

Ultimate and Proximate Explanations of Helping Behavior in the red-cockaded
woodpecker (*Picoides borealis*).

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(ABSTRACT)

One unresolved issue in the study of cooperative breeding is why individuals that delay their own reproduction assist others in raising young. Red-cockaded woodpecker helpers may gain future indirect fitness benefits by increasing survival of breeders, who produce offspring related to the helper in the future. Breeder survival may be enhanced because of general benefits of group living, either because of the helper's own presence or because helping increases the production of fledglings. I demonstrate that breeder survival increases in the presence of helpers and additional young. Helpers may also reduce the workload of the breeder, and this may increase breeder survival as well. I show that breeders spend less time incubating and provisioning young when a helper is present.

Helpers may also gain fitness benefits if once they become breeders, they are assisted by young they previously helped raise. Expected frequencies of reciprocal exchange of helping are low (2%). Slightly higher observed frequencies may be accounted for by preferential helping of kin and effects of territory quality. Reciprocity occurs no more often than expected among helpers unrelated to the young they help raise suggesting that young males do not preferentially help former care-givers. I conclude that helpers do not gain fitness benefits from reciprocity.

I examined the proximate causes of delayed breeding and helping behavior by measuring plasma testosterone (T) and prolactin (PRL) concentrations in female breeders, male breeders, and male helpers during different stages of the reproductive cycle. Among male breeders and helpers, T is low during the nonbreeding stage, peaks during copulation and declines during the incubation and nestling-provisioning stages. Helpers appear physiologically capable of reproducing: their T concentrations are equal to those of breeders. Helpers unrelated to the breeding female have higher T than helper related to her. Sexual inactivity by male helpers is best explained by behavioral suppression. Female breeder, male breeder, and male helper PRL was equal and increased from the nonbreeding stage through the copulation and incubation stages. During the nestling provisioning stage, male breeder and male helper PRL declined, while female PRL continued to increase. I conclude that the physiological bases of helping behavior and parental behavior are the same.

DEDICATION

To my mother, Judith P. Khan, for introducing me to the outdoors.

To my father, M. Saeed Khan, for introducing me to laboratory science.

To my husband, Karl E. Loewenstein, for introducing me to my own capabilities.

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Chapter 1 Introduction

The central point in Lorenz's life work thus seems to me his clear recognition that behaviour is part and parcel of the adaptive equipment of animals; that, as such, its short-term causation can be studied in fundamentally the same way as that of other life processes; that its survival value can be studied just as systematically as its causation; that the study of its ontogeny is similar to that of the ontogeny of structure; and that the study of its evolution likewise follows the same lines as that of the evolution of form.

- Tinbergen 1963

Two major contributions of Konrad Lorenz to the study of behavior are that (1) behavior should be studied like any other trait and (2) behavioral studies consist of four major areas of research: survival value, evolution, physiology, and development. These four areas are neatly divided into two levels of analysis, ultimate and proximate (Alcock and Sherman 1994). My dissertation accepts this paradigm as the most productive way to understand the evolution of behavior and will examine both ultimate and proximate causation in an attempt to explain delayed dispersal and helping behavior in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*). Ultimate questions ask about the evolutionary causes of behavior. I will examine the evolutionary causes of helping behavior by testing hypotheses about the survival advantages and reproductive consequences of helping behavior in Chapters 2 and 3. Proximate questions ask about the immediate causes of behavior such as internal physiological mechanisms and the development of behavioral traits. I will examine the physiological bases of sexual inactivity and alloparental behavior of helpers in Chapter 4. In this chapter, I introduce the conceptual framework used to study the evolution of cooperative breeding (1.1), the basic biology of the red-cockaded woodpecker (1.2), the ultimate hypotheses to explain helping behavior (1.3), and the proximate hypotheses to explain sexual inactivity and alloparental behavior of helpers (1.4).

1.1 Evolution of cooperative breeding

Cooperative breeding is a social system characterized by the presence of adults that exhibit parent-like (helping, alloparental) behavior toward young that are not their genetic offspring, at some or all nests in a population. Cooperative breeding occurs in over 300 avian species from 24 orders and has evolved independently many times (Emlen and Vehrencamp 1983; Brown 1987). Cooperatively breeding species exhibit all combinations of mating systems, ranging from monogamy to polygynandry. In most cases, a monogamous breeding pair is assisted by adult offspring from previous breeding seasons, e.g. red-cockaded woodpeckers (Walters et al. 1988). In a less common form of cooperative breeding, plural breeders from several monogamous pairs build nests on a jointly defended territory, e.g. bell miners (*Manorina melanophrys*; Conrad et al. 1998). Bell miner helpers may be breeders that provision young at nests other than their own, or nonbreeding adults and juveniles without nests. Still other species, like the acorn woodpecker (*Melanerpes formicivorus*), are polygynandrous joint nesters in which two or more females may lay eggs in the same nest, and mate with two or more co-breeding

males (Koenig and Stacey 1990). In these species, some adults are exhibiting parental behavior to some young in the nest and alloparental behavior to others. Clearly, the conditions required for these various forms of cooperative breeding to evolve are quite different.

Although convergent evolution most likely explains the presence of similar cooperative breeding in some sets of species, phylogenetic history is an important factor in other cases. Cooperative breeding occurs in some phylogenetic groups disproportionately more often than expected by convergent evolution alone. In Australia 28% of 266 old endemic Australian passerines are cooperative breeders and in some families cooperative breeding is the norm (e.g. Maluridae; Rowley and Russell 1997). In comparison, cooperative breeding occurs in 3% of all bird and mammal species world wide.

In the most common form of cooperative breeding, such as occurs in the red-cockaded woodpecker, most helpers are nonbreeding individuals that have remained on their natal territory. In these systems, the evolution of cooperative breeding involves two distinct phenomena: (1) young remain on their natal territory, rather than dispersing and (2) the retained young express alloparental behavior (Brown 1987; Emlen 1982a; Emlen 1982b). The ultimate causes for delayed dispersal have been identified in several cooperatively breeding species (Koenig et al. 1992; Komdeur 1992; Walters et al. 1992b). A general framework for the evolution of delayed dispersal, the delayed-dispersal threshold model, has been proposed by Koenig et. al. (1992). This model incorporates factors such as the benefits of philopatry, ecological constraints, and high variation in territory quality within populations (Emlen 1994).

In contrast to our general understanding of delayed dispersal, the evolution of alloparental behavior is poorly understood. The persistence of helping presents an evolutionary paradox because altruistic traits, in this case raising offspring produced by others, should be selected against because of fitness costs to the donor. Hamilton proposed a solution to this paradox with his theory of inclusive fitness, namely that helpers gain indirect benefits by raising offspring of close relatives (i. e., non-descendant kin; Hamilton 1964a; 1964b). He defined inclusive fitness as the sum of direct and indirect fitness benefits. Direct benefits accrue when the helper's survival or production of descendant kin is enhanced. Indirect benefits accrue when helping increases the production of non-descendant kin. Direct and indirect fitness benefits are each comprised of a current and future component depending on the time when the benefits are realized (Brown 1987; Koenig and Mumme 1990).

