 2002). The pay-off theory assumes that individuals with more to gain from winning the contest will be more likely to escalate a fight in order to maintain their rank and their control of the contested resource (Parker 1974; Maynard Smith and Parker 1976; Cant et al. 2006).

Dominance within broods

Often the influence of resource holding potential, status signaling and social experience on dominance are confounded and difficult to separate, especially if measured in adult animals that each have unique genetic, environmental and social backgrounds. Some of these complications can be reduced by looking at dominance hierarchies within sibling groups (Stanback 1994). Siblings from the same brood are expected to have very similar or exactly the same ages, genetic quality, natal territory quality and level of previous social experience (Stanback 1994).

If the benefits of achieving high rank at a young age are great, it is assumed that hierarchy formation will commence as soon as the young are physically capable of domination

(Drummond 2006). For birds, this may be while the young are still in the nest, or soon after fledging (Drummond 2006). This especially applies in situations where the young rely on parents for food, the cost of subordination is high, and the young are confined within a nest or cavity (Drummond 2006).

Asymmetries in competitive ability among brood-mates may be caused by a number of factors. One asymmetry in young birds leading to hierarchy formation is differences in body size, often caused by asynchronous hatching (Stanback 1994; Ellsworth and Belthoff 1999). In extreme cases of hatching asynchrony, the older dominant chicks frequently act violently towards their younger siblings, which often results in starvation or even siblicide (Legge 2000; Drummond 2006). Differences in body size may also be driven by sex-specific factors such as sexual size dimorphism (SSD). For many species, genetically driven SSD after hatching leads quickly to competitive asymmetry (Bortolotti 1986). Additional sex-specific factors contributing to competitive asymmetries among brood-mates include laying order (Bortolotti 1986), the speed of embryonic development (Blanco et al. 2003; Cook and Monaghan 2004), hormones associated with aggression or begging (Sasvari et al. 1999; Goodship and Buchanan 2006), or immune response to parasites (Potti and Merino 1996).

Achieving within-brood dominance has many immediate benefits to nestlings and fledglings. The ability to overpower nest mates allows for greater access to resources provided by parents. Once fledged, dominant individuals may have primary access to food brought by adults or to preferred feeding and roosting sites. In red-winged blackbirds (*Agelaius phoeniceus*), older, more dominant individuals have priority of roost sites, (Weatherhead and Hoysak 1984) and this may also be the case with recently fledged birds, especially when roost sites are limited. Birds that establish dominance at a very young age may also breed earlier than their subordinate

siblings, and therefore might have increased lifetime reproductive success (Rabenold 1990). If the presence of same-sex siblings decreases an individual's future reproductive success through increased competition for mates or nest sites, then young birds may seek to dominate, or even kill their siblings at an early age to reduce competition at that level (Drummond 2006).

Cooperatively breeding birds and the evolution of delayed dispersal

Cooperatively breeding species are defined as species where individuals in addition to the breeding pair assist in rearing offspring. Often these 'helpers-at-the-nest' are retained offspring from previous broods that have delayed their own reproduction, and remained on their natal territory. The evolution of delayed dispersal behavior as the first step toward cooperative breeding has been the subject of numerous theoretical models and demographic studies across a variety of taxa (see review in Koenig et al. 1992). The historically predominant theory explaining why individuals choose to remain on their natal territory rather than disperse is the presence of constraints in the environment that prohibit independent reproduction (Emlen 1982). These constraints could come in the form of a shortage of mates, highly variable environments or habitat saturation (Emlen 1978; Stacey 1979). Many long-term studies strongly support this idea (see review in Hatchwell and Komdeur 2000), and the presence of some ecological constraint is nearly always acknowledged in current explanations for the evolution of delayed dispersal. However, since juveniles from non-cooperatively breeding species often also face similar ecological constraints to independent reproduction, yet they do not delay natal dispersal, additional explanations are required to fully explain why cooperatively breeding birds remain philopatric (Stacey and Ligon 1991).

One explanation is that individuals that delay dispersal benefit directly from living on the natal territory and these benefits outweigh the benefits associated with early dispersal. Intrinsic benefits associated with family associations on the natal territories may play an important role in the retention of juveniles in cooperatively breeding species (Koenig et al. 1992). Possible intrinsic benefits include the relative safety of familiar surroundings, assistance with locating food, nepotism, increased predator detection, access to critical resource (e.g. roost sites) or indirect fitness gained from raising related young. The relative roles of the benefits of philopatry and ecological constraints on the evolution of delayed dispersal is a current area of interest for research on cooperative breeding species.

Intrabrood dominance and cooperative breeding

In many cooperatively breeding bird species, aggressive interactions within recently fledged sibling groups are more common than conflicts among adults. It may be particularly important to establish hierarchies early for these perpetually social species and thereby reduce the cost of constant conflict, which might negate the individual benefits associated with group living (Ligon and Ligon 1990). Frequent aggressive conflicts among fledglings are seen in green woodhoopoes (*Phoeniculus purpureus*, Ligon and Ligon 1990), Arabian babblers (*Turdoides squamiceps*, Carlisle and Zahavi 1986), *Campylorhynchus* wrens (Rabenold 1990), pinyon Jays (*Gymnorhinus cyanocephalus*, Balda and Balda 1978) and red-cockaded woodpeckers (*Picoides borealis*; Hewett Ragheb and Walters 2011).

Establishing dominance at a young age may have a critical influence on long term life history patterns such as natal dispersal strategy (Christian 1970; Gauthreaux 1978). This may be

especially pertinent for cooperatively breeding species since juveniles often select among discrete life history pathways (delay dispersal as a natal helper, disperse and attempt independent reproduction, or float). For some cooperatively breeding species like the red-cockaded woodpecker, dispersal behavior is presumed to be risky and there are extrinsic constraints to early dispersal, such that the lifetime reproductive success of individuals that delay dispersal can equal or exceed that of those attempting to breed earlier (Walters et al. 1992b; Ekman et al. 1999). In gray jays (*Perisoreus canadensis*), a species with delayed dispersal but no helping behavior, dominant juveniles force their subordinate siblings off the natal territory (Strickland 1991). In other species, like the non-cooperative Western screech owl (*Otus kennicottii*), it is more beneficial to leave the natal territory earlier because this increases the chance of finding an available breeding territory, and birds disperse as soon as physiologically ready. In this case, it is the most dominant, highest condition fledgling that is the first to disperse (Ellsworth and Belthoff 1999). In cooperatively breeding Florida scrub-jays (*Aphelocoma coerulescens*) dominant helpers gain breeding opportunities earlier than subordinate helpers, but the breeding opportunity can be obtained through either dispersal or inheritance of the natal territory (Woolfenden and Fitzpatrick 1977). Studying the social factors contributing to natal dispersal decisions in cooperative breeding species will help us to better understand the balance between the benefits associated with philopatry and the costs of natal dispersal, and thus the evolution of this unusual social system (Stacey and Ligon 1991).

STUDY SPECIES: THE RED-COCKADED WOODPECKER

“Wilson called the Cockaded Woodpeckers, *Picus querulus*, and this seems, at first glance, to be a most appropriate name, for, of all of the family, these are not only the most noisy, but their notes are given in a decidedly fretful tone as if the birds were constantly in an irritable state of mind.”

–Arthur Cleveland Bent (1939)

“They are exceedingly quarrelsome, particularly during the breeding season,...[yet] after the lapse of a very little time, birds that have been scolding one another most extensively again alight on the same pine tree and go about their respective businesses in perfect amity.”

-Arthur Cleveland Bent (1939)

Description

The red-cockaded woodpecker is a federally listed endangered species dependent on the mature pine forests of the Southeastern United States. They are relatively small in size (body length approximately 22cm, mass 40-55g) and adult red-cockaded woodpeckers exhibit small to moderate SSD in some linear measures and mass, where males are typically larger and heavier than females (Jackson 1994). Measurements from 40 male and 26 female adults from the North Carolina Sandhills population revealed that males were larger than females in tarsus (2.06 mm greater, and bill length (1.63 mm greater), but tail length was longer for females by 3.20 mm (Pizzoni-Ardemani 1990). Adult males (49.6g, n=61) were 4.1% heavier than females (47.6g, n=36) (Pizzoni-Ardemani 1990). The morphological differences between sexes in this species

are small when compared to other *Picoides* species, like Hairy Woodpeckers and Arizona Woodpeckers (Ligon 1968; Peters and Grubb 1983; Morrison and With 1987).

Individuals of this species are easily identified by their white cheek patches and black and white barred back (Winkler et al. 1995). Adult males have a tiny cockade consisting of a few red feathers near the nape, however, these feathers are normally covered by black crown feathers and not easily observed in the field. Adult females are similar in appearance to males except they lack the red cockade. Juveniles are duller overall when compared to adults, and juvenile males have a dull red crown patch which varies in size among individuals and is replaced by black crown feathers during the first prebasic molt. The crown patch appears between day 12-15 in male nestlings and is absent in females (Jackson 1994). This sexually dimorphic trait unique to the juvenile plumage has been described as an ancestral characteristic and is presumed to have no role in defining social hierarchies (Ligon 1970). However, variation in crown patch size among juvenile males and its function as it relates to dominance has never been directly studied.

Breeding Behavior

Red-cockaded woodpeckers are a cooperatively breeding species that defend large permanent territories consisting of foraging area and a cluster of cavity trees used for roosting and nesting. The number of cavity trees in the cluster varies among groups and sites, and is strongly constrained by the availability of suitable mature living pines in the territory (Carrie et al. 1998). The cavities, excavated only in living pines (a habit unique to this species), are conspicuous because of numerous resin wells maintained around the cavity entrance which produce a thick build-up of pine resin. Cavities can take years, or even decades to complete

(Harding and Walters 2002) because living heartwood is difficult to excavate and work must stop intermittently to allow the sticky pine resin to harden (Walters 1991). Because natural cavities are often constructed at a lower rate than the rate of cavity loss through habitat loss, abandonment after midstory growth, or interspecific competition, cavity availability is a key component of red-cockaded woodpecker population dynamics and may act as an extrinsic ecological constraint to early dispersal and reproduction (Walters 1991; Carrie et al. 1998; Harding and Walters 2002).

Breeding pairs are socially and genetically monogamous (Haig et al. 1994). Eggs are laid starting in late April and ending in early June. Incubation begins prior to clutch completion (Ligon 1970), possibly starting with the laying of the penultimate egg (Jackson 1994). Nestlings hatch after an incubation period of 10-13 days and fledge about 26-28 days after hatching (Winkler et al. 1995). Brood reduction occurs frequently, and in a North Carolina population, a mean clutch size of 3.3 eggs was found to only produce 1.9 fledglings, with most nestling losses occurring before day six (LaBranche and Walters 1994). This is thought to be caused by hatching asynchrony where even a couple of hours variation in hatching time among nestlings can produce large nestling mass differences resulting in the starvation of the latest hatched young (Ligon 1970). Once fledged, young continue to beg and be fed by adults in the group for as long as five months post fledging. This species is usually single brooded although reneating often occurs after nest failure (Jackson 1994). Double-brooding is very rare, and only occurs in some years in some populations (Phillips Jr. et al. 1998).

Social behavior

Frequently, some male fledglings remain on the natal territory and act as nonbreeding helpers while other male and almost all female fledglings disperse in search of breeding opportunities elsewhere (Walters et al. 1988). The cost of dispersal is presumed to be higher than remaining with the natal group, and philopatry is an advantageous strategy for young males because territories are often inherited upon the death of the breeder male (Walters et al. 1992b). Female helpers are rare, and females may disperse either during the fall of their first year or over winter with their family and disperse the following spring (Kesler et al. 2010). Male fledglings with lower body mass relative to brood-mates are more likely to disperse, suggesting that social dominance is an important factor in movement behavior (Pasinelli and Walters 2002). Dominant individuals also may compete for and gain access to cavity roost sites earlier than their subordinate siblings. Little work has been done in this species to identify the specific factors influencing sibling dominance.

Aggressive encounters are commonly observed among recently fledged young and less frequently observed among adults (J.R. Walters, pers. comm.). After placing a caged juvenile in the center of a foreign cluster, Ligon (1970) observed strong aggression towards the caged bird by the juvenile of that cluster but relatively no aggression by adults from the group. Aggressive interactions include perch displacements, pecking and chasing. Adult males are dominant over females and within sexes, older birds are dominant over younger birds (Jackson 1994).

RESEARCH SUMMARY

Not all individuals have the same likelihood of survival or reproduction. Competition among individuals for these opportunities reveals asymmetries in quality resulting in the

formation of dominance hierarchies. These hierarchies act as a form of social selection by partitioning resources among group-living animals. Relative placement within a dominance hierarchy has the potential to strongly influence life history decisions, as the path with the highest fitness benefit may vary for individuals according to their social rank. My dissertation research investigates the factors contributing to competitive asymmetries among brood-mates as well as the short- and long-term consequences of intrabrood social rank. My study species is the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*), a species where juveniles segregate into discrete life history pathways. Our long-term demographic dataset from an individually marked population provides an exciting opportunity to track individuals through time.

Here, I present my study questions and research results as three independent data chapters, each prepared as manuscripts designed for publication. In Chapter 2, I first provide a thorough description of the agonistic behaviors observed among fledgling brood-mates and their adult caregivers. I also investigate the proximate mechanism driving competitive asymmetries among nest-mates leading to social rank assignment. I then examine how intrabrood social rank influences provisioning during the post-fledging dependent period to determine if adults show favoritism towards individuals of a particular social rank. Chapter 2 has already been peer-reviewed and published in the journal *Animal Behaviour*. In Chapter 3, I explore the fitness consequences of intrabrood social rank for male fledglings by using multistate mark-recapture methods to calculate first-year survival and dispersal probabilities for dominant and subordinate brothers. I then compare first-year survival and dispersal probabilities between male and female juveniles using relative nestling mass as a surrogate for social rank to determine if females follow similar patterns of rank-biased dispersal as males. In Chapter 4, I focus on the role of the

nestling social environment in shaping life history strategy. By comparing individuals from broods of different sizes and sexual composition I am able to refine our understanding of the social factors that maintain individual variation in natal dispersal strategies. The three data chapters are followed by a conclusion chapter in which I discuss the broader impacts of this work on our understanding of the role of intrabrood social environment on the evolution of cooperative breeding in birds.

**CHAPTER II. FAVOURITISM OR INTRABROOD COMPETITION? ACCESS TO
FOOD AND THE BENEFITS OF PHILOPATRY FOR RED-COCKADED
WOODPECKERS**

Erin L. Hewett Ragheb and Jeffrey Walters

*This chapter has been published under the same title in the journal *Animal Behaviour*, August 2011, Vol 82, Issue 2, Pages 329-338, and published with permission from Elsevier Limited. <http://www.sciencedirect.com/science/article/pii/S0003347211001928>. Formatting and spelling reflects that required for the journal.

ABSTRACT

In species showing delayed natal dispersal, broodmates vary in natal dispersal timing and strategy, where some choose to disperse early while others delay. In the cooperatively breeding red-cockaded woodpecker, *Picoides borealis*, typically only one juvenile male per brood delays dispersal despite the lifetime fitness benefits associated with delayed dispersal. We sought to determine whether adult favouritism or intrabrood competition over the distribution of natal food resources provides a mechanism for the persistence of individual variation in natal dispersal strategies. We show that fledgling red-cockaded woodpeckers form male-biased, linear dominance hierarchies as a result of frequent aggressive conflicts. For males, high nestling condition relative to male broodmates was a strong predictor of future dominance, and this condition–rank relationship persisted after individuals reached nutritional independence. Adults were never observed interfering with broodmate conflicts, and were only rarely aggressive

towards fledglings. Adults showed no overt favouritism towards offspring when targeting individual fledglings during provisioning early in the postfledging period. However, conflict rates increased with decreasing targeted feeding rates, suggesting that access to resources is an important function of dominance hierarchies. After fledglings were developmentally able to compete for positions near foraging adults, first- and second-ranking males were fed more often than subordinate females. Of the juvenile males surviving to spring, subordinates were more likely to disperse during their first year than were their dominant broodmates. Together, our findings suggest that for young red-cockaded woodpeckers, intrabrood social rank provides a mechanism for prioritized access to natal resources and variation in natal dispersal strategy.

Keywords: benefits of philopatry, delayed dispersal, feeding rates, food allocation, intrafamilial conflict, juvenile aggression, life history strategy, linear dominance hierarchy, Picoides borealis, sibling rivalry

INTRODUCTION

The social environment within family groups is an important but often overlooked factor in the evolution and maintenance of dispersal strategies (Ekman et al. 2002). Tolerance of current offspring by parents and retained offspring from previous broods is a critical step for the development of delayed dispersal behaviour (Ekman and Griesser 2002). Nepotistic behaviour directed towards offspring may create a natal safe haven for birds waiting for reproductive opportunities (Kokko and Ekman 2002; Griesser and Ekman 2004; Griesser and Ekman 2005; Eikenaar et al. 2007). Theory predicts that parents should allocate resources evenly among their brood (Fisher 1930), but extended parental care may provide an opportunity for weaker individuals to gain access to resources if at least one parent directs increased feeding effort

towards late-hatched, or otherwise competitively disadvantaged, young (Gottlander 1987; Ploger and Medeiros 2004). Parents may directly benefit from extended parental care if the offspring they tolerate are better able to attain higher-quality breeding territories or have higher first-year survival (Ekman et al. 1999; Griesser et al. 2006). Alternatively, social interactions with adults on the natal territory may lower the relative benefits of philopatry. In times of food shortage, adults could limit access to resources to all offspring or to a selected subset of offspring, and thereby indirectly encourage early dispersal behaviour (Ekman and Griesser 2002). In situations where increased group size is costly to future reproduction, resident adults would benefit from evicting surplus offspring (Eikenaar et al. 2007).

Social interactions with broodmates may also influence dispersal strategies. Allocation of resources on the natal territory may be determined in part by nestling competition (Mock and Parker 1997). Direct physical aggression (interference competition) or scramble competition for food brought by adults or preferred positions within the nest can result in a biased distribution of resources in both siblicidal (see review in Drummond 2006) and nonsiblicidal species (Gottlander 1987; McRae et al. 1993; Ostreiher 1997; Tanner et al. 2008). In grey jays, *Perisoreus canadensis*, socially dominant siblings expel subordinates and thereby gain full access to stored food on the natal territory and increased winter survival (Strickland 1991).

The cooperatively breeding red-cockaded woodpecker, *Picoides borealis*, presents an unique case where typically only one juvenile male per brood delays dispersal and remains home as a helper, while all other male and female juveniles disperse to search for independent breeding opportunities by their first spring (J. R. Walters, personal observation). Female helpers are uncommon, but their frequency differs between populations (Koenig and Walters 1999). As estimated by a demographic model, young males adopting the delayed dispersal strategy have

equal or slightly higher first-year survival than males that disperse within their first year (Walters et al. 1992b). The probability that early dispersers will obtain a breeding vacancy and become a breeder is very low, and young breeders have poor reproductive success (Walters et al. 1992b). These combined factors lead to greater lifetime reproductive success for young males choosing to delay dispersal and remain on the natal territory during their first year, and thus explain the occurrence of this tactic in this system (Walters et al. 1992b). Since delayed dispersal has beneficial fitness consequences for juvenile males, and only one sibling per brood remains home as a helper, there is the opportunity for competition among broodmates over dispersal strategy. Natal dispersal strategy has been linked to nestling size at banding (age 5–10 days), where male nestlings with lower body mass relative to their brothers are more likely to disperse during their first year (LaBranche 1992; Pasinelli and Walters 2002). Also, males from broods with more male fledglings are more likely to disperse early, suggesting the importance of intrabrood social interactions on dispersal behaviour (Pasinelli and Walters 2002). However, the mechanisms explaining how size differences between broodmates during the nestling and fledgling stages can influence individual dispersal choices remains unknown. The combined roles of adult allocation of resources and intrabrood competition have yet to be applied as possible mechanisms regulating first-year natal dispersal in this system.

Aims and Predictions

In the present study, we sought to explore how social interactions with resident adults and broodmates, particularly during resource allocation, may provide a causal mechanism for individual variation in first-year natal dispersal strategies among broodmates. We present our

research in four parts. In Part 1, we formally describe social conflicts experienced by red-cockaded woodpecker fledglings during the postfledging dependent period. We predicted that, within broods, fledglings would form male-biased dominance hierarchies, given that social dominance of males over females is a species-wide pattern in adults (Jackson 1994). We also predicted that intrabrood conflict would increase with decreasing social distance, since closely matched individuals would have to dispute more frequently to establish and maintain rank. As such, fledgling males should engage in aggressive conflicts more frequently with closely ranked broodmates than with distantly ranked broodmates and adults. These basic behavioural descriptions have not been previously published, yet they are a critical first step in our understanding of how intrabrood social dynamics shape individual life history strategies.

In Part 2, we first explore the link between fledgling social rank during the postfledging dependent period with relative competitive ability as a nestling. We predicted that, within sexes, nestling condition relative to that of broodmates (resource holding power; Parker 1974), would be positively associated with intrabrood social dominance as a fledgling. Second, we assess the permanence of this size–rank relationship by comparing the sizes of male broodmates with known social rank after they were nutritionally independent but still remained with their family on the natal territory.

In Part 3, we address the main question of interest for this paper: how intragroup social interactions contribute to the allocation of food resources among broodmates during the postfledging dependent period. To do this, we examine three nonmutually exclusive hypotheses. First, broodmates control the allocation of food as fledglings through intrabrood competition. Support for this hypothesis includes frequent conflict among broodmates and little or no conflict between adults and fledglings. If broodmates, rather than adults, control allocation of food, then

parents should distribute food evenly among fledglings regardless of social rank or sex early in the postfledging period, when adults control food distribution by targeting sedentary young. However, fledgling food allocation should shift, favouring socially dominant individuals later in the postfledging period after fledglings become developmentally capable of scramble competition near foraging adults. If broodmates use competition to gain access to limited resources, then intrabrood aggression should increase as food availability decreases. The second hypothesis is that adults control distribution of natal resources, favouring low-ranking fledglings as a compensating form of extended parental care. Here, we expect frequent aggression by adults towards fledglings directed primarily at high-condition fledglings, and we expect infrequent aggression among broodmates. If parents favour low-condition young during provisioning, then we expect feeding rates for the lowest-ranking fledglings to be higher than that of their dominant broodmates regardless of the degree of fledgling mobility. Third, adults control the distribution of natal resources postfledging, favouring high-ranking fledglings over their low-ranking broodmates. Under this hypothesis, adult–fledgling aggression would be common and targeted towards subordinate young, and intrabrood conflicts would be rare. Parents would favour dominant fledglings when making feeding decisions and this bias would persist regardless of the degree of fledgling mobility.

Lastly, in Part 4, we extend the three hypotheses introduced in Part 3 by considering how postfledging survival and natal dispersal patterns of fledglings differ according to intrabrood social rank. Here we focus on juvenile males primarily, since only males regularly adopt both the ‘stay and help’ and the ‘depart and search’ strategies. In line with our first hypothesis that intrabrood competition controls access to resources on the natal territory, we predicted that socially dominant fledglings would be more likely to survive through their first winter. Surviving

dominant fledglings would then choose to remain on the natal territory as helpers during their first spring, since this is the life history strategy with greater lifetime fitness benefit in this species. Alternatively, subordinates would be less likely to survive the winter and more likely to disperse by their first spring. Under our second hypothesis that parents control resources and favour subordinate fledglings, we predicted that subordinates would not show reduced overwinter survival as a result of the benefits provided through extended parental care. Also, subordinates surviving the winter should be just as likely, or more likely to remain on the natal territory as their dominant broodmates. The predictions for postfledging survival and dispersal under our third hypothesis match the first; if parents control access to resources and favour dominant fledglings, then we would expect overwinter survival of dominants to be higher than that of subordinates, and subordinates would be more dispersive than dominants.

GENERAL METHODS

Study Population and Species Biology

The study population consists of over 220 individually banded family groups located in the Sandhills region of southcentral North Carolina, U.S.A. The study area covers 110 000 ha and includes the western portion of U.S. Army Fort Bragg, NC, the North Carolina Sandhills Game Lands, Hoffman, NC, and a number of smaller publicly owned sites. This population has been part of a long-term demographic study since 1980, and over 95% of the individuals are banded. Dispersal and survival fates are known for most individuals through annual demographic monitoring and censuses conducted by the Sandhills Ecological Institute (SEI). For a thorough

description of the study area and monitoring techniques see Walters et al. (1988).

Red-cockaded woodpeckers form cooperative family groups consisting of a genetically monogamous breeding pair (Haig et al. 1994) and from zero to four helpers (typically retained male offspring; Ligon 1970; Lennartz et al. 1987; Walters et al. 1988; Walters 1990). Helpers assist with incubation, brooding and fledgling provisioning (Jackson 1994). Adults form male-biased dominance hierarchies, and within sexes, older birds are dominant over younger birds (Jackson 1994). Family groups defend permanent territories surrounding a cluster of cavity trees used for nesting and roosting (Walters 1990; Jackson 1994). Cavity excavation is done exclusively in mature living pine trees (primarily longleaf pine, *Pinus palustris*) and typically takes several years to complete (Harding and Walters 2004). Colonization of areas without existing cavity trees is rare (Walters 2004), suggesting that the limited availability of cavity trees may be a key component driving population dynamics (Walters 1991; Carrie et al. 1998; Harding and Walters 2002), as well as a possible ecological constraint supporting the evolution of delayed dispersal in this species (Emlen 1982; Walters et al. 1992a).

Eggs are laid from late April to early June (Ligon 1970). The incubation period is only 10–13 days and begins with the laying of the second or the penultimate egg, resulting in moderate hatching asynchrony (Ligon 1970; Jackson 1994). Brood reduction occurs frequently, with most nestling loss occurring before day 6 (LaBranche and Walters 1994). If late-hatched nestlings survive, their smaller size relative to their broodmates might negatively influence their ability to compete for resources. Nestlings fledge after 26–29 days (Ligon 1970; Winkler et al. 1995), but continue to beg and be fed by adults for approximately 3 months postfledging (E. L. Hewett Ragheb, personal observation). Nondispersing individuals remain with their families even after reaching nutritional independence. Juveniles choosing to disperse in their first year

vary in the timing of dispersal. Juveniles as young as 1 month postfledging have been located as dispersers during routine monitoring (J. R. Walters, personal observation), while other juveniles are known to overwinter on the natal territory and disperse in early spring before the start of their first breeding season (Kesler et al. 2010).

Field Methods

During 2007–2009, we banded all red-cockaded woodpecker nestlings with both aluminium U.S. Fish and Wildlife Service bands and a unique combination of plastic coloured leg bands when the nestlings were 4–10 days old (aged according to Ligon 1970). Nestlings were returned to the nest immediately after banding to reduce handling stress. We sexed chicks in the nest at age 20 days based on the presence (male) or absence (female) of the red crown patch (Jackson 1994). To assign intrabrood social rank and measure conflict and feeding rates for dependent fledglings, we selected broods containing more than one male fledgling and conducted 30 min focal observations on every fledgling from those broods (Altmann 1974). We sampled every individual once, and all broodmates were sampled on the same day (with the exception of seven broods where focal observations were split across 2–3 days, and one brood with an 11-day span between focal observations). Sampling ages ranged from 30 to 62 days (median = 38 days, all cohorts pooled). All focal observations were started between 0600 and 1030 hours and conducted during periods without rain by a single observer (E.L.H.R.). In 2007, we sampled fledglings in the order of detection, but in 2008–2009, we preselected fledglings randomly to avoid any rank-specific sampling order bias. Only minutes where the focal individual was in sight were counted towards the 30 min sampling time. We excluded periods

when the focal fledgling was separated beyond earshot of other group members and periods of silence and immobilization by all group members after a predator alarm call. The Virginia Tech Institutional Animal Care and Use Committee (10-138-BIOL), the Department of the Interior U.S. Fish and Wildlife Service (TE070846-1, TE070846-2) and the North Carolina Wildlife Resources Commission Division of Wildlife Management (NC-2007ES88, NC-2008ES88, NC-2009ES88, NC-2010ES88) served as the governmental authorities approving ethical treatment of animals for this research.

PART 1: AGONISTIC BEHAVIOUR IN FLEDGLINGS

Methods

During every focal observation, we recorded the type of all dyadic conflicts experienced by the focal individual as well as the identity of the opponent. Winner status was assigned to birds chasing, pecking or perch-displacing their opponent, and loser status was assigned to birds retreating from these attacks. Brood-level numeric ranks were assigned to each fledgling after considering the outcomes of all dyadic conflicts observed for that group. Sixty-seven per cent of all rank assignments were based on the outcome of two or more conflicts, and 66% of all group hierarchies were created by observing conflicts among all possible broodmate dyads. In the event that no conflicts occurred between a particular broodmate dyad during any of the focal sessions, we extended observation time ‘off the clock’ and conducted ad libitum sampling (Altmann 1974) until the critical dyadic conflict was observed (7 groups), or we assumed either hierarchy transitivity (14 groups) or female subordination (2 groups). Hierarchy transitivity was supported

by all groups where at least one conflict was observed between all dyads (65 groups; see Part 1, Results, for supporting rationale for female subordination). For 18 groups, we could not complete focal observations for all broodmates and we assigned rank based on conflicts observed ad libitum by E.L.H.R. or by SEI staff during fledging checks. These broods were included in analyses requiring brood-level numeric rank, but were excluded from analyses requiring conflict or feeding rates. We also recorded all conflicts between the focal individuals and adults, but these interactions were not considered when assigning intrabrood social rank.

To determine whether conflict increases with decreasing social distance, we compared the conflict rates for ‘closely ranked’ and ‘distantly ranked’ dyad pairs. To limit the number of dyad categories, we selected the subset of broods containing only three fledglings. Analyses were run separately for broods containing either all-male fledglings (MMM), or two male and one female fledgling (MMF). We used the GLIMMIX procedure in SAS 9.2 (SAS Institute, Inc., Cary, NC, U.S.A.) to create two generalized linear models (for MMM and MMF broods) fitted to the data using a negative binomial distribution. The dependent variable ‘conflict rate’ was calculated by summarizing the number of conflicts observed during all focal watches for a particular brood and assigning each conflict to the appropriate dyad. The categorical independent variable ‘dyad’ represented social distance where first-ranking (dominant) males paired with second-ranking males (M1 versus M2), or second-ranking males paired with third-ranking males (M2 versus M3) or females (M2 versus F3) were considered ‘closely ranked,’ while first-ranking males paired with third-ranking males (M1 versus M3) or females (M1 versus F3) were ‘distantly ranked’. The categorical covariate ‘family’ was also added to both models to control for the lack of independence among broodmates.

Results

Red-cockaded woodpecker broodmates frequently engaged in aggressive conflicts during the postfledging dependency period (on average 2.79 conflicts per individual per 30 min, for 212 focal observations during 2007–2009). The youngest birds observed engaging in aggressive conflict out of the nest via ad libitum sampling were 28 days of age (approximately 2 days postfledging). Intense conflicts among broodmates waned gradually 3–4 months postfledging (E.L.H.R, personal observation). Conflicts during the postfledging dependency period often consisted of a series of aggressive behaviours in quick succession. In these cases, we categorized the conflict by the behaviour at the conclusion of the agonistic interaction. The following agonistic behaviours were observed during fledgling focal observations (presented with their relative frequency): (1) crest lift (<1%), when the aggressor directs its head towards the recipient while lifting crown feathers; often the bill is open and a unique vocalization is produced; (2) trunk chase (40%), rapid movement towards the recipient by the aggressor where physical contact is avoided because the recipient retreats; (3) pecking (3%), when the aggressor makes physical contact with the recipient with its bill; often feathers on the back or toes are pinched; (4) perch displacement (54%), rapid movement by the aggressor in flight or by crawling towards the recipient, resulting in a flight retreat by the recipient and an exchange of perch space; (5) aerial chase (2%), an aggressive pursuit where both aggressor and recipient are in flight; (6) tumble fight (1%), a physical attack by the aggressor where both members of the pair fall from their perches and grapple while falling towards the ground; the pair typically unlocks before hitting the ground. Juveniles were never observed using the open-wing display (Ligon 1970) during conflicts with each other, although it was displayed frequently in the presence of intruders and during territorial conflicts with neighbours.

Intrabrood fledgling ranks were assigned to 259 fledglings from 99 multiple male broods (38 broods containing at least one female). Social rank assignments typically remained constant throughout our postfledgling sampling period, suggesting that rank reversal is rare. Thirty-three dyads were observed fighting *ad libitum* on additional days either before or after the day of their focal observation. Of these, social rankings of members in 31 dyads (94%) were consistent with those assigned during the focal observation and only two dyads showed evidence of rank reversal. Hierarchies were strongly male biased. Only one of the 30 females that were observed conflicting with a male broodmate was dominant. However, females were observed initiating fights with other females in two female-only broods (not included in this study) as well as in five broods containing more than one female fledgling, and the outcome of these fights resulted in linear dominance hierarchies similar to those observed among males.

We found evidence for increasing intrabrood conflict rate with decreasing social distance for broods containing two males and one female (MMF), but not for all-male broods (MMM). After controlling for family (generalized linear model: $F_{23,46}=1.24$, $N=72$, $P=0.26$), first- and second-ranking males from MMF broods conflicted more frequently with closely ranked subordinate males (M1 versus M2) and female siblings (M2 versus F3), while first-ranking males were less likely to fight with their distantly ranked subordinate sisters (M1 versus F3; generalized linear model: $F_{2,46}=8.21$, $N=72$, $P=0.001$; Fig. 1a). However, after controlling for family (generalized linear model: $F_{10,20}=2.68$, $N=33$ dyads, $P=0.029$), first- and second-ranking males from MMM broods were equally likely to initiate fights with closely ranked (M1 versus M2 and M2 versus M3) and distantly ranked (M1 versus M3) broodmates (generalized linear model: $F_{2,20}=1.25$, $N=33$, $P=0.309$; Fig. 1b).

It was rare for resident adults to show aggression towards juveniles during the sampling

period. There were only 26 attacks towards juveniles by adult family members (as compared to 591 intrabrood conflicts). The majority (21 of 26, 81%) of attacks towards juveniles occurred when adults ‘punished’ offspring that begged too aggressively, by pecking them in the head, and the remaining attacks were trunk chases or perch displacements. Attacks by adults were distributed across all fledgling sexes and ranks (11 dominant males, 10 subordinate males, 4 subordinate females, 1 unidentified fledgling) and initiated by all adults (5 breeder males, 6 breeder females, 5 helper males, 10 unidentified adult family members).

PART 2: SIZE AND SOCIAL RANK

Methods

At banding (see General Methods, Field Methods), we measured nestling mass and leg length. The length of the right leg (rather than tarsus length) was measured and defined as the space between the distal edge of the last complete scale before the toes and the end of the intertarsal joint including the thick heel callus found on nestling red-cockaded woodpeckers. For the 2008 cohort, we also collected mass and linear measures from pairs of male broodmates with known social rank 3–6 months postfledging (after they had reached nutritional independence). We captured each juvenile male by quietly placing a net over the entrance to its roost cavity before dawn. During capture we collected mass, tarsus (standard adult measure) and culmen length. Tarsus and culmen measures were collected twice on the same side of the body and the average value was used in analysis. Broodmate pairs were captured within 3 days of each other, with two exceptions: members of one pair were captured 5 days apart and those of another pair

were captured 17 days apart.

To test our prediction that nestling condition is positively associated with the probability of becoming socially dominant, we created a nominal logistic regression with ‘social rank’ as the dependent variable and ‘condition score’ as the independent variable, using the program JMP 8.0 (SAS Institute, Inc.). ‘Social rank’ was binary (dominant or subordinate); individuals classified as dominant were socially dominant over all siblings, and individuals classified as subordinate were socially submissive to at least one sibling. Condition was calculated as nestling mass (g) divided by the length of the right leg (mm) measured at banding. Since we were interested only in an individual’s condition relative to that of its broodmates, we calculated relative nestling condition as an individual’s residual from the mean condition for all male broodmates.

As a measure of the persistence of a size–rank relationship, we determined whether male broodmate pairs had morphological size differences according to their fledgling social rank even after reaching nutritional independence. We used three separate analysis of variance tests to identify the relationship of dependent variables relative ‘mass score,’ relative ‘tarsus score’ and relative ‘culmen score’ with the independent variable ‘social rank’ (JMP). Relative linear measure scores were calculated as an individual’s residual value from the pair mean. To determine whether dominant and subordinate brothers varied in relative condition after nutritional independence, we used ANOVA to identify the relationship of the dependent variable ‘condition score’ and the independent variable ‘social rank’. We calculated condition in two ways: first by dividing the mass by tarsus, then by dividing mass by culmen. Relative condition scores were calculated as the individual’s residual value from the pair mean. All means are presented with their standard error (alpha level=0.05).

Results

Among male broodmates, the probability that a nestling would become the socially dominant brood member as a fledgling was positively associated with relative condition at banding (logistic regression: $\chi^2_1=21.56$, $N=196$, $P<0.001$; Fig. 2). The predicted probability that a male nestling with above-average nestling condition would become dominant as a fledgling ranged from 47 to 86%, while males with below-average condition had only a 3–46% probability of becoming the dominant brother.

The morphological measurements of eight juvenile male broodmate pairs captured after nutritional independence (15 August–5 December) also revealed differences in size according to fledgling social rank. Dominant individuals had heavier mass scores (1.41 ± 0.50 g versus 1.41 ± 0.50 g; ANOVA: $F_{1,14}=15.97$, $N=16$, $P=0.001$) and marginally longer tarsus scores (0.21 ± 0.15 mm versus -0.21 ± 0.15 mm; ANOVA: $F_{1,14}=3.68$, $N=16$, $P=0.076$) than their subordinate broodmate. There was no difference between broodmate pairs in culmen length score (dominant: -0.10 ± 0.20 mm; subordinate: 0.10 ± 0.20 mm; ANOVA: $F_{1,14}=0.48$, $N=16$, $P=0.500$). Condition scores were higher for dominant brothers when calculated as mass divided by culmen (0.082 ± 0.04 g/mm versus -0.082 ± 0.04 g/mm; ANOVA: $F_{1,14}=10.79$, $N=16$, $P=0.005$; Fig. 3). When condition was calculated as mass divided by tarsus, dominant brothers had only marginally higher condition scores (0.046 ± 0.03 g/mm versus -0.046 ± 0.03 g/mm; ANOVA: $F_{1,14}=3.70$, $N=16$, $P=0.075$; Fig.3).

PART 3: ALLOCATION OF FOOD

Methods

To assess the allocation of food given to fledglings by adults during the postfledging dependent period, we recorded the number and type of all feeding events during each focal observation (see General Methods, Field Methods). We categorized each feeding event as either targeted feeding, where a provisioning adult gathers food items and then flies to locate and feed a stationary fledgling, or approach feeding, where a foraging adult feeds the nearest begging fledgling following closely on the same branch. We identified the timing of the developmental shift between targeted feeding and approach feeding by plotting the proportion of targeted feedings per focal against postfledging age at the time of observation. We found a substantial drop in the mean proportion of targeted feedings after 8–9 days postfledging (Fig. 4).

To determine whether adults feed fledglings equally across sexes and ranks, we created a generalized linear mixed model fitted to the data using a Poisson error distribution (SAS) with the dependent variable ‘targeted feedings’ and the independent fixed variable ‘sex–rank’ and random variable ‘family’. Only the subset of broods sampled at 4–9 days postfledging were included since this is the developmental period when target feeding is predominant (Fig. 4). The number of target feedings was calculated as the total number of target feedings received by the focal individual during its 30 min focal observation. The ‘sex–rank’ variable consisted of the following four categories: (1) first-ranking males, (2) second-ranking males, (3) third- and fourth-ranking males and (4) third- and fourth-ranking females. The categorical covariate ‘family’ was added as a random effect to control for unexplained variation among broods.