Individuals in different species may help for different reasons, which makes resolving the issue of the evolution of alloparental behavior difficult (Emlen 1991). As a consequence, general explanations of the evolution of alloparental behavior probably do not exist. For example, helping behavior has probably evolved in the white-fronted bee-eater (*Merops bullockoides*) because helpers gain substantial indirect inclusive fitness benefits by increasing the production of non-descendant kin by their groups (Emlen 1992). In contrast, helping behavior by males unrelated to the breeders in the pied kingfisher (*Ceryle rudis*) has probably evolved because these helpers gain direct fitness benefits by increasing the probability of future mating with the female they helped (Reyer 1984).

The most appropriate approach to the study of the evolution of helping is to determine the relative importance of various possible fitness benefits of helping in a variety of species (Brown 1987; Emlen 1991; Cockburn 1998). Nine hypotheses, each describing a possible fitness benefit of helping behavior, have been proposed to explain the evolution of alloparental behavior (Table 1: Brown 1987; Emlen and Wrege 1989). These hypotheses have directed research on helping behavior in most cooperatively breeding species, including the red-cockaded woodpecker. Each hypothesis describes a possible fitness benefit of alloparental behavior (Fig. 1).

The red-cockaded woodpecker is a good species in which to study helping behavior for two reasons. First, the red-cockaded woodpecker's system is relatively 'primitive'. Cooperative breeding is only represented by one species in the genus *Picoides*, indicating that this breeding system has probably evolved *de novo* within the red-cockaded woodpecker. Also, in red-cockaded woodpeckers, male fledglings may practice either of two dispersal strategies. Some males stay on their natal territory and help, but others disperse and search for a breeding vacancy, as is typical of species that are not cooperative breeders. In other species, delayed dispersal is the norm, and other secondary behaviors have evolved that increase the benefits of delayed dispersal and helping. For example, acorn woodpecker helpers increase the pay-off of delayed dispersal through secondary behaviors such as communal nesting and sharing mates. Examining the benefits of helping in a primitive cooperative breeder enable one to distinguish between the benefits that initially select for alloparental behavior versus additional benefits that have arisen through subsequent evolution.

Secondly, remarkably complete demographic data have been collected from my study population of red-cockaded woodpeckers. Using these data, I can examine the behavior of individuals and determine how these behaviors influenced their fitness. The demography of my study population in the Sandhills of North Carolina has been monitored continuously for 20 years (1980-1999). These monitoring efforts have resulted in a study population of individually marked woodpeckers whose life-histories are documented from the time they hatch until their death.

1.2 Red-cockaded woodpecker

Ecology

The red-cockaded woodpecker is a cooperatively breeding species endemic to the pine savannas of the southeastern United States, favoring longleaf pine (*Pinus palustris*) systems. The longleaf pine ecosystem is fire-maintained forcing the woodpecker to depend on living pine for its livelihood because snags (standing, dead trees) are scarce. Although this species prefers longleaf pine, it also uses loblolly (*P. taeda*), slash (*P. echinata*), Virginia (*P. virginiana*), pond (*P. serotina*), and pitch (*P. rigida*) pine.

The red-cockaded woodpecker is unique because it relies almost exclusively on living pine for roosting, nesting, and foraging (Conner 1995). Red-cockaded woodpeckers prefer to excavate cavities in live old-growth pines (>80 yrs) because old trees have the necessary

heartwood diameter to accommodate a cavity, and they are usually infected with red-heart fungus (*Phellinus pini*), which presumably makes cavity excavation easier (Conner and Rudolph 1995). In addition, red-cockaded woodpeckers prefer old growth pine for foraging, most likely because of the large surface area and looser bark which accommodates a greater diversity of arthropod prey (Jackson 1994).

Cavity excavation is a laborious and time-consuming activity that requires on average 1.8 to 13.1 years to complete, depending on the pine species and geographic location (Conner and Rudolph 1995; Harding 1997). Excavation takes such a long time because the woodpeckers must cope with pine resin that seeps from the cavity entrance during excavation. Cavity excavation is conducted in bursts of activity, usually during the warmer season, interrupted by long periods of inactivity while the woodpeckers wait for the tree to heal the wounds they have created (Harding 1997). Eventually, the sapwood surrounding the cavity entrance becomes inundated with dried resin, preventing any new resin from flowing. These birds also use a living pine's copious resin flow to their own advantage. The woodpeckers maintain small wounds (resin wells) above, below and around the cavity entrance, that create a sappy barrier that is an effective defense against climbing rat snakes (Rudolph et al. 1990).

The red-cockaded woodpecker's dependence on cavities is a critical factor in the evolution of delayed dispersal in this species. Red-cockaded woodpeckers compete for territories containing existing cavity trees (Copeyon et al. 1991), rather than construct new ones because cavities take so long to excavate (Conner and Rudolph 1995; Harding 1997). Thus, the continued association of young with the natal territory after fledging is related to variation in habitat quality based on availability of cavities for roosting and nesting (Walters et al. 1992a). Young males who choose to remain on high quality territories, namely those with already existing cavities, are staking their position for ensuing competition for breeding vacancies. If they disperse immediately following fledging, they may be unable to obtain a territory with cavities and will have lower life-time reproductive success than if they had waited to reproduce on a high quality territory because of the time required to excavate cavities before breeding can ensue. Red-cockaded woodpeckers that delay dispersal tend to occur on high quality territories and their decision to remain may be influenced by cues of intense competition such as territorial intrusion by floaters (Walters et al. 1992b).

Social system

Red-cockaded woodpeckers occur in groups that consist of a single breeding female, a dominant male breeder, and up to 4 subordinate, nonbreeding helpers, most of which are male (Lennartz et al. 1987; Ligon 1970; Walters 1990; Walters et al. 1988). The breeding system is monogamous, even in groups in which male helpers are unrelated to the breeding female (Haig et al. 1994). Not all breeding groups have helpers and most groups that do have only a single helper (Walters et al. 1992b).

Male and female fledglings practice one of two life-history strategies. Young may disperse in their first year and search for breeding vacancies. Alternatively, young may choose to

remain on their natal territories and become helpers. Most female fledglings that survive disperse and acquire breeding status in their first year, although female helpers sometimes occur. Roughly one-fourth of surviving male fledglings disperse in their first year, whereas the remaining three-fourths remain on the natal territory as helpers. Some of these dispersing males acquire a breeding position in their first year, others acquire territories but not a mate (solitary males), and the remainder acquire neither a territory nor a mate (floaters).

Helpers acquire breeding status either through inheritance of the natal territory or by filling neighboring breeding vacancies (Walters et al. 1988). Helpers tend to be previous offspring of either the breeding male or both breeders, but sometimes they help more distant relatives, such as older siblings. Occasionally, helpers are unrelated to those they help (5%). Helpers participate in territory defense, construction, and maintenance of nest cavities, incubation, brooding, feeding nestlings, and tending fledglings. Helpers have been shown to significantly improve the reproductive success of the breeding pair (Lennartz et al. 1987; Heppell et al. 1994).

Conservation and Management

The decline of the red-cockaded woodpecker parallels the decimation of the longleaf pine forests. Only 3% of the 90 million acres of longleaf pine forest that once covered the southeastern United States remain today. The industrial revolution in the late 1800's heralded the nearly complete destruction of these forests for timber, railroad ties, naval stores, agricultural land, and pine plantations (Sandhills Area Land Trust 1997). As early as 1919 biologists recognized that the red-cockaded woodpecker was in trouble, and it has been listed as a federally endangered species since 1973 (Jackson 1995).

Although habitat destruction is the cause of the initial decline of the species, fire suppression and the limited availability of old trees in regenerated even-aged forests are responsible for more recent declines. Fire suppression encourages development of hardwood midstory, reduction of ground cover and generally changes the pine savanna ecosystem considerably. Red-cockaded woodpeckers will abandon their cavities, and eventually their territories, when hardwoods encroach on the cavities, presumably because of the increased risks of predation (Jackson 1994; Walters 1991).

Twenty-five years of research on the red-cockaded woodpecker identified cavities as the limiting factor to population growth and therefore the key to recovery of this species (Walters 1991). Concurrent research on the ecology of the longleaf pine ecosystem has identified frequent fire as a critical component for maintaining ecosystem health. Therefore, short-term management for the red-cockaded woodpecker involves replacing cavities lost to natural disasters (e. g. hurricanes) on existing territories, and creating new cavity clusters to encourage the formation of new groups, thereby increasing population size (Walters et al. 1992a; Walters 1991; Copeyon et al. 1991). Long-term management for the red-cockaded woodpecker requires frequent prescribed burning during the growing season, protection of old trees for future use by the birds, and regeneration of natural forests (James 1995). Biologists have provided the road

map to recovery for the red-cockaded woodpecker. However the fate of this unique species will be determined by public and private landowners and policy makers.

1.3 Ultimate explanations of helping behavior

1.3.1 Current indirect benefit

Increased inclusive fitness

Helpers may increase their fitness by raising closely related offspring. This hypothesis predicts that (1) helpers substantially increase the reproductive success of the breeding pair and (2) helpers are closely related to the recipients of their aid. In species where helpers have a choice among nests to aid, this hypothesis predicts that helpers will choose the closest relative's nest.

In many cooperatively breeding species helpers increase the reproductive success of the breeding pair that they assist (Table 2). That some of these species gain current indirect benefits from raising closely related offspring is well documented (Table 3). Many of the studies that demonstrate that helpers gain indirect benefits from the increased production of non-descendant kin have been criticized because results may be confounded by breeder age and territory quality (Cockburn 1998). In many species, old breeders have higher reproductive success than young breeders (Curio 1983). If individuals preferentially help older breeders or are more likely to become helpers on high quality territories, the effect of the helper on reproductive success is likely to be confounded by these factors. In the few studies in which breeder age, experience and territory quality were controlled, either through experimental manipulation (Mumme 1992) or statistical techniques (Heppell et al. 1994; Koenig and Mumme 1987), the conclusion that helpers gain significant indirect benefits from the increased production of non-descendant kin is strongly supported.

The conclusion that indirect fitness benefits are important for the evolution of alloparental behavior has been affirmed with new technological advances. The invention of polymerase chain reaction (PCR), which amplifies very small DNA samples, in conjunction with DNA fingerprinting has allowed researchers to determine paternity in many cooperative breeding systems. DNA fingerprinting has affirmed that helpers are usually related to the offspring they help raise, thereby gaining indirect fitness benefits from the production of non-descendant kin in the red-cockaded woodpecker (Haig et al. 1994), bell miner (Conrad et al. 1998), noisy miner (*Manorina melanocephala*; Poldmaa et al. 1995), bicolor wren (*Campylorhynchus griseus*; Haydock et al. 1996), and Florida scrub-jay (Quinn et al. 1999).

DNA fingerprinting has also demonstrated high levels of extra-pair fertilizations in some cooperatively breeding species, causing some researchers to reevaluate the importance of indirect inclusive fitness benefits. Shared paternity was discovered in the stripe-backed wren (*Campylorhynchus nuchalis*) demonstrating that helpers gain current direct benefits in the form of direct reproduction (Rabenold et al. 1990). High levels of extra-pair fertilizations between females and extra- group males were documented in the splendid fairy-wren (65%, *Malurus*

splendens; Brooker and Rowley 1995) and superb fairy-wren (76%, *Malurus elegans*; Dunn et al. 1995), suggesting that helping in these species may be selected through direct fitness benefits.

In summary, the immediate indirect fitness benefits of helping through the increased production of non-descendant kin have been documented for several avian cooperatively breeding species, including the red-cockaded woodpecker. A single red-cockaded woodpecker helper increases the reproductive output of a breeding pair by 0.39 fledglings per year (Heppell et al. 1994). These extra fledglings are non-descendant kin of the helper, because helpers do not participate in breeding (Haig et al. 1994) and helpers are usually related to the breeding pair. To date this has been the only benefit of helping behavior known to apply to red-cockaded woodpecker helpers. In this dissertation I test several other possible fitness benefits of helping behavior.

1.3.2 Future indirect benefits

Increased inclusive fitness

Group size

Helpers may gain future indirect benefits by enhancing breeder survivorship through benefits of group living, such as increased predator detection and increased foraging efficiency (see reviews by Roberts 1996; Elgar 1989). Individuals in larger groups may enjoy the same or improved predator detection rate while scanning for predators less frequently (Pulliam 1973). If an individual spends less time scanning for predators more time becomes available for other activities, notably foraging. That decreased vigilance for predators can result in increased feeding rate has been demonstrated in the downy woodpecker (*Picoides pubescens*), a species that joins mixed-species foraging flocks in the winter (Sullivan 1984). An alternative, but not mutually exclusive explanation for group size effects is that as group size decreases, an individual's risk of predation declines (i.e., dilution effect; reviewed in Inman and Krebs 1987).

Foraging efficiency may increase as a result of large group size, independent of the effect of group size on vigilance for predators. For example, an individual's foraging rate may increase through local enhancement; group members observe where other animals are feeding and use that information to find food themselves (Krebs et al. 1972). Local enhancement has been demonstrated in several vertebrate species (Roberts 1996).