Using the same age subset of broods as above, we then tested our prediction that conflict rates should increase with decreasing feeding rates. We created a generalized linear model fitted to the data using a Poisson error distribution (SAS) with the dependent variable ‘alpha–beta

conflict number' and the independent variable 'mean target feedings'. We defined 'alpha–beta conflict number' as the total number of conflicts observed between the two highest-ranking males in each brood during the sum of both focal observations (1 h), and 'mean target feedings' as the number of target feedings per individual per focal observation averaged across all fledglings in the group (including females).

To test our prediction that intrabrood dominance hierarchies result in prioritized access to resources for dominant individuals later in the postfledging period, we compared the number of approach feedings for individuals with different sex–ranks from broods that were at least 10 days postfledging. We used a generalized linear mixed model fitted to the data using a Poisson error distribution (SAS) with the dependent variable 'approach feedings' and the independent fixed variable 'sex–rank' and random variable 'family.' Definitions for feeding rates, sex–rank categories and family covariates were the same as the targeted feeding analysis above.

Results

After controlling for variation among families, adults showed no strong favouritism towards particular fledglings when target feeding (generalized linear mixed model: $F_{3, 39}=1.47$, $N=66$, $P=0.2383$; Fig. 5a). The frequency of aggressive conflicts between first- and second-ranking male broodmates increased with decreasing mean targeted feeding rate (generalized linear model: $F_{1, 22}=17.18$, $N=24$, $P<0.001$). The beta coefficient (slope) for the effect of feeding rate (per 30 min) on alpha–beta conflict rate (per hour) was -0.2657 (confidence interval: -0.3986, -0.1327). After controlling for family variation, there was a positive association between approach feeding rate and intrabrood sex–rank (generalized linear mixed model: $F_{3, 84}=16.64$, $N=143$, $P<0.001$; Fig. 5b). First- and second-ranking males obtained more food than did females

(Tukey-Kramer post hoc test; $P < 0.001$). Third-/fourth-ranking males had approach feeding rates that were marginally lower than first-ranking males (Tukey-Kramer post hoc test; $P=0.0525$) but overlapped those of other males and females (Tukey-Kramer post hoc test; Fig. 5b).

PART 4: SOCIAL RANK AND DISPERSAL

Methods

We recorded the presence and location of focal individuals with known rank during the annual population-wide breeding season census conducted by SEI staff. Every red-cockaded woodpecker family group within the study area was visited between April and August and all associated group members were recorded. Juveniles were designated as (1) missing, (2) natal helper or (3) dispersed, following Walters (1990). Missing birds were not located with any group within the study area and were probably dead. This assumption comes from the low probability of dispersal off the study area estimated at 6% by Walters et al. (1988). Natal helpers were observed with their family on the natal territory during the breeding season and not observed associating with another group. Dispersers were located on non-natal territories as either new territory holders (oldest or only male on territory) or nonterritory holders (subordinate male on new territory or nonassociated floater).

First, to determine whether intrabrood sex and social rank as a fledgling influences postfledging survival, we used a likelihood ratio test (JMP) on each cohort to compare the status of individuals at the breeding season census according to their social rank as fledglings. Individual status was either 'alive' (natal helpers and dispersers pooled) or 'dead' (missing). Sex-ranks were split into three levels: dominant male (highest-ranking brood member),

subordinate male (second through fourth ranking) and subordinate female (third and fourth ranking). Subordinates were lumped within sexes to meet the cell count requirements for likelihood ratio tests. Second, to determine whether intrabrood social rank as a fledgling influences the probability of dispersal by first spring, we used a likelihood ratio test (JMP) to compare the proportion of dominant and subordinate brothers from all cohorts that were either found alive on their natal territory or found alive and dispersed.

Results

For the 2007 and 2008 cohorts, dominant males, subordinate males and females were equally likely to survive to the breeding season census (likelihood ratio test: 2007: $\chi^2_1=3.3$, $N=79$, $P=0.183$; 2008: $\chi^2_1=2.0$, $N=88$, $P=0.370$; Fig. 6). For the 2009 cohort, however, dominant males had higher first-year survival than subordinate males and females (likelihood ratio test: $\chi^2_1=10.3$, $N=93$, $P=0.006$; Fig. 6). When considering natal dispersal patterns during the first year, all juvenile females that were alive by the spring census had dispersed from their natal territory. Of the juvenile males surviving their first year, subordinate males were more likely to be found dispersed than were their dominant brothers (all cohorts pooled, likelihood ratio test: $\chi^2_1=9.6$, $N=80$, $P=0.002$; Fig. 7). Only four of 45 (9%) dominant males surviving to their first spring were observed off their natal territory, while 13 of 35 (37%) of subordinates were found dispersed. In both of the above analyses only one brood had more than one subordinate male survive to the breeding season census; therefore, no corrections were necessary to account for the nonindependence of broodmates within the lumped subordinate category.

DISCUSSION

Our results suggest that intrabrood competition, rather than adult favouritism towards low-quality young or high-quality young, provides a mechanism to account for variation in natal dispersal strategies for red-cockaded woodpeckers. Only a few other studies have looked at intrabrood social status and dispersal behaviour in species where delayed dispersal is the preferred strategy (Strickland 1991; Ekman et al. 2002). Our study is the first to add the influence of social rank on the acquisition of natal resources as a possible explanation for dispersal of subordinate young.

The results of our focal observations support the intrabrood competition hypothesis by revealing frequent aggressive interactions among broodmates during the postfledging dependent period. These conflicts resulted in intrabrood dominance hierarchies that were male biased according to our prediction and similar to intrabrood dominance hierarchies in other nonsiblicidal species (e.g. Arcese and Smith 1985; Carlisle and Zahavi 1986). In the case of mixed-sex broods, dyad-level conflict frequency increased with decreasing social distance. Social dominance for male fledglings was predicted by high nestling condition relative to that of other male broodmates, supporting our prediction that physical competitive ability corresponds with hierarchy formation in this species. We suspect that dominance hierarchies are established before fledging because postfledging rank reversals were rarely observed during focal watches, fighting among siblings was occasionally observed within the cavity, and some nestlings fledged with patches of crown feathers missing (E.L.H.R., personal observation). Subordinate males remained smaller and in lower condition than their dominant broodmates even after reaching nutritional independence, suggesting that the relationship between size and social rank is more than a temporary effect. This is the first study to specifically describe the agonistic behaviours

and social structure among juvenile red-cockaded woodpecker broods.

Interestingly, parents and adult siblings from previous broods (helpers) rarely showed aggression towards subordinate juveniles. The existence of a strict age-based hierarchy among males from different broods creates a situation where the only uncertainty in rank requiring resolution is that among broodmates. Although adult aggression towards juveniles is rare during the postfledging dependent period, another opportunity for agonistic behaviour between adults and young may occur the following spring before the egg-laying period, when the majority of subordinate juveniles disperse. Occasional aggression by the breeding male towards retained juvenile males has been observed at this time, but it is unclear whether this aggression facilitates eviction of retained juveniles, or is used as a form of mate guarding or social reinforcement of nonbreeding helper status (E.L.H.R., personal observation). Previous research revealed that the number of adult male helpers does not influence the probability of natal dispersal for juvenile males (Pasinelli and Walters 2002), again supporting the idea that the within-brood social environment, rather than the entire social environment, is critical in determining dispersal strategy in this system.

Additional evidence supporting the hypothesis of intrabrood competition over natal resources comes from the observed shift in food distribution in favour of dominant fledglings with increasing fledgling mobility. Parents distributed food evenly when target feeding, but after 8–9 days postfledging, broodmates used scramble competition to gain access to favoured perches near foraging adults, and as a result, dominant males had higher feeding rates than subordinate females. The argument that social rank is linked to access to resources in this system is further strengthened by the relationship between food availability and aggression. The number of aggressive conflicts between the two highest-ranking males is higher in groups with low

targeted-feeding rates, suggesting that aggressive behaviours between brothers is initially driven by reduced food availability even though access to provisioned food is not controlled by social rank until later in the fledging period.

Patterns of natal dispersal for dominant and subordinate fledglings also follow our predictions under the intrabrood competition hypothesis, where subordinate males are more likely to disperse by spring than are their dominant male broodmates. If enough natal resources are denied to subordinates, dispersal may actually be favoured as the strategy with the most potential for success. Natal dispersal behaviour in goshawks, *Accipiter gentilis*, was delayed for individuals given food supplementation compared to those without (Kenward et al. 1993); a similar link may exist between access to natal food and the likelihood of dispersal in young red-cockaded woodpeckers. However, it may be that physical condition drives dispersal of subordinate young in this system rather than limited access to food per se. Subordinates continue to have lower condition as juveniles, but this may be due to carryover effects from their reduced condition as a nestling, or a result of persistent social aggression by dominants, not just limited access to food brought by parents. An additional explanation for the dispersal of subordinates beyond reduced access to food might simply be the avoidance of aggressive siblings. Because of repeated acts of physical aggression by broodmates, it may be adaptive for subordinates to disperse, rather than continually challenge a superior sibling and incur the associated costs (Strickland 1991; Ekman et al. 2002; Kilner and Drummond 2007).

Evidence for hierarchy functions beyond access to food may lie in rates of conflict between all-male and mixed-sex broods. We found that social distance within the brood hierarchy lessened the number of conflicts with the dominant bird only if the distant sibling was female. Conflict rates among dyads in all-male broods showed no difference according to social

distance. If aggression among dyads functions only in competition for food, dominant males should perceive distantly ranked males and females similarly since both are competitors for shared food. Additionally, if access to food were the only driver of natal dispersal, then we might predict that subordinate dispersal would occur primarily during the postfledging dependent period, since this is when access to food is denied. Instead, dispersal timing varies and many juveniles wait until spring to disperse (Kesler et al. 2010), implying that the social hierarchy may also function as a mechanism for competition over helper positions on the natal territory.

The costs associated with subordination mentioned above lend this system to comparison with research from siblicidal species. In red-cockaded woodpeckers, subordinate juveniles get fed at reduced rates and have lower condition as independents, resulting in reduced natal survival in some years. In addition, more subordinates choose the apparently inferior tactic of dispersing in their first year rather than remaining on their natal territory as a helper (Walters et al. 1992b). Despite the potential costs of subordination, subordinate red-cockaded woodpecker juveniles were never observed initiating a conflict, let alone fighting back vigorously. The severity of sibling aggression is thought to be a result of the size and structure of the nursery (nest, pond etc.; Mock and Parker 1997), and the relative mobility of postfledging young and their ability to escape the area of conflict may explain the lower incidence of resistance in red-cockaded woodpeckers compared to siblicidal species.

Our second hypothesis of extended parental care favouring subordinate young was partially supported in 2007 and 2008, when postfledging survival was equivalent for juveniles regardless of sex–rank. Remaining on the natal territory over the winter may protect subordinate offspring from fatal consequences associated with reduced feeding rates during the dependent period. However, in one year (2009), dominant individuals experienced enhanced survival. The

mean target-feeding rates per individual per focal (\pm SE) were 2.77 ± 0.64 , 3.28 ± 0.59 and 4.30 ± 0.49 for 2007, 2008 and 2009, respectively. Although the means did not vary statistically across years (ANOVA: $F_{2,63}=2.01$, $N=66$, $P=0.1423$), target-feeding rates tended to be higher in 2009. This is interesting, because it suggests that only dominant individuals experience the additional benefits of a plentiful food year, potentially because of their ability to monopolize foraging adults later in the postfledging period when approach feeding is predominant feeding type.

In our third hypothesis, we proposed that adults may favour high-ranking fledglings, and while we did not observe any overt parental favouritism in this direction, adults may actually contribute to intrabrood competition as conspirators by setting up situations favourable for sibling competition (Forbes and Thornton 1997; Forbes and Mock 2000). Much about this system supports the idea of parental concurrence with intrabrood competition. First, adults probably control the degree of hatching asynchrony and therefore impose a physical competitive disadvantage to later-hatched young. In this way, parents may produce a set of ‘core’ offspring and then overproduce a set of ‘marginal’ young in order to optimize their annual fitness in the face of environmental uncertainty (Mock and Forbes 1995). Parents may benefit from the production of marginal offspring in years where reproductive conditions are unexpectedly favourable (resource tracking hypothesis: Temme and Charnov 1987) or when one or more core offspring become injured or die (insurance hypothesis: Doward 1962; Cash and Evans 1986). Second, at no observable stage did adults appear to dramatically correct for hatching asynchrony by favouring the lower-condition, subordinate offspring when making feeding decisions. Immediately after fledging, adults have the opportunity to openly choose among young when making feeding decisions, yet they did not strongly favour any particular sex or rank. Once

approach feeding became the dominant feeding type, adults fed the nearest fledgling, rather than seeking another less competitive offspring, again reinforcing the hierarchy rather than acting counter to it. The biased distribution of food resources to particular offspring, as determined by their placement in the dominance hierarchy, may serve as an indirect method of downward adjustment of brood size in times when food resources are low (Mock and Forbes 1995). By letting broodmates compete over perching locations and by rewarding the victors, adults let the fledglings become self-selected survivors and therefore they 'kill by proxy' rather than directly adjusting brood size (e.g. infanticide, neglect; Mock and Forbes 1995). Third, adults in our study were never observed interfering with sibling conflicts and they only rarely punished overtly aggressive begging young. The above findings suggest that in years with limited resources, adults may use sibling competition to optimize their investment.

Parents may also support intrabrood competition that results in more frequent early dispersal of subordinate broodmates even when this strategy results in reduced fledgling fitness. Although breeding pairs with helpers are more likely to produce young (Reed and Walters 1996) and have reduced incubation and feeding workloads (Khan and Walters 2002), these benefits may wane if group size becomes too large. If competition over local resources causes diminishing returns on offspring retention, then adults may favour a mixture of dispersal strategies among their young such that not all offspring delay dispersal. It may be that the benefits of offspring retention vary with relative offspring quality and that the social hierarchy increases the probability that breeders will retain as helpers only the highest-quality male offspring from each brood.

Juvenile dominance hierarchies in red-cockaded woodpeckers may initially be established as a framework to distribute immediate food resources and to sort amongst young in

times of reduced food availability. The same hierarchy may then function to determine dispersal roles within broods. Early social environment and the balance of natal resources among broodmates may be as important to natal dispersal decisions as environmental conditions and nearby breeding vacancies and should therefore be considered in future efforts to understand the evolution of dispersal behaviour.

ACKNOWLEDGEMENTS

We thank the staff and associates of the Sandhills Ecological Institute for their dedication in the field: Kerry Brust, Stephen Anchor, Jay Carter, Vivian Genovese, Michelle Jusino, Matthew King and Jennifer Maynard. We also thank U.S. Army Fort Bragg Endangered Species Branch, Jackie Britcher and Jessie Schillaci, and the North Carolina Sandhills Gamelands and Wildlife Resources Commission, Brady Beck. Committee members, James Fraser, Dana Hawley and John Philips provided helpful advice throughout the development of the project and Cas Eikenaar contributed many thoughtful improvements to the manuscript. Funding for this project was provided by the U.S. Department of Defense Marine Corp Base Camp Lejuene (J.R.W.) and the Virginia Tech Graduate School (E.L.H.R.).

FIGURE CAPTIONS

Figure 1. Conflict rates among dyads with differing social distances from (a) mixed-sex broods of three ($N=24$ broods) and (b) all-male broods of three ($N=11$ broods). Least squares mean \pm SE conflicts per hour calculated from generalized linear model controlling for family. Dyad members and their relative social distance (close or distant) are presented on the X axis. Different letters above bars represent statistically significant differences as determined by a Tukey–Kramer post hoc test.

Figure 2. Predicted cumulative probability of becoming the socially dominant fledgling for male broodmates according to relative nestling condition score (grey shaded portion; $N=196$ fledglings). Probability estimates taken from binary logistic regression of social rank (dominant, subordinate) versus relative condition score (g/mm).

Figure 3. Two measures of relative condition for juvenile male broodmate pairs after nutritional independence according to fledgling social rank. Black bars: dominant males; open bars: subordinates. Nestling condition was calculated as mass divided by leg length; independent juvenile condition was calculated as mass divided by culmen and as mass divided by tarsus. Relative condition scores were calculated as an individual's residual condition from the pair mean. Values are means + SE.

Figure 4. Shift in feeding type with increasing postfledging development for fledgling male and female red-cockaded woodpeckers. Mean proportion of targeted feedings per individual focal observation + SE is plotted against postfledgling age. Age categories are in 2-day bins. Numbers

above or below each mean value represent the number of individual focal observations completed during that age category ($N=191$).

Figure 5. Influence of sex–rank on (a) targeted-feeding and (b) approach-feeding rates for fledglings 4–9 days postfledging and >10 days postfledging, respectively. Least squares means + SE are presented from generalized linear models of feeding rates per 30 min with ‘sex–rank’ and ‘family’ covariates. Sex–rank categories are presented on the X axis. Different letters above bars represent statistically significant differences as determined by Tukey–Kramer post hoc test.

Figure 6. Postfledging survival of juvenile red-cockaded woodpeckers split by sex and social rank as a fledgling. Black bars: dominant males; grey bars: subordinate males; white bars: subordinate females. Numbers above bars represent the total number of individuals in each category at the time of fledgling rank assignment. Significance values represent differences in proportion surviving according to sex–rank within cohorts.

Figure 7. Breeding season settlement locations of juvenile male red-cockaded woodpeckers surviving to their first spring by intrabrood social rank as fledglings. Black shaded area denotes the proportion of birds located on new territories during breeding season census (dispersed: dominant, $N=4$; subordinate, $N=13$). Grey shaded area denotes the proportion of birds found remaining on natal territory during breeding season census (natal helper: dominant, $N=41$; subordinate, $N=22$).

Figure 2. 1 Conflict rates among dyads with differing social distances

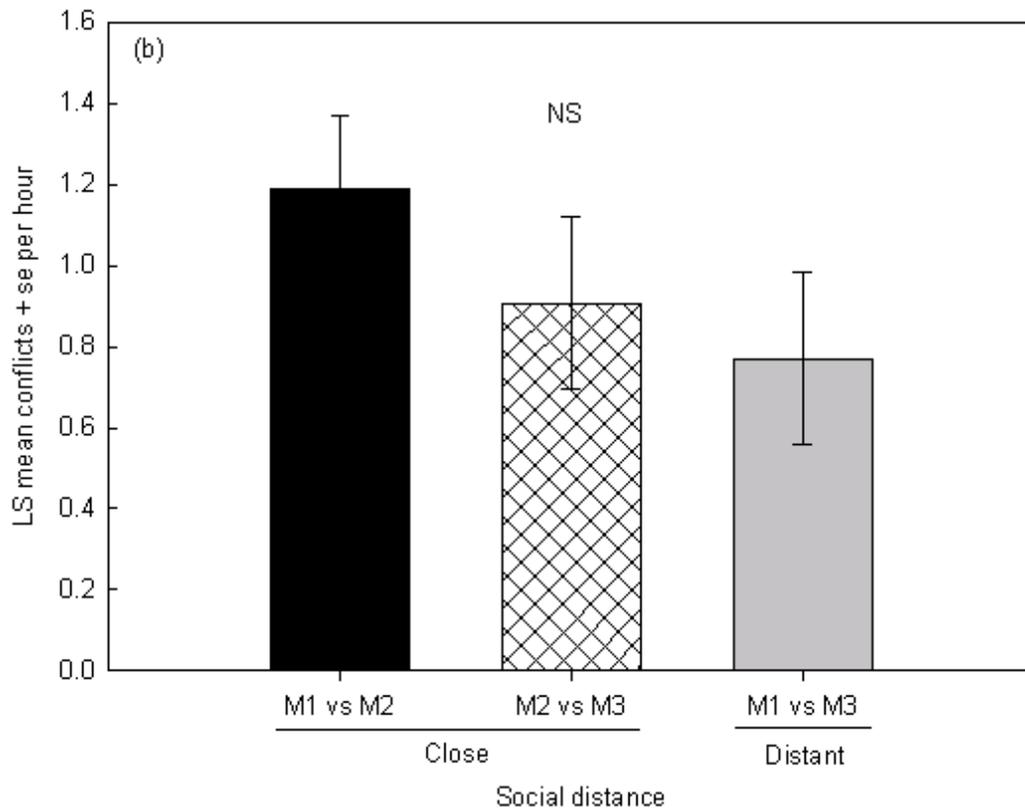
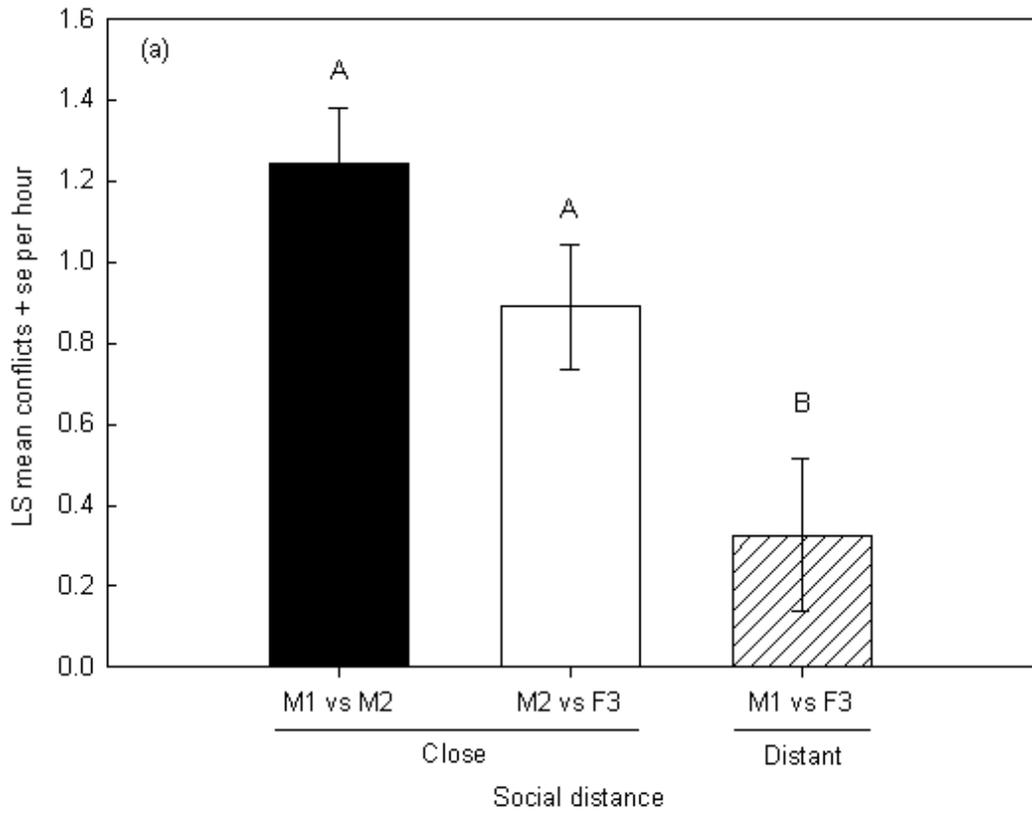


Figure 2. 2 Predicted cumulative probability of becoming the socially dominant fledgling.

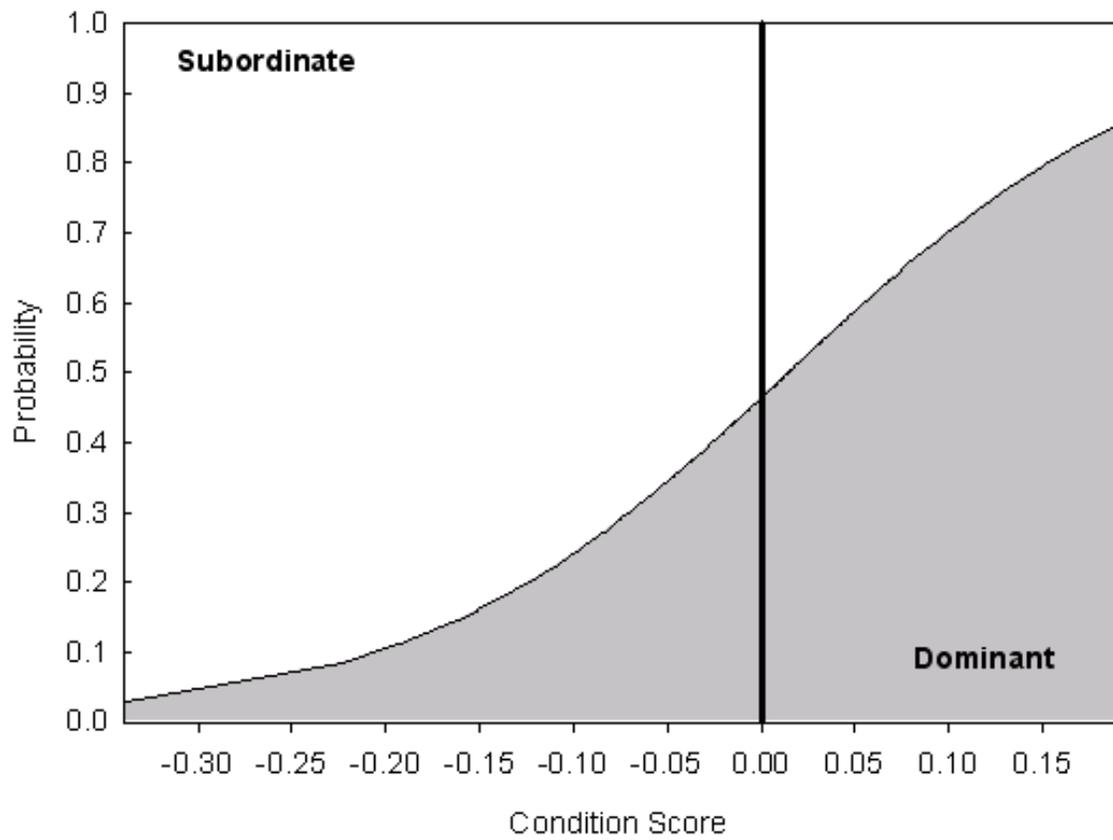


Figure 2. 3 Two measures of relative condition for independent juvenile males.

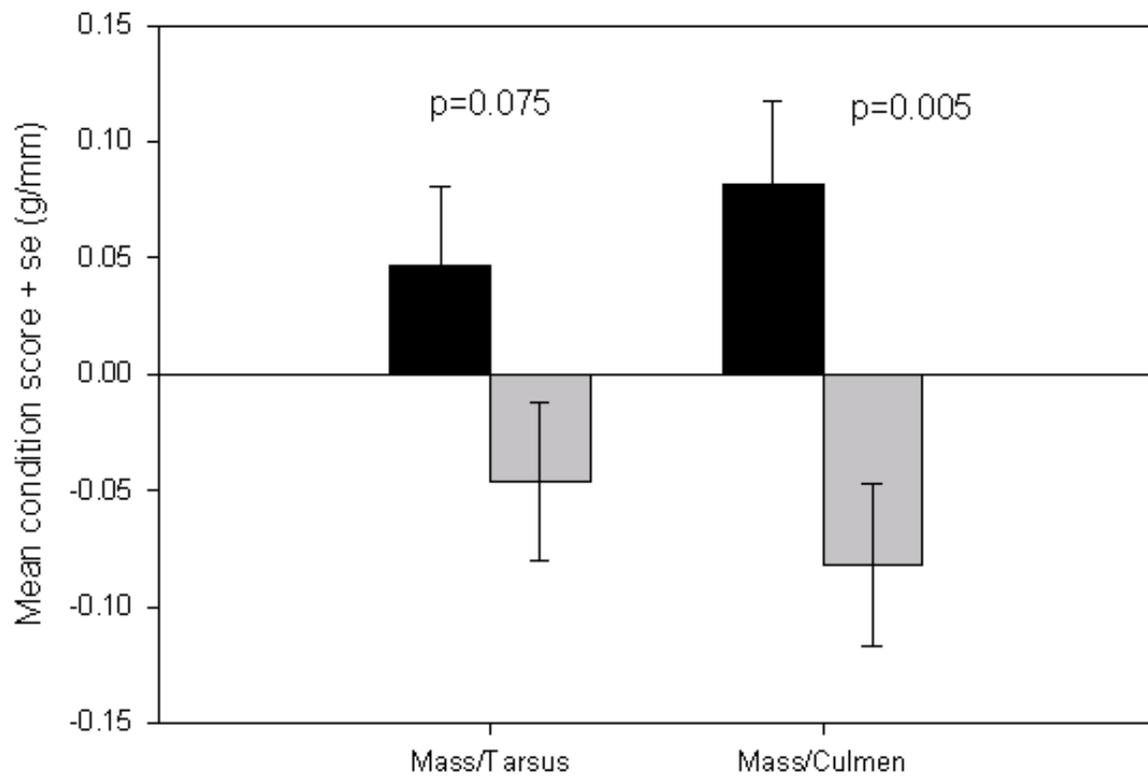


Figure 2. 4 Shift in feeding type with increasing postfledging development

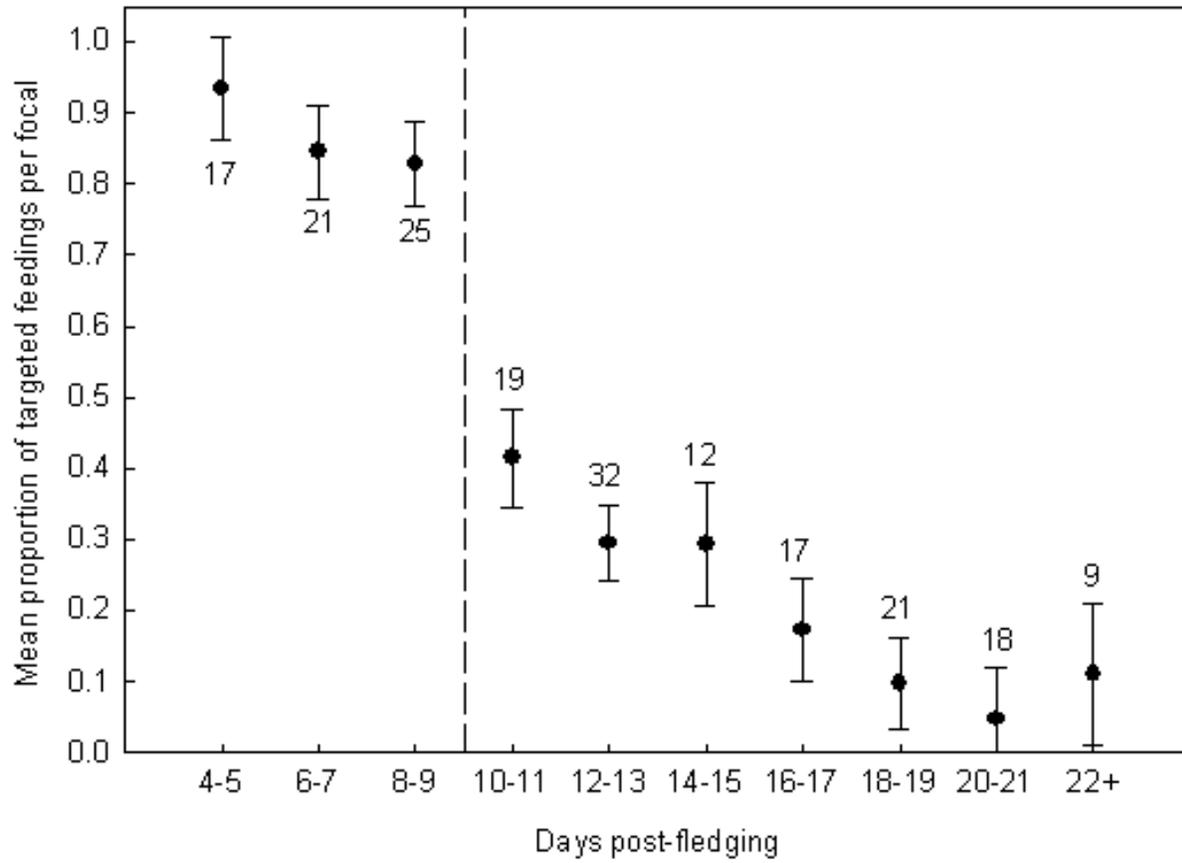


Figure 2. 5 Targeted- (a) and approach-feeding (b) rates.

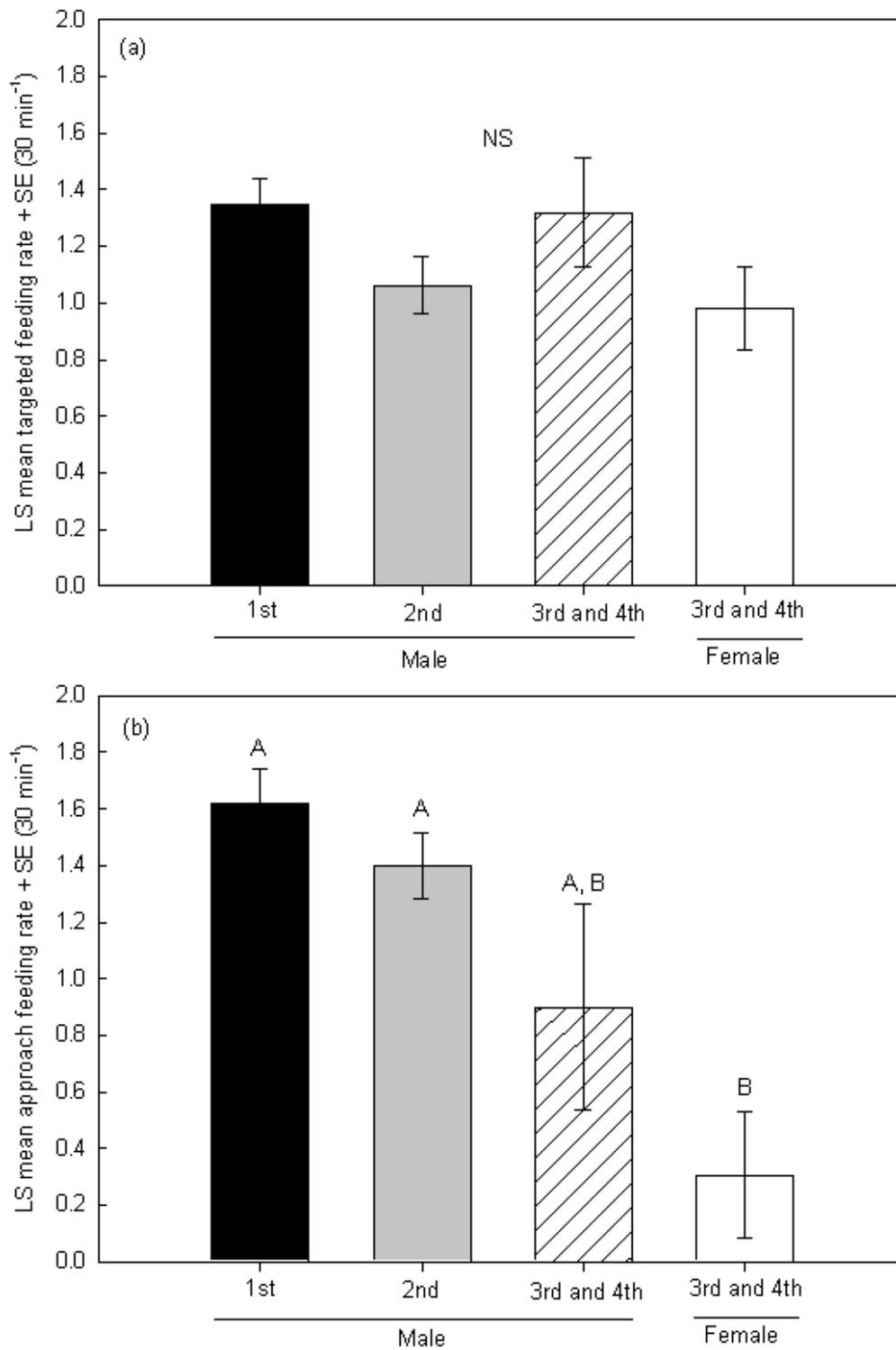


Figure 2. 6 Postfledging juvenile survival

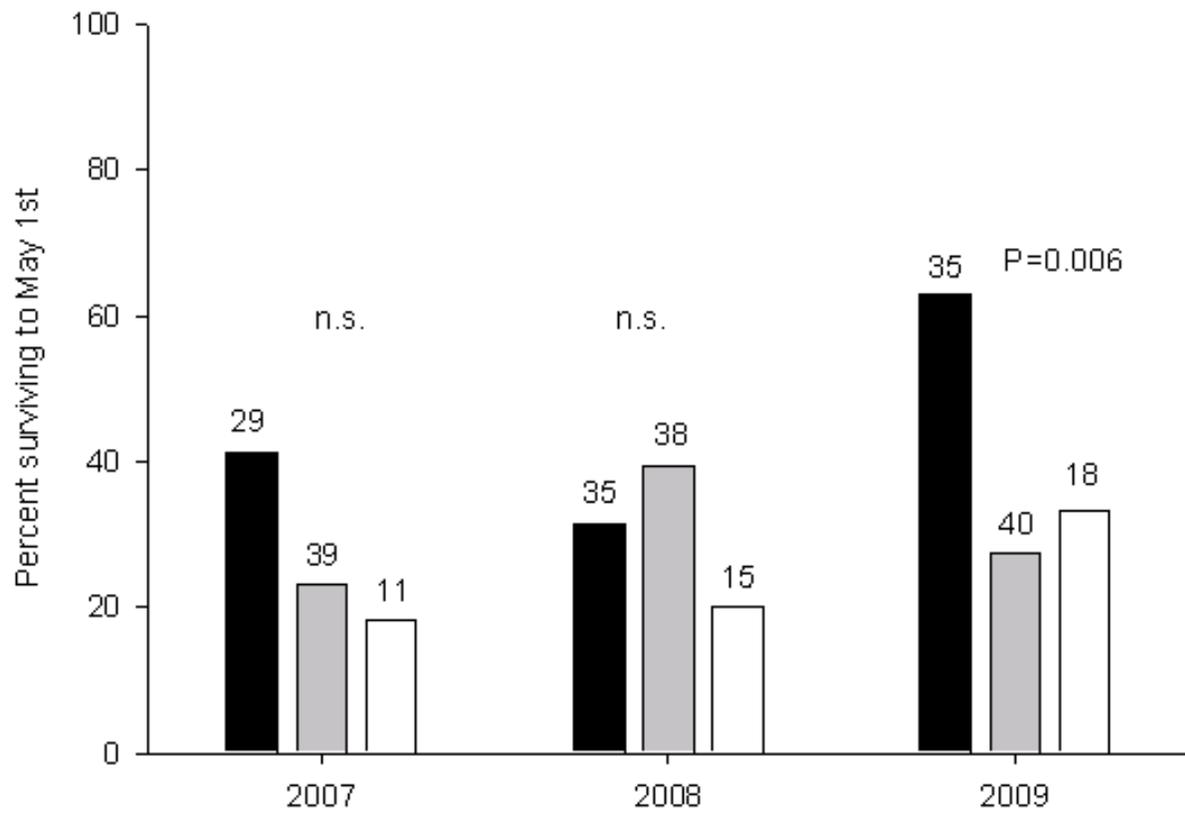
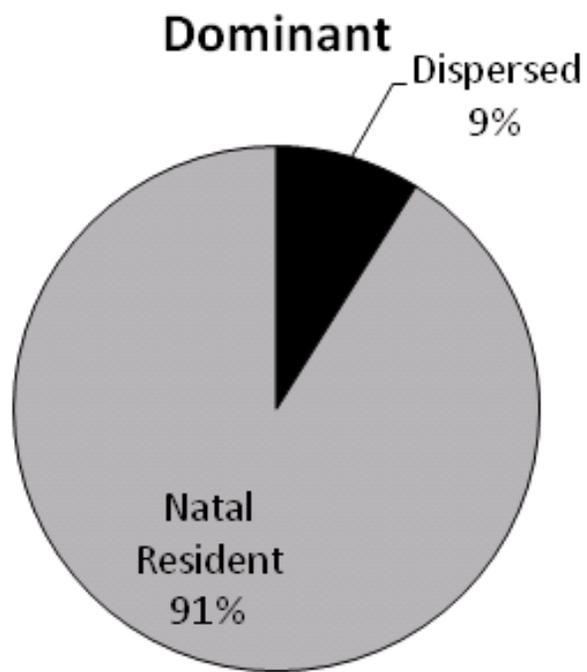
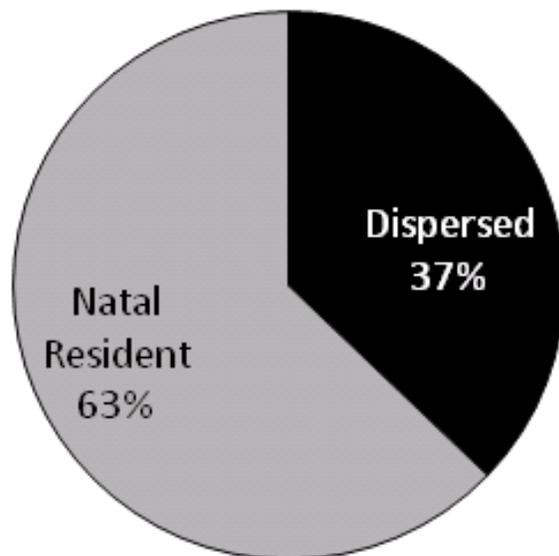


Figure 2. 7 Breeding season settlement locations of juvenile males.