Helpers may increase group size through production of extra fledglings. Alternatively, the presence of the helpers themselves may increase the survivorship of breeders, regardless of the helper's effects on fledgling production. This hypothesis predicts that (1) helpers are closely related to the breeders in a group and (2) breeder survival increases as a function of group size.

Enhancement of breeder survival through group size effects was first demonstrated in the acorn woodpecker. Koenig and Mumme (1987) controlled for territory quality and previous breeding experience in a log-linear analysis of breeder survivorship and showed that male breeder survivorship is significantly enhanced by the presence of nonbreeding adult helpers.

Koenig and Stacey (1990) estimate that one-third of the fitness benefits accrued by acorn woodpecker helpers is derived from the helper's enhancement of the survival of related male breeders in the group.

Reduced workload

Helpers may also enhance breeder survivorship by reducing the breeder's energy expenditure during the breeding season. This hypothesis is usually tested by measuring nestling feeding rates because this is the most conspicuous energy-demanding behavior performed by breeders. This hypothesis predicts that (1) helpers are closely related to the breeders in a group, (2) breeders adjust their contributions to nestling care in response to nonbreeding adults and (3) breeder survival is enhanced in the presence of a helper.

Helper effects on breeder workload are summarized for several cooperatively breeding species in Table 4. Since helpers assist with provisioning, if the total provisioning rate of groups with helpers is statistically equivalent to that of groups without helpers, then one or both breeders are adjusting their effort to the presence of helpers. In several species, breeders adjust their workload in the presence of helpers so that the total provisioning rate is unchanged. In others, total provisioning significantly increases in the presence of a helper, yet one or both breeders reduces its workload. In cases where total provisioning rates are higher in groups with helpers and where breeders do not adjust their effort, brood loss is often attributed to starvation (Reyer 1980; Woolfenden and Fitzpatrick 1984; Koenig and Mumme 1987; Heinsohn et al. 1987; Emlen et al. 1991b). Breeders reduce their workload when helpers are present in 14 of the 23 species studied (Table 4) suggesting that reduced workload is a common benefit for breeders in groups with helpers.

Although many studies demonstrate that breeders reduce their workload in the presence of a helper, only four studies document a concomitant increase in breeder survival: white-browed sparrow weaver (*Plocepasser mahali*; Lewis 1982), splendid fairy-wren (Rowley and Russell 1997), bicolor wren (*Campylorhynchus griseus*; Austad and Rabenold 1985; Rabenold 1990), and pied kingfisher (Reyer 1984). Whether a breeder's survival is enhanced directly because of reduced workload is difficult to determine because of the confounding factor of territory quality and the difficulty of measuring breeder workloads.

For analyses of breeder survival the effects of territory quality may be controlled by multivariate regression (acorn woodpecker; Koenig and Mumme 1987) or experimentation. For example, Woolfenden and Fitzpatrick (1984) reported that Florida scrub-jay (*Aphelocoma coerulescens*) breeders living in pairs die at about 1.5 times the rate of those living in groups of three or more. If groups with helpers tend to occur on high quality territories and simple pairs on low quality territories, this pattern may be a function of territory quality and not the presence of helpers. Evidence that territory quality influences breeder survival was provided by Mumme (1992) who found no difference between the survival of Florida scrub-jay breeders in experimental groups from which non-breeders were removed (96.8% survival) and those in control groups containing non-breeders (95.2% survival).

Effects of reduced breeder workload on breeder survivorship may be difficult to demonstrate because nestling provisioning may not be an accurate indicator of a breeder's total energy budget. Breeding birds may spend their time and energy on several different activities such as foraging and territory defense in addition to nestling provisioning. Breeders that reduce nestling provisioning in the presence of helpers may use their surplus energy and time on other equally demanding activities, such as territory defense. The benefits of reduced workload might result from these activities rather than from enhanced survival.

Few studies have documented future indirect fitness benefits because of the difficulties in separating the effects of territory quality from the effects of helpers on breeder survival. Future indirect benefits can be quite substantial (e.g. acorn woodpecker), indicating that careful studies of the effects of helpers on breeder survivorship are necessary. Red-cockaded woodpecker helpers may gain future indirect benefits by enhancing the survival of related breeders. I document the effect of helpers on breeder workloads and examine breeder survival as a function of group size in Chapter 2.

1.3.3 Future direct benefits

A helper may gain three types of future direct fitness benefits. First, helping may improve an individual's probability of surviving to breed. Second, alloparental behavior may increase the future reproductive success of the individual. Third, helping behavior may increase an individual's future probability of breeding. Below I discuss each type of future benefit and describe specific hypotheses (e.g. mechanisms) by which a helper may gain these benefits.

Improved probability of surviving to breed

Group size effects

This hypothesis proposes that helpers augment the production of young, thereby increasing group size and enhancing their own survival through the general benefits of group living, such as increased foraging efficiency, enhanced predator detection, and improved protection from predators through dilution effects (Pulliam and Caraco 1984). This hypothesis predicts that: (1) helping augments group size and (2) helper survival is higher in larger groups than in small ones (Emlen 1991). The ability of helpers to augment group size was discussed above. Here I discuss whether group size affects a helper's own survival.

Although many studies report positive effects of group size on survival, these results are likely to be confounded by territory quality. Removing territory quality effects is important for distinguishing between reasons an individual delays dispersal and reasons an individual helps. If helper survival is a function of territory quality but not group size, individuals can gain this advantage without engaging in alloparental behavior.

The hypothesis that helper survival is enhanced through the general benefits of group living is not supported in many cooperatively breeding species. Helper survival does not increase as a function of group size in the acorn woodpecker (Koenig and Mumme 1987), bicolor wren (Rabenold 1990), pinyon jay (*Gymnorhinus cyanocephalus*; Marzluff and Balda 1990) or white-fronted bee-eater (Emlen and Wrege 1989) (Table 5). Benefits from increased foraging efficiency may be limited because young cooperative breeders are often inefficient at finding food for themselves (Heinsohn 1991; Poiani 1993; Langen 1996). Safety from predators, through dilution effects, may not operate at the small group sizes typical of most cooperatively breeding species. However, this effect may apply to cooperative breeders that typically live in large groups, such as the Australian miners (*Manorina spp.*), who often live in groups numbering over twenty individuals.

Red-cockaded woodpecker helpers may gain direct benefits because helping increases the probability of the helper surviving to breed. This analysis is not included in my dissertation because of the intractable problem that the effect of group size on helper survival is confounded by territory quality. High quality territories are correlated with the presence of helpers and higher production of fledglings. Therefore, examination of the hypothesis that helpers gain survival benefits from augmenting group size through the production of 'extra' fledglings must wait until an indicator of territory quality, independent of the number of adults or fledglings is determined.

Pay-to-stay

The pay-to-stay hypothesis states that a helper must compensate the breeder by helping raise the offspring on that territory in order to gain access to critical resources on the territory. The pay-to-stay hypothesis assumes that helpers will have higher survival by living on a territory with which they are familiar. Helping reduces the cost to the breeder of having an extra individual using resources on the territory. This hypothesis predicts that a breeder will try to evict any non-helping individual. In 1991, Emlen noted that no compelling evidence of differential treatment of helpers versus non-helpers had been observed, but the data were scant. Little additional work has specifically addressed this hypothesis, yet it routinely appears as an explanation for observed alloparental behavior (Marzluff and Balda 1992; Poiani 1993; Khan and Walters 1997).

The best evidence for the pay-to-stay hypothesis was demonstrated in the pied kingfisher. Reyer (1986) observed that pied kingfisher helpers unrelated to the breeding pair that were not carrying fish to feed nestlings were more frequently attacked by the breeding male than unrelated helpers with fish. Furthermore, breeders only accept unrelated helpers when the risk of brood loss to starvation is high (Reyer and Westerterp 1985). These observations suggest that feeding unrelated offspring is a payment to the breeding male for access to his nesting territory.

The first experimental test of the pay-to-stay hypothesis was conducted on superb fairy-wrens (Mulder and Langmore 1993). Helpers were removed for 24 hours and aggression by the dominant male toward the 'non-helper' was measured at three different stages of the reproductive cycle: nonbreeding, fertilization/incubation, and nestlings/dependent fledglings. No aggression

was observed during nonbreeding season removals, only 50% of the groups exhibited aggression during the fertilization/incubation stage, and the highest levels of aggression occurred during the nestlings/dependent fledglings stage (Mulder and Langmore 1993). This pattern is consistent with the pay-to-stay hypothesis. Alternatively, dominant males may be aggressive toward the ‘non-helpers’ because both are competing for extra-group copulations (Dunn et al. 1995; Green et al. 1995). Males from other groups have been documented to father up to 76% of young in a brood (Rowley and Russell 1997).

Although the superb fairy-wren experiment is intriguing, removal experiments do not adequately test the pay-to-stay hypothesis. Specifically, one can not determine if the group is unable to recognize the missing member and therefore treats it as an intruder, or if the group is responding to lack of help. This hypothesis could be properly tested in a species where non-helping auxiliaries are common (Emlen 1991). The white-throated magpie jay (*Calocitta formosa*), a large, Neotropical corvid, may be such a species, since helper contributions to nestling feeding are highly variable with some individuals not contributing at all (Innes and Johnston 1996). The pay-to-stay hypothesis may also be tested through phenotypic engineering in which non-helping auxiliaries are created through hormonal manipulation. This could be accomplished by increasing the metabolism of the auxiliary by elevating its thyroid hormone levels so that the individual must consume all of the food it obtains (Schoech, pers comm.). Alternatively, a hormone blocking chemical that interferes with prolactin, such as metapyrone, might be used to manipulate levels of alloparental behavior within populations. Prolactin is a hormone often associated with parental and possibly alloparental behavior in birds (Vleck et al. 1991; Schoech et al. 1996b).

The pay-to-stay hypothesis remains an intriguing explanation for helping in cooperatively breeding species. Several studies provide suggestive evidence that pay-to-stay is operating. Pay-to-stay may be likely in species where the breeding male experiences a decrease in fitness (e.g. cuckoldry) as a direct result of sharing his territory with extra adult males. This question needs to be addressed in species with some level of extra-pair paternity and natural variation in levels of alloparental behavior, or in species where helping contributions can be manipulated.

The pay-to-stay hypothesis remains untested in the red-cockaded woodpecker, in part because potentially harmful manipulative experiments generally are prohibited for this endangered bird. Pay-to-stay is not likely to be an important hypothesis to explain helping in this species because (1) helpers are generally closely related to the breeding male, (2) this species is genetically monogamous, and (3) evidence of conflict between the breeding male and helper is lacking. I will not consider this hypothesis further.

Increased future reproductive success

Skills hypothesis

Helping may be a learning experience that benefits an individual once it attains breeder status by improving relevant skills. The skills hypothesis predicts that first-time breeders with

helping experience will have higher reproductive success than first-time breeders without helping experience. This benefit is frequently cited without supporting empirical evidence (Skutch 1961; Brown et al. 1978; Lawton and Guindon 1981). Analyses of benefits of helping experience must first separate helping experience from breeding experience and identify effects of age independent of experience. Only four studies have adequately tested the skills hypothesis in cooperatively breeding birds and the results are mixed. Helping experience had no effects on subsequent reproductive success of first time breeders in white-fronted bee-eaters (Emlen and Wrege 1989), and western bluebirds (*Sialia mexicana*; Dickinson et al. 1996). However, helping experience has strong effects on reproductive success in the Seychelles warbler (*Acrocephalus sechellensis*; Komdeur 1996), and long-tailed tit (*Aegithalos caudatus*; Hatchwell et al. 1999).

Many studies have demonstrated that helpers acquire important skills during the time they remain on their natal territory. Foraging skills improve with age in bell miners (Poiani 1993), brown jay (*Psilorhinus morio*; Lawton and Guindon 1981), white-winged chough (*Corcorax melanorhamphus*; Heinsohn et al. 1987; Heinsohn 1991) and white-throated magpie jays (Langen 1996). We do not know, however, if these skills translate into improved reproductive success.

Helping experience may improve a helper's future reproductive success only in those species in which helpers, but not non-helpers, gain experience with particularly important skills. Nest-building may be one such skill. Female Seychelles warblers that help gain experience building nests that non-helpers do not (Komdeur 1996). Male long-tailed tits that help at successful nests learn the criteria for a good nest site. Male breeders that fail in their first attempt, and help at a successful nest, improve their choice of nest location in subsequent breeding attempts, whereas failed breeders who do not help show no such improvement (Hatchwell et al. 1999). Incubation and provisioning young apparently are skills that require little practice, whereas foraging is a skill critical to reproductive success that improves markedly with age in many species but is not linked to helping experience.

In red-cockaded woodpeckers, experiences gained by helpers but not floaters or solitary males are limited to incubating eggs and provisioning young. I previously tested the skills hypothesis in the red-cockaded woodpecker and found that first time breeders with one year of helping experience and first time breeders without helping experience have equal reproductive success (Khan and Walters 1997). I concluded that red-cockaded woodpeckers do not gain skills that enhance their future reproductive success as a result of helping experience and therefore that this benefit does not apply to this species.

Reciprocal exchange of helping

Helping may improve a helper's future reproductive success if reciprocal exchanges of helping occur between helpers and previous beneficiaries of the helper's assistance (Ligon and Ligon 1978; Wiley and Rabenold 1984). The reciprocity hypothesis predicts that nestlings and fledglings that receive aid will preferentially aid the individuals that raised them.