Subordinate



CHAPTER III. THE ROLE OF INTRABROOD SOCIAL ENVIRONMENT ON POST-FLEDGING SURVIVAL AND NATAL DISPERSAL IN RED-COCKADED WOODPECKERS: A MULTISTATE MARK-RECAPTURE STUDY

Erin L. Hewett Ragheb and Jeffrey R. Walters

ABSTRACT

Despite the benefits of philopatry for some cooperatively breeding birds, many juveniles still disperse during their first year. To determine how this individual variation is influenced by intrabrood social environment, we studied first-year survival and natal dispersal in the red-cockaded woodpecker (*Picoides borealis*), a cooperatively breeding species that establishes male-biased fledgling dominance hierarchies. We generated behavioral predictions for individuals according to their intrabrood rank under hypotheses regarding the adaptive consequences of dispersal timing. First, delaying dispersal is favored because of high direct benefits of philopatry gained during the first year postfledgling. Second, early dispersal is favored in order to secure breeding vacancies. Third, delaying dispersal is favored because of lifetime fitness benefits obtained beyond the first year. Our results reveal that natal survival favored males, and within juvenile males, dominant brood-mates had higher first-year survival. Both sexes dispersed more in the spring than fall, and females were more dispersive than males. Within male brood-mates, subordinates were more likely to disperse than dominants, but subordinates delayed dispersal in situations where all dominants died over the winter. Together, these results suggest that overwintering on the natal territory is the preferred strategy for both sexes supporting our first hypothesis. However, overwinter survival estimates within sexes were similar for natal residents and established fall dispersers. Also, dispersal timing within the first

year had no influence on the probability of obtaining a breeding position by the first breeding season for either sex, suggesting that delayed dispersal may result from increased lifetime fitness benefits generated beyond the first year following the predictions of our third hypothesis. *Key words:* benefits of philopatry, condition, delayed dispersal, intrafamilial conflict, juvenile aggression, life history strategy, linear dominance hierarchy, multistate mark-recapture, *Picoides borealis*, sibling rivalry.

INTRODUCTION

In species where ecological constraints limit independent reproduction on high quality habitats, young birds may choose to disperse and become non-territorial floaters, join flocks of other young non-breeding individuals, or wait on the natal territory for available breeding vacancies in the neighborhood. Remaining on the natal territory is a common strategy for the approximately 3% of bird species known to live in extended family groups (Emlen 1982). For cooperatively breeding species, many of these retained offspring become helpers at the nest by contributing to the care of related young (Emlen 1982). Within species that exhibit delayed natal dispersal, many offspring still choose to disperse early, yet this individual variation is only recognized in a few models attempting to explain the evolution of delayed dispersal (Kokko and Johnstone 1999; Ekman et al. 2002). Much of this individual variation may be caused by sex specific differences in dispersal strategy (Alonso et al. 1998; Green and Cockburn 2001), especially when the costs and benefits associated with delayed dispersal differ between the sexes (Daniels and Walters 2000a; Hawn et al. 2007).

In addition, variation in dispersal timing may be explained by differences in competitive ability. If immediate dispersal is the preferred strategy because it leads to an increased

probability of territory acquisition (Drent 1984; Ellsworth and Belthoff 1999), then individuals should attempt dispersal as early as physiologically ready and dominant, high condition individuals may be the first to disperse within their brood (Ellsworth and Belthoff 1999). Early dispersers may also be more aggressive relative to unrelated juveniles within their cohort (Duckworth and Badyaev 2007), or more independent foragers (Middleton and Green 2008). Here, competitive superiority is related to increased access to breeding vacancies, and competitively inferior individuals may need to make the best-of-a-bad-situation by remaining on the natal territory in order to reach the necessary conditional threshold (Alonso et al. 1998). This was observed in brood-mate pairs of male acorn woodpeckers (*Melanerpes formicivorus*), where the smaller, subordinate male was more likely to become a helper in situations where one delayed dispersal and the other dispersed (Koenig et al. 2011). Alternatively, if remaining on the natal territory is the preferred strategy, resulting in greater access to breeding vacancies, or increased lifetime reproductive success, then delayed dispersal may be the strategy adopted by competitively superior individuals (Strickland 1991; Ekman et al. 2002). In either of these cases, delayed dispersal would only be favored if the benefits of remaining home outweigh the benefits of early dispersal for that particular class of individual (Stacey and Ligon 1991; Koenig et al. 1992).

Red-cockaded woodpeckers (*Picoides borealis*) are a cooperatively breeding species in which breeding opportunities are limited by the number of available nest cavities in the environment (Walters et al. 1992a). Since individuals must acquire a breeding position at a territory with an established cavity tree, only a fraction of juveniles surviving to the following breeding season become breeders. Surviving juveniles demonstrate a variety of life history strategies by their first breeding season. Some male fledglings remain at the natal territory as

non-breeding helpers while other male and almost all female fledglings disperse, becoming breeders or unrelated helpers on non-natal territories or floaters (Walters et al. 1988). As estimated by a demographic model, young males adopting the delayed dispersal strategy have higher first-year survival than birds dispersing within their first year (Walters et al. 1992b). This is likely a result of increased mortality risks associated with dispersal, although this assumption is difficult to test because it is difficult to differentiate between early dispersal resulting in mortality and mortality on the natal territory. Also, the probability that early dispersers will obtain a breeding vacancy and become a breeder is very low, and first year males that attempt to breed often have poor reproductive success (Walters et al. 1992b). As a result, young males that delay dispersal can have equal or even slightly higher lifetime fitness than individuals that disperse within their first year, providing an explanation for how delayed dispersal could persist in this system (Walters et al. 1992b).

In addition to the variation among juvenile males in the probability of first-year dispersal, juveniles of either sex choosing to disperse vary in the timing of dispersal within that first year. Juveniles as young as 1 month post-fledging have been located as dispersers during routine monitoring (J. R. Walters, personal observation), while others are known to overwinter on the natal territory and disperse in early spring immediately before the start of their first breeding season (Kesler et al. 2010).

Aims and predictions

In this study we explore the role of intrabrood social environment on post-fledging survival and natal dispersal behavior by generating predictions under three hypotheses for the adaptive significance of delayed dispersal behavior (Table 1). Our first hypothesis is that

delaying dispersal and overwintering on the natal territory during the first year of life is adaptive because conditions on the natal territory are more favorable for survival than conditions off the natal territory (Stacey and Ligon 1991). For birds choosing to remain on the natal territory through their first winter, juveniles with greater competitive ability and/or social rank will have higher post-fledging natal survival than their brood-mates, since access to some natal resources varies according to intrabrood social rank (Hewett Ragheb and Walters 2011). If competitively inferior individuals within the brood are denied access to the benefits of philopatry, then they will be more likely to disperse within their first year than their superior brood-mates (Hewett Ragheb and Walters, 2011; Pasinelli and Walters 2002). Likewise, the propensity for dispersal in subordinates should be flexible, based on current access to natal resources. Subordinates should be more likely to delay natal dispersal if their superior brood-mate died or dispersed from the natal territory. We also predict that first-year survival will be lower for early dispersing juveniles than those overwintering on the natal territory. Lastly, if we assume that individuals that overwinter on their natal territory benefit physically from their extended period of philopatry, we predict that spring dispersers will be more likely to out-compete fall dispersers for access to breeding vacancies during their first breeding season..

Our second hypothesis proposes that leaving the natal territory early within the first year is adaptive because securing high quality breeding vacancies early is critical (Ellsworth and Belthoff 1999; Raihani et al. 2008). This hypothesis follows the ‘best-of-a-bad-job’ strategy for delayed dispersal as suggested for acorn woodpeckers (Koenig et al. 2011). Similar to the prediction under the first hypothesis, access to resources on the natal territory will vary with intrabrood social rank and competitively superior individuals will be in higher condition (Hewett Ragheb and Walters 2011) and therefore have higher natal survival than their inferior brood-

mates. Here, we predict that the survival cost associated with dispersal to be low, since birds will disperse as early as they are physiologically ready, rather than being forced to leave. Lastly, we predict that competitively superior individuals will disperse earlier than their subordinate brood-mates and early dispersers will be more likely to fill breeding vacancies than individuals that overwinter on the natal territory.

Alternatively, our third hypothesis proposes that delaying natal dispersal is adaptive, not because of any direct benefits of philopatry gained during the first year (access to resources or protection from predators), but rather through increased lifetime fitness effects (indirect fitness benefits of helping, increased probability of obtaining high quality breeding territory in neighborhood or through inheritance (Walters et al. 1992b)). Competition may still occur among brood-mates over access to natal food resources, but the ultimate benefit associated with high intrabrood social rank is the ability to remain on the natal territory as a helper. Whether or not natal survival varies among brood-mates according to intrabrood social rank is not a specific prediction under this hypothesis. However, the probability and timing of natal dispersal will vary according to social rank, and competitively superior individuals will be more likely to delay dispersal than their inferior brood-mates. Under this hypothesis, the dispersal costs for individuals that become helpers for at least one year before dispersing may be equal to or lower than for individuals that disperse within their first year. Dispersal risk could be reduced for delayed dispersers if they are more likely to eventually find breeding vacancies in their natal neighborhood, and there is a relationship between dispersal distance and familiarity of habitat with the probability of disperser survival. However, this is not a necessary component of this hypothesis. We would predict that the dispersal costs for individuals dispersing within their first

year to be the same, regardless of dispersal timing. Under this hypothesis, first-year dispersers will rarely fill reproductive roles regardless of the timing of first-year dispersal.

In Part 1 of this paper we compare models representing our predictions for the effect of competitive ability (relative condition) and intrabrood social rank on post-fledging survival and natal dispersal strategy in males using a multistate mark-recapture analysis. Then, again using only males, we examine the flexibility of individual dispersal strategies based on the intrabrood social environment before spring dispersal. In Part 2, we use both male and female juveniles to address our remaining predictions concerning the influence of sex and competitive ability (relative mass) on dispersal strategy, the timing of natal dispersal within the first year, and the reproductive roles of first-year dispersers.

MATERIALS AND METHODS

Biology of study species

Red-cockaded woodpeckers form cooperative family groups consisting of a breeding pair and zero to four helpers (typically retained male offspring; Ligon 1970; Lennartz et al. 1987; Walters et al. 1988; Walters 1990). Dominance hierarchies within groups of adults are formed where males are dominant over females, and within sexes, older birds are dominant over younger birds (Jackson 1994). Breeding pairs are socially and genetically monogamous (Haig et al. 1994). Family groups defend permanent territories surrounding a cluster of cavity trees used for nesting (Walters 1990; Jackson 1994) and roosting (Jackson 1994). Cavity excavation is done exclusively in mature living pine trees (primarily longleaf pine, *Pinus palustris*) and usually takes several years to complete (Conner and Rudolph 1995; Harding and Walters 2002, 2004).

Colonization of areas without existing cavity trees is rare (Walters 2004), suggesting that the limited availability of cavity trees may be a key component driving population dynamics (Walters 1991; Carrie et al. 1998; Harding and Walters 2002) as well as a possible ecological constraint supporting the evolution of delayed dispersal (Emlen 1982; Walters et al. 1992a). Clutches of 3-4 eggs are laid starting mid-April, incubation lasts only 10-13 days and nestlings fledge after 26-29 days (Ligon 1970; Winkler et al. 1995). Once fledged, young continue to beg and are fed by adults in the group for as long as five months post fledging (Ligon 1970), but intense begging behavior stops by mid-late September when the young are presumed to forage independently (E.L.H.R. personal observation).

Study populations

Our primary study area covers 110,000 hectares in the Sandhills region of south-central North Carolina including the western portion of U.S. Army Fort Bragg (FB), U.S. Army Training Facility Camp Mackall (MACK), and the North Carolina Sandhills Game Lands in Hoffman (SGL) as well as a number of smaller publicly and privately owned sites (SOPI and MINOR). The study population contains over 220 family groups included in a long-term demographic study since 1980, and annually more than 95% of the individuals are banded with unique color band combinations. The Sandhills Ecological Institute (SEI) currently collects basic reproductive data, and dispersal and survival fates are known for most individuals through an annual breeding season census. For a thorough description of the study area and monitoring techniques see Walters et al. (1988).

Several cohort samples from within the Sandhills population were selected for use in this study. The first three cohort samples (CS1-CS3 from 2007-2009, respectively) consisted of a subset of juveniles with known intrabrood social ranks from broods containing at least two males in the FB, MACK and SGL study areas. These juveniles were specifically chosen and sampled as part of a three year study on social dominance and natal dispersal (Hewett Ragheb and Walters 2011). The fourth (CS4) and fifth (CS5) cohort samples consisted of all juveniles from the FB 1984 and 1985 cohorts, respectively. The sixth (CS6) and seventh (CS7) cohort samples consisted of all juveniles from the SOPI 1984 and 1985 cohorts, respectively. CS4 through CS7 were part of a population-wide winter census study, where all family groups were monitored in December-January and the locations of juveniles recorded.

The second study area covers over 34,000 hectares of coastal plain habitat along the southeastern coast of North Carolina on Marine Corps Base Camp Lejeune (CL). This population of more than 70 family groups has been part of an annual monitoring program since 1986, and annually more than 95% of the population is individually marked with unique color band combinations. For a more detailed description of the study area and population see Zwicker and Walters (1999). A single cohort sample was used from this population (CS8), and it consisted of all fledglings from the 2007 cohort. In addition to the standard breeding season census, CS8 was included in a population-wide winter (January) census where every known family group was visited and the location of all individuals, including dispersed fledglings, recorded.

General methods

Red-cockaded woodpecker groups were monitored for nesting during the breeding season on 7-10 day cycles starting the third week of April. Additional visits were scheduled such that all

nestlings could be banded between ages 5-10 days. All nestlings were banded with both aluminum USFWS bands and a unique combination of plastic colored leg bands. In addition to standard mass measurements, the length of the right leg was measured (CS1-CS3 only, Hewett Ragheb and Walters 2011). Nests were visited again when nestlings were age 20 days and the sexes of all nestlings were identified based on the presence (male) or absence (female) of a red crown patch (CS1- CS3 only). Fledging confirmation observations were conducted within the first two weeks of fledging, and, for CS4-CS8, fledgling sex was also determined at this time. Groups were visited a second time if the number of observed fledglings differed from the number expected based on the previous nest check. See Walters et al. (1988) for further details.

PART 1: Intra brood social environment (males only)

Social rank assignment

For CS1-CS3, groups containing more than one male fledgling were selected from the population and 30-minute focal observations (Altmann 1974) were conducted on every fledgling from those broods. All focal observations were conducted between 0600 and 1030 by a single observer (E.L.H.R.) during periods without rain. All conflicts during the focal observation were recorded, and the winner and loser of each conflict were assigned. Numeric ranks (where 1 represents the most dominant individual) were assigned to individuals based on the outcome of conflicts with siblings using information gathered during all focal observations for siblings in that group. More complicated indices of dominance were not required, since rank reversals were exceptionally rare and sibling groups were never larger than four individuals, making rank assignments simple (See Hewett Ragheb and Walters 2011 for full methodology).

Live re-sighting

Encounter histories were created for every juvenile male with known intrabrood social rank from CS1-CS3. Individuals entered the study (“initial capture”) at the date of intrabrood social rank assignment. We returned to all of the original natal focal groups in July, December and May and recorded the presence or absence of focal juveniles. We visited active territories during routine monitoring work in June and July and recorded any focal juveniles located off their natal territories. We may have missed focal birds during visits to their natal cluster because they were foraging (Kesler et al. 2010). We made no effort to locate individuals off the natal territory in December. In the spring, we located dispersed individuals during the population-wide breeding season census (May-August). Dispersal off the study area is relatively infrequent and estimated at 6% annually by Walters et al. (1988).

For every sampling occasion, focal birds were categorized into one of two states. Any bird observed foraging and associating with its natal family group was considered a natal resident. Birds found alone or associating with a group on a territory that was not their original natal territory were considered dispersed. The success of such dispersal events from a reproductive standpoint (i.e., whether or not dispersers bred the following year) was not considered when making this classification. No individuals in the CS1-CS3 samples that were observed off the natal territory were ever seen on their natal territory again; therefore we assume that permanent dispersal events were not confused with temporary forays (Kesler et al. 2010).

Multistate mark-recapture model

To estimate apparent survival (Φ) and recapture probability (p) for natal territory residents and dispersers, we used a multistate mark-recapture analysis in Program MARK (MARK; White and Burnham 1999; White et al. 2006), where recapture refers to live re-sighting events occurring during sampling occasions. The multistate approach also allowed us to estimate the probability that an individual will transition from natal resident (N) to disperser (D) (Ψ^{ND}) or from disperser to natal resident (Ψ^{DN}) states. This procedure assumes a first-order Markov chain process where mortality is modeled as taking place before movement, all movement between states occurs at the same point in the sampling interval and detection occurs instantaneously within a sampling occasion (Brownie et al. 1993).

In order to generate a biologically relevant candidate model set based on *a priori* knowledge of the system (Anderson 2008), we used a 4-stage model selection procedure in which we first established the basic structure of the general model by incorporating three likely covariates (cohort, fledging date and condition relative to the population) based on our understanding of post-fledging natal survival (Stage 1) and dispersal probability (Stage 2). For the remaining stages, we used the best supported model(s) generated after stages 1 and 2 to construct models representing some of our predictions for natal survival (Stage 3) and dispersal probability (Stage 4). Where there was ambiguity regarding selection of a single best model, all models where $\Delta QAIC_c < 2$ were retained for use in future stages (Anderson 2008).

For all models, the probability of recapture for the two states was considered equal and constant across seasons ($p^{N=D}(\cdot)$), where p is the probability of recapture, $N=D$ represents no difference between natal resident and disperser states, and (\cdot) represents constancy over seasons. The exception was the December sampling occasion where the probability of recapture was fixed to zero in the disperser state because no effort was made to locate dispersed individuals. Since

we were interested in estimating survival separately for birds in the natal resident and disperser states, we included a state effect on apparent survival. Apparent survival for natal residents was modeled as variable across seasons ($\Phi^N(t)$), where t equals variation among sampling occasions, and apparent survival for birds in the disperser state as constant across season ($\Phi^D(\cdot)$). While seasonal variation in disperser survival ($\Phi^D(t)$) may be likely, small sample sizes of dispersers during some sampling occasions prevented reliable estimation of season-specific apparent survival. The transition rate from natal resident to disperser for all models varied with season ($\Psi^{ND}(t)$). Since no birds in our study were ever observed to return to the natal territory once dispersed, the probability of transition from disperser to natal resident was modeled as constant and fixed to zero ($\Psi^{DN}(0)$). To summarize, the structure of the starting model was:

$$\Phi^N(t) \Phi^D(\cdot) p^{N=D}(\cdot) \Psi^{ND}(t) \Psi^{DN}(0).$$

To generate the model set for Stage 1, all possible additive combinations of three general covariates were added to the natal survival term ($\Phi^N(t)$): ‘cohort’ (2007, 2008, and 2009) representing annual variation, ‘flg’ representing fledging date within a season, and ‘conpop’ representing condition relative to the population mean. We estimated date of fledging as date of banding + (26 days-estimated age at banding) (Ligon 1970). Condition scores represent the focal individual’s residual from the linear regression of nestling mass against nestling leg length at banding using the expanded sample of all nestlings banded from 2007 to 2009 (n=932). For focal individuals missing leg length measurements (and ‘conpop’ scores; N=21), we assigned the mean value of condition relative to the population (-0.0186 g/mm). To generate the model set for Stage 2, all possible additive combinations of the general covariates ‘cohort,’ ‘flg,’ and ‘conpop’ were added to the dispersal probability term ($\Psi^{ND}(t)$) in the best supported model(s) from Stage 1.

Stage 3 of model selection involved comparing models representing predictions about the role of relative competitive ability or intrabrood social rank on natal survival by adding covariates to the natal survival term in the best supported model(s) from Stage 2. Since we know that condition relative to brood-mates at banding is correlated with dominance among male brood-mates (Chapter II), the role of relative condition and social rank were assessed by comparing separate models. To explore our prediction that individuals in high physical condition relative to their brood-mates at banding will have higher apparent natal survival as fledglings, we created models containing a continuous covariate for nestling condition relative to male brood-mates ('conbro') on the apparent natal survival term. Condition was calculated as mass divided by leg length. Relative condition was calculated as the focal individual's difference from the mean nestling condition of all male brood-mates. For focal individuals missing leg length measurements (and 'conbro' scores; N=21), we assigned the mean value of condition relative to male brood-mates (0 g/mm). Then, to examine our prediction that males with high social rank relative to their brothers will have higher natal survival, we created models containing a categorical covariate for social rank ('rank') on the apparent natal survival term. The rank covariate was created by splitting all focal males into two groups (dominant or subordinate), where dominant individuals were socially superior to all siblings (numeric rank 1) and subordinates were subordinate to at least one sibling (numeric ranks 2-4). Models containing 'conbro' or 'rank' in the natal survival term (Φ^N) were compared using QAIC_c scores and only the most supported model(s) from Stage 3 were retained for use in Stage 4.

For Stage 4, we used the best supported model(s) from Stage 3 to create models representing predictions about the role of relative competitive ability on natal dispersal probabilities. To determine whether dispersal probability varies with condition relative to brood-

mates, we created models where ‘conbro’ was added to the dispersal probability term. Then, models representing the prediction that subordinate individuals will be more likely to disperse than their dominant brothers were created by adding the covariate ‘rank’ to the dispersal probability term. Models containing ‘conbro’ or ‘rank’ in the probability of dispersal term (Ψ^{ND}) were then compared using QAIC_c scores. Model likelihoods and model weights (w_i) were calculated to further interpret the relative support for various models in the set.

Models were compared within stages based Akaike’s Information Criterion (AIC_c) corrected for small sample size (Anderson 2008). To account for possible overdispersion of the data, we tested the goodness of fit of the starting model using the median \hat{c} test in MARK. In cases when $\hat{c} \approx 1$, overdispersion is absent and no correction is required; in cases when $\hat{c} > 1$, we calculated the quasi AIC_c (QAIC_c) by manually adjusting the value of \hat{c} (Cooch and White 2010). Lower AIC_c or QAIC_c scores are assigned to models with stronger support relative to the other models in the set (Anderson 2008).

The effect of general covariates, ‘cohort’, ‘flg’, ‘conpop,’ and ‘conbro’ on apparent natal survival (Part 1) and natal dispersal (Part 2) probabilities were evaluated based on whether or not they improved model fit (models with $\Delta\text{QAIC}_c < 2$ are considered equivalent) as well as the direction and strength of their beta coefficient estimates (slope and 95% confidence intervals from the final highest ranking model). We calculated model-averaged estimates and unconditional 95% confidence intervals for parameters Φ^N , Φ^D , p and Ψ^{ND} (Buckland et al. 1997). Mean values for general covariates were used when generating model-averaged parameter estimates. Parameter estimates were interpreted based on model-averaged point estimates and unconditional 95% confidence intervals. Although a large number of models were created, only

the best fitting models or those required for comparison of predictions are presented in the results section (but see online *Supplementary Data* Table S1 for list of all models in candidate set).

Role of current social environment on dispersal strategy

In order to assess the role of sibling presence on dispersal behavior, we compared the natal social environment for subordinate males that were recorded as either dispersed or delaying dispersal in the population-wide breeding season census following their hatch year using a likelihood ratio chi-square test (JMP, Version 8. SAS Institute Inc., Cary, NC). For this analysis, detection rates were assumed to be 100% for both dispersers and natal residents. Natal social environment was split into two possible categories; cases where subordinate males came from natal territories where at least one socially superior brother remained on the natal territory in the spring, and cases where all socially superior siblings were absent (either dead or dispersed) in the spring. Birds surviving to the breeding season census were pooled across cohorts (2007-2009).

PART 2: Intra brood social environment (both sexes)

Live re-sighting

To assess the role of sex on juvenile survival and the approximate timing of natal dispersal, we compared the locations of juveniles during two population-wide census periods which serve as snapshots of bird movement in the population. Male and female juveniles from CS4-CS8 were first sampled during the routine fledging check for their family (see General methods). The entire population was then censused in winter (December-January) and again

during the subsequent breeding season census (BS1: Apr-August). For each sampling occasion after fledging, individuals were recorded as belonging to one of three states: dead (missing from population during sampling occasion and never observed alive at a later sampling occasion), dispersed (discovered roosting or foraging with members of a non-natal group and never again observed at the natal territory), or natal (observed roosting or foraging with natal family group).

Dispersal paths were assigned to individuals based on the timing of transition between these states. ‘Fall dispersers’ were missing from their natal territory during the winter census and discovered on a non-natal territory at least once during either the winter or breeding season censuses. ‘Spring dispersers’ were seen on their natal territory during the winter census and found on a non-natal territory during the breeding season census. ‘Natal residents’ were still on their natal territory during the breeding season census. We included only individuals with known paths. Here, we did not use formal mark-recapture methods that account for detection probability since there were only two sampling intervals and the sampling occasions post-fledging were population-wide (resulting in a very high probability of detecting birds if they were alive). For statistical analysis, we used SAS 9.2 software (SAS Institute Inc, Cary, NC, U.S.A.).

Estimates of survival and dispersal probability

Survival probability was estimated for three juvenile subgroups. In the first subgroup, survival was estimated from the end of the fledge check period to the winter census (July-Dec) and included all individuals known to have fledged from CS4-CS8. In the second subgroup, survival was estimated from the end of the winter census to the breeding season census (Jan-May) and included only juveniles known to be alive as dispersers. In the third subgroup, survival was also estimated from Jan-May, but only included juveniles known to be alive on their natal

territory during the winter census. To determine how survival probability differs between these subgroups and sexes, we created nine binary logistic regression models (Proc GLIMMIX; SAS) where the binary probability of survival was the dependent variable and sex, subgroup, cohort sample (CS4-CS8), and a sex*subgroup interaction term were the independent covariates.

Natal dispersal probability was estimated for the July-Dec interval for all juveniles known to have fledged from CS4-CS8 and the Jan-May interval for all juveniles known to be alive on their natal territory during the winter census. To determine how natal dispersal probability differs between sexes and among time interval-location subgroups, we created four binary logistic regression models (Proc GLIMMIX; SAS) where the binary probability of dispersal (natal vs. dispersed) was the dependent variable and sex, subgroup (July-Dec vs. Jan-May), and a sex*subgroup interaction term were the independent covariates. Variation among cohort samples could not be assessed for the probability of natal dispersal because models containing the cohort covariate contained too many parameters and would not converge.

For both survival and dispersal, all possible additive combinations of independent covariates were used to create the candidate model sets. We tested the goodness-of-fit of the most parameterized model by calculating the deviance statistic \hat{c} (Pearson X^2/df) as a measure of overdispersion. Model selection was based on relative AIC_c or $QAIC_c$ model ranks as described in the methods for the mark-recapture analysis (Part 1). Estimated probabilities were converted from interval rates to monthly rates for presentation where:

$$\text{monthly probability} = \text{interval probability}^{1/\# \text{ months in the interval}}$$

Role of relative nestling mass on dispersal strategy

To determine if intrabrood nestling mass differences can be used as a predictor for eventual dispersal strategy and how this may differ between the sexes, we compared the relative sizes of nestlings at banding for juveniles surviving to the breeding season census according to their adopted dispersal path. We created nine multinomial logistic regression models (Proc GLIMMIX; SAS) where dispersal path (fall disperser, spring disperser or natal resident) was the categorical dependent variable and sex, relative mass, cohort sample (CS4-CS8), and a sex*relative mass interaction term were the independent covariates. Relative mass scores were calculated as a nestling's residual from the mean mass of all siblings of either sex known to have fledged. Relative mass has been used as a surrogate for intrabrood social rank in similar studies on other species (Stanback 1994; Koenig et al. 2011), and in red-cockaded woodpeckers, there is a relationship between relative condition at banding and fledgling intrabrood social rank among male brood-mates (Chapter II). All possible additive combinations of these terms were used to create the candidate model set and models were compared using the same information theoretic approach as described in Part 2: Estimates of survival and dispersal probability.

Dispersal strategy and first-year reproductive role

We used CS4-CS8 again to assess how sex and dispersal path (fall disperser, spring disperser and natal resident) influences first-year reproductive roles. We assigned birds surviving to the breeding season census into four categories based on their reproductive role in the population: (1) breeders, (2) solitary individuals, (3) helpers, or (4) floaters. Breeders were individuals who were either the oldest or the only adult holding an active territory with a mate.

We only considered social position when making this classification, not actual nesting effort or success. Breeders obtain this social position through territory inheritance (if natal resident) or by dispersing and replacing the previous breeder. Solitary individuals were birds holding an active territory lacking other group members. Helpers were individuals residing on an active territory held by a pair of breeders. The helper social position is obtained by remaining on the natal territory, often with related individuals, or by dispersing and becoming an unrelated helper in another group. Only within-group social position, not participation in helping behavior was considered when making this classification. Floaters were dispersed individuals that were not accepted as members by any existing family groups and held no territory. See Walters et al. (1988) for expanded description of reproductive roles.

RESULTS

PART 1: Intra brood social environment (males only)

Estimates of survival and dispersal probability

Two-hundred and fourteen juvenile males from 98 broods were assigned social ranks and entered into the mark-recapture study (Table 2). The starting model (model 1; Table 3) fit the data with minimal overdispersion (median \hat{c} value = 1.25 ± 0.12 sampling SE). We evaluated 64 nested models (Stage 1: Models 1-8, Stage 2: Models 9-36, Stage 3: Models 37-50, Stage 4: Models 51-64; online *Supplemental Data*, Table S1). The model-averaged parameter estimates and unconditional 95% confidence intervals (CI) for the monthly probability of recapture (constant across state and sampling interval) was 0.966 (CI: 0.914-0.987); the monthly

probability of apparent survival for dispersers (constant across sampling interval) was 0.936 (CI: 0.786-0.983).

Natal survival was higher for birds that fledged earlier in the season than those fledging late. This is indicated by Stage 1 and Stage 2 of model selection, where all models containing the fledge date ('flg') covariate in the natal survival term were a better fit than those without (Model 5 vs. 2, $\Delta\text{QAIC}_c=3.8125$; Table 3), and there was a negative relationship between fledge date and apparent natal survival (Model 51, slope = -3.2691 (CI: -5.7014,-0.8369)). Natal survival varied by cohort and our estimates for natal survival were improved slightly by the addition of 'cohort' to models in Stage 1 (Model 5 vs. 3, $\Delta\text{QAIC}_c=0.9729$; Table 3). Natal survival was reduced in 2007 compared with 2009 (Model 51, slope = -0.6189 (CI: -1.1700, -0.0677)), but there was no difference between 2008 and 2009 (Model 51, slope = -0.3634 (CI: -0.8840, 0.1575)). Natal survival did not appear to vary with nestling condition relative to the population, as the addition of the 'conpop' covariate to the natal survival term did not improve the fit of models in Stage 1 (Model 8 vs. 5, $\Delta\text{QAIC}_c= -1.2178$; Table 3). The probability of dispersal did not vary with cohort, fledging date or condition relative to the population as none of three general covariates improved model fit when added to the dispersal probability term in Stage 2 ('flg': Model 5 vs. 10, $\Delta\text{QAIC}_c= -1.9510$; 'cohort': Model 5 vs. 9, $\Delta\text{QAIC}_c= -1.9510$; conpop': Model 5 vs. 11, $\Delta\text{QAIC}_c= -1.6940$; Table 3).

Stage 3 revealed evidence that first-year natal survival is better predicted by fledgling social rank than condition relative to brood-mates. Adding condition relative to brothers ('conbro') to the best fitting models from Stage 2 did not improve model fit (e.g. Model 5 vs. 44, $\Delta\text{QAIC}_c= -1.719$; Table 3), while adding social rank ('rank') did (e.g. Model 5 vs. 37, $\Delta\text{QAIC}_c=3.107$; Table 3). Stage 4 revealed strong evidence that social rank better predicts the

probability of dispersal than condition relative to brood-mates. Adding condition relative to brothers ('conbro') to the best fitting models from Stage 3 did not improve model fit (e.g. Model 37 vs. 58, $\Delta\text{QAIC}_c = -2.1182$; Table 3), while adding social rank ('rank') did (e.g. Model 37 vs. 51, $\Delta\text{QAIC}_c = 6.740$; Table 3).

Apparent monthly natal survival (Φ^N) was lowest for both dominant and subordinate juveniles during the June-July interval and increased during the Aug-Dec and Jan-May intervals (Figure 2). Apparent survival remained constant between the Aug-Dec and Jan-May intervals. For all intervals, subordinate males had lower estimated natal survival probability estimates than their dominant brothers but with considerable overlap in unconditional 95% confidence intervals (Figure 2). The probability of natal dispersal (Ψ^{ND}) varied with sampling interval and was higher during the January-May interval than the June-July or August-December intervals (Figure 3). Across all intervals, subordinate males had higher dispersal estimates than their dominant brothers, but this difference is most striking across the Jan-May interval when subordinate males are 3.75 times more likely to disperse than their dominant brothers (Figure 3). Again, there was considerable overlap in unconditional 95% confidence intervals likely due to the relatively small number of dispersing individuals.

Role of current social environment on dispersal strategy

Of the 36 subordinate males that survived to their first spring, those that dispersed were more likely to have a socially superior male brood-mate remaining on the natal territory during the breeding season census than those that delayed dispersal (Likelihood ratio test: $X^2_{1} = 10.5$, $N = 36$, $P = 0.001$). Ten of 14 (71%) dispersing subordinate males had socially superior male brood-mates remaining on the natal territory, and the remaining four (29%) individuals dispersed

even though their dominant brother was missing from the natal territory by the first breeding season census. Eighteen of 22 (82%) subordinate males that delayed dispersal had socially superior brothers that were dead, while only four (18%) cohabitated the natal territory with a socially superior brother.

PART 2: Intra brood social environment (both sexes)

Estimates of survival and dispersal probability

Of 242 male and 216 female fledglings from CS4-CS8, 228 male and 201 female fledglings with known dispersal paths were included in analyses (Figure 1). Cohort samples varied in the proportion of fledglings with known paths. Paths were known for 86% of males and 79% of females in CS4, 97% of males and 100% of females in CS6, 100% of males and females in CS5 and CS7, and 96% of males and 98% of females in CS8.

The best supported model for post-fledging survival probability included both sex and subgroup terms but not the interaction between sex and subgroup (AIC_c weight=0.475; Table 4). The second ranking model was close ($\Delta AIC_c=1.91$) and contained only the subgroup term (AIC_c weight=0.183). Estimates generated from the best fitting model reveal slightly higher monthly survival probabilities for males than for females in each subgroup but with considerable overlap in 95% confidence intervals (Figure 4). Monthly survival estimates were nearly equivalent across the three subgroups (Jun-Dec, all fledglings; Jan-May, overwinter dispersers; and Jan-May overwinter natal residents). Overwinter dispersers in Jan-May had slightly lower monthly survival rates compared with the other two subgroups, but with considerable overlap in 95% confidence intervals.

The best supported model for natal dispersal probability contained sex, subgroup and the interaction between sex and subgroup. This model was strongly supported relative to the other models (AIC_c weight=1.000; Table 5). According to estimates generated from the best fitting model, females were more likely to disperse than males in both intervals (Figure 5). This difference is most striking during Jan-May when the monthly dispersal probability for females was 9.5 times higher than for males.

Role of relative nestling mass on dispersal strategy

One hundred twenty-one male and 96 female juveniles with relative nestling mass scores survived to the breeding season census (Figure 1). The best-supported model for dispersal probability indicated that dispersal path was influenced by nestling sex, relative mass and the interaction between sex and relative mass (AIC_c weight=0.862; Table 6). The strength of these slope coefficients varied according to pair wise comparisons of dispersal paths (Table 7). Males with low relative mass and all females were more likely to disperse in the fall than remain home (Table 7, Figure 6). Birds dispersing in the spring differed from natal residents by sex only, where females were again more likely than males to disperse, but relative mass did not influence dispersal path (Table 7, Figure 6). For dispersing individuals, the timing of dispersal (fall vs. spring) was predicted by relative mass for males only, where low-mass males were more likely to disperse in the fall than spring, but female dispersal timing was uncorrelated with relative nestling mass (Table 7, Figure 6). For females, the most common dispersal path was spring dispersal, followed by fall dispersal and then becoming a natal resident (Figure 6). For males, becoming a natal resident was the most common dispersal path, followed by fall dispersal for low-mass males and then spring dispersal (Figure 6).

Dispersal path and first-year reproductive role

Of the 429 total fledglings from CS4-CS8, 118 males and 82 females survived to the breeding season census. There was no statistical difference in the distribution of breeding roles between fall and spring dispersing males (Likelihood ratio chi-square: $X^2_{1}=0.03$, $N=27$, $P=0.8632$). Of the males that dispersed in the fall and survived to the breeding season census ($n=13$), 54% became breeders, 23% solitary, 15% helpers and 8% floaters. Of the similar number of males that survived their first year and waited until the spring to disperse ($n=14$), 57% became breeders, 14% solitary, 21% helpers and 7% floaters. The majority of surviving males remained on the natal territory through the breeding season census ($n=91$), and, of these, 92% were natal helpers, 7% inherited the natal territory as breeders and 1% remained on the natal territory as solitary individuals (Figure 1a). Of the females that dispersed in the fall and survived to the breeding season census ($n=22$), 73% became breeders, while the remaining 27% became floaters. Over twice as many females waited until the spring to disperse ($n=51$), and, of these, 84% became breeders, 2% helpers and 14% floaters. There is no statistical difference in the distribution of status classes between fall and spring dispersers (Likelihood ratio chi-square: $X^2_{1}=0.84$, $N=72$, $P=0.3593$). Very few females chose to delay dispersal and remain on the natal territory through the breeding season census ($n=9$), and 100% of these females became helpers at their natal group (Figure 1b).