Increased reproductive success resulting from reciprocal exchange of helping has been demonstrated in the green woodhoopoe (*Phoeniculus purpureus*) and more recently has been suggested for the white-winged chough. Neither species seems to gain large indirect benefits by raising non-descendant kin because helpers are often unrelated to their beneficiaries. Green woodhoopoe breeders receive aid in acquiring territories and raising young from subordinate birds with whom they formed alliances when they were helpers (Ligon and Ligon 1978; Ligon and Ligon 1983). White-winged choughs require large groups to ensure reproductive success and they usually disperse in groups. Large groups raid small groups, resulting in kidnapping of fledglings that are incorporated into the group. It may be beneficial to nonbreeding helpers to recruit and establish special bonds with as many young as possible so that they may later aid the helper in dispersal and breeding (Heinsohn 1991).

The hypothesis that helpers gain future direct benefits from assistance by previous recipients of helping behavior has been rejected for most cooperatively breeding birds in which it has been studied. For example, pinyon jays (*Gymnorhinus cyanocephalus*) receive aid from beneficiaries only 1.1% of the time (Marzluff and Balda 1990). White-fronted bee-eater breeders who had been helpers for at least one year had no higher probability of being aided than breeders who had never helped (Emlen and Wrege 1989). This hypothesis also has been rejected for Arabian babblers (*Turdoides squamiceps*; Zahavi 1990), hoatzin (*Opisthocomus hoazin*; Strahl and Schmitz 1990), Mexican jays (*Aphelocoma ultramarina*; Brown 1987), and western bluebirds (Dickinson et al. 1996). In the latter species no birds were observed to subsequently assist those who helped raise them.

In the strictest sense, reciprocity requires that individual A perform a costly behavior for the benefit of individual B, and that in the future individual B return the favor with an equally costly behavior that benefits individual A (reciprocal altruism, Trivers 1971). Reciprocal altruism is not a stable behavioral strategy because individuals that do not reciprocate (cheaters who do not incur a cost) gain the greatest benefit. Reciprocal altruism has not been conclusively demonstrated in any cooperatively breeding bird to date, because all studies have failed to demonstrate that alloparental behavior incurs a fitness cost (Koenig 1988). Recently, however, a cost of helping has been demonstrated in the white-winged chough, in which one-year old helpers in small groups lose mass in proportion to the amount of time they spend incubating (Heinsohn and Legge 1999). How should one categorize the (1) cases in which reciprocal exchange has been documented (see above), but no cost of helping behavior demonstrated and (2) cases in which a breeder is not specifically aided by previous beneficiaries of their aid, but reliably receives aid from young nonbreeding birds, as has been described for the stripe-backed wren (Rabenold, 1985)? These instances may best be described as no-cost cooperation (*sensu* Dugatkin 1997; by-product mutualism, *sensu* West-Eberhard 1975; pseudo-reciprocity, *sensu* Connor 1986). No-cost cooperation occurs when cooperation provides immediate net benefits that outweigh the benefit of cheating (Dugatkin 1997). For example, demographics and patterns of kinship create a reliable association of young stripe-backed wrens whose best option is to participate as nonbreeding aid-givers with older breeders who offer indirect fitness rewards for helping (Wiley and Rabenold 1984).

Reciprocity is a rare future direct benefit of helping in most cooperatively breeding species. It is likely to be important only in species that exhibit low levels of relatedness between

helpers and the recipients of their aid and in species in which large group sizes are necessary to ensure successful reproduction. Neither condition applies to red-cockaded woodpeckers. In Chapter 3, I calculate the frequency of reciprocal exchanges of helping in three red-cockaded woodpecker populations to determine if helpers benefit when they become breeders from assistance from young they previously helped raise.

Increased future probability of breeding

Territory acquisition

The territory acquisition hypothesis states that recipients of a helper's assistance may increase the probability that the helper will breed in the future, by aiding the helper in acquiring a territory. This hypothesis predicts that (1) helpers augment group size and (2) the presence of subordinate helpers increases the probability that the dominant helper will acquire a territory.

A helper may acquire a territory in three ways, territorial budding, territorial inheritance and dispersal. I treat the first two mechanisms here and the last in the next section. Territorial budding was first described for the Florida scrub-jay by Woolfenden (1978). In this species, helpers augment group size, larger groups increase their territory size and eventually the dominant male helper acquires a small portion of the enlarged parental territory. This mechanism of acquiring a territory is common in the Florida scrub-jay: 38% of male helpers obtain breeding positions in this way (Woolfenden and Fitzpatrick 1990). Territorial budding has also been described in the hooded crow in which 60% of two year-year old birds obtained territories within the boundaries of the parental territory (*Corvus cornix*; Grabovsky 1986), Galapagos mockingbird (*Nesomimus parvulus*; Kinnaird and Grant 1982), brown treecreeper (*Climacteris picumnus*; Noske 1991), and hoatzin (Strahl and Schmitz 1990).

Territorial inheritance has been documented in virtually every cooperative breeder studied, for example, stripe-backed wrens (Rabenold 1985), jungle babblers (*Turdoides striatus*; Gaston 1978a), Mexican jays (Brown 1987), and Seychelle warblers (Komdeur 1992). It is not clear from any of these studies, however, that the probability of territory inheritance is a function of helping rather than an incidental by-product of delayed dispersal. Territory inheritance depends on breeder survival, not the actions of subordinate helpers.

I did not test the hypothesis that helping improves the future probability that male red-cockaded woodpeckers will become breeders through territorial budding because territorial budding is too rare in this species to result in a significant benefit. Budding occurs on only 0-2% of territories each year, and the annual probability of acquiring a breeding position through budding is only 1%, compared to 14% through dispersal and 15% through inheritance (Walters 1990).

Joint dispersal

The recipients of a helper's aid may disperse with the helper and assist it in competition for territories. This hypothesis predicts that (1) previous recipients of help form coalitions with their benefactors and (2) coalitions are more effective at acquiring territories than single individuals. This mechanism is expected to increase the future probability of breeding in cooperatively breeding species where breeding opportunities are limited by habitat constraints.

Joint dispersal was first described for the green woodhoopoe. Its role in this species and the white-winged chough were discussed above (See Reciprocity). In the green woodhoopoe, helpers disperse in coalitions with several younger, same-sex, subordinate birds that they helped raise. Older helpers who disperse in groups have a higher probability of obtaining territories and breeding positions than birds that disperse alone (Ligon and Ligon 1990). Helpers also gain substantial future direct benefits from joint dispersal and subsequent territory acquisition in the white-winged chough (see above), acorn woodpecker (Hannon et al. 1985; Koenig and Mumme 1987), and Arabian babbler (Zahavi 1990).