DISCUSSION

Our results provide partial support for the first and third hypothesis for the adaptive role of delayed dispersal behavior. Overwintering on the natal territory is the preferred strategy for

both male and female juvenile red-cockaded woodpeckers, and the probability of fall dispersal as well as the decision to remain on the natal territory as a helper the following spring is strongly influenced by intrabrood social rank between and within sexes following our predictions under our first hypothesis. However, first year survival and the probability of filling a breeder vacancy by the first breeding season does not vary between individuals dispersing in fall and spring, suggesting that delayed dispersal behavior may also result from increased lifetime fitness benefits generated by remaining on the natal territory beyond the first year, in addition to the immediate benefits gained during the first year as suggested in our third hypothesis. Here we discuss the predictions generated under our three hypotheses for the adaptive significance of natal dispersal strategy.

Intrabrood social rank and natal survival

As predicted by our first and second hypotheses, intrabrood social rank between sexes and within males is an important predictor of monthly natal survival. Natal survival for juvenile males is slightly higher across all intervals than for females. This difference in survival has been explained in other species as a consequence of sexual dimorphism favoring larger male nestlings (Green and Cockburn 2001; Koenig et al. 2001a), where larger offspring should incur a survival cost due to higher energy requirements associated with maintaining their size (Fisher 1958). This exception may also be the case in red-cockaded woodpeckers since intrabrood dominance hierarchies are male-biased, but additional descriptive work is required to determine the degree of sexual dimorphism in the nestling stage and its consequences for post-fledging survival. Within males, natal survival is slightly lower for subordinate males compared to their dominant

brothers. This is similar to the findings for pairs of acorn woodpecker juveniles, where dominant males had much higher overwinter survival than their subordinate brothers (Koenig et al. 2011).

Although nestling condition relative to brothers and fledgling social dominance are positively correlated for juvenile male red-cockaded woodpeckers (Hewett Ragheb and Walters 2011), it is rank that appears to best explain these survival patterns. Intra-brood social rank corresponds to access to food during the post-fledging dependent period where subordinate females are fed less than dominant males, and subordinate males are fed at intermediate rates (Hewett Ragheb and Walters 2011). If socially mediated access to food (both between and within sexes) drives post-fledging survival, then it is not surprising that social rank is a better explanatory variable than relative mass or condition since it is a more direct measure of competitive ability in a family-specific context. This is an important addition to our current understanding of the predictors of post-fledging survival since many previous studies examine only mass or condition differences between young (Green and Cockburn 2001; Koenig et al. 2001a; Koenig et al. 2011). Stanback (1994) found that in acorn woodpeckers intra-brood social rank has no effect on post-fledging survival, and both sexes are equally likely to be dominant. However, a study using a larger dataset with relative nestling size as a surrogate for social dominance revealed higher post-fledging survival rates for larger brood-mates (Stanback 1991). An alternative explanation for reduced natal survival of females and subordinate males may be their increased dispersal behavior, if the transient phase of dispersal turns out to have a significant mortality cost (see *Costs of dispersal* below). A second alternative is that reduced survival with inferior social rank may stem from the direct consequences of frequent physical attacks, rather than decreased access to food. Although the rate of aggressive conflict among brood-mates gradually decreases by 3-4 months post-fledging (E.L.H.R., personal observation),

it is possible that even occasional aggressive interactions or the threat of attack is enough to increase stress hormone levels or mortality rates for subordinates.

Natal dispersal

Our estimates for first year natal dispersal probability reveal large variation between and within the sexes, where socially and competitively inferior individuals are more likely to disperse within their first year than their superior brood-mates. This finding supports the predictions from our first hypotheses where individuals with low intrabrood social placement shift from natal philopatry to dispersal as a result of decreased access to direct benefits of the natal territory. It also supports our third hypothesis where individuals compete to remain on the natal territory in order to obtain the future lifetime fitness benefits associated with this strategy (Walters et al. 1992b).

Females are more likely to disperse than males during both the fall and spring intervals corresponding to the strongly female-biased dispersal patterns found previously in this (Walters 1990) and most other bird species (reviewed in Greenwood 1980). The near-obligate first year dispersal observed in female red-cockaded woodpeckers may be driven by intersexual differences in the long term benefits of philopatry (Moore and Ali 1984; Daniels and Walters 2000a). Males that delay dispersal have increased lifetime fitness (Walters et al. 1992b) and an opportunity to inherit the natal territory. On the other hand, it is not clear that delayed dispersal leads to increased lifetime fitness in females. Females rarely delay dispersal long enough to inherit, and even then, their ability to inherit is restricted by inbreeding avoidance. Since females will only breed with an unrelated male, a young helper female would only be able to inherit her natal territory upon the death or departure of the breeding female and all related males. While

this may set up a situation where early dispersal is preferred by females (following our second hypothesis) in order to compete for breeding vacancies, the majority of females overwinter on the natal territory and then disperse in the spring. This implies that overwintering on the natal territory is the preferred strategy for both sexes.

The timing of female natal dispersal does not show a strong relationship with relative nestling mass. What causes the variation in dispersal strategies between fall and spring dispersing females is not clear. Observations of female-only broods and broods containing multiple females reveal social hierarchy formation and frequent physical aggression similar to that seen with males (E.L.H.R. personal observation). It is possible that intrabrood social rank drives dispersal in females, but unlike males, relative nestling mass does not serve as an adequate proxy for rank.

Relatively few studies have looked specifically at the role of intrabrood female aggression and its impact on natal dispersal. Cooperatively breeding pied babbler (*Turdoides bicolor*) females are more aggressive than males, and within females, aggressive individuals disperse early (Raihani et al. 2008), unlike the dispersal patterns observed in red-cockaded woodpecker females. In Siberian jays (*Perisoreus infaustus*) and Western screech-owls (*Otus kennicottii*), socially dominant siblings were more likely to remain on the natal territory regardless of sex (Ellsworth and Belthoff 1999; Ekman et al. 2002). In acorn woodpeckers (*Melanerpes formicivorus*), there is no sex bias in intrabrood social dominance, and both sexes frequently become philopatric helpers (Stanback 1994). In red-cockaded woodpeckers there is a strong sex bias in social dominance, and the effect of social rank on dispersal may apply first between sexes then within sexes. If this is the case, we would predict that the rare instances when females remain as helpers occur in female-only broods since this is the only situation where a

female can be the highest ranking brood-member. Support for this prediction is observed in red-cockaded woodpeckers from the Sandhills population where females raised in broods of one are the most likely to delay natal dispersal (Chapter IV). This scenario was proposed for gray jays (*Perisoreus canadensis*), but the proportion of philopatric females in the population does not support this idea (Strickland 1991).

Within juvenile males, natal dispersal probability varies with intrabrood social rank, where subordinate males were more likely to disperse over all intervals than their dominant brother. Intrabrood social rank is a better predictor of dispersal strategy than relative condition, confirming earlier assumptions regarding the social mechanism behind individual variation in dispersal (Pasinelli and Walters 2002). Furthermore, subordinate males shift their dispersal strategy contingent on the presence of their dominant brother, which provides additional support to the idea that dispersal strategies are flexible rather than fixed based on physical traits as a nestling (relative mass or hatch order etc.).

Costs of dispersal

Monthly survival for dispersed juvenile males (94%; ranks and sampling intervals pooled) was equivalent to monthly natal survival for dominant males (94%) and slightly higher than monthly natal survival for subordinate males (90-91%) after the initial month post-fledging. Similarly, monthly survival for male and female dispersers was not reduced compared to natal residents. This is contrary to our first hypothesis that suggests the direct benefits of philopatry increase the probability of surviving the winter and provide a proximate mechanism for the evolution of delayed dispersal behavior. This is also contrary to the assumption that natal dispersal has a substantial mortality cost (Johnson and Gaines 1990; Walters et al. 1992b;

Stamps 2001). Reduced survival during dispersal movement is seen in mammals as a result of human activity (Devillard and Bray 2009) or predation (VanVuren and Armitage 1994).

Also, mortality associated with dispersal of breeding female red-cockaded woodpeckers was more than double that of non-dispersing breeding females (Daniels and Walters 2000b).

The equivalent survival probabilities for natal residents and dispersers observed after settlement on established territories suggests that any survival costs associated with natal dispersal are borne during the transient phase, and not subsequent to movement. Equivalent overwinter survival was also found between philopatric and settled dispersing yellow-bellied marmots (*Marmota flaviventris*; VanVuren and Armitage 1994) and red-bellied woodpeckers (Cox and Kesler 2010). However, there is growing evidence that natal dispersal does not necessarily have a substantial mortality cost even during the transient phase. Early foray activity by juvenile red-bellied woodpeckers (Cox and Kesler 2010) and transient dispersal activity in juvenile ruffed grouse (*Bonasa umbellus*; Small et al. 1993) did not result in increased mortality. In the former case most juvenile mortality occurred on the natal territory in the first few weeks after fledging, and thus was not linked to foray behavior or whether juveniles moved early or stayed longer on the natal territory. The same may be true of red-cockaded woodpeckers, which also exhibit juvenile forays before permanent natal dispersal (Kesler et al. 2010). Lower survival of subordinates may be due to competition with brood-mates on the natal territory rather than their greater predilection to disperse.

Alternatively, it may be that we underestimated dispersal mortality due to our inability to find individuals during the transient stage prior to establishment at a new territory. Dispersing juveniles that die before detection are included in natal mortality under the assumptions of multistate mark-recapture models (Brownie et al. 1993) resulting in elevated estimates of natal

mortality. Increased population-wide censuses or studies using radio telemetry during the first few months post-fledging are needed to distinguish these possibilities. When scaled for comparison, our multistate mark-recapture natal survival estimates for juvenile red-cockaded woodpecker males are nearly identical to weekly post-fledging natal survival estimates from a unique radio telemetry study on fledgling red-bellied woodpeckers (*Melanerpes erythrocephalus*) (Cox and Kesler 2010). This similarity with a radio telemetry study provides support for the accuracy of our estimates of dispersal probability versus natal mortality.

Our natal survival estimates for juvenile male red-cockaded woodpeckers are lowest during the first month post-fledging then increased and stabilized during the remainder of the year, a temporal pattern commonly observed in studies of post-fledging survival (Green and Cockburn 2001; Yackel Adams et al. 2006). We detected only a negligible increase in monthly natal survival with age in Part 2, but this temporal pattern was diluted when spread across our five month sampling interval (June-Dec) instead of 1 month (June-July; Part 1). The difference between monthly and whole-season survival highlight the importance of evaluating both the early and late fledging period when calculating post-fledging survival in woodpeckers. Sampling only during the early weeks would result in underestimation of survival estimates and important life history patterns may be missed when estimating across larger sampling intervals.

Low natal survival immediately after fledging may be a result of increased vulnerability to predators (Cox and Kesler 2010). Fledgling red-cockaded woodpeckers are noticeably less agile in flight and foraging locomotion than adults (E.L. H.R. personal observation). They also frequently emit predatory alarm calls when near any fast flying bird (including non-predators such as mourning doves (*Zenaida macroura*); E.L.H.R. personal observation), suggesting that,

while they exhibit heightened caution, their ability to accurately identify predators may be limited during the first weeks after fledging (see also Rajala et al. 2003).

First-year reproductive roles

Remaining as a helper on the natal territory is the most common strategy for male first year survivors. However, for males that do disperse and survive to the breeding season census, dispersal timing (fall versus spring) does not appear to impact the probability of filling a breeding role in the spring. For surviving females, remaining on the natal territory is a rarely adopted strategy, and the majority of females disperse by their first spring. Of the surviving dispersers, spring dispersal is more common and these females have a slightly, but insignificantly higher probability of becoming breeders. This suggests that for females, dispersal timing does not impact reproductive role in the spring. These findings do not support the directional predictions generated by our first and second hypotheses. However, these findings are also consistent with our third hypothesis. If the benefits of delayed dispersal come with increased lifetime fitness as a result of remaining on the natal territory beyond the first breeding season, we would not expect to see variation in the probability of filling a breeding vacancy regardless of the timing of first-year dispersal. If this study was extended several years, we might expect to detect a bias in reproductive roles favoring delayed dispersing individuals that would eventually lead to the equal or slightly higher measures of lifetime fitness for delayed dispersers calculated by Walters et al. (1992b).

Conclusion

Intrabrood dominance influences access to natal food resources (Hewett Ragheb and Walters 2011), first-year natal survival and the probability of delayed dispersal behavior (this study). Together, these results provide supporting evidence for direct benefits of philopatry for competitively superior individuals remaining on the natal territory during their first winter. However, this study also reveals that the direct benefits of philopatry during the first year are not sufficient to singularly explain the observed patterns of first-year survival and reproductive roles during the first breeding season. It is unclear if natal dispersal carries the heavy survival cost assumed previously, and the timing of first year dispersal does not influence the likelihood of obtaining a breeder vacancy during the first breeding season. Nevertheless, remaining on the natal territory at least through the first winter appears to be the preferred strategy for both males and females. For males, dispersal in the spring may be driven largely by social pressure from a dominant brood-mate, and competition among siblings may be over access to the lifetime fitness benefits associated with residing on the natal territory beyond the first year rather than direct benefits obtained during the first year.

FUNDING

This work was supported by the U.S. Department of Defense, Marine Corps Base Camp Lejeune and Department of the Army, Fort Bragg to J.R.W.; the National Science Foundation (BSR-8307090) to J.R.W.; the Virginia Tech Bailey Fund to J.R.W., and the Virginia Tech Graduate School to E.L.H.R.

ACKNOWLEDGMENTS

We thank all past and current field staff working with both the Sandhills and Camp Lejeune study populations for their contribution to the red-cockaded woodpecker long-term demographic data set. Particularly, the staff and associates from the Sandhills Ecological Institute: K. Brust, S. Anchor, J. H. Carter III, V. Genovese, M. Jusino, M. King and J. Maynard. Kevin Rose and K. Hudgins conducted the winter censuses at Camp Lejeune analyzed in this study. We also thank the U.S. Army Fort Bragg Endangered Species Branch: J. Britcher and J. Schillaci, the North Carolina Sandhills Gamelands and Wildlife Resources Commission: B. Beck; and the natural resource managers at Marine Corp Base Camp Lejeune: Craig Tenrbink, Gary Haight, John Townson and Bill Rogers. James Fraser, D. Hawley, J. Philips and C. Eikenaar provided helpful advice throughout the development of the project. We thank V. Garcia, J. Cohen and D. Catlin for their patient assistance with mark-recapture analysis methods. The Virginia Tech Institutional Animal Care and Use Committee (10-138-BIOL, 01-080-BIOL), the Department of the Interior U.S. Fish and Wildlife Service (TE070846-1, TE070846-2) and the North Carolina Wildlife Resources Commission Division of Wildlife Management (NC-2007ES88, NC-2008ES88, NC-2009ES88, NC-2010ES88) served as the governmental authorities approving ethical treatment of animals for this research.

FIGURE CAPTIONS

Figure 1: Flow charts representing dispersal paths for male (a) and female (b) fledglings from CS4-CS8. Numbers in parentheses represent sample sizes for each category and percentages listed near arrows represent the percentage of birds from the category at the start of the arrow that selected a particular path. Shaded columns represent time intervals where population-wide censuses were conducted. Roles during the breeding season census (far right column) were assigned based on social position, not on actual reproductive effort.

Figure 2: Apparent monthly natal survival (Φ^N) for 98 dominant (white bars) and 116 subordinate (hashed bars) juvenile males from CS1-CS3 across three sampling intervals. Model-averaged parameter estimates and unconditional 95% confidence intervals were calculated using QAIC_c weights from 64 multistate mark-recapture models. For all models, recapture probability was constrained as constant across time and state ($p^{N=D}(\cdot)$); no effort was made to locate dispersed individuals during the December sampling occasion and the probability of recapture was fixed at zero for that occasion. The probability of surviving in the dispersing state was constant over time ($\Phi^D(\cdot)$), and the probability of transition from disperser to natal resident states was fixed at zero ($\Psi^{DN}(0)$). Covariates added to the natal survival (Φ^N) and dispersal probability terms (Ψ^{ND}) during the 4-part model selection procedure include: seasonal variation (t), annual variation (cohort), fledging date (flg), nestling condition relative to the population (conpop), intrabrood social rank (rank) and condition relative to brood-mates (conbro). Dominant males were socially dominant to all brood-mates and socially subordinate males were subordinate to at least one brood-mate.

Figure 3: Monthly dispersal probability (Ψ^{ND}) with for 98 dominant (white bars) and 116 subordinate (hashed bars) juvenile males from CS1-CS3 across three sampling intervals. Model-averaged parameter estimates and unconditional 95% confidence intervals were calculated using QAIC_c weights from 64 multistate mark-recapture models. For all models, recapture probability was constrained as constant across time and state ($p^{N=D}(\cdot)$); no effort was made to locate dispersed individuals during the December sampling occasion and the probability of recapture was fixed at zero for that occasion. The probability of surviving in the dispersing state was constant over time ($\Phi^D(\cdot)$), and the probability of transition from disperser to natal resident states was fixed at zero ($\Psi^{DN}(0)$). Covariates added to the natal survival (Φ^N) and dispersal probability terms (Ψ^{ND}) during the 4-part model selection procedure include: seasonal variation (t), annual variation (cohort), fledging date (flg), nestling condition relative to the population (conpop), intrabrood social rank (rank) and condition relative to brood-mates (conbro). Dominant males were socially dominant to all brood-mates and socially subordinate males were subordinate to at least one brood-mate.

Figure 4: Monthly juvenile survival for juvenile males (white bars) and females (hashed bars) from CS4-CS8 across three time-location subgroups. Estimates and 95% confidence intervals generated from the highest-ranking binary logistic regression model for monthly juvenile survival (shown in bold in Table 4) using AIC_c model selection on nine candidate models. The dependent variables included in model selection were sex, subgroup (July-Dec, Jan-May overwinter dispersers, Jan-May overwinter natal residents), cohort (CS4-CS8) and a sex*subgroup interaction term. The Jul-Dec subgroup includes all fledglings with known dispersal paths (228 male, 201 female). The first Jan-May subgroup includes all juveniles that

were alive and dispersed during the winter census (17 male, 36 female) and the second includes all juveniles that were alive on their natal territory during the winter census (134 male, 87 female).

Figure 5: Monthly dispersal probability for juvenile males (white bars) and females (hashed bars) from CS4-CS8 across two time-location subgroups. Estimates and 95% confidence intervals generated from the highest-ranking binary logistic regression model for monthly juvenile survival (shown in bold in Table 5) using AICc model selection on four candidate models. The dependent variables included in model selection were sex, subgroup (July-Dec, Jan-May), and a sex*subgroup interaction term. The Jul-Dec subgroup includes all individuals known to have fledged (228 male, 201 female), and the Jan-May subgroup includes all juveniles that were alive on their natal territory during the winter census (134 male, 87 female).

Figure 6: The predicted probability that a juvenile will become a fall disperser (dotted line), spring disperser (dashed line) or natal resident (solid line) as a function of relative nestling mass at banding (g). Sample includes 96 female (a) or 122 male (b) juveniles from CS4-CS8 known to have fledged and survived to the breeding season census. Predicted probability curves were calculated from the beta estimates of the highest-ranking multinomial logistic regression model (shown in bold in Table 6) using AICc model selection on nine candidate models. The dependent variables included in model selection were sex, cohort sample (CS; CS4-CS8), and nestling mass relative to the brood mean (mass).

Figure 3. 1 Fledgling dispersal paths.

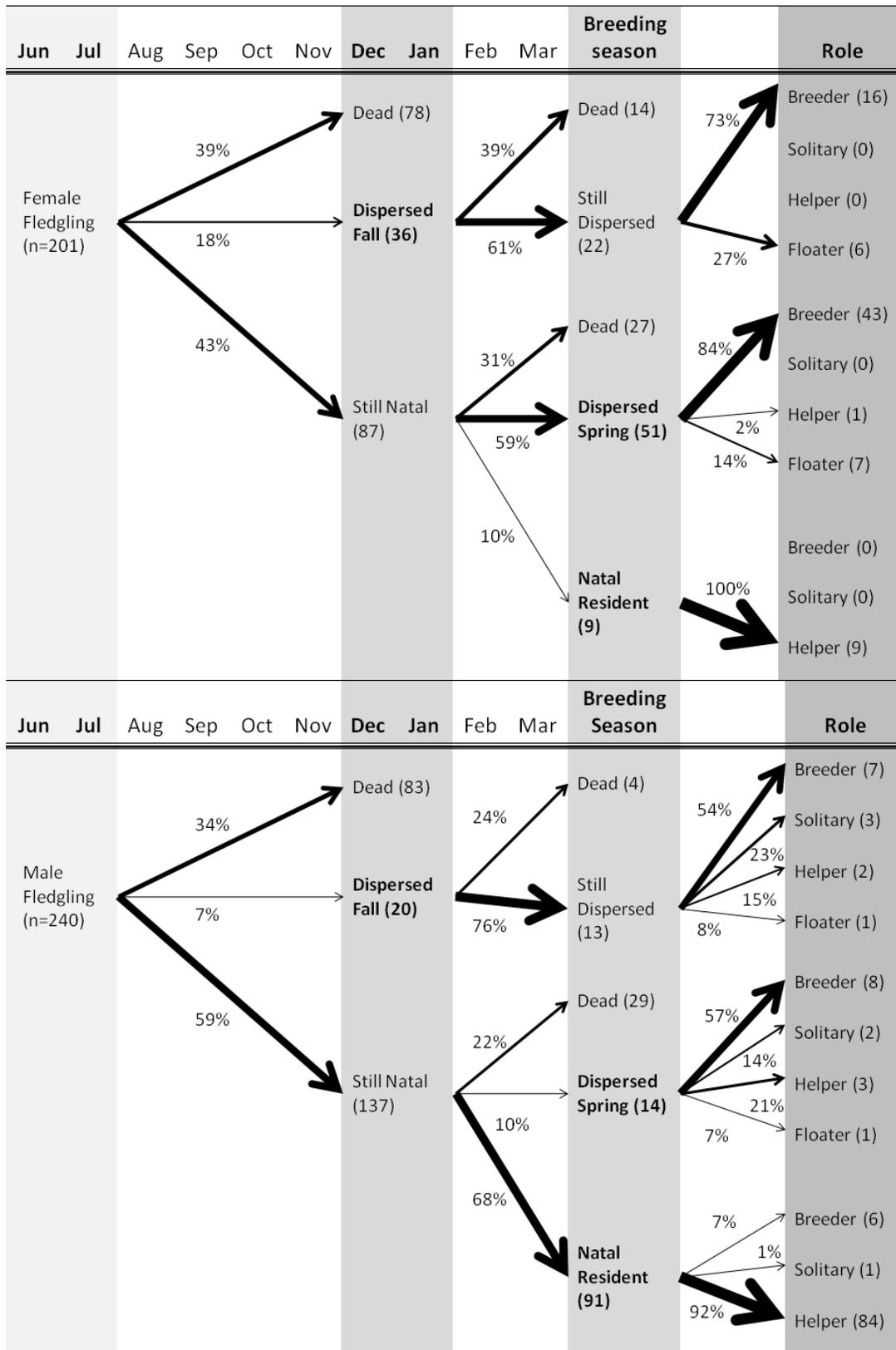


Figure 3. 2 Apparent monthly survival for juvenile males.

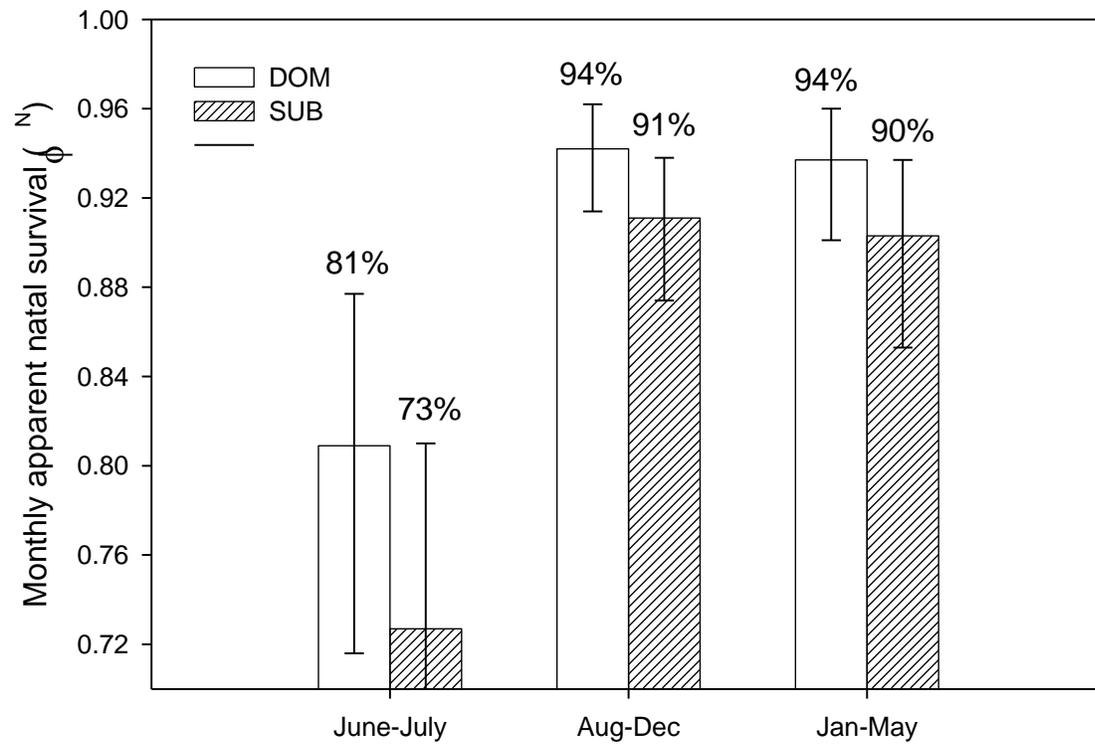


Figure 3. 3 Monthly dispersal probability for juvenile males.

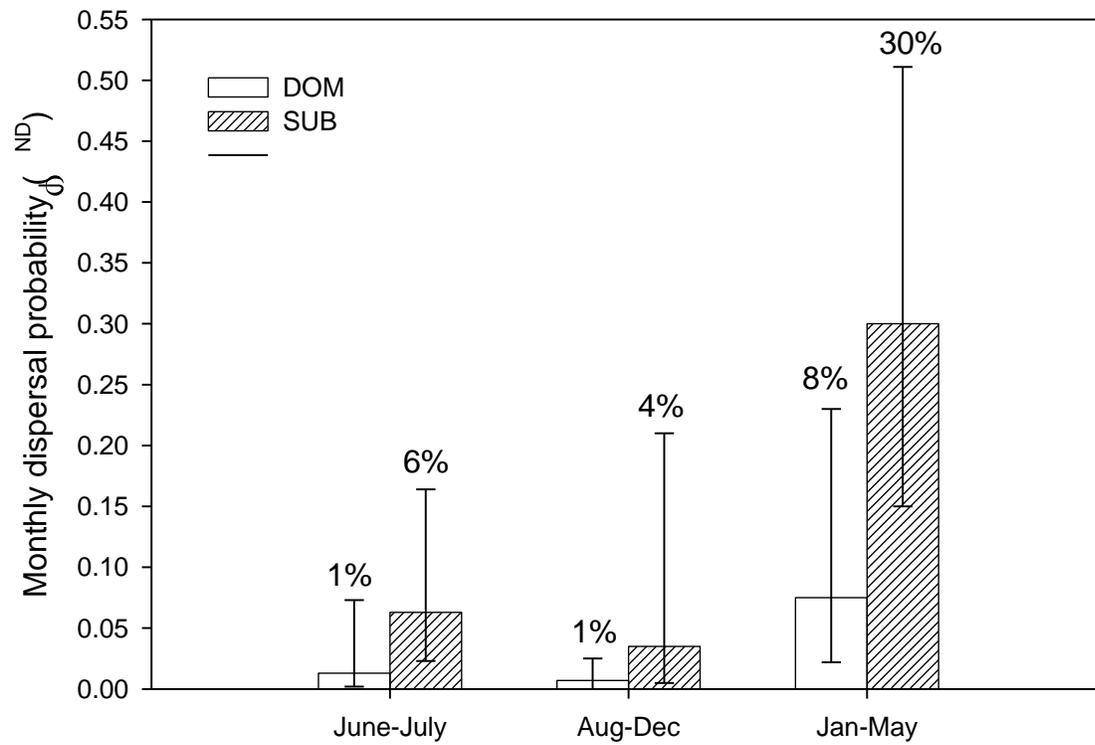


Figure 3. 4 Monthly survival for juvenile males and females.

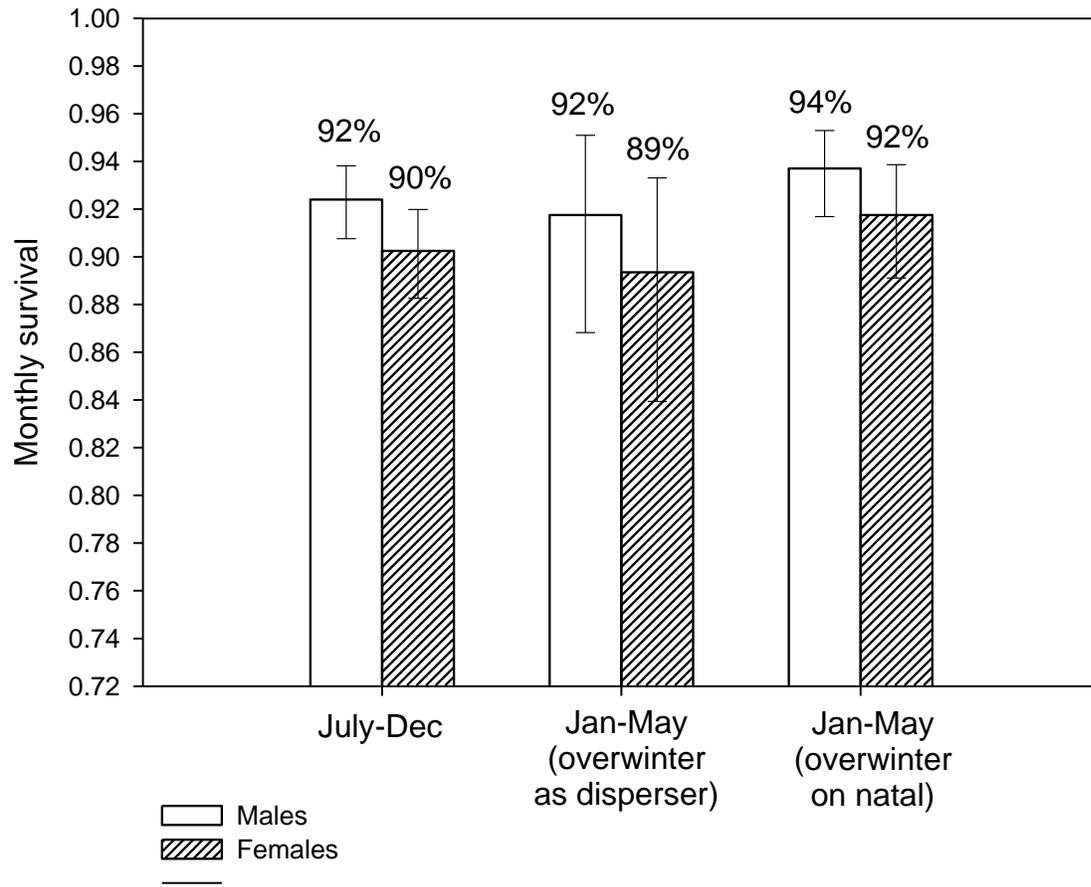


Figure 3. 5 Monthly dispersal probability for juvenile males and females.

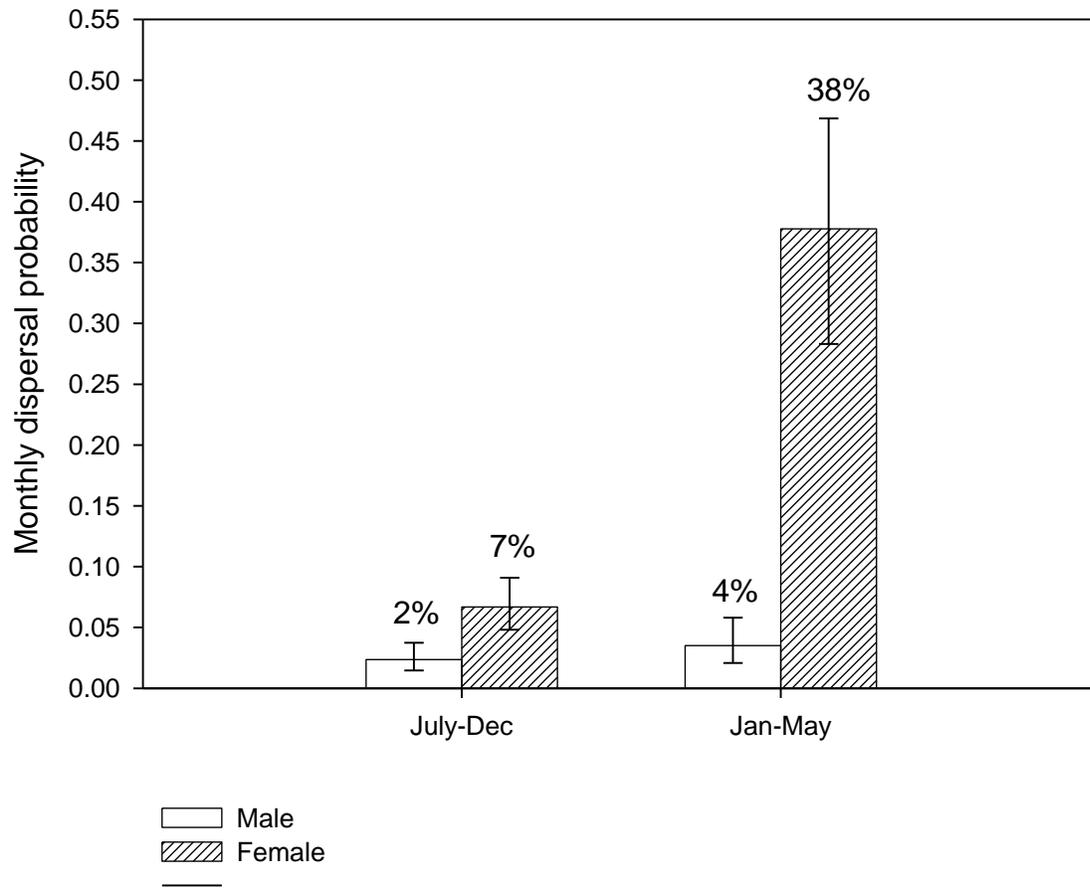


Figure 3. 6 Predicted probability of dispersal path by mass.

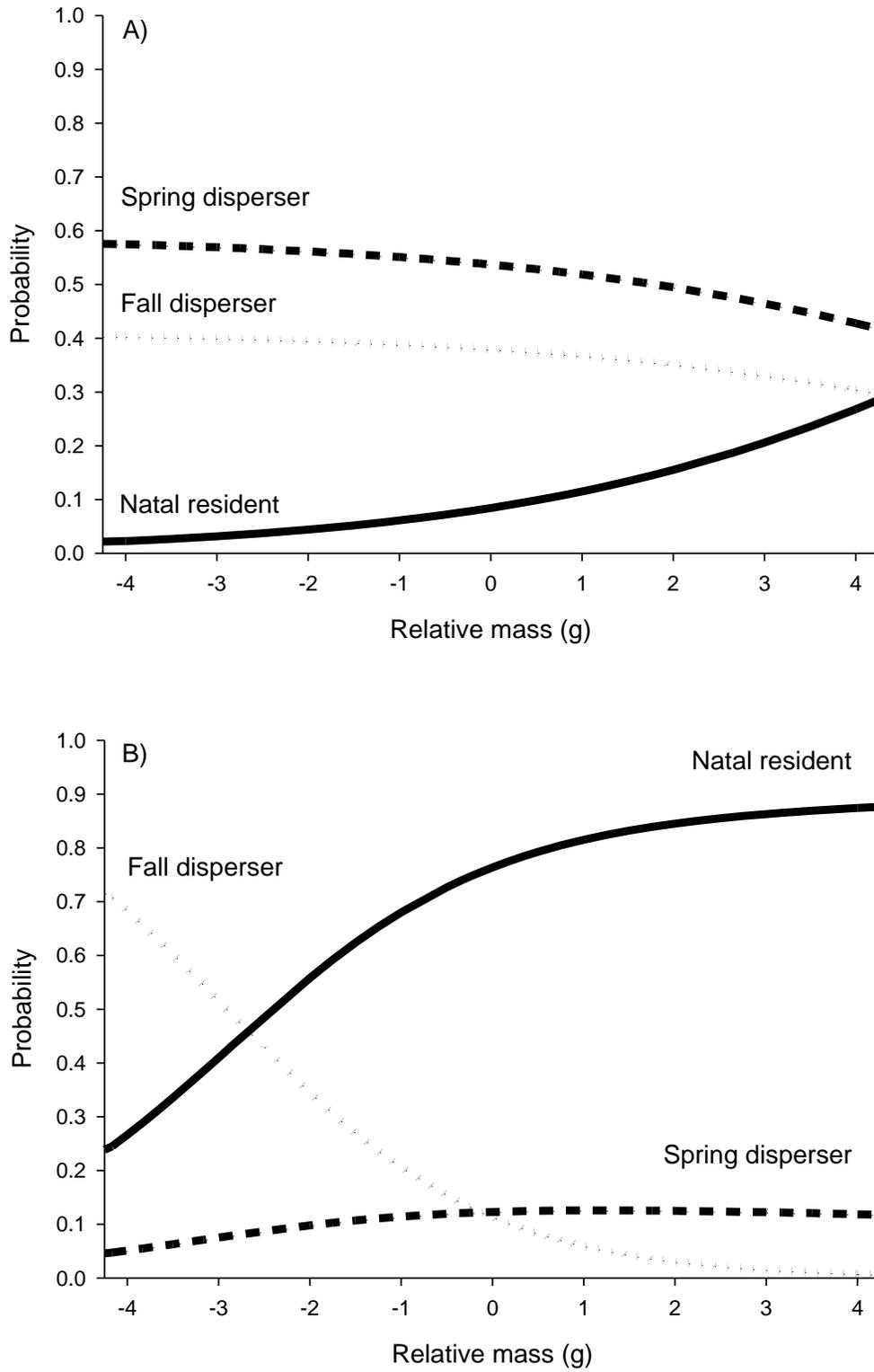


Table 3. 1: Predictions of hypotheses for adaptive significance of delayed dispersal behavior

Predictions	Hypothesis 1 “Intrinsic benefits”	Hypothesis 2 “Best-of-a-bad-job”	Hypothesis 3 “Lifetime reproductive success”
First-year natal survival	Dominants have higher natal survival than subordinates	Dominants have higher natal survival than subordinates	No specific predictions
First-year dispersal survival	Survival higher for natal residents than dispersers	Survival equal for natal residents and dispersers	Survival equal or higher for natal residents than dispersers
First-year dispersal probability	Subordinates more likely to disperse than dominants.	Dominants more likely to disperse than subordinates	Subordinates more likely to disperse than dominants
First-year dispersal timing	Subordinates disperse earlier (fall) and dominants later (spring)	Dominants disperse earlier (fall) and subordinates later (spring)	No specific predictions
Yearling breeder probability	Higher for late (spring) dispersers than early (fall) dispersers	Higher for early (fall) dispersers than late (spring) dispersers	Low for both early (fall) and late (spring) dispersers

Table 3. 2 Number of juvenile male natal and disperser resightings for the North Carolina Sandhills population (2007-2009).