I did not test the hypothesis that alloparental behavior improves the future probability that red-cockaded woodpeckers will acquire a breeding position through joint dispersal because this phenomenon also is too rare to result in a significant benefit in this species. Joint dispersal has been observed only 12 times in 2600 group-years of observation. Therefore, this benefit, like territory acquisition through budding, can be eliminated for the red-cockaded woodpecker.

Access to mates

Helping may increase an individual's access to mates when mates are a limited resource. This hypothesis predicts a skewed adult sex ratio and an increased probability of helpers acquiring a mate compared to non-helpers. A helper may acquire a mate in two ways: (1) the helper mates with the opposite-sexed breeder or (2) the helper mates with opposite-sexed offspring that it helped raise.

This hypothesis was first described by Reyer (1984) to explain the occurrence of unrelated helpers in his study population of pied kingfishers. He demonstrated that secondary unrelated helpers gained substantial future direct benefits by mating with the breeding female in subsequent years. Secondary helpers gained the breeding position by replacing or displacing the breeding male.

The hypothesis that helping increases a helper's access to mates is also supported in the rifleman (*Acanthisitta chloris*) and bell miner. The rifleman is a small, hole nesting passerine that does not exhibit delayed dispersal, yet on 15% of the breeding territories unrelated auxiliary adults feed young at nests. The presence of helpers significantly decreased female mortality and male helpers often paired with female offspring from a nest at which they helped (Sherley 1990).

Bell miners are a highly social colonial species in which several breeding pairs occupy slightly overlapping home ranges that they share with nonbreeding offspring and immigrants.

Helpers provision young at several of the nests in their home range and widowed females preferentially pair with the unmated male helper that provisioned them the most (Clarke 1989).

It is unlikely that red-cockaded woodpeckers gain future direct benefits from an increased future probability of breeding through access to mates. Helping is unlikely to increase a red-cockaded woodpecker helper's access to mates because (1) red-cockaded woodpeckers are monogamous (Haig et al., 1994), (2) helpers are usually related to the breeding female in the group and (3) the breeding system is not characterized by a shortage of females. Therefore, I do not address this hypothesis.

1.4 Proximate explanations of delayed breeding and helping

In contrast to the many studies of cooperatively breeding species that have closely examined the evolutionary reasons for delayed breeding and alloparental behavior (Brown 1987; Koenig and Mumme 1990; Emlen 1991; Cockburn 1998), as yet there have been few physiological studies of proximate mechanisms underlying cooperative breeding behavior. Low concentrations of reproductive hormones appear to be the proximate bases of delayed breeding in mammalian (Creel et al. 1992; Roberts et al. 1996) and avian cooperatively breeding species (Reyer et al. 1986; Mays et al. 1991; Schmidt et al. 1991; Schoech et al. 1991, 1996a; Wingfield et al. 1991; Poiani and Fletcher 1994). Other studies suggest that prolactin plays a role in the proximate basis of alloparental behavior (Brown and Vleck 1998; Vleck et al. 1991; Schoech et al. 1996b).

Hormones of the hypothalamo-pituitary-gonadal axis are likely mediators of sexual inactivity and alloparental behavior in cooperatively breeding species. Evidence linking the gonadal steroid testosterone to sexual behavior implicates its role in the physiological bases of delayed breeding in males. Testosterone concentrations are strongly correlated with some reproductive behaviors in most avian species (Wingfield and Farner 1993). Examples include mate guarding in the male barn swallow (*Hirundo rustica*; Saino and Moller 1995) and frequency of epaulet exposure, sexual chases and aggressive encounters with other males in the red-winged blackbird (*Aegialius phoeniceus*; Johnsen 1998). Testosterone implants increase singing in male Lapland longspurs (*Calcarius lapponicus*; Hunt et al. 1997) and induce male-like singing in female European starlings (*Sturnus vulgaris*; Hausberger et al. 1995) and budgerigars (*Melopsittacus undulatus*; Nespor et al. 1996).

The physiological mechanism regulating helping may be mediated by the anterior pituitary protein hormone, prolactin. Growing evidence relating prolactin to the expression of parental behavior in mammals, birds and fish makes prolactin a likely regulator of alloparental behavior (reviewed in de Vlaming 1979; Buntin 1998). Circulating prolactin concentrations correlate with incubation, brooding and provisioning in avian species (Goldsmith 1990; Yves et al. 1994). In species with sex-role reversal in which males alone care for young, males exhibit prolactin levels similar to those of females of other species in which females are the primary care-givers (Oring et al. 1986a, b; Fivizzani et al. 1990). Administration of exogenous prolactin induces parental behavior in several species including domestic fowl (*Gallus domesticus*, Riddle

et al. 1935), turkey (*Meleagris gallapavo*; El Halawani et al. 1986; Youngren et al. 1991), and the ring dove (*Streptopelia risoria*; Buntin 1993).

1.4.1 Testosterone and delayed breeding

Four hypotheses have been proposed to explain the proximate control of delayed breeding of helpers in cooperatively breeding species: delayed maturation, physiological suppression, behavioral suppression and absence of stimulation. These hypotheses are not mutually exclusive and several may be operating in a particular species. First I review the reproductive endocrinology of males in monogamous breeding systems. Then, I will introduce the four hypotheses and describe the predictions about expected testosterone concentrations derived from each.

At the onset of the breeding season, triggered by increasing day-length after the winter solstice, the hypothalamus secretes gonadotropin releasing hormone (GnRH) which stimulates the anterior pituitary to secrete follicle stimulating hormone (FSH) and luteinizing hormone (LH), both which control the development of the avian testes. FSH acts on the Sertoli cells in the seminiferous tubules to promote the maturation of sperm, while LH induces the interstitial Leydig cells to synthesize and secrete testosterone. Complete gonadal development and expression of secondary sex characteristics correspond with maximum plasma concentrations of LH and testosterone (T). In monogamous birds with biparental care, FSH, LH and T decline during the parental phase of the breeding cycle. Late in the breeding season, males may become photo-refractory, meaning that they no longer respond to increasing photo-period. When males become photo-refractory, FSH, LH and sex steroid concentrations decline, and the gonads regress and become non-functional (reviewed in Wingfield and Farner 1993).

Delayed maturation

Helpers may be incapable of reproducing because they are sexually immature (delayed maturation; Reyer et al. 1986). As described above, most birds undergo annual recrudescence of the testes during the breeding season. During the nonbreeding season the regressed testes are non-functional and do not produce testosterone. In this season, male helpers and breeders are expected to exhibit similar testosterone concentrations because neither have functional gonads at this time. In contrast, during the breeding season, breeder testosterone concentrations are expected to be high, while reproductively immature male helpers are expected to exhibit testosterone concentrations similar to the nonbreeding season.