Month	Dominant				Subordinate				Total focal birds ^c
	New rank assignment ^a	Natal resights	Disperser resights ^b	Dominant total ^c	New rank assignment ^a	Natal resights	Disperser resights ^b	Sub. total ^c	
June	74	74	0	74	91	91	0	92	165
July	24	87	0	87	25	82	5	87	174
December	0	60	-	60	0	49	-	49	109
May	0	40	4	44	0	22	13	35	79

^aNumber of fledgling males assigned with intrabrood social rank in month *i* and entered into study as focal bird.

^bNumber of focal birds observed on non-natal territories. Excludes juveniles observed on neighboring territories during territorial conflicts. No attempt was made to locate dispersed individuals in December.

^cNumber of focal birds known to exist in population during month *i*.

Table 3. 3 Selected multistate mark-recapture models for natal survival and dispersal for juvenile males with known intrabrood social rank from CS1-CS3.

Final Rank	Model	Apparent Natal Survival (Φ^N)	Dispersal (Ψ^{ND})	QAIC _c	Δ QAIC _c	QAIC _c weight	Model likelihood	K	QDeviance
1	51	Rank+cohort+flg+t	Rank+t	579.237	0.000	0.233	1.000	13	552.398
2	53	Rank+cohort+flg+conpop+t	Rank+t	580.021	0.784	0.158	0.676	14	551.051
3	52	Rank+flg+t	Rank+t	580.073	0.837	0.154	0.658	11	557.468
4	54	Rank+flg+conpop+t	Rank+t	580.234	0.998	0.142	0.607	12	555.517
5	55	Rank+cohort+flg+t	Rank+conpop+t	581.047	1.810	0.094	0.405	14	552.077
6	57	Rank+cohort+flg+t	Rank+flg+t	581.328	2.091	0.082	0.352	14	552.358
7	56	Rank+cohort+flg+t	Rank+cohort+t	581.510	2.273	0.075	0.321	15	550.399
8	37	Rank+cohort+flg+t	t	585.977	6.741	0.008	0.034	12	561.260
13	58	Rank+cohort+flg+t	Conbro+t	587.896	8.659	0.003	0.013	13	561.057
19	5	Cohort+flg+t	t	589.084	9.848	0.002	0.007	11	566.479
23	3	Flg+t	t	590.057	10.821	0.001	0.005	9	571.646
24	8	Cohort+flg+conpop+t	t	590.302	11.066	0.001	0.004	12	565.585
26	11	Cohort+flg+t	Conpop+t	590.778	11.542	0.001	0.003	12	566.061
27	44	Conbro+cohort+flg+t	t	590.803	11.566	0.001	0.003	12	566.086
28	9	Cohort+flg+t	Cohort+t	591.021	11.784	0.001	0.003	13	564.182
29	10	Cohort+flg+t	Flg+t	591.035	11.799	0.001	0.003	12	566.318
40	1	t	t	592.343	13.107	0.000	0.001	8	576.015
48	2	Cohort+t	t	592.897	13.660	0.000	0.001	10	572.393

Models shown represent the 8 top-ranking models (95% of QAIC_c weight for all models), and 10 additional models useful for

comparison (shown below empty row in table). For all models, recapture probability was constrained as constant across time and state ($p^{N=D}(\cdot)$) probability of surviving in the dispersing state was constant over time ($\Phi^D(\cdot)$), and probability of transition from disperser to natal resident states was fixed at zero ($\Psi^{DN}(0)$). Covariates added to the natal survival (Φ^N) and dispersal probability terms (Ψ^{ND})

during the 4-part model selection procedure include: seasonal variation (t), annual variation (cohort), fledging date (flg), nestling condition relative to the population (conpop), intrabrood social rank (rank) and condition relative to brood-mates (conbro). A median- \hat{c} goodness-of-fit test on the starting model (1) revealed minor overdispersion. AIC scores were manually adjusted for overdispersion (QAIC; $\hat{c}=1.245$) and corrected for small sample size (QAIC_c). Models are shown with the QAIC_c score, change in QAIC_c score (Δ QAIC_c), Δ QAIC_c weight, model likelihood, the number of estimable parameters (K) and model deviance (QDeviance).

Table 3. 4 Binary logistic regression models for the probability of first-year survival

Model	AIC _c	ΔAIC _c	ΔAIC _c weight	Model likelihood	K	-2log(L)
1 SEX+SUBGROUP	883.51	0	0.475	1.000	4	875.45
2 SUBGROUP	885.42	1.91	0.183	0.385	3	879.38
3 SEX+ SUBGROUP+SEX* SUBGROUP	886.64	3.13	0.099	0.209	6	874.52
4 SEX	886.67	3.16	0.098	0.206	2	882.65
5 SEX+CS+ SUBGROUP	887.11	3.60	0.078	0.165	8	870.91
6 CS+ SUBGROUP	889.08	5.57	0.029	0.062	7	874.92
7 SEX+CS	890.16	6.65	0.017	0.036	6	878.04
8 SEX+CS+ SUBGROUP +SEX* SUBGROUP	890.20	6.69	0.017	0.035	10	869.88
9 CS	892.92	9.41	0.004	0.009	5	882.83

Sample includes juveniles known to have fledged from CS4-CS8 (male=228, female=201). The most parameterized model (model 8) was a good fit to the data (Pearson $X^2/df = 1.01$). AIC scores were corrected for small sample size (AIC_c). For all models, the binary dependent variable is juvenile state (alive, dead). The fixed covariates are ‘sex,’ cohort sample (‘CS’; CS4-CS8) and time-location subgroup (‘subgroup’; July-Dec (all fledglings), Jan-May (juveniles known to overwinter as dispersers), Jan-May (juveniles known to overwinter as natal residents)). Only birds alive during the July-Dec sampling interval were included in the Jan-May subgroups. Models are shown with AIC_c score, change in AIC_c score (ΔAIC_c), ΔAIC_c weight, model likelihood, the number of estimable parameters (K) and model deviance (-2log(L)).

Table 3. 5 Binary logistic regression models for the probability of natal dispersal.

Model	AIC _c	Δ AIC _c	Δ AIC _c weight	Model likelihood	K	-2log(L)
1 SEX+SUBGROUP+SEX* SUBGROUP	396.17	0	1.000	1.000	4	338.17
2 SEX+ SUBGROUP	414.03	17.86	0.000	0.000	3	407.98
3 SEX	446.26	50.09	0.000	0.000	2	442.23
4 SUBGROUP	494.44	98.27	0.000	0.000	2	490.41

Sample includes juveniles known to have fledged from CS4-CS8 (male=228, female=201). The most parameterized model (1) was a good fit to the data (Pearson $X^2/df=1.01$). AIC scores were corrected for small sample size (AIC_c). Column statistics are the same as described in Table 4. The binary dependent variable is juvenile state (dispersed, natal resident). The fixed covariates are ‘sex’ and time-location subgroup (‘subgroup’; July-Dec (all fledglings surviving to the winter census), Jan-May (all juveniles surviving to the breeding season census)). All mortality was assumed to take place on the natal territory before the census period.

Table 3. 6 Multinomial logistic regression models for the probability that a juvenile will belong to the fall disperser, spring disperser or natal resident ‘dispersal path states.’

Model	AIC _c	Δ AIC _c	Δ AIC _c weight	Model likelihood	K	-2log(L)
1 MASS+SEX+SEX*MASS	348.42	0	0.862	1.000	8	332.42
2 MASS+SEX	353.27	4.85	0.076	0.088	6	340.87
3 MASS+SEX+CS+SEX*MASS	353.93	5.51	0.055	0.064	16	319.21
4 MASS+SEX+CS	358.19	9.77	0.007	0.008	14	328.11
5 SEX	366.33	17.91	0.000	0.000	4	358.14
6 SEX+CS	369.25	20.83	0.000	0.000	12	343.72
7 MASS	447.38	98.96	0.000	0.000	4	439.19
8 MASS+CS	448.85	100.43	0.000	0.000	12	423.32
9 CS	466.81	118.39	0.000	0.000	10	445.74

Sample includes juveniles known to have fledged from CS4-CS8 and survived to the breeding season census (male=121, female=96).

The most parameterized model (3) was a good fit to the data (Pearson $X^2/df=0.96$). AIC scores were corrected for small sample size (AIC_c). Column statistics are the same as described in Table 4. The dependent variable is dispersal path state (‘fall dispersal,’ ‘spring dispersal’ or ‘natal resident’). The covariates are ‘sex,’ cohort sample (‘CS’; CS4-CS8), and nestling mass relative to the brood mean (mass).

Table 3. 7 Coefficient estimates from the highest ranking multinomial logistic regression model of dispersal path state (shown in bold in Table 6)

Variable	Fall dispersal vs. natal resident			Spring dispersal vs. natal resident			Fall vs. spring dispersal		
	β	LCI	UCI	β	LCU	UCI	β	LCU	UCI
Mass	-0.7121	-1.07	-0.36	-0.0429	-0.35	0.26	-0.669	-1.1	-0.23
Sex	3.4102	2.35	4.46	3.6784	2.68	4.68	-0.268	-1.21	0.68
Sex*Mass	0.3682	-0.19	0.92	-0.303	-0.82	0.22	0.6712	0.19	1.15
Intercept	-1.9067	-2.57	-1.24	-1.8272	-2.44	-1.22	-0.079	-0.92	0.76

Sample includes juveniles known to have fledged from CS4-CS8 and survived to the breeding season census (male=121, female=96). See Table 6 footnote for description of dependent and independent variables. Columns represent the pair-wise probabilities that a juvenile will belong to the fall dispersal vs. natal resident, spring dispersal vs. natal resident or fall dispersal vs. spring dispersal states. The estimated coefficients (β) are given with lower and upper 95% confidence intervals (alpha level=0.05). Coefficients for variables with 95% confidence intervals that do not include zero are in bold. Sex is modeled with male as the dummy variable.

**CHAPTER IV. NESTLING COMPETITIVE ENVIRONMENT INFLUENCES DEGREE
OF SEXUAL SIZE DIMORPHISM AND FEMALE HELPING BEHAVIOR IN RED-
COCKADED WOODPECKERS**

Erin L. Hewett Ragheb and Jeffrey R. Walters

ABSTRACT

The social milieu experienced by developing nestlings has the potential to influence their growth and life history strategy, particularly if competitive ability differs between the sexes. Here, we used 16 years of red-cockaded woodpecker demographic data from two populations to examine the degree of sexual size-dimorphism in nestlings and the effect of natal brood sex-ratios on several life history traits. Models for nestling mass and leg length revealed only a very slight size bias towards males. However, females were only lighter than males when raised in mixed sex broods, suggesting that the subtle sexual dimorphism observed in nestling leg length may give males a competitive advantage over their sisters. The natal competitive environment had no effect on survival or recruitment success. Nestlings of either sex were equally likely to fledge from single- or mixed-sex broods. In addition, natal brood sex-ratio did not influence the probability of first-year survival or the probability of recruitment for either sex, or the quality of the recruitment territory for females. The probability of female helping behavior varied with natal sex-ratio, but for only one, not both populations. In the Sandhills, females from singleton broods were the most likely to become natal helpers, but females from the Camp Lejeune population were equally likely to delay dispersal regardless of natal competitive environment. Differences in the availability of breeding vacancies may explain the observed patterns of dispersal behavior. Sandhills females with greater access to breeding positions favor dispersal

except in natal situations with no brood-mate competitors while Camp Lejeune females with less access to breeding positions are more likely to delay dispersal regardless of their natal social environment. *Key words: benefits of philopatry, cooperative breeding, sex-ratio, delayed dispersal, intrafamilial conflict, life history strategy, nestling competition, Picoides borealis, sibling rivalry*

INTRODUCTION

The competitive environment experienced early in development may maintain individual variation among brood-mates and influence individual life history strategy. In birds, the natal competitive environment may vary across broods due to the degree of hatching asynchrony (Bryant and Tatner 1990), brood size (Nilsson and Svensson 1996), or the availability of shared resources (Cook et al. 2000; Brzek and Konarzewski 2001). Within broods, sex-specific sibling interactions may result in variable growth or survival of individual offspring (see review in Uller 2006). The sexual composition of the brood can alter levels of aggression and sex-specific mortality (Bortolotti 1986; Mock and Parker 1997; Nathan et al. 2001; Lee et al. 2010) as well as parental provisioning behavior (Michler et al. 2010).

Asymmetries in competitive ability among brood-mates may be caused by a number of sex-specific factors including laying order (Bortolotti 1986), the speed of embryonic development (Blanco et al. 2003; Cook and Monaghan 2004), hormones associated with aggression or begging (Sasvari et al. 1999; Goodship and Buchanan 2006), or immune response to parasites (Potti and Merino 1996). One more obvious difference between the sexes confounding competitive ability is the degree of sexual size dimorphism (SSD). For many species, genetically driven SSD after hatching leads quickly to competitive asymmetry

(Bortolotti 1986). Traditionally, species with strong SSD were the focus for research on SSD and biased sex-ratios (Fisher 1930). Because nestlings of the larger sex are more expensive energetically to rear, and require greater parental investment, they can be more vulnerable to poor rearing conditions than their smaller, less expensive brood-mates (see review in Clutton-Brock 1985), although this was not always found to be the case (see review in Jones et al. 2009). More recently, experiments manipulating rearing conditions for species with small to moderate SSD revealed competitive asymmetries favoring the slightly larger sex (Oddie 2000; Rowland et al. 2007). For song sparrows (*Melospiza melodia*), the increased competitive environment created through brood parasitism by brown-headed cowbirds (*Molothrus ater*) results in differential mortality of females raised in mixed-sex broods (Zanette et al. 2005). In cooperatively breeding acorn woodpeckers, the sex-ratio of juveniles at independence is male biased as a result of differential growth and resulting competitive superiority of larger male nestlings over females (Koenig et al. 2001b). In these cases, the slightly larger sex has a competitive advantage during scramble competition, enough to cause the smaller sex to suffer, yet without the burden of costly energetic demands as observed in species with large SSD. In sexually monomorphic species, no general rules have been generated thus far to predict which sex, if either will be competitively superior or more sensitive to poor rearing conditions (Rosivall et al. 2010). In monomorphic collared flycatchers (*Ficedula albicollis*), male nestlings suffered more than their sisters in poor rearing conditions (Rosivall et al. 2010), while in zebra finches (*Taeniopygia guttata*) females were more likely to die in experimentally enlarged broods than males (Kogel 1997).

Regardless of the proximate causes of sex-specific competitive asymmetries, the competitive environment created by natal sex-ratio may have important long-term demographic

consequences. If nestlings of the less competitive sex are raised in a high-competition environment, they are likely to be lower quality and suffer from sub-lethal fitness effects after fledging (Oddie 2000). Relative nestling mass, or mass at fledging often correlates positively to adult size (Koenig et al. 2011), post-fledging survival (Tinbergen and Boerlijst 1990; Koenig et al. 2011), recruitment probability (Verboven and Visser 1998; Cleasby et al. 2010), status within fledgling dominance hierarchies (Stanback 1994; Hewett Ragheb and Walters 2011), and natal dispersal strategy (Pasinelli and Walters 2002). In some studies, however, the brood sexual composition had no influence on fledging timing (Radersma et al. 2011) or nestling mortality (Rowland et al. 2007). In cooperative breeding species where some, but not all offspring delay natal dispersal, the natal competitive environment may be critical in determining which offspring stay and which disperse (Hewett Ragheb and Walters 20XX; See Chapter 3)). Studies are needed that can link competitive asymmetries during development to long-term fitness by tracking individuals raised under various rearing conditions (Uller 2006).

Here, we use 16 years of demographic data for red-cockaded woodpeckers (*Picoides borealis*) from two study populations to examine the effect of natal competitive environment on long-term life history traits. Adult red-cockaded woodpeckers exhibit moderate SSD (Pizzoni-Ardemani 1990; Jackson 1994), yet there have been no studies describing SSD in nestlings, and it is unknown if SSD drives pre-fledging competitive interactions or vice versa. Red-cockaded woodpecker fledglings form male-biased linear dominance hierarchies and higher social rank results in increased access to perches near foraging adults and higher provisioning rates (Hewett Ragheb and Walters 2011). Within males, condition at banding relative to brood-mates is a strong predictor of fledgling intrabrood dominance rank and subordinates are more likely to disperse within their first year than dominants (Hewett Ragheb and Walters 2011). Delayed

dispersal behavior in juvenile females is a relatively rare life history strategy (only 1% of all female fledglings; (Walters et al. 1988)), and juvenile females are more likely to successfully disperse by their first breeding season than males (31% versus 13% for juvenile males; Walters et al. 1988). This sex-bias in dispersal strategy has been attributed to a number of factors such as inbreeding avoidance (Pusey 1987; Daniels and Walters 2000a) or sex-biases in competition over breeding vacancies (Walters et al. 1992b). The relative benefits of philopatry (Stacey and Ligon 1991) may vary among the sexes as subordinate female fledglings have reduced access to natal resources (Hewett Ragheb and Walters 2011) and territory inheritance opportunities (Walters et al. 1992b). Together, these findings suggest that for red-cockaded woodpeckers, sex-specific competitive asymmetries among nestlings have the potential to strongly influence long-term fitness traits. Our large cohort sample (16 years) and ability to track individuals within the population throughout their lifetime provide us with a rare opportunity to detect even subtle long-term effects of early rearing conditions.

Aims and predictions

In Part 1, our aim is to explore the degree of SSD in nestling red-cockaded woodpeckers and its relationship with early competitive environment. As a preliminary inquiry, we compare models of male and female nestling growth from ages 4-11 days to determine if the sexes exhibit different patterns of nestling growth as measured by mass and leg length. Then, to assess interactions between sex, size and competitive environment, we compare mass and leg length of male and female nestlings from same- and mixed-sex broods, using increasing brood size as a surrogate for increasing competitive pressure. We first hypothesize that SSD is inherent for

nestlings and the larger sex is more vulnerable to poor rearing conditions since there are inadequate resources available to support their larger size. Here, we predict that SSD will be evident in both single- and mixed-sex broods but the degree of SSD will decrease with increasing brood size.

Second, we hypothesize that SSD is inherent for nestlings and the larger sex will be less vulnerable to poor rearing conditions because increased physical size provides an important competitive advantage during scramble competition over resources in the nest. Here, we again predict SSD to be present in both small single- and mixed-sex broods, but the degree of SSD will increase with increasing brood size in mixed sex broods as the smaller sex is out-competed by their siblings of the large sex. We do not expect the degree of SSD to change with increasing brood size for single-sex broods.

Alternatively, our third hypothesis is that there is no inherent nestling SSD, rather any observed SSD is a product of the sex-specific competitive environment. One sex is still more vulnerable to poor rearing conditions but for reasons not related to initial physical size. Here, we predict that no SSD will exist between males and females raised in small broods, but as brood size increases the more vulnerable sex will be smaller in both single- and mixed sex broods. The degree of SSD may be stronger in mixed-sex broods than single sex broods if the less vulnerable sex takes competitive advantage of their opposite-sex sibling's weakness. Lastly, we hypothesize that there is no inherent SSD in nestlings and no sex-bias in vulnerability to poor rearing conditions. Here, we predict there to be no SSD regardless of brood size or competitive environment, although nestling size may decrease with increasing brood size.

In Part 2, we explore our hypothesis that the nestling competitive environment has long-term consequences and influences life history traits affecting fitness. To begin, we first

determine which brood sex-ratios are most common over the 16 years in our study and assess if this distribution differs from expected under random *ZW* chromosomal sex determination. Then, under the above hypotheses, we first predict that if a competitively inferior sex exists, it would be more likely to fledge from single-sex than mixed-sex broods. Second, we predict that individuals raised in broods with different sex-ratios and sizes will vary in post-fledging survival, recruitment probability and the quality of the recruitment territory (females only), where individuals of the least competitive sex would have the highest measures of fitness when raised in broods where the competitive environment is the least harsh (smaller broods and fewer number of competitively superior brood-mates).

Lastly, in Part 3, we hypothesize that delayed dispersal is the preferred strategy for juvenile females similar to that shown previously for males (Walters et al. 1992b), but competition on the natal territory with socially dominant brood-mates prohibits philopatry in most cases. Here we predict that only solitary females or dominant females from female-only broods would have the opportunity to remain home as a helper, and therefore the probability of delayed dispersal will be higher for females from these brood sex-ratio types. Alternatively, if first-year natal dispersal is the preferred strategy for juvenile females for reasons such as inbreeding avoidance, or sex-biases in competition for breeding vacancies or probability of territory inheritance, then we predict that all juvenile females would be equally likely to disperse regardless of their natal sex-ratio type.

METHODS

Study population and species biology

Our primary study area covers 110,000 hectares in the Sandhills region of south-central North Carolina including the western portion of U.S. Army Fort Bragg, U.S. Army Training Facility Camp Mackall, and the North Carolina Sandhills Game Lands in Hoffman, North Carolina as well as a number of smaller publicly and privately owned sites. The study population contains over 220 family groups included in a long-term demographic study since 1980. The second study area covers over 34,000 hectares of coastal plain habitat along the southeastern coast of North Carolina on Marine Corps Base Camp Lejeune. This study population of over 70 family groups has been part of an annual monitoring program since 1986. Consistently for both study populations, over 95% of the population is banded with unique color band combinations. Field staff band all new nestlings and collect basic reproductive data each year. Dispersal and survival fates are known for most individuals through an annual population-wide breeding season census. For a thorough description of the study areas and monitoring techniques see Walters et al. (1988), and Zwicker and Walters (1999).

Red-cockaded woodpeckers form cooperative family groups consisting of a genetically monogamous breeding pair (Haig et al. 1994) and 0-4 helpers (typically retained male offspring; (Ligon 1970; Lennartz et al. 1987; Walters et al. 1988; Walters 1990). Helpers assist with incubation, brooding and fledgling provisioning (Jackson 1994). Adults form male-biased dominance hierarchies and within sexes, older birds are dominant over younger birds (Jackson 1994). Family groups defend permanent territories surrounding a cluster of cavity trees used for nesting and roosting (Walters 1990; Jackson 1994). Cavity excavation is done exclusively in mature living pine trees (primarily longleaf pine, *Pinus palustris*) and typically takes several years to complete (Harding and Walters 2004). Colonization of areas without existing cavity

trees is rare (Walters 2004), suggesting that the limited availability of cavity trees may be a key component driving population dynamics (Walters 1991; Carrie et al. 1998; Harding and Walters 2002), as well as a possible ecological constraint supporting the evolution of delayed dispersal in this species (Emlen 1982; Walters et al. 1992a).

Eggs are laid from late April to early June (Ligon 1970). The incubation period is only 10-13 days and begins with the laying of the second or the penultimate egg, resulting in moderate hatching asynchrony (Ligon 1970; Jackson 1994). Brood reduction occurs frequently, with most nestling loss occurring before day six (LaBranche and Walters 1994). Nestlings fledge after 26-29 days (Ligon 1970; Winkler et al. 1995), but continue to beg and be fed by adults for approximately three months post-fledging (E.L.H.R., personal observation). Non-dispersing individuals remain with their families even after reaching nutritional independence. Typically only one male per brood remains at the natal territory as a non-breeding helper while other male and almost all female fledglings disperse, becoming breeders or unrelated helpers on non-natal territories or floaters (Walters et al. 1988; Hewett Ragheb and Walters 20XX: See Chapter 3). Juveniles dispersing in their first year vary in their timing of dispersal. Juveniles as young as 1 month post-fledging have been located as dispersers during routine monitoring (J.R.W., personal observation), while other juveniles are known to overwinter on the natal territory and disperse in early spring before the start of their first breeding season (Kesler et al. 2010).

Adult red-cockaded woodpeckers exhibit small to moderate SSD in some linear measures and mass, where males are typically larger and heavier than females. Measurements from 40 male and 26 female adults from the Sandhills population reveal that males were larger than females in tarsus (2.06 mm greater, and bill length (1.63 mm greater), but tail length was longer

for females by 3.20 mm (Pizzoni-Ardemani 1990). Adult males (49.6g, n=61) were 4.1% heavier than females (47.6g, n=36) (Pizzoni-Ardemani 1990).

Field Methods

For both study populations, we monitored red-cockaded woodpecker groups for nesting during the breeding season on 7-10 day cycles starting the third week of April. We banded all nestlings with both aluminum USFWS bands and a unique combination of plastic colored leg bands between the ages of 4-11 days (aged according to Ligon 1970). In addition to standard mass measurements, the length of the right leg was measured (2007-2009 Sandhills cohorts only; see Hewett Ragheb and Walters 2011 for methodology). For the Sandhills population (2007-2009 cohorts only), nests were visited again when nestlings were age 20 days and the sexes of nestlings were identified based on the presence (male) or absence (female) of a red crown patch (Jackson 1994). For all nests at both study populations, we confirmed fledging success and sex for all banded individuals by recording all individuals in the natal group within two weeks of the estimated fledging date (age 26 days). Groups were visited a second time if the number of observed fledglings differed from expected based on the previous nest check. See Walters et al. (1988) for further details.

To measure post-fledging survival and recruitment, we recorded the presence, location and reproductive role of individuals during population-wide breeding season census conducted annually by field staff. Every red-cockaded woodpecker family group in both study populations was visited between April and August and all associated group members were recorded. In another analysis on the Sandhills population, the same breeding season census data were

combined with additional summer and winter censuses and mark-recapture methods were used to calculate the monthly detection probabilities for juvenile males (Hewett Ragheb and Walters 20XX; See Chapter 3: Part 1). Monthly detection of juvenile males was very high (0.936 (95% CI: 0.786-0.983)) suggesting we have a strong ability to reliably detect living individuals on their natal territories using our current field observation methods. Birds that were not located in the study areas were assumed to be dead based on our high detection rates and the low probability of off-site dispersal (estimated at 6% annually for the Sandhills population by Walters et al. (1988)). We assigned reproductive roles to all birds surviving to each breeding season census based on their location and social status in the population: 1) Social breeders were either the oldest or only adult defending an active territory with an opposite-sex mate. Social breeders may or may not have actually attempted reproduction during the year of classification. 2) Natal helpers were non-breeders that delayed dispersal and remained on their natal territory held by a pair of breeders. The degree of relatedness to the current breeding pair and the performance of helping behaviors were not required when making this classification. 3) Non-breeder/non-natal helpers were dispersed individuals that were either solitary on an active territory, helpers at a non-natal territory or floating between or intruding on active territories and were not accepted as members by any existing family group. See Walters et al. (1988) for expanded description of reproductive roles.

Statistical analysis

Part 1: Sexual size dimorphism in nestlings

To examine the degree of SSD for nestling red-cockaded woodpeckers, we used a subsample of broods where the sex and mass of all banded nestlings was known from the Sandhills population (1994-2009). This includes any brood where brood reduction occurred before banding, and excludes all broods with brood reduction after banding but before the fledging observation when sex was determined. Broods containing one or more nestlings too small at the time of banding to fit leg bands (runts) were excluded since the sex and identity of unmarked birds cannot be confidently confirmed after fledging. Only broods banded between ages 4-11 days were included since nestlings banded before or after this range were very rare in our sample.

We first generated two models to test for age and sex specific differences in nestling size (mass and leg length) for nestlings banded at ages 4-11 days. We generated age- and sex-specific nestling size estimates and 95% confidence intervals from two linear regression models with dependent variables nestling mass and leg length and independent covariates 'sex', 'banding age' and the interaction 'sex*banding age' (JMP Software Version 9.0; SAS Institute Inc., Cary, NC, 1989-2010; JMP). Size differences between the sexes at particular ages were detected using a Tukey-Kramer post-hoc test ($\alpha=0.05$).

Then, to examine how intrabrood competitive environment (brood size and the presence of opposite-sex brood-mates) may influence nestling size, we divided and analyzed the broods in our sample according to whether or not they contained single- or mixed-sex nestlings. For each scenario we generated the same 38 linear mixed models to explain nestling mass and leg length (Proc MIXED; SAS 9.2; SAS Institute Inc., Cary, NC, USA; SAS). All models contained the random effect variable 'family' representing the family group in a given natal year to control for relatedness of siblings, and the fixed effect variable 'age' to control for the effect of banding age

on nestling size. In addition, models in the candidate set contained all possible additive combinations of the following fixed effect covariates: ‘cohort’ (year of banding), ‘brood’ (the number of nestlings in the brood at the time of banding), ‘sex’ (as assigned at fledging), ‘brmale’ (the age of the breeder male), ‘helpers’ (the number of helpers in the family during the natal year) and the multiplicative interaction between brood and sex, ‘brood*sex.’ The ‘brmale’ and ‘helpers’ covariates were added to examine any possible effect of parental and territory quality on nestling size, since they are both positively associated with reproductive success (Walters 1990). We restricted our sample for this analysis to include only broods where the age of the breeder male was known exactly.

We generated Akaike Information Criterion (AIC) corrected for small sample size (AIC_c) for each model in the set and compared models based on differences in this value (ΔAIC_c), model likelihood and model weight following Anderson (2008). Models with lower AIC_c scores relative to the other models in the set were considered to be more likely given the dataset. We calculated model-averaged parameter estimates and unconditional 95% confidence intervals for all covariate regression coefficients (slopes) and predicted response values (mass and leg length). Only models with model weights greater than 0.01 were included when generating model averaged estimates. When plotting model averaged estimates according to a subset of particular covariates, we used the mean values of the remaining covariates. We assessed the covariate effect sizes by comparing regression coefficients and their unconditional 95% confidence intervals. Although a large number of models were created, only the best fitting models (model weights ≥ 0.01) or those required for comparison of hypotheses are presented in the results (but see Appendices 1-4 for complete model sets).

Part 2: Natal brood sex-ratios and individual fitness

To determine if the distribution of brood sex-ratios within each brood size observed in our study differed from expected under random ZW chromosomal sex determination, we used a likelihood ratio chi-square test (JMP) on all broods where the sexes of all banded nestlings were known for the Sandhills and Camp Lejeune populations (1994-2009; populations analyzed separately).

To determine if nestling competitive environment influences fledging success we compared the probability of fledging for nestlings of each sex according to their natal brood composition type (single- or mixed-sex). We ran a likelihood ratio chi-square test (JMP) using only broods where all banded nestlings were sexed at the day 20 crown patch check (Sandhills, 2007-2009 cohorts only). For the Sandhills population (1994-2009), we next considered the effect of the natal brood sex-ratio on the probabilities of several life history events by generating separate logistic regression models (Proc GLIMMIX; SAS) for each sex using the following binary response variables: 1) first year survival, 2) social breeder recruitment, and 3) recruitment to a territory containing helpers (females only). In all models, brood sex-ratio was the independent categorical variable. First year survival was determined by the presence or absence of juveniles on the population-wide breeding season census. When calculating social breeder recruitment we restricted our sample taking into account the possibility of delayed reproduction. Males often delay first reproduction, but 96% of all males that fill breeder vacancies do so by their seventh year (Figure 1). Therefore, we considered males to be successful social breeder recruits when they had filled a breeder vacancy at least once by their seventh year and restricted our cohort sample to 1994-2003 since only these males would have the opportunity to become social breeders within that timeframe. Since 96% of all females that fill breeder vacancies do so

by their third spring (Figure 1), social breeder recruitment was assigned to females that become social breeders by their third spring and we restricted our cohort sample to 1994-2008. As a surrogate for the quality of the first year recruitment territory for females, we assessed the presence or absence of at least one helper at the territory where they first filled a breeder vacancy (second or third year recruits; 1994-2008 cohorts only). We assumed territories containing at least one helper were more established and of higher quality than territories containing only a breeding pair. We used the Tukey-Kramer post-hoc test adjusted for multiple comparisons ($\alpha=0.10$) and the degree of overlap in 95% confidence intervals to make inferences about survival differences among brood sex-ratio types.

Part 3: Female helping behavior

To determine if female helping behavior is related to early competitive environment, we ran a fourth type of logistic regression model on juvenile females from the Sandhills and Camp Lejeune populations separately where we predicted the probability of delaying dispersal and remaining as a natal helper (Proc GLIMMIX; SAS). Brood sex-ratio was the independent categorical variable. Delayed dispersal status was assigned to individuals that were still found on their natal territory as helpers during the population-wide breeding season census following their hatch year. Actual participation in helping behavior was not required for this classification. Post-hoc testing was similar to Part 2.

RESULTS

Part 1: Sexual size dimorphism in nestlings

From the Sandhills population (1994-2009), 1484 male and 1547 female nestlings from 1256 broods met the criteria for inclusion. The mean proportion of males fledged from these broods did not differ from that expected under parity ($0.4924 \pm 0.0097\text{SE}$; likelihood ratio chi-square: $\chi^2_1=0.350$, $N=6062$, $p=0.5540$). From our growth model, nestling mass increases with age at banding (ANOVA; $F_{6,3024}=474.47$, $p<0.0001$), and although nestling sex alone is not a significant predictor of mass (ANOVA; $F_{1,3029}=3.846$, $p=0.5978$), the rate of increase with age differs between males and females (ANOVA; sex*age interaction: $F_{6,3024}=224.73$, $p=0.0230$; Figure 2). This effect is likely driven by the size difference on day nine, where males are larger than females; however, for all other ages, males and females demonstrate strikingly similar patterns of nestling mass growth (Tukey-Kramer post hoc test). On the banding age with the most robust sample size (day 7), male nestlings were approximately 2.6% heavier than females, although according to the post-hoc test, this difference is not statistically significant.

Of the 2007-2009 Sandhills broods (374 male, 378 female nestlings) included in the leg length growth model, nestling leg length increases with banding age (ANOVA; $F_{6,745}=108.42$, $p<0.0001$); with a marginally non-significant trend for males to be larger than females (ANOVA; $F_{1,750}=3.362$, $p=0.0671$). The rate of increase with age was different between the sexes (ANOVA; sex*age interaction: $F_{6,745}=2.57$, $p=0.0127$; Figure 3). However, for any given age, the sexes did not differ in leg length after adjusting for multiple comparisons (Tukey-Kramer post hoc test). On the banding age with the most robust sample size (day 7), nestling leg length was 1.4% longer for males than females, although according to the post-hoc test, this difference is not statistically significant.

The degree of SSD in nestling red-cockaded woodpecker mass varied according to brood composition (Figure 4). Our model selection procedure from single-sex broods resulted in 11 of 36 models with AIC_c weights greater than 0.01 (Table 1). The top-ranking model (18) had 37% of the total model weight and indicated that nestling mass varies with age (included in all models), cohort and the age of the breeder male, but does not vary with nestling sex (Table 1). Eight of 36 models from the mixed-sex dataset had AIC_c weights greater than 0.01 (Table 2). The top-ranking model (33) had 33% of the total model weight and indicated that nestling mass varies with age (included in all models), cohort, brood size, the number of helpers and nestling sex (Table 2). However, since models in addition to the top-ranking model showed some support in both brood type analyses (Tables 1 and 2), model-averaged regression coefficients and their unconditional 95% confidence intervals were generated to interpret the influence of individual covariates on nestling mass (Table 3). For both single-sex and mixed-sex broods, mean nestling mass increased with banding age, varied among cohorts, and decreased with increasing brood size (Table 3). In either scenario, there was no support for the effect of the number of helpers and age of the breeder male on nestling mass (Table 3). For broods containing only single sex nestlings, there was no support for nestling mass differences between the sexes (Table 3). Mixed broods had strong support for a sex difference in mass, where male nestlings were heavier than females (Table 3). The interaction between brood size and sex was not supported in either brood composition scenario (Table 3).

In the subset of broods with leg length measures (374 males, 378 females), the relationship between the degree of SSD in nestling red-cockaded woodpecker leg length and brood composition is less clear than with nestling mass (Figure 5). Our model selection procedure for single-sex broods resulted in 15 of 36 models with AIC_c weights greater than 0.01

(Table 4). The top-ranking model (9) had 28% of the total model weight and indicated that nestling mass varies with age (included in all models), cohort and nestling sex (Table 4). Twenty-two of 36 models from mixed-sex broods had AICc weights greater than 0.01 (Table 5). Two models (9, 5) shared the top-ranking position. Each had only 10% of the total model weight (Table 5) and contained age (included in all models), and sex. Model 9 also indicated that nestling leg length varies with cohort (Table 5). Again, many models showed some support and therefore model-averaged regression coefficients and their unconditional 95% confidence intervals were generated (Table 6). Leg length increased with banding age for both single-sex (15 models with weights > 0.01; Table 4) and mixed-sex (22 models with weights > 0.01; Table 5) broods (Table 6). Leg length varied among cohorts only for single-sex broods (Table 6). Unlike nestling mass, there was no support for the effect of brood size on leg length in either scenario (Table 6). Similar to the pattern seen with nestling mass, there is support for the effect of sex on leg length only in mixed sex broods (Table 6). However, the model-averaged regression coefficients are close enough to zero in both scenarios to question whether this difference is biologically meaningful (Table 6). In both scenarios, the model-averaged estimates for leg length were 1.4% longer for males than females, suggesting that brood composition does not affect the effect size of SSD in leg length. The support for the sex covariate in only mixed-sex broods thus may be an artifact of a more robust sample size for mixed sex broods rather than a true biological difference between brood composition scenarios. There was no support for the effect of the number of helpers, the interaction between brood size and sex, or the age of the breeder male on leg length for either brood composition scenario (Table 6).

Part 2: Natal brood sex-ratio and individual fitness

In the Sandhills (1994-2009), we observed 16 brood sex-ratio types from 1435 broods where the sex of all banded nestlings was known (Figure 6). There was no difference between the number of brood sex-ratio types observed and the number expected under random ZW chromosomal sex determination within each brood size (likelihood ratio tests; one nestling: $X^2_1=0.072$, $N=347$, $p=0.7878$; two nestlings: $X^2_2=0.763$, $N=1199$, $p=0.6829$; three nestlings: $X^2_3=4.240$, $N=1132$, $p=0.2367$; four nestlings: $X^2_4=4.557$, $N=191$, $p=0.3358$; five nestlings: $N=2$, statistics not available; Figure 6). At Camp Lejeune, we observed only 13 brood sex-ratio types (0_4 and five nestling broods were never observed) from 1107 broods where the sex of all banded nestlings was known. Similar to the Sandhills, the observed distribution of brood sex-ratio types did not differ from expected within each brood size (likelihood ratio tests; one nestling: $X^2_1=0.060$, $N=151$, $p=0.8058$; two nestlings: $X^2_2=3.867$, $N=527$, $p=0.1447$; three nestlings: $X^2_3=1.686$, $N=300$, $p=0.6400$; four nestlings: $X^2_4=1.586$, $N=29$, $p=0.8113$; not shown). The mean brood size differed between populations; the number of nestlings at banding was larger in the Sandhills (mean: 2.671 ± 0.0135) than Camp Lejeune (mean: 2.439 ± 0.0209 ; likelihood ratio test: $X^2_4=33.534$, $N=1937$, $P<0.0001$; not shown).

There was no difference in fledging success according to brood composition (single or mixed-sex) in either sex in the Sandhills (2007-2009 only). The percent of male nestlings surviving from the day 20 crown patch check to the fledge check observation (within two weeks post-fledging) was 92% for single-sex broods and 89% for mixed-sex broods, but this difference between brood types was not statistically significant (mean survival=90%; $X^2_1=1.416$, $N=372$, $p=0.2341$). The same non-significant pattern was observed in females where the percentage of

nestlings surviving to fledge was 92% for single-sex broods and 90% for mixed-sex broods (mean survival=91%; $X^2_1=0.290$, $N=351$, $p=0.500$).

In the Sandhills population, first-year survival did not differ according to brood sex-ratio type for either sex (logistic regression; males: $X^2_9=9.74$, $N=1484$, $p=0.3725$; females $X^2_9=9.63$, $N=1547$, $p=0.3813$). The mean probability of first year survival was higher for males ($0.45 \pm 0.01SE$) than females ($0.33 \pm 0.01SE$). There was no difference in the probability that a male nestling would fill a breeding vacancy by his seventh year across brood sex-ratio types (logistic regression; $X^2_9=5.37$, $N=785$, $p=0.8002$: mean= $0.2433 \pm 0.02SE$). The mean probability that a female nestling would fill a female breeder vacancy by her third spring was $0.2809 \pm 0.01SE$, and did not differ across natal brood sex-ratio types (logistic regression; $X^2_9=7.09$, $N=1406$, $p=0.6273$). Females who fill breeder vacancies by their second or third year are equally likely to join a recruitment group containing helpers regardless of their natal sex-ratio (logistic regression; $X^2_9=5.05$, $N=372$, $p=0.8286$; mean: $0.3065 \pm 0.02SE$).

Part 3: Female helping behavior

For female fledglings in the Sandhills, the probability of becoming a natal helper differs according to natal brood sex-ratio (logistic regression; $X^2_9=23.49$, $N=1545$, $P=0.0054$; Figure 7a). Females from single nestling broods had the highest probability of remaining as a natal helper ($0.1127 \pm 0.04SE$ vs. $0.0265 \pm 0.004SE$ (mean across all female fledglings)). The difference in dispersal probability among sex-ratio types persists when looking only at females that survived to their first breeding season (logistic regression; $X^2_9=23.49$, $N=506$, $P=0.0195$; not shown), and females from single nestling broods are still the most likely to delay dispersal

(0.2759 ± 0.0830 vs. 0.0810 ± 0.01 SE (mean across all female first-year survivors)). At Camp Lejeune, the probability that a female fledgling will become a natal helper was 3.6 times more likely than in the Sandhills (mean: $0.09667 \pm 0.0124SE$ vs. $0.0265 \pm 0.0041SE$); however, unlike the Sandhills, there was no difference across natal brood sex-ratio types (logistic regression; $X^2_{8}=4.03$, $N=569$, $P=0.8538$; Figure 7b). There was still no difference in the probability of female helping behavior according to sex-ratio type when looking only at females that survived to their first breeding season (logistic regression; $X^2_{8}=5.21$, $N=253$, $P=0.738$; not shown).

DISCUSSION

Sexual-size dimorphism and competitive environment

Our growth model revealed subtle SSD for both mass and leg length, where males were slightly heavier and structurally larger than females. Our size measures are consistent with the direction of SSD observed for adults in this species (Pizzoni-Ardemani 1990; Jackson 1994). However, the magnitude of SSD observed for nestlings in the Sandhills population (males were 2.6% heavier and 1.4% larger than females; this study) was not as strong as previously reported for adults (males 4.1% heavier and 3.6% larger than females; (Pizzoni-Ardemani 1990; Jackson 1994)). This suggests that some sex-biased growth must take place after the age 4-11 day banding period. If the degree of SSD increases gradually over time we should also be cautious of our use of banding size as a surrogate for “inherent SSD” or SSD at hatching. It is still possible that there is no SSD at hatching, but competitive asymmetries in an asynchronous brood during the period of rapid growth from hatching to day 4 will result in subtle, but measurable

differences in size at banding. Until more is known about possible sex-biases in laying- or hatching-order in this species, our explanations of the proximate origin of SSD before ages 4-7 days will remain speculative. While the degree of SSD immediately at hatching is unknown, and sexual differences in size is very subtle between the ages 4-11 days, our analysis reveals that these subtle differences are flexible based on natal competitive environment.

While mass and leg length differed between the sexes in the growth models, we were able to distinguish the influence of competitive environment on the degree of SSD by splitting broods according to the number of nestlings and their sexual composition. The degree of SSD in leg length did not differ with increasing brood size, or sexual composition, suggesting that the larger structural size of males observed in nestling red-cockaded woodpeckers may be a more stable physical quality, and less vulnerable to rearing conditions. However, nestling mass decreased with increasing brood size for both sexes, supporting our assumption that larger broods are more competitive rearing environments. Males and females raised in broods without competition (singletons) exhibited no SSD in mass. Females were lighter than males only when reared in mixed-sex broods indicating that intrabrood competition between opposite-sex siblings has important consequences for access to natal resources. In mixed-sex broods, the structural size advantage of males may result in females being more vulnerable to the increased competition within larger broods. These findings complement the male-biased competitive superiority of red-cockaded woodpecker males observed in the fledgling (Hewett Ragheb and Walters 2011) and adult stages (Jackson 1994). Together, these results most strongly support the predictions from our second hypothesis where SSD is inherent in the nestling stage (but only subtly), and the smaller sex (female) suffers in situations with increased competition as a result of losing to siblings of the larger sex during scramble competition. This pattern is in line with other studies

of species exhibiting subtle SSD (Oddie 2000; Koenig et al. 2001b; Zanette et al. 2005), but contrary to our first hypothesis that the larger sex is more vulnerable to poor rearing conditions. Fisher's (1930) prediction that the larger sex suffers under poor rearing conditions as a result of the higher investment required by parents may not entirely apply in this system since nestlings compete amongst themselves for access to resources, and the allocation of resources is not solely determined by parental choice

Early competitive environment and future life history traits

Despite increased SSD among male and female nestlings raised in mixed-sex broods, we observed little impact of the natal competitive environment on measures of survival and recruitment, contrary to our predictions. First, the sex composition of the brood (single- or mixed-sex) did not affect the probability that male or female nestlings sexed during the crown patch check (day 20) would survive to fledge (day 26). However, we might not expect to see substantial mortality during this short interval so late in the brooding stage, since daily rates of partial brood loss are drastically higher during the short interval between hatching and day 6 (between 1.8-3.2% daily) than the longer interval from day 7 to fledging (between 0.3-0.7% daily; LaBranche and Walters 1994). A closer examination of sex-biased mortality early in the nestling stage would require genetic sexing techniques, since the sexually dimorphic plumage of nestlings is not reliably distinguishable until age 20 days (E.L.H.R, personal observation). Although we were not able to directly detect sex-biased mortality in the nest, the population-level fledgling sex-ratio did not differ from parity (49% male), and the distribution of sex-ratio types within each brood size did not differ from expected under random ZW chromosomal sex

determination, suggesting no sex bias in nestling mortality. An alternative explanation is that there is a sex-bias in nestling mortality, but it is obscured by a corresponding sex-bias in the primary (egg) sex-ratio, where more females are produced to offset high rates of female mortality. However, a simple look at our long-term dataset does not support this scenario. Broods experiencing no brood reduction (the number of eggs in the complete clutch equals the number of fledglings) revealed a sex-ratio of 0.4890 which does not differ from parity (Sandhills population 1994-2009: Likelihood ratio test, $X^2_1=0.375$, $N=1540$ nestlings, $p=0.5401$). It may be however, that these broods were reared under conditions of relatively high resource availability (hence no brood reduction), and it is possible that sex-biases in either the primary (egg) sex-ratio or nestling mortality are subject to annual variation in resources. A more thorough examination of the interaction between annual food availability and the degree of sex-biased nestling mortality may help to better understand the intrabrood competitive environment.

Second, fledglings of either sex were equally likely to survive to their first breeding season regardless of the sex-ratio of their natal brood. Males had higher rates of first year survival than females, consistent with other studies (Walters 1990; Hewett Ragheb and Walters 2011), but within sexes, the nestling competitive environment did not appear to affect an individual's ability to survive through their first winter. For the analysis in this study, the locations of individuals on the breeding season census were not taken into account, only presence. As discussed later in this section and elsewhere (Hewett Ragheb and Walters 2011), the intrabrood competitive environment may play an important role in determining dispersal strategies. Dispersing away from unfavorable competitive situations on the natal territory may be a way to increase first-year survival.

Third, the natal sex-ratio did not affect the probability of recruitment for either sex. Males were equally likely to fill a breeder vacancy at least once within their first seven years and females within their first three years regardless of the competitive environment of their natal brood. The quality of the recruitment territory for females recruiting as second year birds also did not vary with natal brood sex-ratio, suggesting that the competitive environment at home does not give dispersing individuals a competitive advantage when obtaining breeder vacancies.

Female helping behavior

Lastly, natal sex-ratio did influence the probability that a female fledgling will become a natal helper during her first breeding season in one but not both populations. Since females are almost exclusively subordinate to males, and dispersal in juvenile males is strongly linked to intrabrood fledgling rank, we would expect only solitary females or dominant females from all-female broods to be in the social position to remain home as a helper as outlined in the predictions of our first hypothesis. This was partially supported in the Sandhills where females from singleton broods had the highest rates of philopatry (11% of fledglings survived their first year and then delayed dispersal). One might suppose that these philopatric singleton females are produced by younger breeders than their dispersing counterparts since the number of fledglings produced increases with breeder age (Walters 1990). If young breeders produce smaller broods, they may also produce nestlings of low physiological quality as an result of parental inexperience and therefore their offspring may require extra time on the natal territory before successful dispersal. Our data do not support this idea however, since nestling mass decreases with increasing brood size and singleton nestlings of either sex were the heaviest on average (Figure

4). Increased philopatry of singleton females in the Sandhills suggests that the presence of any brood-mate competitor, regardless of sex or quantity, discourages philopatric behavior, and may provide an additional explanation for why this strategy remains so rare.

Across all broods, however, the rates of female philopatry were not as high as we would predict if females exhibited the same preference for delayed dispersal as males, but were constrained by social inferiority. If this were the case, then approximately 91% of dominant females (from singleton or female-only broods) that survived to their first breeding season would delay dispersal (as calculated for males; (Hewett Ragheb and Walters 2011)). However, if we look at female first year survivors from our Sandhills dataset and calculate the theoretical number of those females that could be dominant over their brood-mates, given their natal brood sex-ratio type (assuming subordination to male brood-mates, only one dominant female per female-only brood and equal first-year survival for dominant and subordinate females), only 21% of theoretically dominant females delay dispersal. These lower observed rates of female helping behavior in the Sandhills confirm our initial hypotheses that other factors are important in determining female dispersal strategy and intrabrood competition is not the primary explanation for sex-biased delayed dispersal.

Contrary to the Sandhills, at Camp Lejeune no difference in female helping probability was observed among natal sex-ratio types despite a much higher mean probability of female helping behavior. This higher rate of female helping behavior at Camp Lejeune relative to the Sandhills has previously been reported (Koenig and Walters 1999). We anticipated that this difference could arise as an artifact of the smaller average clutch size at Camp Lejeune creating more singleton female broods, but this was not the case, as female helpers were not disproportionately from singleton broods.

Alternatively, differences in female helping behavior observed between populations may come from differences in the ecological constraints to independent reproduction, more specifically, the relative availability of breeding vacancies for females. In Camp Lejeune, adult female survival is higher resulting in lower rates of female breeder turnover (J.R.W.). If competition over available breeder vacancies is high enough, delayed dispersal may become the preferred strategy for females. In the Sandhills, independent reproduction for females is less constrained by the availability of breeding vacancies and dispersal is more likely to be the preferred strategy for all females. Singleton females appear to be the slight exception. Unhindered access to natal resources may encourage higher rates of philopatry for these females on the basis of the intrinsic benefits of delayed dispersal (Stacey and Ligon 1991; Koenig et al. 1992).

A better understanding of the behavior of dominant females would be particularly informative when comparing female dispersal behavior between these two populations. Socially dominant individuals are presumed to have first choice among life history strategies and therefore, comparing strategies of individuals according to their social rank will help us understand which strategy is preferred for a given population at a given point in evolutionary time. Unfortunately, in this study we do not know the social ranks of females from broods containing more than one female. The relationship between mass relative to brood-mates and dispersal strategy appears to be less clear in females than in males, although females that are very heavy relative to their siblings show a very slightly increased probability of delayed dispersal (Sandhills and Camp Lejeune combined; Chapter III: Part 2: Figure 6). Intra-brood dominance may be a stronger predictor of delayed dispersal for females than brood composition. Interestingly, at Camp Lejeune even females from mixed-sex broods frequently delay dispersal,

suggesting that the presence of a male brood-mate may not completely prevent remaining on the natal territory. It may be that dominance relationships within sexes may be more influential in determining dispersal strategies than relationships between sexes. On the other hand, the sexes may differ in the factors they consider when making dispersal decisions. While male dispersal strategy seems tightly linked with both relative mass and intrabrood social rank, females may make dispersal decisions based primarily on ecological factors and secondarily on social factors.

Conclusion

Red-cockaded woodpecker nestlings exhibit very subtle structural SSD that results in increased SSD in mass for nestlings in mixed-sex broods. While females are smaller than their brothers when raised together, we were unable to detect any deleterious effects of the natal competitive environment in any measures of survival or recruitment probability. The probability of female helping behavior was influenced by natal competitive environment; however, the pattern was not consistent across populations. Previously, the evolution of female-biased dispersal in red-cockaded woodpeckers has been attributed to inbreeding avoidance, sex-biases in competition over breeding vacancies, or the relative payoff between philopatry and dispersal (Walters et al. 1992a). Our findings provide support for several factors acting on different scales. For females, it is possible that the number of available breeding vacancies acts on the population to set the level of competition among dispersed yearlings and the probability of recruitment. This in turn influences the balance between the costs and benefits of dispersal and may alter dispersal decisions, even for females from highly competitive natal environments.

ACKNOWLEDGEMENTS

We thank all past and current field staff working with both the Sandhills and Camp Lejeune study populations for their contribution to the red-cockaded woodpecker long-term demographic data set. Particularly, the staff and associates from the Sandhills Ecological Institute: K. Brust, S. Anchor, J. H. Carter III, V. Genovese, M. Jusino, M. King and J. Maynard. Kevin Rose and K. Hudgins conducted the winter censuses at Camp Lejeune analyzed in this study. We also thank the U.S. Army Fort Bragg Endangered Species Branch: J. Britcher and J. Schillaci, the North Carolina Sandhills Gamelands and Wildlife Resources Commission: B. Beck; and the natural resource managers at Marine Corp Base Camp Lejeune: C. Tenbrink, G. Haught, J. Townson and B. Rogers. J. Fraser, D. Hawley, J. Philips and C. Eikenaar provided helpful advice throughout the development of the project. We thank V. Garcia, J. Cohen and D. Catlin for their patient assistance with mark-recapture analysis methods. The Virginia Tech Institutional Animal Care and Use Committee (10-138-BIOL, 01-080-BIOL), the Department of the Interior U.S. Fish and Wildlife Service (TE070846-1, TE070846-2) and the North Carolina Wildlife Resources Commission Division of Wildlife Management (NC-2007ES88, NC-2008ES88, NC-2009ES88, NC-2010ES88) served as the governmental authorities approving ethical treatment of animals for this research.

FIGURE CAPTIONS

Figure 1: Distribution of social recruitment ages for male (black bars) and female (gray bars) red-cockaded woodpeckers from the Sandhills population (1994-2009). Cumulative percentages of age at first reproduction are shown as solid (female) and dashed (males) lines. Social recruitment was assigned to individuals the first year they filled a social breeder vacancy at an established territory cohabited by an opposite-sex adult.

Figure 2: Nestling mass growth models for female (black circles) and male (white circles) red-cockaded woodpecker nestlings ages 4-11 days from the Sandhills population (1994-2009). Values represent least squares mean mass (g) at banding and 95% confidence intervals from a linear model for nestling mass containing independent variables sex, age (in days) and a sex*age interaction term. Bars at bottom of graph represent sample size for female (black bars, N=1547) and male (white bars, N=1484) nestlings. Star represents statistical difference ($p < 0.05$) in mean mass between the sexes as determined by a Tukey-Kramer post-hoc test.

Figure 3: Nestling leg length growth models for female (black circles) and male (white circles) red-cockaded woodpecker nestlings ages 4-11 days from the Sandhills population (1994-2009). Values represent least squares mean leg length at banding and 95% confidence intervals from a linear model for nestling mass containing independent variables sex, age and a sex*age interaction term. Bars at bottom of graph represent sample size for female (black bars, N=378) and male (white bars, N=374) nestlings (1994-2009).

Figure 4: Mean predicted mass (g) for female (white bars) and male (hashed bars) red-cockaded woodpecker nestlings (4-11 days) from the Sandhills population (1994-2009) as a function of brood size for single sex (a) and mixed sex (b) broods. Model-averaged parameter estimates and their unconditional 95% confidence intervals were generated from linear mixed models in the candidate model sets with AIC_c weights greater than 0.01. All models included the random effect covariate ‘family’ to control for non-independence of brood-mates and the fixed covariate ‘age’ to control for variation in the age at banding. Additional fixed covariates included: annual variation (cohort), the age of the breeder male (male), brood size (brood), nestling sex (sex), the number of helpers on the natal territory at the time of rearing (helpers), and a brood size and sex interaction term (brood*sex).

Figure 5: Mean predicted leg length (mm) for female (white bars) and male (hashed bars) red-cockaded woodpecker nestlings (4-11 days) from the Sandhills population (1994-2009) for single sex (a) and mixed sex (b) broods. Model-averaged parameter estimates and their unconditional 95% confidence intervals were generated from linear mixed models in the candidate model sets with AIC_c weights greater than 0.01. All models included the random effect covariate ‘family’ to control for non-independence of brood-mates and the fixed covariate ‘age’ to control for variation in the age at banding. Additional fixed covariates included: annual variation (cohort), the age of the breeder male (male), brood size (brood), nestling sex (sex), the number of helpers on the natal territory at the time of rearing (helpers), and a brood size and sex interaction term (brood*sex).

Figure 6: Distribution of brood sex-ratio types from 1435 red-cockaded woodpecker broods from the Sandhills population (1994-2009) where the sex of all banded nestlings is known. Values represent the number of broods observed in the population (black bars) and the number of broods expected under random ZW chromosomal sex determination (gray bars) within each brood size category. Brood sex-ratio types are denoted by the number of males subscripted by number of females.

Figure 7: The proportion of fledgling females remaining on their natal territories as helpers during their first breeding season according to natal brood sex-ratio type for the Sandhills (a) and Camp Lejeune (b) populations (1994-2009). In the Sandhills, 41 of 1545 (2.7%) female fledglings survived to their first breeding season and became natal helpers (sample sizes: $0_1=71$, $0_2=281$, $1_1=254$, $0_3=191$, $1_2=355$, $2_1=210$, $0_4=12$, $1_3=85$, $2_2=72$, $3_1=14$) In Camp Lejeune, 55 of 569 (9.7%) female fledglings survived to their first breeding season and became natal helpers (sample sizes: $0_1=39$, $0_2=126$, $1_1=151$, $0_3=75$, $1_2=94$, $2_1=59$, $0_4=0$, $1_3=9$, $2_2=12$, $3_1=4$). Values represent the least squared mean probability and 95% confidence intervals from binary logistic regression models of the probability of becoming a natal helper with the independent categorical variable brood sex-ratio. Brood sex-ratio types are denoted by the number of males subscripted by number of females. Bars that do not share a common letter are statistically different according to a Tukey-Kramer post-hoc test ($p<0.10$).

Figure 4. 1 Distribution of social recruitment ages.

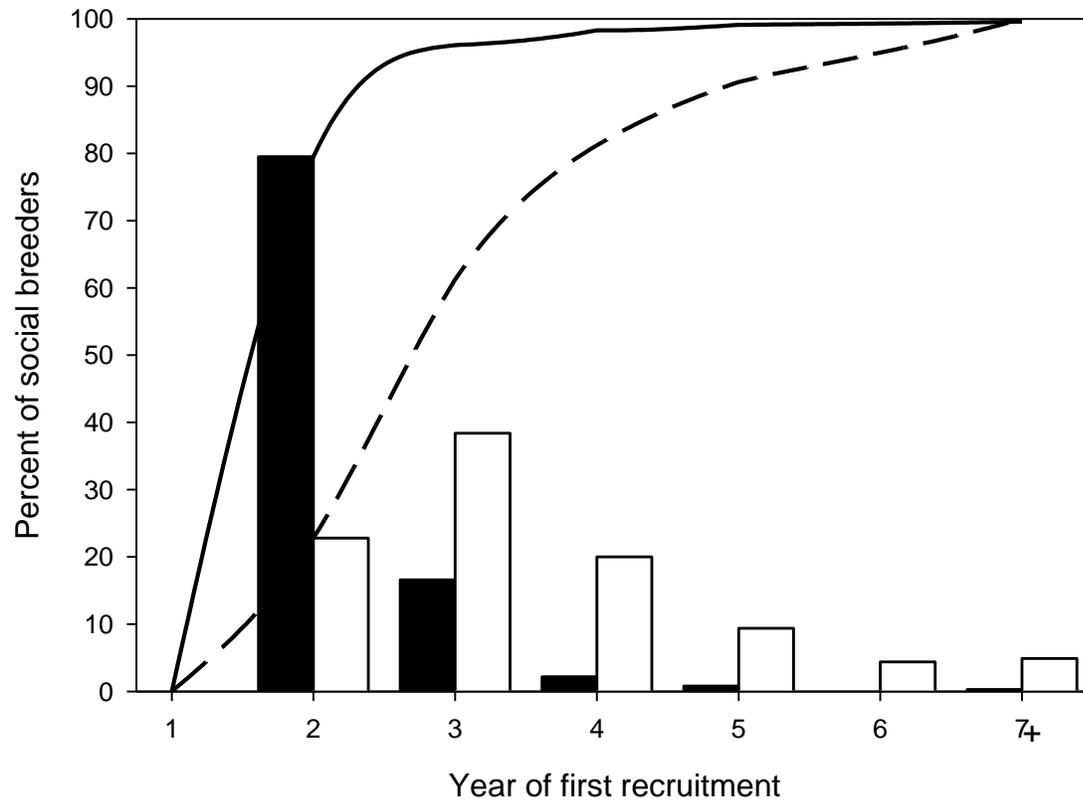


Figure 4. 2 Nestling mass growth models.

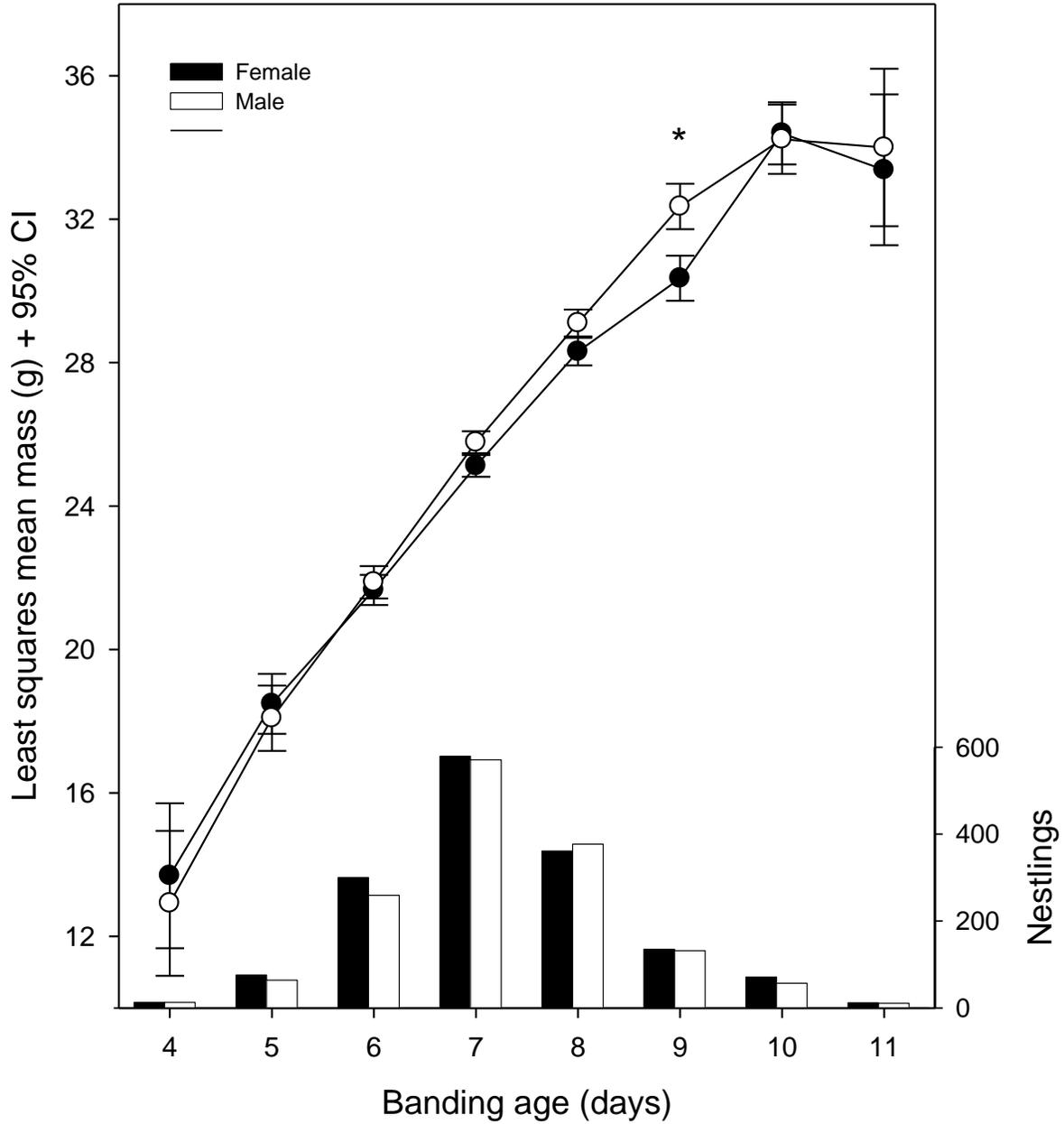


Figure 4. 3 Nestling leg length growth models.

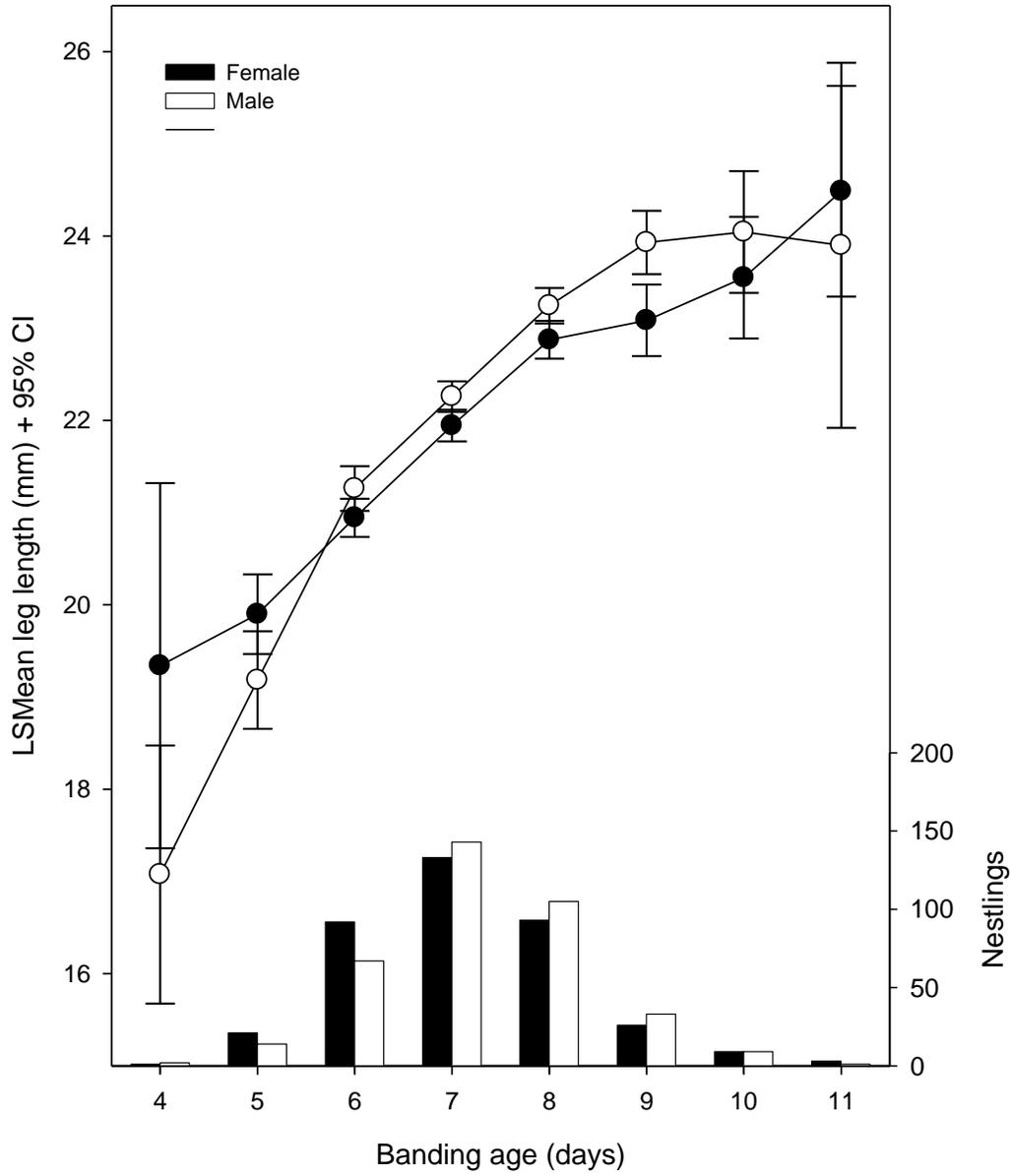


Figure 4. 4 Predicted nestling mass

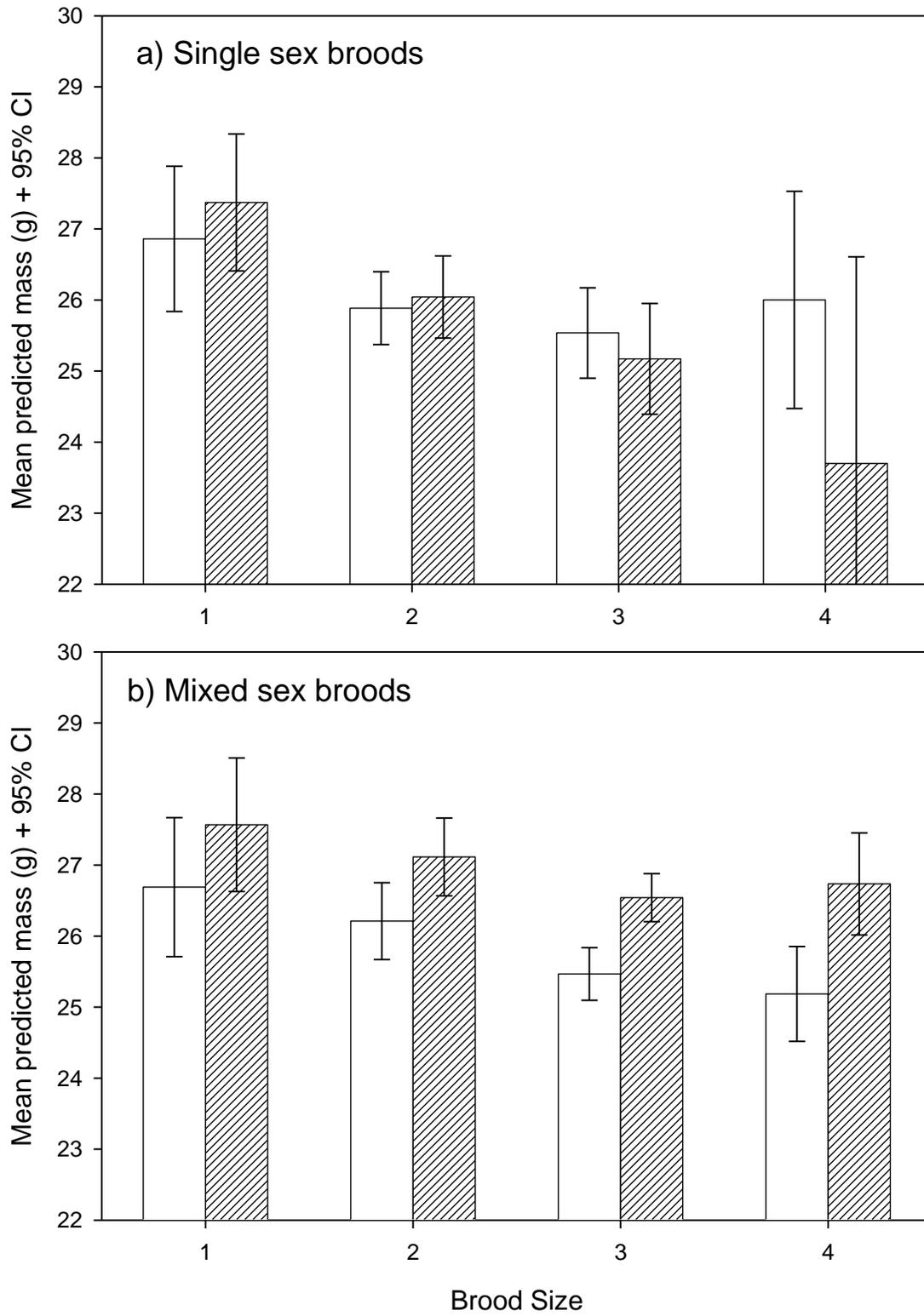


Figure 4. 5 Predicted nestling leg length.

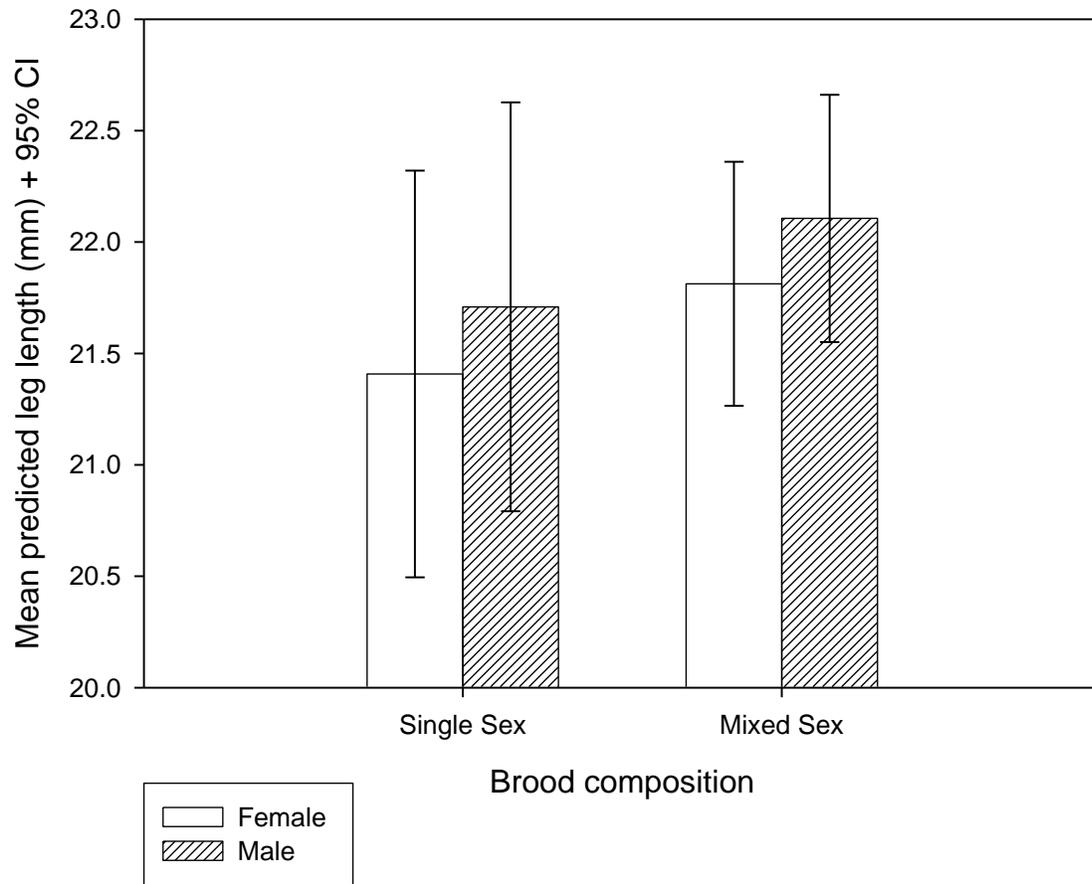


Figure 4. 6 Distribution of brood sex-ratio types.

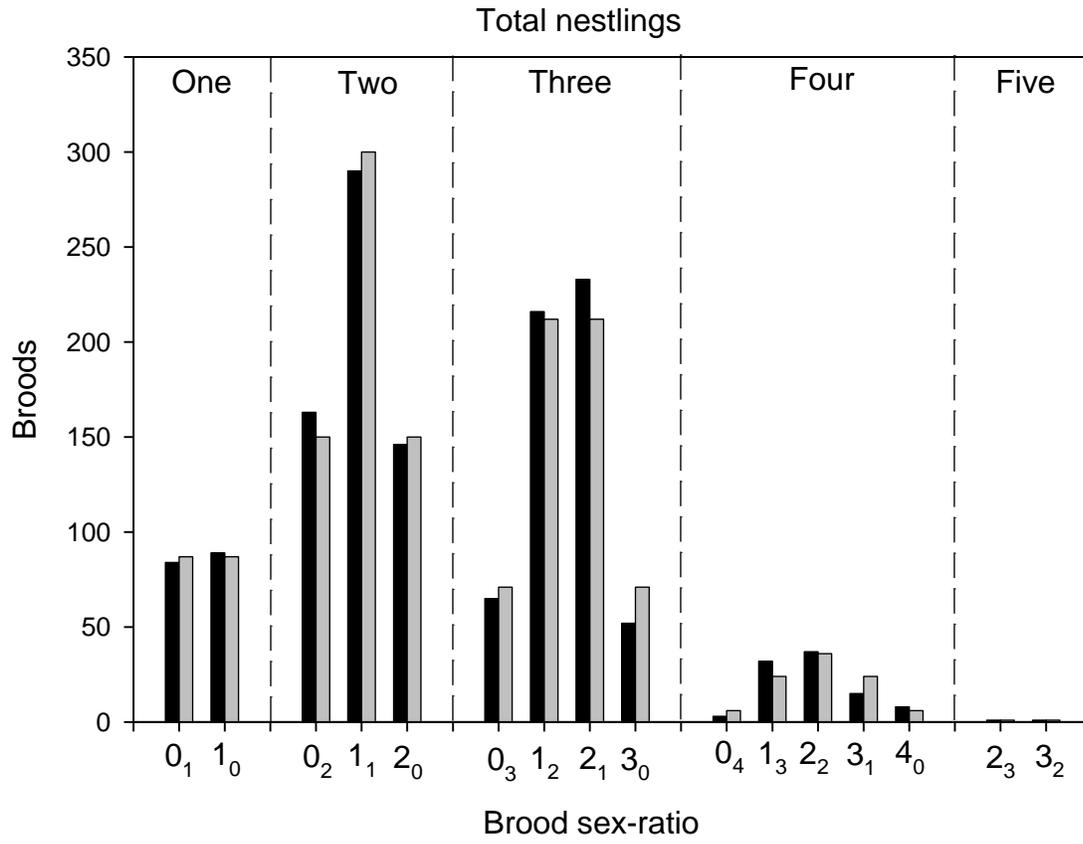


Figure 4. 7 Natal helping behavior in female fledglings

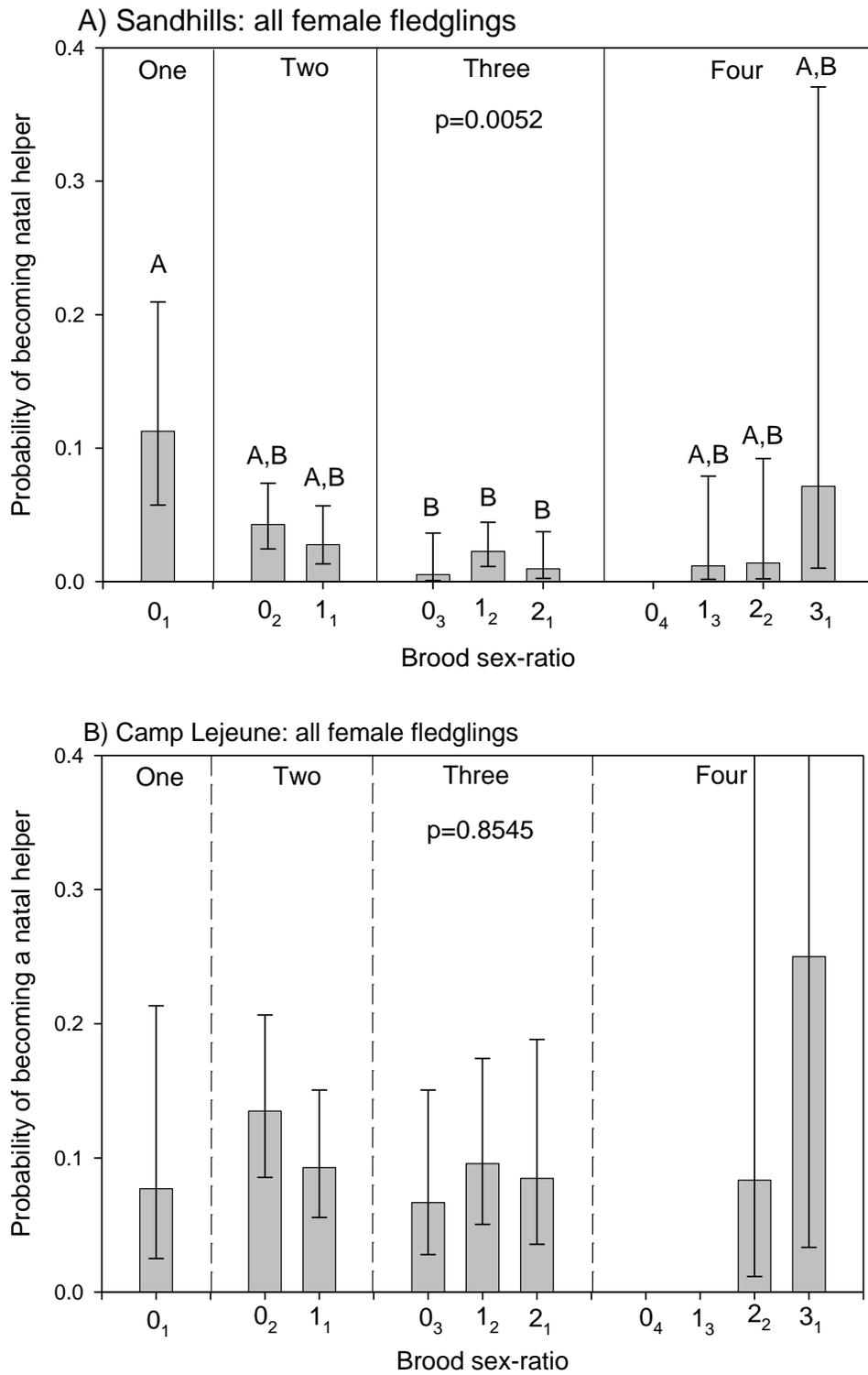


Table 4. 1 Select linear mixed models for nestling red-cockaded woodpecker mass from broods containing only single-sex nestlings (1994-2009).

Rank	No.	Model	AIC _c	ΔAIC _c	Model weight	Model likelihood	K	-2log(L)
1	18	Age Cohort Male Brood	5427.1	0.0	0.366	1.000	21	5384.2
2	31	Age Cohort Male Brood Sex	5428.7	1.6	0.164	0.449	22	5383.7
3	8	Age Cohort Brood	5429.6	2.5	0.105	0.287	20	5388.8
4	32	Age Cohort Male Brood Sex Brood*Sex	5429.8	2.7	0.095	0.259	23	5382.7
5	37	Age Cohort Male Brood Sex Helpers	5430.8	3.7	0.058	0.157	23	5383.7
6	23	Age Cohort Brood Helpers	5430.9	3.8	0.055	0.150	21	5388.0
7	21	Age Cohort Brood Sex	5431.0	3.9	0.052	0.142	21	5388.1
8	38	Age Cohort Male Brood Sex Helpers Brood*Sex	5431.9	4.8	0.033	0.091	24	5382.7
9	22	Age Cohort Brood Sex Brood*Sex	5432.1	5.0	0.030	0.082	22	5387.1
10	33	Age Cohort Brood Sex Helpers	5432.3	5.2	0.027	0.074	22	5387.3
11	34	Age Cohort Brood Sex Helpers Brood*Sex	5433.5	6.4	0.015	0.041	23	5386.4
31	1	Age	5475.7	48.6	0.000	0.000	4	5467.6

Models shown represent the 11 top-ranking models (95% of AIC_c weight) and the starting model (1; listed below blank row in table).

All models included the random effect covariate ‘family’ to control for non-independence of brood-mates and the fixed covariate ‘age’ to control for variation in the age at banding. Additional fixed covariates included: annual variation (cohort), the age of the breeder male (male), brood size (brood), nestling sex (sex), the number of helpers on the natal territory at the time of rearing (helpers), and a brood size and sex interaction term (brood*sex). Models are shown with the AIC_c score, change in AIC_c score (ΔAIC_c), model weight, model likelihood, number of estimable parameters (K), and model deviance (-2log(L)).

Table 4. 2 Select linear mixed models for nestling red-cockaded woodpecker mass from broods containing mixed-sex nestlings (1994-2009).

Rank	No.	Model	AICc	Δ AICc	Model weight	Model likelihood	K	-2Log(L)
1	33	Age Cohort Brood Sex Helpers	11378.3	0.0	0.329	1.000	22	11333.8
2	34	Age Cohort Brood Sex Helpers Brood*Sex	11379.3	1.0	0.199	0.607	23	11332.7
3	37	Age Cohort Male Brood Sex Helpers	11380.3	2.0	0.121	0.368	23	11333.8
4	21	Age Cohort Brood Sex	11380.4	2.1	0.115	0.350	21	11337.9
5	38	Age Cohort Male Brood Sex Helpers Brood*Sex	11381.3	3.0	0.073	0.223	24	11332.7
6	22	Age Cohort Brood Sex Brood*Sex	11381.4	3.1	0.070	0.212	22	11336.9
7	31	Age Cohort Male Brood Sex	11381.8	3.5	0.057	0.174	22	11337.3
8	32	Age Cohort Male Brood Sex Brood*Sex	11382.8	4.5	0.035	0.105	23	11336.3
35	1	Age	11475.8	97.5	0.000	0.000	4	11467.8

Models shown represent the 8 top-ranking models (95% of AIC_c weight) and the starting model (1; listed below blank row in table).

All models included the random effect covariate ‘family’ to control for non-independence of brood-mates and the fixed covariate ‘age’ to control for variation in the age at banding. Additional fixed covariates included: annual variation (cohort), the age of the breeder male (male), brood size (brood), nestling sex (sex), the number of helpers on the natal territory at the time of rearing (helpers), and a brood size and sex interaction term (brood*sex). Column statistics are the same as described in Table 1.

Table 4. 3 Results from linear mixed models for nestling mass with model weights greater than 0.01 from single-sex and mixed-sex broods.

Covariate	Single sex scenario			Mixed sex scenario		
	β	LCL	UCL	β	LCL	UCL
Intercept	3.055	1.340	4.771	4.604	3.167	6.041
Banding age	3.358	3.152	3.564	3.150	2.978	3.321
Cohort: 1994 vs. 2009	1.177	-0.008	2.361	-0.248	-1.087	0.590
1995 vs. 2009	-0.062	-0.968	0.844	-0.733	-1.693	0.228
1996 vs. 2009	0.059	-1.191	1.309	-0.211	-1.137	0.714
1997 vs. 2009	1.483	0.444	2.522	1.989	1.077	2.900
1998 vs. 2009	0.475	-0.677	1.628	0.336	-0.482	1.154
1999 vs. 2009	0.877	-0.121	1.874	1.229	0.392	2.067
2000 vs. 2009	-0.310	-1.253	0.633	0.144	-0.730	1.019
2001 vs. 2009	-1.617	-2.631	-0.603	-0.993	-1.917	-0.068
2002 vs. 2009	-0.219	-1.179	0.740	-0.225	-0.995	0.545
2003 vs. 2009	1.295	0.171	2.418	0.538	-0.358	1.433
2004 vs. 2009	0.625	-0.250	1.501	0.208	-0.557	0.973
2005 vs. 2009	-0.287	-1.168	0.595	0.204	-0.629	1.037
2006 vs. 2009	-0.682	-1.544	0.180	0.141	-0.597	0.878
2007 vs. 2009	-2.184	-2.985	-1.383	-1.100	-1.914	-0.286
2008 vs. 2009	0.164	-0.666	0.993	-0.204	-0.909	0.500
Brood size	-0.713	-1.059	-0.367	-0.551	-0.823	-0.278
Sex (female vs. male)	-0.040	-0.231	0.151	-0.502	-0.626	-0.379
Helpers	0.011	-0.135	0.157	0.190	-0.131	0.511
Brood size*sex	0.030	-0.160	0.220	-0.033	-0.167	0.100
Breeder male age	0.069	-0.046	0.183	0.003	-0.042	0.048

Model averaged regression coefficients (β) presented with their unconditional lower (LCL) and upper (UCL) 95% confidence intervals

generated from linear mixed models in the candidate model sets (single sex, mixed sex) with AIC_c weights greater than 0.01. All

models included the random effect covariate ‘family’ to control for non-independence of brood-mates (not shown) and the fixed covariate ‘age’ to control for variation in the age at banding. Additional fixed covariates included: annual variation (cohort), brood size (brood), nestling sex (sex), the number of helpers on the natal territory at the time of rearing (helpers), a brood size and sex interaction term (brood*sex), and the age of the breeder male (male). Covariates with strong support (confidence intervals do not include zero) are highlighted with bold text.

Table 4. 4 Select linear mixed models for nestling red-cockaded woodpecker leg length from broods containing only single-sex nestlings (1994-2009).

Rank	No.	Model name	AICc	Δ AICc	Model weight	Model likelihood	K	-2LogL
1	9	Age Cohort Sex	596.5	0.0	0.279	1.000	7	582.0
2	21	Age Cohort Brood Sex	598.3	1.8	0.113	0.407	8	581.6
3	19	Age Cohort Male Sex	598.4	1.9	0.108	0.387	8	581.7
4	24	Age Cohort Sex HELPERS	598.5	2.0	0.102	0.368	8	581.9
5	22	Age Cohort Brood Sex Brood*Sex	598.6	2.1	0.097	0.350	9	579.7
6	2	Age Cohort	600.1	3.6	0.046	0.165	6	587.7
7	31	Age Cohort Male Brood Sex	600.2	3.7	0.044	0.157	9	581.4
8	33	Age Cohort Brood Sex HELPERS	600.4	3.9	0.040	0.142	9	581.6
9	32	Age Cohort Male Brood Sex Brood*Sex	600.7	4.2	0.034	0.122	10	579.6
10	34	Age Cohort Brood Sex Helpers Brood*Sex	600.7	4.2	0.034	0.122	10	579.7
11	10	Age Cohort HELPERS	601.8	5.3	0.020	0.071	7	587.3
12	8	Age Cohort Brood	601.9	5.4	0.019	0.067	7	587.4
13	7	Age Cohort Male	602.0	5.5	0.018	0.064	7	587.5
14	37	Age Cohort Male Brood Sex HELPERS	602.4	5.9	0.015	0.052	10	581.4
15	38	Age Cohort Male Brood Sex HELPERS Brood*Sex	602.9	6.4	0.011	0.041	11	579.6
20	1	Age	615.6	19.1	0.000	0.000	4	607.4

Models shown represent the 15 top-ranking models (95% of AIC_c weight) and the starting model (1; listed below blank row in table).

All models included the random effect covariate ‘family’ to control for non-independence of brood-mates and the fixed covariate ‘age’ to control for variation in the age at banding. Additional fixed covariates included: annual variation (cohort), the age of the breeder male (male), brood size (brood), nestling sex (sex), the number of helpers on the natal territory at the time of rearing (helpers), and a

brood size and sex interaction term (brood*sex). Models are shown with the AIC_c score, change in AIC_c score (ΔAIC_c), model weight, model likelihood, number of estimable parameters (K), and model deviance ($-2\log(L)$).

Table 4. 5 Select linear mixed models for nestling red-cockaded woodpecker leg length from broods containing mixed-sex nestlings (1994-2009).

Rank	No.	Model name	AICc	Δ AICc	Model likelihood	Model weight	K	-2LogL
1	9	Age Cohort Sex	1356.2	0.0	1.000	0.102	7	1342.0
2	5	Age Sex	1356.2	0.0	1.000	0.102	5	1346.0
3	15	Age Brood Sex Brood*Sex	1356.5	0.3	0.861	0.088	7	1342.2
4	24	Age Cohort Sex HELPERS	1356.7	0.5	0.779	0.079	8	1340.4
5	22	Age Cohort Brood Sex Brood*Sex	1356.9	0.7	0.705	0.072	9	1338.5
6	17	Age Sex HELPERS	1357.1	0.9	0.638	0.065	6	1344.9
7	34	Age Cohort Brood Sex Helpers Brood*Sex	1357.3	1.1	0.577	0.059	10	1336.9
8	30	Age Brood Sex HELPERS Brood*Sex	1357.5	1.3	0.522	0.053	8	1341.1
9	12	Age Male Sex	1358.2	2.0	0.368	0.037	6	1346.0
10	14	Age Brood Sex	1358.2	2.0	0.368	0.037	6	1346.0
11	21	Age Cohort Brood Sex	1358.3	2.1	0.350	0.036	8	1341.9
12	19	Age Cohort Male Sex	1358.3	2.1	0.350	0.036	8	1342.0
13	26	Age Male Brood Sex Brood*Sex	1358.5	2.3	0.317	0.032	8	1342.2
14	33	Age Cohort Brood Sex HELPERS	1358.8	2.6	0.273	0.028	9	1340.4
15	38	Age Cohort Male Brood Sex HELPERS Brood*Sex	1358.9	2.7	0.259	0.026	11	1336.3
16	32	Age Cohort Male Brood Sex Brood*Sex	1358.9	2.7	0.259	0.026	10	1338.4
17	28	Age Male Sex HELPERS	1359.0	2.8	0.247	0.025	7	1344.8
18	29	Age Brood Sex HELPERS	1359.1	2.9	0.235	0.024	7	1344.9
19	36	Age Male Brood Sex Helpers Brood*Sex	1359.4	3.2	0.202	0.021	9	1341.0
20	37	Age Cohort Male Brood Sex HELPERS	1360.1	3.9	0.142	0.014	10	1339.8
21	25	Age Male Brood Sex	1360.2	4.0	0.135	0.014	7	1346.0
22	31	Age Cohort Male Brood Sex	1360.3	4.1	0.129	0.013	9	1341.9
25	1	Age	1366.7	10.5	0.005	0.001	4	1358.6

Models shown represent the 22 top-ranking models (95% of AIC_c weight) and the starting model (1; listed below blank row in table). All models included the random effect covariate ‘family’ to control for non-independence of brood-mates and the fixed covariate ‘age’ to control for variation in the age at banding. Additional fixed covariates included: annual variation (cohort), the age of the breeder male (male), brood size (brood), nestling sex (sex), the number of helpers on the natal territory at the time of rearing (helpers), and a brood size and sex interaction term (brood*sex). Column statistics are the same as described in Table 1.

Table 4. 6 Results from linear mixed models for nestling leg length.

Covariate	Single sex scenario			Mixed sex scenario		
	β	LCL	UCL	β	LCL	UCL
Intercept	15.139	13.876	16.402	15.739	14.846	16.632
Banding age	0.922	0.794	1.050	0.855	0.755	0.954
Cohort: 2007 vs. 2009	-0.624	-0.991	-0.256	-0.095	-0.327	0.136
2008 vs. 2009	0.202	-0.136	0.540	0.065	-0.108	0.239
Brood size	0.053	-0.183	0.290	0.004	-0.117	0.125
Sex (female vs. male)	-0.150	-0.316	0.017	-0.147	-0.228	-0.065
Helpers	0.005	-0.071	0.080	0.039	-0.086	0.164
Brood size*sex	-0.056	-0.363	0.251	-0.037	-0.166	0.092
Breeder male age	0.002	-0.022	0.027	-0.001	-0.023	0.021

Model averaged regression coefficients (β) are shown with their unconditional lower (LCL) and upper (UCL) 95% confidence

intervals generated from linear mixed models in the candidate model sets (single sex, mixed sex) with AIC_c weights greater than 0.01.

All models included the random effect covariate ‘family’ to control for non-independence of brood-mates (not shown) and the fixed covariate ‘age’ to control for variation in the age at banding. Additional fixed covariates included: annual variation (cohort), brood size (brood), nestling sex (sex), the number of helpers on the natal territory at the time of rearing (helpers), a brood size and sex interaction term (brood*sex), and the age of the breeder male (male). Covariates with strong support (confidence intervals do not include zero) are highlighted with bold text.

CHAPTER V. CONCLUSIONS

Erin L. Hewett Ragheb

When reproductive opportunities are restricted by an ecological constraint, juveniles from some bird species respond by delaying dispersal and remaining on their natal territory (Emlen 1982). In cooperatively breeding species, these retained offspring then assist in caring for offspring on the natal territory, but helping behavior and delayed dispersal are not always linked (e.g. Ekman et al. 1999). The decision to remain home in the face of ecological constraint is an important first step in the evolution of cooperative breeding. Most non-cooperative bird species disperse early and if individuals are unable to find a suitable breeding territory they become nonbreeding floaters in the population, rather than remaining on the natal territory (Stacey and Ligon 1991). Intrinsic benefits associated with family associations on the natal territories may play an important role in the retention of juveniles. One of the broader goals of this dissertation research was to better understand the role of intrinsic benefits of philopatry on delayed dispersal behavior.

One benefit of philopatry that may influence dispersal behavior in cooperatively breeding species is increased access to food resources through either familiarity with the environment (local knowledge) or increased foraging ability mediated by group effects (Walters et al. 1992b). Access to food resources on the natal territory has been directly linked to dispersal behavior in Western bluebirds (*Sialia mexicana*) where the experimental removal of mistletoe (*Phoradendron villosum*), a critical winter food resource, resulted in higher rates of winter natal dispersal for juvenile males (Dickinson and McGowan 2005). The overall quality of the natal

territory has also been proposed as an important factor in dispersal decisions, where individuals from high quality territories will remain philopatric, and individuals from low quality territories will disperse and search despite ecological constraints to independent breeding (Stacey and Ligon 1991). The maintenance of both strategies in cooperatively breeding species has been attributed to this variability in territory quality (Stacey and Ligon 1991).

However, for sibling red-cockaded woodpeckers the general quality of the natal territory is the same. Since they were raised on the same territory, in the same neighborhood and population, they should also experience similar ecological constraints to independent reproduction. Siblings should also match in their ability to perceive and access available breeder vacancies in the neighborhood. Furthermore, dispersal distance in red-cockaded woodpeckers is strongly heritable but modulated by ecological or social factors (Pasinelli et al. 2004). Since breeding pairs are strictly monogamous (Haig et al. 1994), siblings should also share parentage and the tendency to disperse certain distances, but the probability or timing of dispersal may still vary within broods. Therefore, general measures of habitat or parental quality need to be considered to control for between brood variation in dispersal strategy but cannot be used to explain the observed patterns of within-brood variation.

Our research highlights the importance of intrabrood social rank on individual access to food resources on the natal territory where socially dominant individuals have greater access to food brought by adults during the postfledging dependent period than subordinates. (Chapter II). If increased access to food resources is one of the primary benefits of philopatry for juvenile red-cockaded woodpeckers, and subordinate individuals have restricted access during the post-fledging dependent period, they may become more dispersive in the fall as a result (See discussion in Chapter II). While variation in habitat or parental quality among territories may

still be important when comparing the probability of dispersal between broods, we showed that the variation in dispersal strategies within a territory driven by intrabrood social rank differences is sufficient to regularly produce both dispersal strategies among males.

Future research should attempt to identify other resources critical to juveniles that might factor into an individual's decision to delay dispersal. While biased access to food on the natal territory may be enough to drive intrabrood variation in fall dispersal patterns, other resources may be involved in the explanation of spring dispersal decisions. One probable resource that may influence the intrinsic quality of the natal territory throughout the first year is access to a cavity for roosting. Red-cockaded woodpeckers roost singly in cavities not already occupied by a socially dominant individual or an interspecific kleptoparasite (Kappes 1997). When cavities are limited in a cluster, dominant individuals gain prioritized access to roost sites by evicting subordinates who are then forced to roost in the open (E.L.H.R., personal observation). Intersexual rank differences are often great enough that even a hatch year male can displace the breeding female from her roost cavity (Jackson 1994). Obtaining a high quality roost cavity soon after fledging may have substantial survival benefits, especially through the winter months.

Another important consideration driving increased dispersal of subordinate juveniles that cannot be ignored is the direct influence of aggressive physical conflicts among brood-mates. Adults on the natal territory rarely attack juveniles (Chapter II) and in this way, the natal territory may provide a safe haven for young as described previously in other species with delayed dispersal (Kokko and Ekman 2002). However, for subordinate individuals, if the frequency of aggressive conflicts is great enough, the natal territory may no longer be a safe haven. Negative effects of intrabrood conflicts include physical injury (extreme examples from siblicidal species; see review in Mock and Parker 1997) or elevated stress hormone levels (Martinez-Padilla et al.

2004; Blanco et al. 2006). Elevated levels of stress hormone corticosterone has been observed in birds during the restless period prior to migration (Landys et al. 2004) and may be involved with increased locomotor activity prior to natal dispersal (Belthoff and Dufty 1998). Physical aggression from dominant brood-mates may also result in the forced eviction of subordinate offspring (Strickland 1991) and early dispersal may not be a voluntary choice as it is often presented.

The dispersal patterns observed among red-cockaded woodpecker juveniles in this study appear to be driven primarily by nestling sex, where females are more dispersive than males. Secondly, within sexes, the decision to disperse in the fall may be driven by rank-specific access to food resources during the post-fledging dependent period, or in combination with the direct effect of physical attack. Although access to food may vary with intrabrood social rank beyond the post-fledging dependent period, access to other resources (e.g. roost cavities) or elevated stress hormone levels as a result of direct physical attack may drive spring dispersal decisions.

The research presented in this dissertation also improves our understanding of delayed dispersal behavior in red-cockaded woodpeckers because it provides strong evidence that delayed dispersal during the first year is the preferred strategy for juvenile males. This idea was previously presented by the equal or slightly higher lifetime fitness granted to philopatric males compared to early dispersers (Walters et al. 1992b) More support comes from the propensity of juvenile males to delay dispersal when they have high mass relative to their brood-mates (Pasinelli and Walters 2002). Our research adds to these findings by describing the role that intrabrood social rank plays as a predictor of individual life history strategy variation. Socially dominant males demonstrate much higher probabilities of delayed dispersal (Chapter II). In

addition, subordinate males existing on natal territories where their dominant siblings have died or dispersed (rare) are much more likely to delay dispersal (Chapter III). This suggests that individual dispersal decisions are flexible, and assessed based on current social conditions rather than physical traits fixed at birth or correlated with initial social status.

If delayed dispersal is the preferred strategy for juvenile male red-cockaded woodpeckers as our research suggests, that implies that early dispersal must be the inferior strategy. We might then say that early dispersers are making the 'best-of-a-bad-situation' because their low social rank results in a reduction of the benefits normally associated with philopatry and possibly eviction from the natal territory. However, delayed dispersal as a life history strategy is also frequently described as making the 'best-of-a-bad-situation' since independent reproduction should ultimately be the preferred strategy but ecological constraints prohibit this option (Alonso et al. 1998). This is the case with acorn woodpeckers, where if only one brother from a pair remained home as a helper, it is much more likely to be the subordinate male (Koenig et al. 2011). This suggests that delayed dispersal is a way for individuals of inferior quality to wait and prepare for dispersal, contrary to our findings with red-cockaded woodpeckers.

As discussed in Chapter III, the direct benefits of philopatry gained during the first year may not be the only factor driving delayed dispersal; rather lifetime fitness benefits accumulated over time may be more important. First year males that do obtain breeding vacancies have distinctly poor reproductive success and survival (Walters et al. 1992b). In addition, older female breeders appear to avoid pairing with young males (Daniels and Walters 2000b), suggesting that physical or social maturity or experience gained through age is critical to successful breeding. We propose then, for first year males, the optimal strategy is to delay reproduction on the natal territory even if a nearby breeder vacancy is available. For dominant males in this system, the

“bad situation” they are trying to make the best of may not only be the reduced availability of breeding vacancies, but also the high cost of first year reproduction. For subordinate males this becomes a “very bad situation” because in addition to habitat saturation and the high cost of first-year reproduction, their social status within the family removes some or all of the benefits associated with waiting at home. This suggests that natal dispersal by subordinates is not so much the result of lifted ecological constraints as it might be for dominant juveniles when they chose to disperse (Walters et al. 1992a) rather it is the result of the lack of benefits of philopatry. Here on a very fine scale (differences in social placement among siblings) we are able to identify the relative roles of intrinsic benefits and extrinsic constraints on the maintenance of multiple dispersal strategies in red-cockaded woodpeckers.

SUMMARY

This research contributes to a greater understanding of the relative contribution of intrinsic benefits versus extrinsic constraints as current pressures influencing individual dispersal decisions in red-cockaded woodpeckers. This evaluation of the relative contribution of factors driving delayed dispersal is preferred over attempting to eliminate one factor from the explanation of the evolution of delayed dispersal (Koenig et al. 1992). While a single factor is unlikely to explain the general evolution of delayed dispersal behavior, single influential factors may reveal themselves when comparing species or populations with different dispersal patterns (Koenig et al. 1992). Our comparison of individuals with different dispersal patterns within the same brood proved to be an exciting opportunity to identify additional factors important to dispersal pressure in this species, primarily intrabrood social rank.

LITERATURE CITED

- Alonso, J. C., Martin, E., Alonso, J. A. & Morales, M. B.** 1998. Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. *Behavioral Ecology*, **9**, 243-252.
- Altmann, J.** 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227-267.
- Anderson, D. R.** 2008. *Model Based Inference in the Life Sciences*. New York: Springer.
- Arcese, P. & Smith, J. N. M.** 1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. *Journal of Animal Ecology*, **54**, 817-830.
- Balda, R. P. & Balda, J.** 1978. The care of young Pinon Jays (*Gymnorhinus cyanocephalus*) and their integration into the flock. *Journal of Ornithology*, **119**, 146-171.
- Belthoff, J. R. & Dufty, A. M.** 1998. Corticosterone, body condition and locomotor activity: a model for dispersal in screech-owls. *Animal Behaviour*, **55**, 405-415.
- Bent, A. C.** 1939. Life Histories of North American Woodpeckers. *United States National Museum Bulletin* 174.
- Blanco, G., Frias, O., Martinez, J., Lemus, J. A., Merino, R. & Jimenez, B.** 2006. Sex and rank in competitive brood hierarchies influence stress levels in nestlings of a sexually dimorphic bird. *Biological Journal of the Linnean Society*, **88**, 383-390.
- Blanco, G., Martinez-Padilla, J., Davila, J. A., Serrano, D. & Vinuela, J.** 2003. First evidence of sex differences in the duration of avian embryonic period: consequences for sibling competition in sexually dimorphic birds. *Behavioral Ecology*, **14**, 702-706.
- Bortolotti, G. R.** 1986. Influence of Sibling Competition on Nestling Sex-Ratios of Sexually Dimorphic Birds. *American Naturalist*, **127**, 495-507.

- Brownie, C., Hines, J. E., Nichols, J. D., Pollock, K. H. & Hestbeck, J. B.** 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics*, **49**, 1173-1187.
- Bryant, D. M. & Tatner, P.** 1990. Hatching Asynchrony, Sibling Competition and Siblicide in Nestling Birds - Studies of Swiftlets and Bee-Eaters. *Animal Behaviour*, **39**, 657-671.
- Brzek, P. & Konarzewski, M.** 2001. Effect of food shortage on the physiology and competitive abilities of sand martin (*Riparia riparia*) nestlings. *Journal of Experimental Biology*, **204**, 3065-3074.
- Buckland, S. T., Burnham, K. P. & Augustin, N. H.** 1997. Model selection: An integral part of inference. *Biometrics*, **53**, 603-618.
- Cant, M. A., English, S., Reeve, H. K. & Field, J.** 2006. Escalated conflict in a social hierarchy. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2977-2984.
- Carlisle, T. R. & Zahavi, A.** 1986. Helping at the nest, allofeeding and social-status in immature Arabian babblers. *Behavioral Ecology and Sociobiology*, **18**, 339-351.
- Carrie, N. R., Moore, K. R., Stephens, S. A. & Keith, E. L.** 1998. Influence of cavity availability on red-cockaded woodpecker group size. *Wilson Bulletin*, **110**, 93-99.
- Cash, K. J. & Evans, R. M.** 1986. Brood reduction in the American white pelican (*Pelecanus erythrorhynchos*). *Behavioral Ecology and Sociobiology*, **18**, 413-418.
- Chase, I. D., Bartolomeo, C. & Dugatkin, L. A.** 1994. Aggressive Interactions and Inter-Contest Interval - How Long Do Winners Keep Winning. *Animal Behaviour*, **48**, 393-400.

- Chase, I. D., Tovey, C., Spangler-Martin, D. & Manfredonia, M.** 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 5744-5749.
- Christian, J. J.** 1970. Social subordination, population density, and mammalian evolution. *Science*, **168**, 84-90.
- Cleasby, I. R., Nakagawa, S., Gillespie, D. O. S. & Burke, T.** 2010. The influence of sex and body size on nestling survival and recruitment in the house sparrow. *Biological Journal of the Linnean Society*, **101**, 680-688.
- Clutton-Brock, T. H.** 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**, 131-133.
- Conner, R. N. & Rudolph, D. C.** 1995. Excavation dynamics and use patterns of red-cockaded woodpecker cavities: relationships with cooperative breeding. In: *Red-cockaded Woodpecker: recovery, ecology and management*. (Ed. by D. L. Kulhavy, R. G. Hooper & R. Costa), pp. 343-352. Nacogdoches, Texas, USA: Center for Applied Studies, College of Forestry, Stephen F. Austin State University.
- Cooch, E. & White, G. C.** 2010. Program MARK: a gentle introduction, 9th revision.
- Cook, M. I. & Monaghan, P.** 2004. Sex differences in embryo development periods and effects on avian hatching patterns. *Behavioral Ecology*, **15**, 205-209.
- Cook, M. I., Monaghan, P. & Burns, M. D.** 2000. Effects of short-term hunger and competitive asymmetry on facultative aggression in nestling black guillemots *Cephus grylle*. *Behavioral Ecology*, **11**, 282-287.
- Cox, A. S. & Kesler, D. C.** 2010. Natal dispersal and survival of red-bellied woodpeckers in a fragmented landscape. Masters thesis, University of Missouri.

- Daniels, S. J. & Walters, J. R.** 2000a. Inbreeding depression and its effects on natal dispersal in Red-cockaded Woodpeckers. *Condor*, **102**, 482-491.
- Daniels, S. P. & Walters, J. R.** 2000b. Between-year breeding dispersal in red-cockaded woodpeckers: multiple causes and estimated cost. *ECOLOGY*, **81**, 2473-2484.
- Devillard, S. & Bray, Y.** 2009. Assessing the effect on survival of natal dispersal using multistate capture-recapture models. *ECOLOGY*, **90**, 2902-2912.
- Dickinson, J. L. & McGowan, A.** 2005. Winter resource wealth drive's delayed dispersal and family-group living in western bluebirds. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2423-2428.
- Doward, D. F.** 1962. Comparative biology of the white booby and the brown booby *Sula* spp. *atascension*. *Ibis*, **103b**, 174-220.
- Drent, P. J.** 1984. Mortality and dispersal in summer and its consequences for the density of great tits *Parus major* at the onset of autumn. *Ardea*, **72**, 127-162.
- Drummond, H.** 2006. Dominance in vertebrate broods and litters. *Quarterly Review of Biology*, **81**, 3-32.
- Duckworth, R. A. & Badyaev, A. V.** 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 15017-15022.
- Eikenaar, C., Richardson, D. S., Brouwer, L. & Komdeur, J.** 2007. Parent presence, delayed dispersal, and territory acquisition in the Seychelles warbler. *Behavioral Ecology*, **18**, 874-879.

- Ekman, J., Bylin, A. & Tegelstrom, H.** 1999. Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. *Proceedings of the Royal Society of London B*, **266**, 911-915.
- Ekman, J., Bylin, A. & Tegelstrom, H.** 2000. Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behavioral Ecology*, **11**, 416-420.
- Ekman, J., Eggers, S. & Griesser, M.** 2002. Fighting to stay: the role of sibling rivalry for delayed dispersal. *Animal Behaviour*, **64**, 453-459.
- Ekman, J. & Griesser, M.** 2002. Why offspring delay dispersal: experimental evidence for a role of parental tolerance. *Proceedings of the Royal Society of London B*, **269**, 1709-1713.
- Ellsworth, E. A. & Belthoff, J. R.** 1999. Effects of social status on the dispersal behaviour of juvenile western screech-owls. *Animal Behaviour*, **57**, 883-892.
- Emlen, S. T.** 1978. The Evolution of Cooperative Breeding in Birds. In: *Behavioural Ecology, an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 245-281.
- Emlen, S. T.** 1982. The evolution of helping. I. An ecological constraints model. *American Naturalist*, **119**, 29-39.
- Fisher, R. A.** 1930. *The genetical theory of natural selection*. Oxford: Oxford University Press.
- Fisher, R. A.** 1958. *The genetical theory of natural selection*. Oxford: Oxford University Press.
- Forbes, L. S. & Thornton, S.** 1997. Why parent birds play favorites. *Nature*, **390**, 351-352.
- Forbes, S. & Mock, D. W.** 2000. A tale of two strategies: life-history aspects of family strife. *Condor*, **102**, 23-34.
- Gauthreaux, S. A.** 1978. *The Ecological Significance of Behavioral Dominance*. New York: Plenum Press.

- Gill, F. B.** 2003. *Ornithology*, Second edn. New York: W.H. Freeman and Company.
- Goodship, N. M. & Buchanan, K. L.** 2006. Nestling testosterone is associated with begging behaviour and fledging success in the pied flycatcher, *Ficedula hypoleuca*. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 71-76.
- Gottlander, K.** 1987. Parental feeding-behavior and sibling competition in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica*, **18**, 269-276.
- Green, D. J. & Cockburn, A.** 2001. Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology*, **70**, 505-514.
- Greenwood, P. J.** 1980. Mating Systems, Philopatry and Dispersal in Birds and Mammals. *Animal Behaviour*, **28**, 1140-1162.
- Griesser, M. & Ekman, A.** 2004. Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, **67**, 933-939.
- Griesser, M. & Ekman, J.** 2005. Nepotistic mobbing behaviour in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, **69**, 345-352.
- Griesser, M., Nystrand, M. & Ekman, J.** 2006. Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society B*, **273**, 1881-1886.
- Guhl, A. M.** 1968. Social inertia and social stability in chickens. *Animal Behaviour*, **16**, 219-232.
- Guhl, A. M. & Ortman, L. L.** 1953. Visual patterns in the recognition of individuals among chickens *The Condor*, **55**.
- Haig, S. M., Walters, J. R. & Plissner, J. H.** 1994. Genetic-evidence for monogamy in the cooperatively breeding red-cockaded woodpecker. *Behavioral Ecology and Sociobiology*, **34**, 295-303.

- Harding, S. R. & Walters, J. R.** 2002. Processes regulating the population dynamics of red-cockaded woodpecker cavities. *Journal of Wildlife Management*, **66**, 1083-1095.
- Harding, S. R. & Walters, J. R.** 2004. Dynamics of cavity excavation by red-cockaded woodpeckers. In: *Red-cockaded Woodpecker: Road to Recovery* (Ed. by R. Costa & S. J. Daniels), pp. 412-422. Blaine: Hancock House Publishers Inc.
- Hatchwell, B. J. & Komdeur, J.** 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, **59**, 1079-1086.
- Hawn, A. T., Radford, A. N. & du Plessis, M. A.** 2007. Delayed breeding affects lifetime reproductive success differently in male and female green woodhoopoes. *Current Biology*, **17**, 844-849.
- Hegner, R. E.** 1985. Dominance and anti-predator behaviour in blue tits (*Parus caeruleus*). *Animal Behaviour*, **33**, 762-768.
- Hewett Ragheb, E. L. & Walters, J. R.** 2011. Favouritism or intrabrood competition? Access to food and the benefits of philopatry for red-cockaded woodpeckers. *Animal Behaviour*, **82**, 329-338.
- Jackson, J. A.** 1994. The red-cockaded woodpecker (*Picoides borealis*). In: *The Birds of North America* (Ed. by A. Poole & F. Gill). Philadelphia: The Academy of Natural Sciences, Washington D.C.: The American Ornithologists' Union.
- Johnson, M. L. & Gaines, M. S.** 1990. Evolution of Dispersal - Theoretical-Models and Empirical Tests Using Birds and Mammals. *Annual Review of Ecology and Systematics*, **21**, 449-480.
- Jones, K. S., Nakagawa, S. & Sheldon, B. C.** 2009. Environmental Sensitivity in Relation to Size and Sex in Birds: Meta-Regression Analysis. *American Naturalist*, **174**, 122-133.

- Kappes, J. J.** 1997. Defining cavity-associated interactions between red-cockaded woodpeckers and other cavity-dependent species: Interspecific competition or cavity kleptoparasitism? *Auk*, **114**, 778-780.
- Kenward, R. E., Marcstrom, V. & Karlbom, M.** 1993. Postnestling behavior in goshawks, *Accipiter gentilis*. I. The causes of dispersal. *Animal Behaviour*, **46**, 365-370.
- Kesler, D. C., Walters, J. R. & Kappes, J. J.** 2010. Social influences on dispersal and the fat-tailed dispersal distribution in red-cockaded woodpeckers. *Behavioral Ecology*, **21**, 1337-1343.
- Khan, M. Z. & Walters, J. R.** 2002. Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). *Behavioral Ecology and Sociobiology*, **51**, 336-344.
- Kilner, R. M. & Drummond, H.** 2007. Parent-offspring conflict in avian families. *Journal of Ornithology*, **148**, S241-S246.
- Koenig, W., Walters, E. & Haydock, J.** 2011. Fitness consequences of within-brood dominance in the cooperatively breeding acorn woodpecker. *Behavioral Ecology and Sociobiology*, 1-10.
- Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. & Stanback, M. T.** 1992. The Evolution of Delayed Dispersal in Cooperative Breeders. *Quarterly Review of Biology*, **67**, 111-150.
- Koenig, W. D., Stanback, M. T., Haydock, J. & Kraaijeveld-Smit, F.** 2001a. Nestling sex ratio variation in the cooperatively breeding acorn woodpecker. *Behavioral Ecology and Sociobiology*, **49**, 357-365.

- Koenig, W. D., Stanback, M. T., Haydock, J. & Kraaijeveld-Smit, F.** 2001b. Nestling sex ratio variation in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*). *Behavioral Ecology and Sociobiology*, **49**, 357-365.
- Koenig, W. D. & Walters, J. R.** 1999. Sex-ratio selection in species with helpers at the nest: the repayment model revisited. *The American Naturalist*, **153**, 124-130.
- Kogel, C. H. D.** 1997. Long-Term Effects of Brood Size Manipulation on Morphological Development and Sex-Specific Mortality of Offspring. *Journal of Animal Ecology*, **66**, 167-178.
- Kokko, H. & Ekman, J.** 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *American Naturalist*, **160**, 468-484.
- Kokko, H. & Johnstone, R. A.** 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 571-578.
- LaBranche, M. S.** 1992. Asynchronous hatching, brood reduction and sex ratio biases in red-cockaded woodpeckers. Ph.D. dissertation, North Carolina State University.
- LaBranche, M. S. & Walters, J. R.** 1994. Patterns of mortality in nests of red-cockaded woodpeckers in the Sandhills of southcentral North Carolina. *Wilson Bulletin*, **106**, 258-271.
- Landys, M. T. M., Wingfield, J. C. & Ramenofsky, M.** 2004. Plasma corticosterone increases during migratory restlessness in the captive white-crowned sparrow *Zonotrichia leucophrys gambelli*. *Hormones and Behavior*, **46**, 574-581.

- Lee, S. I., Hwang, Y., Lee, J. & Choe, J. C.** 2010. Unusual pattern of sex-specific mortality in relation to initial brood sex composition in the black-billed magpie *Pica pica*. *Journal of Avian Biology*, **41**, 139-146.
- Legge, S.** 2000. Siblicide in the cooperatively breeding laughing kookaburra (*Dacelo novaeguineae*). *Behavioral Ecology and Sociobiology*, **48**, 293-302.
- Lennartz, M. R., Hooper, R. G. & Harlow, R. F.** 1987. Sociality and cooperative breeding of red-cockaded woodpecker, *Picoides borealis*. *Behavioral Ecology and Sociobiology*, **20**, 77-88.
- Ligon, J. D.** 1968. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. *Auk*, **85**, 203-215.
- Ligon, J. D.** 1970. Behavior and breeding biology of the red-cockaded woodpecker. *The Auk*, **87**, 255-278.
- Ligon, J. D. & Ligon, S. H.** 1990. Green Woodhoopoes: life history traits and sociality. In: *Cooperative Breeding in Birds: long-term studies of ecology and behavior* (Ed. by P. B. Stacey & W. D. Koenig), pp. 32-65. Cambridge: Cambridge University Press.
- Martinez-Padilla, J., Martinez, J., Davila, J. A., Merino, S., Moreno, J. & Millan, J.** 2004. Within-brood size differences, sex and parasites determine blood stress protein levels in Eurasian Kestrel nestlings. *Functional Ecology*, **18**, 426-434.
- Maynard Smith, J. & Parker, G. A.** 1976. Logic of Asymmetric Contests. *Animal Behaviour*, **24**, 159-175.
- McRae, S. B., Weatherhead, P. J. & Montgomerie, R.** 1993. American robin nestlings compete by jockeying for position. *Behavioral Ecology and Sociobiology*, **33**, 101-106.

- Michler, S. P. M., Bleeker, M., van der Velde, M., Both, C., Komdeur, J. & Tinbergen, J. M.** 2010. Parental provisioning in relation to offspring sex and sex ratio in the great tit (*Parus major*). *Behaviour*, **147**, 1355-1378.
- Middleton, H. A. & Green, D. J.** 2008. Correlates of postfledging survival, the timing of dispersal, and local recruitment in American Dippers. *Canadian Journal of Zoology- Revue Canadienne De Zoologie*, **86**, 875-881.
- Mock, D. W. & Forbes, L. S.** 1995. The Evolution of Parental Optimism. *Trends in Ecology & Evolution*, **10**, 130-134.
- Mock, D. W. & Parker, G. A.** 1997. *The evolution of sibling rivalry*, 1st edn. New York: Oxford University Press.
- Moore, J. & Ali, R.** 1984. Are Dispersal and Inbreeding Avoidance Related. *Animal Behaviour*, **32**, 94-112.
- Morrison, M. L. & With, K. A.** 1987. Interseasonal and Intersexual Resource Partitioning in Hairy and White-Headed Woodpeckers. *Auk*, **104**, 225-233.
- Nathan, A., Legge, S. & Cockburn, A.** 2001. Nestling aggression in broods of a siblicidal kingfisher, the laughing kookaburra. *Behavioral Ecology*, **12**, 716-725.
- Nilsson, J. A. & Svensson, M.** 1996. Sibling competition affects nestling growth strategies in marsh tits. *Journal of Animal Ecology*, **65**, 825-836.
- Oddie, K. R.** 2000. Size matters: competition between male and female great tit offspring. *Journal of Animal Ecology*, **69**, 903-912.
- Oliveira, R. F., McGregor, P. K. & Latruffe, C.** 1998. Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 1045-1049.

- Ostreiher, R.** 1997. Food division in the Arabian babbler nest: adult choice or nestling competition? *Behavioral Ecology*, **8**, 233-238.
- Parker, G. A.** 1974. Assessment Strategy and the Evolution of Fighting Behaviour. *Journal of Theoretical Biology*, **47**, 223-243.
- Pasinelli, G., Schiegg, K. & Walters, J. R.** 2004. Genetic and environmental influences on natal dispersal distance in a resident bird species. *American Naturalist*, **164**, 660-669.
- Pasinelli, G. & Walters, J. R.** 2002. Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. *ECOLOGY*, **83**, 2229-2239.
- Peters, W. D. & Grubb, T. C.** 1983. An experimental analysis of sex-specific foraging in the Downy Woodpecker *Picoides pubescens*. *ECOLOGY*, **64**, 1437-1443.
- Phillips Jr., L. F., Tomcho Jr., J. & Walters, J. R.** 1998. Double-clutching and double-brooding in Red-cockaded Woodpeckers in Florida. *Florida Field Naturalist*, **26**, 109-140.
- Pizzoni-Ardemani, A.** 1990. Sexual dimorphism and geographic variation in the red-cockaded woodpecker (*Picoides borealis*). M.Sc. thesis, North Carolina State University.
- Ploger, B. J. & Medeiros, M. J.** 2004. Unequal food distribution among great egret *Ardea alba* nestlings: parental choice or sibling aggression? *Journal of Avian Biology*, **35**, 399-404.
- Potti, J. & Merino, S.** 1996. Parasites and the ontogeny of sexual size dimorphism in a passerine bird. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **263**, 9-12.
- Pusey, A. E.** 1987. Sex-Biased Dispersal and Inbreeding Avoidance in Birds and Mammals. *Trends in Ecology & Evolution*, **2**, 295-299.

- Rabenold, K. N.** 1990. Campylorhynchus wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savanna. In: *Cooperative Breeding in Birds: long-term studies of ecology and behavior* (Ed. by P. B. Stacey & W. D. Koenig), pp. 158-196. Cambridge: Cambridge University Press.
- Radersma, R., Tinbergen, J. M. & Komdeur, J.** 2011. Do brood sex ratio, nestling development and sex affect fledging timing and order? An experimental study on great tits. *Animal Behaviour*, **81**, 69-75.
- Raihani, N. J., Ridley, A. R., Browning, L. E., Nelson-Flower, M. J. & Knowles, S.** 2008. Juvenile Female Aggression in Cooperatively Breeding Pied Babblers: Causes and Contexts. pp. 452-458.
- Rajala, M., Ratti, O. & Suhonen, J.** 2003. Age differences in the response of willow tits (*Parus montanus*) to conspecific alarm calls. *Ethology*, **109**, 501-509.
- Reed, J. M. & Walters, J. R.** 1996. Helper effects on variance components of fitness in the cooperatively breeding red-cockaded woodpecker. *The Auk*, **113**, 608-616.
- Rosivall, B., Szollosi, E., Hasselquist, D. & Torok, J.** 2010. Males are sensitive - sex-dependent effect of rearing conditions on nestling growth. *Behavioral Ecology and Sociobiology*, **64**, 1555-1562.
- Rowland, E., Love, O. P., Verspoor, J. J., Sheldon, L. & Williams, T. D.** 2007. Manipulating rearing conditions reveals developmental sensitivity in the smaller sex of a passerine bird, the European starling *Sturnus vulgaris*. *Journal of Avian Biology*, **38**, 612-618.
- Sasvari, L., Hegyi, Z. & Peczely, P.** 1999. Brood reduction in white storks mediated through asymmetries in plasma testosterone concentrations in chicks. *Ethology*, **105**, 569-582.

- Small, R. J., Holzwart, J. C. & Rusch, D. H.** 1993. Are Ruffed Grouse More Vulnerable to Mortality during Dispersal. *ECOLOGY*, **74**, 2020-2026.
- Sridhar, H., Beauchamp, G. & Shanker, K.** 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, **78**, 337-347.
- Stacey, P. B.** 1979. Habitat saturation and communal breeding in the acorn woodpecker. *Animal Behaviour*, **27**, 1153-1166.
- Stacey, P. B. & Ligon, J. D.** 1991. The Benefits-of-Philopatry Hypothesis for the Evolution of Cooperative Breeding - Variation in Territory Quality and Group-Size Effects. *American Naturalist*, **137**, 831-846.
- Stamps, J. A.** 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols). Oxford: Oxford University Press.
- Stanback, M. T.** 1991. Causes and consequences of nestling size variation in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*). University of California at Berkeley.
- Stanback, M. T.** 1994. Dominance within Broods of the Cooperatively Breeding Acorn Woodpecker. *Animal Behaviour*, **47**, 1121-1126.
- Strickland, D.** 1991. Juvenile dispersal in gray jays - dominant brood member expels siblings from natal territory. *Canadian Journal of Zoology*, **69**, 2935-2945.
- Tanner, M., Kolliker, M. & Richner, H.** 2008. Differential food allocation by male and female great tit, *Parus major*, parents: are parents or offspring in control? *Animal Behaviour*, **75**, 1563-1569.

- Temme, D. H. & Charnov, E. L.** 1987. Brood size adjustment in birds - economical tracking in a temporally varying environment. *Journal of Theoretical Biology*, **126**, 137-147.
- Tinbergen, J. M. & Boerlijst, M. C.** 1990. Nestling Weight and Survival in Individual Great Tits (Parus-Major). *Journal of Animal Ecology*, **59**, 1113-1127.
- Uller, T.** 2006. Sex-specific sibling interactions and offspring fitness in vertebrates: patterns and implications for maternal sex ratios. *Biological Reviews*, **81**, 207-217.
- Van Doorn, G. S., Hengeveld, G. M. & Weissing, F. J.** 2003. The evolution of social dominance - I: Two-player models. *Behaviour*, **140**, 1305-1332.
- VanVuren, D. & Armitage, K. B.** 1994. Survival of Dispersing and Philopatric Yellow-Bellied Marmots - What Is the Cost of Dispersal. *Oikos*, **69**, 179-181.
- Verboven, N. & Visser, M. E.** 1998. Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos*, **81**, 511-524.
- Walters, J. R.** 1990. Red-cockaded woodpeckers: a 'primitive' cooperative breeder. In: *Cooperative Breeding in Birds* (Ed. by P. B. Stacey & W. D. Koenig). Cambridge: Cambridge University Press.
- Walters, J. R.** 1991. Application of ecological principles to the management of endangered species - the case of the red-cockaded woodpecker. *Annual Review of Ecology and Systematics*, **22**, 505-523.
- Walters, J. R.** 2004. Unusual dynamics in a rapidly increasing population of red-cockaded woodpeckers at Camp Lejeune, North Carolina. In: *Red-cockaded Woodpecker: Road to Recovery* (Ed. by R. Costa & S. J. Daniels). Blaine: Hancock House
- Walters, J. R., Copeyon, C. K. & Carter, J. H.** 1992a. Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *The Auk*, **109**, 90-97.

- Walters, J. R., Doerr, P. D. & Carter, J. H.** 1988. The cooperative breeding system of the red-cockaded woodpecker. *Ethology*, **78**, 275-305.
- Walters, J. R., Doerr, P. D. & Carter, J. H.** 1992b. Delayed dispersal and reproduction as a life-history tactic in cooperative breeders - fitness calculations from red-cockaded woodpeckers. *American Naturalist*, **139**, 623-643.
- Weatherhead, P. J. & Hoysak, D. J.** 1984. Dominance Structuring of a Red-Winged Blackbird Roost. *Auk*, **101**, 551-555.
- White, G. C. & Burnham, K. P.** 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120-139.
- White, G. C., Kendall, W. L. & Barker, R. J.** 2006. Multistate survival models and their extensions in Program MARK. *Journal of Wildlife Management*, **70**, 1521-1529.
- Wilson, E. O.** 1975. Dominance Systems. In: *Sociobiology*. Cambridge: Belknap Press.
- Winkler, H., Christie, D. A. & Nurney, D.** 1995. *Woodpeckers: An identification guide to the woodpeckers of the world*, 1st edn. Boston: Houghton Mifflin Company.
- Woolfenden, G. E. & Fitzpatrick, J. W.** 1977. Dominance in the Florida Scrub Jay. *The Condor*, **79**, 1-12.
- Yackel Adams, A. A., Skagen, S. K. & Savidge, J. A.** 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. *ECOLOGY*, **87**, 178-188.
- Zanette, L., MacDougall-Shakleton, E., Clinchy, M. & Smith, J. N. M.** 2005. Brown-headed cowbirds skew host offspring sex ratios. *ECOLOGY*, **86**, 815-820.
- Zwicker, S. M. & Walters, J. R.** 1999. Selection of pines for foraging by red-cockaded woodpeckers. *Journal of Wildlife Management*, **63**, 843-852.

APPENDIX A

Appendix A. 1 Multistate mark-recapture models for natal survival and dispersal for juvenile males with known intrabrood social rank from CS1-CS3.

Model	Apparent Natal Survival (Φ^N)	Dispersal (Ψ^{ND})	QAICc	Δ QAICc	QAICc weight	Model likelihood	K	QDeviance
<i>Stage 1: Addition of general covariates to natal survival term</i>								
5	Cohort+flg+t	t	589.084	0.000	0.318	1.000	11	566.479
3	Flg+t	t	590.057	0.973	0.196	0.615	9	571.646
8	Cohort+flg+conpop+t	t	590.302	1.218	0.173	0.544	12	565.585
7	Flg+conpop+t	t	590.626	1.542	0.147	0.463	10	570.123
1	t	t	592.343	3.259	0.062	0.196	8	576.015
2	Cohort+t	t	592.897	3.813	0.047	0.149	10	572.393
4	Conpop+t	t	593.468	4.384	0.036	0.112	9	575.057
6	Cohort+conpop+t	t	594.634	5.550	0.020	0.062	11	572.029
<i>Stage 2: Addition of general covariates to dispersal term</i>								
5	Cohort+flg+t	t	589.084	0.000	0.137	1.000	11	566.479
3	Flg+t	t	590.057	0.973	0.084	0.615	9	571.646
8	Cohort+flg+conpop+t	t	590.302	1.218	0.074	0.544	12	565.585
7	Flg+conpop+t	t	590.626	1.542	0.063	0.463	10	570.123
11	Cohort+flg+t	Conpop+t	590.778	1.694	0.059	0.429	12	566.061
9	Cohort+flg+t	Cohort+t	591.021	1.937	0.052	0.380	13	564.182
10	Cohort+flg+t	Flg+t	591.035	1.951	0.052	0.377	12	566.318
18	Flg+t	Conpop+t	591.730	2.645	0.036	0.266	10	571.226
16	Flg+t	Cohort+t	591.822	2.737	0.035	0.254	11	569.216
25	Cohort+flg+conpop+t	conpop+t	591.985	2.900	0.032	0.235	13	565.146
17	Flg+t	Flg+t	591.992	2.908	0.032	0.234	10	571.489
23	Cohort+flg+conpop+t	Cohort+t	592.252	3.167	0.028	0.205	14	563.282

24	Cohort+flg+conpop+t	Flg+t	592.261	3.177	0.028	0.204	13	565.423
13	Cohort+flg+t	Cohort+Conpop+t	592.278	3.193	0.028	0.203	14	563.308
32	Flg+conpop+t	Conpop+t	592.283	3.199	0.028	0.202	11	569.678
30	Flg+conpop+t	Cohort+t	592.405	3.321	0.026	0.190	12	567.688
31	Flg+conpop+t	Flg+t	592.569	3.485	0.024	0.175	11	569.964
14	Cohort+flg+t	Flg+conpop+t	592.665	3.581	0.023	0.167	13	565.826
20	Flg+t	Cohort+conpop+t	593.049	3.964	0.019	0.138	12	568.331
12	Cohort+flg+t	Cohort+flg+t	593.152	4.068	0.018	0.131	14	564.182
27	Cohort+flg+conpop+t	Cohort+conpop+t	593.483	4.399	0.015	0.111	15	562.372
34	Flg+conpop+t	Cohort+conpop+t	593.595	4.511	0.014	0.105	13	566.757
21	Flg+t	Flg+conpop+t	593.601	4.517	0.014	0.105	11	570.996
28	Cohort+flg+conpop+t	Flg+conpop+t	593.879	4.794	0.012	0.091	14	564.909
19	Flg+t	Cohort+flg+t	593.933	4.848	0.012	0.089	12	569.215
35	Flg+conpop+t	Flg+conpop+t	594.162	5.078	0.011	0.079	12	569.445
26	Cohort+flg+conpop+t	Cohort+flg+t	594.393	5.308	0.010	0.070	15	563.282
15	Cohort+flg+t	Cohort+flg+conpop+t	594.405	5.321	0.010	0.070	15	563.294
33	Flg+conpop+t	Cohort+flg+t	594.526	5.441	0.009	0.066	13	567.687
22	Flg+t	Cohort+flg+conpop+t	595.162	6.077	0.007	0.048	13	568.323
29	Cohort+flg+conpop+t	Cohort+flg+conpop+t	595.620	6.536	0.005	0.038	16	562.358
36	Flg+conpop+t	Cohort+flg+conpop+t	595.718	6.634	0.005	0.036	14	566.748

Stage 3: Effects of social rank and condition relative to male broodmates on natal survival

37	Rank+cohort+flg+t	t	585.977	0.000	0.190	1.000	12	561.260
39	Rank+cohort+flg+conpop+t	t	586.751	0.773	0.129	0.679	13	559.912
38	Rank+flg+t	t	586.814	0.836	0.125	0.658	10	566.310
40	Rank+flg+conpop+t	t	586.976	0.999	0.116	0.607	11	564.371
41	Rank+cohort+flg+t	Conpop+t	587.693	1.716	0.081	0.424	13	560.854
42	Rank+cohort+flg+t	Cohort+t	587.930	1.952	0.072	0.377	14	558.960
43	Rank+cohort+flg+t	Flg+t	587.941	1.963	0.071	0.375	13	561.102
5	Cohort+flg+t	t	589.084	3.107	0.040	0.212	11	566.479
3	Flg+t	t	590.057	4.080	0.025	0.130	9	571.646
8	Cohort+flg+conpop+t	t	590.302	4.325	0.022	0.115	12	565.585

7	Flg+conpop+t	t	590.626	4.649	0.019	0.098	10	570.123
11	Cohort+flg+t	Conpop+t	590.778	4.801	0.017	0.091	12	566.061
44	Conbro+cohort+flg+t	t	590.803	4.826	0.017	0.090	12	566.086
9	Cohort+flg+t	Cohort+t	591.021	5.043	0.015	0.080	13	564.182
10	Cohort+flg+t	Flg+t	591.035	5.058	0.015	0.080	12	566.318
45	Conbro+flg+t	t	591.757	5.779	0.011	0.056	10	571.253
46	Conbro+cohort+flg+conpop+t	t	592.337	6.359	0.008	0.042	13	565.498
48	Conbro+cohort+flg+t	Conpop+t	592.502	6.524	0.007	0.038	13	565.663
47	Conbro+flg+conpop+t	t	592.686	6.709	0.007	0.035	11	570.081
49	Conbro+cohort+flg+t	Cohort+t	592.753	6.776	0.006	0.034	14	563.783
50	Conbro+cohort+flg+t	Flg+t	592.765	6.788	0.006	0.034	13	565.927

Stage 4: Effects of social rank and condition relative to male broodmates on natal dispersal

51	Rank+cohort+flg+t	Rank+t	579.237	0.000	0.237	1.000	13	552.398
53	Rank+cohort+flg+conpop+t	Rank+t	580.021	0.784	0.160	0.676	14	551.051
52	Rank+flg+t	Rank+t	580.073	0.837	0.156	0.658	11	557.468
54	Rank+flg+conpop+t	Rank+t	580.234	0.998	0.144	0.607	12	555.517
55	Rank+cohort+flg+t	Rank+conpop+t	581.047	1.810	0.096	0.405	14	552.077
57	Rank+cohort+flg+t	Rank+flg+t	581.328	2.091	0.083	0.352	14	552.358
56	Rank+cohort+flg+t	Rank+cohort+t	581.510	2.273	0.076	0.321	15	550.399
37	Rank+cohort+flg+t	t	585.977	6.741	0.008	0.034	12	561.260
39	Rank+cohort+flg+conpop+t	t	586.751	7.514	0.006	0.023	13	559.912
38	Rank+flg+t	t	586.814	7.577	0.005	0.023	10	566.310
40	Rank+flg+conpop+t	t	586.976	7.740	0.005	0.021	11	564.371
41	Rank+cohort+flg+t	Conpop+t	587.693	8.456	0.003	0.015	13	560.854
58	Rank+cohort+flg+t	Conbro+t	587.896	8.659	0.003	0.013	13	561.057
42	Rank+cohort+flg+t	Cohort+t	587.930	8.693	0.003	0.013	14	558.960
43	Rank+cohort+flg+t	Flg+t	587.941	8.704	0.003	0.013	13	561.102
60	Rank+cohort+flg+conpop+t	Conbro+t	588.686	9.449	0.002	0.009	14	559.716
59	Rank+flg+t	Conbro+t	588.721	9.484	0.002	0.009	11	566.115
61	Rank+flg+conpop+t	Conbro+t	588.899	9.662	0.002	0.008	12	564.182
62	Rank+cohort+flg+t	Conbro+conpop+t	589.400	10.164	0.001	0.006	14	560.430

63	Rank+cohort+flg+t	Conbro+cohort+t	589.830	10.593	0.001	0.005	15	558.719
64	Rank+cohort+flg+t	Conbro+flg+t	589.845	10.608	0.001	0.005	14	560.875

Models listed in order first by stage, then by QAICc rank. Models with $\Delta QAICc$ values < 2 (shown in bold) were retained for use in proceeding stages (see main text *Methods: Multistate mark-recapture model*). A median- \hat{c} goodness-of-fit test on the starting model (1) revealed minor overdispersion. AIC scores were manually adjusted for overdispersion (QAIC; $\hat{c}=1.245$) and corrected for small sample size (QAIC_c). Models are shown with the QAIC_c score, change in QAIC_c score ($\Delta QAICc$), $\Delta QAICc$ weight, model likelihood, the number of estimable parameters (K) and model deviance (QDeviance). For all models, recapture probability was constrained as constant across time ($p(\cdot)$), probability of surviving in the dispersing state was constant over time ($\Phi^D(\cdot)$), and probability of transition from disperser to natal resident states was fixed at zero ($\Psi^{DN}(0)$).

APPENDIX B

Appendix B. 1 Mass for single-sex scenario

Rank	No.	Model	AICc	Δ AICc	Model weight	Model likelihood	K	-2log(L)
1	18	Age Cohort Male Brood	5427.1	0.0	0.366	1.000	21	5384.2
2	31	Age Cohort Male Brood Sex	5428.7	1.6	0.164	0.449	22	5383.7
3	8	Age Cohort Brood	5429.6	2.5	0.105	0.287	20	5388.8
4	32	Age Cohort Male Brood Sex Brood*Sex	5429.8	2.7	0.095	0.259	23	5382.7
5	37	Age Cohort Male Brood Sex Helpers	5430.8	3.7	0.058	0.157	23	5383.7
6	23	Age Cohort Brood Helpers	5430.9	3.8	0.055	0.150	21	5388.0
7	21	Age Cohort Brood Sex	5431.0	3.9	0.052	0.142	21	5388.1
8	38	Age Cohort Male Brood Sex Helpers Brood*Sex	5431.9	4.8	0.033	0.091	24	5382.7
9	22	Age Cohort Brood Sex Brood*Sex	5432.1	5.0	0.030	0.082	22	5387.1
10	33	Age Cohort Brood Sex Helpers	5432.3	5.2	0.027	0.074	22	5387.3
11	34	Age Cohort Brood Sex Helpers Brood*Sex	5433.5	6.4	0.015	0.041	23	5386.4
12	7	Age Cohort Male	5442.5	15.4	0.000	0.000	20	5401.7
13	2	Age Cohort	5443.2	16.1	0.000	0.000	19	5404.5
14	19	Age Cohort Male Sex	5443.7	16.6	0.000	0.000	21	5400.8
15	9	Age Cohort Sex	5444.2	17.1	0.000	0.000	20	5403.4
16	20	Age Cohort Male Helpers	5444.3	17.2	0.000	0.000	21	5401.4
17	10	Age Cohort Helpers	5445.2	18.1	0.000	0.000	20	5404.4
18	24	Age Cohort Sex Helpers	5446.2	19.1	0.000	0.000	21	5403.3
19	11	Age Male Brood	5459.2	32.1	0.000	0.000	6	5447.1
20	4	Age Brood	5459.2	32.1	0.000	0.000	5	5449.2
21	26	Age Male Brood Sex Brood*Sex	5460.4	33.3	0.000	0.000	8	5444.3
22	15	Age Brood Sex Brood*Sex	5460.4	33.3	0.000	0.000	7	5446.3
23	14	Age Brood Sex	5460.9	33.8	0.000	0.000	6	5448.8
24	25	Age Male Brood Sex	5461.0	33.9	0.000	0.000	7	5446.9
25	27	Age Male Brood Helpers	5461.1	34.0	0.000	0.000	7	5447.0
26	16	Age Brood Helpers	5461.1	34.0	0.000	0.000	6	5449.1
27	30	Age Brood Sex Helpers Brood*Sex	5462.3	35.2	0.000	0.000	8	5446.2

28	36	Age Male Brood Sex Helpers Brood*Sex	5462.4	35.3	0.000	0.000	9	5444.2
29	29	Age Brood Sex Helpers	5462.8	35.7	0.000	0.000	7	5448.7
30	35	Age Male Brood Sex Helpers	5462.9	35.8	0.000	0.000	8	5446.8
31	1	Age	5475.7	48.6	0.000	0.000	4	5467.6
32	3	Age Male	5476.9	49.8	0.000	0.000	5	5466.8
33	5	Age Sex	5477.0	49.9	0.000	0.000	5	5466.9
34	6	Age Helpers	5477.6	50.5	0.000	0.000	5	5467.5
35	12	Age Male Sex	5478.3	51.2	0.000	0.000	6	5466.2
36	13	Age Male Helpers	5478.3	51.2	0.000	0.000	6	5466.2
37	17	Age Sex Helpers	5478.9	51.8	0.000	0.000	6	5466.8
38	28	Age Male Sex Helpers	5479.7	52.6	0.000	0.000	7	5465.6

Appendix B. 2 Mass for mixed-sex scenario

Rank	No.	Model	AICc	Δ AICc	Model weight	Model likelihood	K	-2Log(L)
1	33	Age Cohort Brood Sex Helpers	11378.3	0.0	0.329	1.000	22	11333.8
2	34	Age Cohort Brood Sex Helpers Brood*Sex	11379.3	1.0	0.199	0.607	23	11332.7
3	37	Age Cohort Male Brood Sex Helpers	11380.3	2.0	0.121	0.368	23	11333.8
4	21	Age Cohort Brood Sex	11380.4	2.1	0.115	0.350	21	11337.9
5	38	Age Cohort Male Brood Sex Helpers Brood*Sex	11381.3	3.0	0.073	0.223	24	11332.7
6	22	Age Cohort Brood Sex Brood*Sex	11381.4	3.1	0.070	0.212	22	11336.9
7	31	Age Cohort Male Brood Sex	11381.8	3.5	0.057	0.174	22	11337.3
8	32	Age Cohort Male Brood Sex Brood*Sex	11382.8	4.5	0.035	0.105	23	11336.3
9	9	Age Cohort Sex	11392.7	14.4	0.000	0.001	20	11352.3
10	24	Age Cohort Sex Helpers	11394.2	15.9	0.000	0.000	21	11351.8
11	19	Age Cohort Male Sex	11394.8	16.5	0.000	0.000	21	11352.3
12	29	Age Brood Sex Helpers	11398.3	20.0	0.000	0.000	7	11384.3
13	30	Age Brood Sex Helpers Brood*Sex	11399.4	21.1	0.000	0.000	8	11383.3
14	14	Age Brood Sex	11400.1	21.8	0.000	0.000	6	11388.0
15	35	Age Male Brood Sex Helpers	11400.2	21.9	0.000	0.000	8	11384.1
16	36	Age Male Brood Sex Helpers Brood*Sex	11401.2	22.9	0.000	0.000	9	11383.1
17	15	Age Brood Sex Brood*Sex	11401.2	22.9	0.000	0.000	7	11387.1
18	25	Age Male Brood Sex	11401.9	23.6	0.000	0.000	7	11387.9
19	26	Age Male Brood Sex Brood*Sex	11403.0	24.7	0.000	0.000	8	11387.0
20	5	Age Sex	11413.7	35.4	0.000	0.000	5	11403.7
21	17	Age Sex Helpers	11415.3	37.0	0.000	0.000	6	11403.3
22	12	Age Male Sex	11415.6	37.3	0.000	0.000	6	11403.5
23	28	Age Male Sex Helpers	11416.8	38.5	0.000	0.000	7	11402.8
24	23	Age Cohort Brood Helpers	11438.6	60.3	0.000	0.000	21	11396.1
25	8	Age Cohort Brood	11440.7	62.4	0.000	0.000	20	11400.3
26	18	Age Cohort Male Brood	11442.1	63.8	0.000	0.000	21	11399.7
27	2	Age Cohort	11453.7	75.4	0.000	0.000	19	11415.4
28	10	Age Cohort Helpers	11455.3	77.0	0.000	0.000	20	11414.9

29	7	Age Cohort Male	11455.8	77.5	0.000	0.000	20	11415.4
30	20	Age Cohort Male Helpers	11457.2	78.9	0.000	0.000	21	11414.8
31	16	Age Brood Helpers	11459.8	81.5	0.000	0.000	6	11447.7
32	4	Age Brood	11461.5	83.2	0.000	0.000	5	11451.5
33	27	Age Male Brood Helpers	11461.6	83.3	0.000	0.000	7	11447.5
34	11	Age Male Brood	11463.4	85.1	0.000	0.000	6	11451.4
35	1	Age	11475.8	97.5	0.000	0.000	4	11467.8
36	6	Age Helpers	11477.5	99.2	0.000	0.000	5	11467.4
37	3	Age Male	11477.7	99.4	0.000	0.000	5	11467.7
38	13	Age Male Helpers	11479.0	100.7	0.000	0.000	6	11467.0

Appendix B. 3 Leg length for single-sex scenario

Rank	No.	Model name	AICc	Δ AICc	Model weight	Model likelihood	K	-2LogL
1	9	Age Cohort Sex	596.5	0.0	0.279	1.000	7	582.0
2	21	Age Cohort Brood Sex	598.3	1.8	0.113	0.407	8	581.6
3	19	Age Cohort Male Sex	598.4	1.9	0.108	0.387	8	581.7
4	24	Age Cohort Sex HELPERS	598.5	2.0	0.102	0.368	8	581.9
5	22	Age Cohort Brood Sex Brood*Sex	598.6	2.1	0.097	0.350	9	579.7
6	2	Age Cohort	600.1	3.6	0.046	0.165	6	587.7
7	31	Age Cohort Male Brood Sex	600.2	3.7	0.044	0.157	9	581.4
8	33	Age Cohort Brood Sex HELPERS	600.4	3.9	0.040	0.142	9	581.6
9	32	Age Cohort Male Brood Sex Brood*Sex	600.7	4.2	0.034	0.122	10	579.6
10	34	Age Cohort Brood Sex Helpers Brood*Sex	600.7	4.2	0.034	0.122	10	579.7
11	10	Age Cohort HELPERS	601.8	5.3	0.020	0.071	7	587.3
12	8	Age Cohort Brood	601.9	5.4	0.019	0.067	7	587.4
13	7	Age Cohort Male	602.0	5.5	0.018	0.064	7	587.5
14	37	Age Cohort Male Brood Sex HELPERS	602.4	5.9	0.015	0.052	10	581.4
15	38	Age Cohort Male Brood Sex HELPERS Brood*Sex	602.9	6.4	0.011	0.041	11	579.6
16	23	Age Cohort Brood HELPERS	603.8	7.3	0.007	0.026	8	587.2
17	18	Age Cohort Male Brood	603.9	7.4	0.007	0.025	8	587.3
18	20	Age Cohort Male HELPERS	604.0	7.5	0.007	0.024	8	587.3
19	5	Age Sex	615.1	18.6	0.000	0.000	5	604.8
20	1	Age	615.6	19.1	0.000	0.000	4	607.4
21	12	Age Male Sex	616.6	20.1	0.000	0.000	6	604.2
22	14	Age Brood Sex	617.2	20.7	0.000	0.000	6	604.8
23	17	Age Sex HELPERS	617.2	20.7	0.000	0.000	6	604.8
24	3	Age Male	617.2	20.7	0.000	0.000	5	606.9
25	6	Age Helpers	617.5	21.0	0.000	0.000	5	607.3
26	4	Age Brood	617.7	21.2	0.000	0.000	5	607.4
27	15	Age Brood Sex Brood*Sex	618.7	22.2	0.000	0.000	7	604.2

28	25	Age Male Brood Sex	618.7	22.2	0.000	0.000	7	604.2
29	28	Age Male Sex HELPERS	618.7	22.2	0.000	0.000	7	604.2
30	29	Age Brood Sex HELPERS	619.3	22.8	0.000	0.000	7	604.8
31	11	Age Male Brood	619.3	22.8	0.000	0.000	6	606.9
32	13	Age Male HELPERS	619.3	22.8	0.000	0.000	6	606.9
33	16	Age Brood HELPERS	619.6	23.1	0.000	0.000	6	607.2
34	26	Age Male Brood Sex Brood*Sex	620.4	23.9	0.000	0.000	8	603.7
35	35	Age Male Brood Sex Helpers	620.8	24.3	0.000	0.000	8	604.1
36	30	Age Brood Sex HELPERS Brood*Sex	620.8	24.3	0.000	0.000	8	604.2
37	27	Age Male Brood HELPERS	621.4	24.9	0.000	0.000	7	606.9
38	36	Age Male Brood Sex Helpers Brood*Sex	622.5	26.0	0.000	0.000	9	603.7

Appendix B. 4 Leg length for mixed-sex scenario

Rank	No.	Model name	AICc	Δ AICc	Model likelihood	Model weight	K	-2LogL
1	9	Age Cohort Sex	1356.2	0.0	1.000	0.102	7	1342.0
2	5	Age Sex	1356.2	0.0	1.000	0.102	5	1346.0
3	15	Age Brood Sex Brood*Sex	1356.5	0.3	0.861	0.088	7	1342.2
4	24	Age Cohort Sex HELPERS	1356.7	0.5	0.779	0.079	8	1340.4
5	22	Age Cohort Brood Sex Brood*Sex	1356.9	0.7	0.705	0.072	9	1338.5
6	17	Age Sex HELPERS	1357.1	0.9	0.638	0.065	6	1344.9
7	34	Age Cohort Brood Sex Helpers Brood*Sex	1357.3	1.1	0.577	0.059	10	1336.9
8	30	Age Brood Sex HELPERS Brood*Sex	1357.5	1.3	0.522	0.053	8	1341.1
9	12	Age Male Sex	1358.2	2.0	0.368	0.037	6	1346.0
10	14	Age Brood Sex	1358.2	2.0	0.368	0.037	6	1346.0
11	21	Age Cohort Brood Sex	1358.3	2.1	0.350	0.036	8	1341.9
12	19	Age Cohort Male Sex	1358.3	2.1	0.350	0.036	8	1342.0
13	26	Age Male Brood Sex Brood*Sex	1358.5	2.3	0.317	0.032	8	1342.2
14	33	Age Cohort Brood Sex HELPERS	1358.8	2.6	0.273	0.028	9	1340.4
15	38	Age Cohort Male Brood Sex HELPERS Brood*Sex	1358.9	2.7	0.259	0.026	11	1336.3
16	32	Age Cohort Male Brood Sex Brood*Sex	1358.9	2.7	0.259	0.026	10	1338.4
17	28	Age Male Sex HELPERS	1359.0	2.8	0.247	0.025	7	1344.8
18	29	Age Brood Sex HELPERS	1359.1	2.9	0.235	0.024	7	1344.9
19	36	Age Male Brood Sex Helpers Brood*Sex	1359.4	3.2	0.202	0.021	9	1341.0
20	37	Age Cohort Male Brood Sex HELPERS	1360.1	3.9	0.142	0.014	10	1339.8
21	25	Age Male Brood Sex	1360.2	4.0	0.135	0.014	7	1346.0
22	31	Age Cohort Male Brood Sex	1360.3	4.1	0.129	0.013	9	1341.9
23	35	Age Male Brood Sex Helpers	1361.1	4.9	0.086	0.009	8	1344.8
24	2	Age Cohort	1366.6	10.4	0.006	0.001	6	1354.4
25	1	Age	1366.7	10.5	0.005	0.001	4	1358.6
26	10	Age Cohort HELPERS	1367.1	10.9	0.004	0.000	7	1352.8
27	6	Age Helpers	1367.7	11.5	0.003	0.000	5	1357.6
28	20	Age Cohort Male HELPERS	1368.3	12.1	0.002	0.000	8	1352.3

29	8	Age Cohort Brood	1368.6	12.4	0.002	0.000	7	1354.3
30	7	Age Cohort Male	1368.6	12.4	0.002	0.000	7	1354.4
31	3	Age Male	1368.7	12.5	0.002	0.000	5	1358.6
32	4	Age Brood	1368.7	12.5	0.002	0.000	5	1358.6
33	23	Age Cohort Brood HELPERS	1369.1	12.9	0.002	0.000	8	1352.8
34	13	Age Male HELPERS	1369.6	13.4	0.001	0.000	6	1357.5
35	16	Age Brood HELPERS	1369.8	13.6	0.001	0.000	6	1357.6
36	18	Age Cohort Male Brood	1370.6	14.4	0.001	0.000	8	1354.3
37	11	Age Male Brood	1370.8	14.6	0.001	0.000	6	1358.6
38	27	Age Male Brood HELPERS	1371.7	15.5	0.000	0.000	7	1357.5