The delayed maturation hypothesis has not been supported by studies of cooperatively breeding species to date. Helpers often exhibit lower testosterone concentrations than breeders but young birds are capable of reproducing when given the opportunity. In the bell miner, some male helpers had low plasma concentrations of androgens, but had sperm producing gonads

(Poiani and Fletcher 1994). One-year-old breeders have been documented in the Florida scrub-jay (Schoech et al 1996a), Harris' hawk (Mays et al. 1991), and pied kingfisher (Reyer et al. 1986). Furthermore, helpers are not always young birds. In the Australian magpie, helpers may be either subadults that have androgen concentrations lower than breeders or they may be adults who have androgen concentrations identical to breeders (Schmidt et al. 1991).

Physiological suppression

Helpers may be physiologically incapable of reproducing because of poor body condition and/or high levels of stress (physiological suppression; Wingfield et al. 1991). Corticosterone secreted in response to stress inhibits an individual's reproductive physiology and behavior (Moore and Miller 1984; Moore and Zoeller 1985; Moore et al. 1991). According to this hypothesis helpers experience stress as a result of their interaction with dominant breeders. This hypothesis is different from that of delayed maturation because helpers are limited by their physical environment (e.g. nutritional, social) rather than by their ontogeny. The physiological suppression hypothesis predicts that helpers will exhibit (1) poor body condition (e. g. mass, fat deposits, molt indices), (2) lower plasma testosterone concentrations than breeders and (3) higher plasma corticosterone concentrations than breeders.

The physiological suppression hypothesis has not been supported by previous studies of cooperatively breeding birds either. Baseline concentrations of corticosterone did not differ between breeders and nonbreeders in the Florida scrub-jay (Schoech et al. 1997), white-browed sparrow weaver (Wingfield et al. 1991) or Harris' hawk (Mays et al. 1991). These results may be explained by the stability of the social hierarchy in cooperatively breeding species. Subordinate birds sampled in newly formed groups exhibit high plasma corticosterone concentrations, but this pattern disappears once the hierarchy becomes established, despite continued aggression between group members (Siegel 1980; Mench and Ottinger 1991).

Behavioral suppression

Helpers may be capable of reproducing, but are prevented from reproducing because of behavioral interactions with other group members (behavioral suppression; Brown 1978; Mumme et al. 1983; Emlen and Wrege 1988). If helpers are capable of reproducing and are prevented from doing so only by behavioral interactions, there will be no differences between testosterone concentrations of male helpers and male breeders. Possible means of behavioral suppression include mate-guarding by the breeding male and/or lack of receptivity by the breeding female. That male helpers will attempt to mate with the breeding female is one prediction that distinguishes the behavioral suppression hypothesis from other hypotheses to explain delayed breeding.

Behavioral suppression has been suggested to explain lack of breeding by male helpers unrelated to the breeding female in the pied kingfisher and the Harris' hawk. In the pied kingfisher, helper males that are unrelated to the breeding female are chased out of the nesting

area by male breeders during the egg-laying period when the breeding female is fertile (Reyer et al. 1986). In the Harris' hawk, adult helper males that attempt to copulate with the alpha female have little success, suggesting that breeding females are unreceptive to copulation attempts by subordinate males (Mays et al. 1991).

Absence of stimulation

Delayed breeding by helpers may be caused by the absence of appropriate stimulation (Reyer et al. 1986; Schoech et al. 1996a). Social stimuli, such as interactions with a mate, are often important in synchronizing, stimulating and integrating reproductive physiology and behavior (Wingfield and Farner 1993). Male helpers may not acquire fully functioning testes if they do not receive appropriate social stimuli from their interactions with females. This hypothesis cannot be easily distinguished from the delayed maturation or physiological suppression hypotheses by measuring plasma testosterone concentrations because all three hypotheses predict low testosterone concentrations in helpers.

The absence of stimulation hypothesis has been examined experimentally by manipulating endogenous testosterone concentrations of nonbreeding males and the estradiol concentrations of nonbreeding females in the Florida scrub-jay (Schoech et al. 1996a). Male non-breeders exposed to estradiol-enhanced females exhibited higher plasma testosterone concentrations than did control males. Analogous results were obtained for female nonbreeders in the presence of testosterone-enhanced males. These results clearly suggest that one of the reasons these nonbreeding Florida scrub-jays do not attain full breeding condition is because they are not exposed to the necessary stimuli.

In Chapter 4, I investigate the hormonal correlates of delayed breeding in the red-cockaded woodpecker by comparing plasma testosterone concentrations of male helpers to those of male breeders. These data combined with behavioral data from the literature, are used to determine which of the four proximate mechanisms just described best explains delayed breeding in the red-cockaded woodpecker. The relatedness of the helper to the breeder of the opposite sex has been shown to influence the testosterone concentration of helpers in other species (pied kingfisher, Reyer et al. 1986; Harris' hawk, Mays et al. 1991). These results indicate that the proximate bases of delayed breeding may differ among helpers. To assess the importance of helper relatedness to the breeding female, I compared plasma testosterone concentrations of helpers that were unrelated to the breeding female to those of helpers related to her.

1.4.2 Prolactin, parental behavior and alloparental behavior

A relationship between prolactin and parental behavior is widely accepted (reviews in Buntin 1986; Ball 1990; Goldsmith 1990). Because prolactin mediates parental behavior, and in some species parental and alloparental behavior are functionally identical, prolactin is likely to mediate alloparental behavior as well. Two of the most common alloparental behaviors are incubating eggs and feeding nestlings. Here I describe the seasonal pattern of prolactin secretion

in avian species and the experimental and correlative evidence that demonstrates the role of prolactin in incubation and nestling provisioning behavior. Finally, I discuss how examining the physiological bases of alloparental behavior may provide evidence that it is an adaptive trait, modified from parental behavior and maintained by natural selection.

Prolactin is a protein hormone secreted by the anterior pituitary. In most species, the initial seasonal increase of plasma prolactin concentration during the breeding season is caused by increasing photo-period (Goldsmith and Hall 1980; Ebling et al. 1982; Boswell et al. 1995). During the breeding season in most species, female plasma prolactin concentrations reach a maximum during egg-laying and incubation, and males exhibit a similar pattern (Wingfield and Farner 1993). As the breeding season progresses, plasma prolactin concentration and the expression of parental behavior decline concomitantly, but the timing of the decline is variable. The decline of prolactin may be endogenously timed, such that it declines after a set period of time, as in the *Diomedea* albatrosses (Hector and Goldsmith 1982), pied flycatcher (Silverin and Goldsmith 1984), and king penguin (Garcia et al. 1996).

That prolactin secretion is affected by non-photic stimuli is demonstrated by prolactin concentration declining in response to an anesthetized brood patch or the absence of eggs (Goldsmith 1983). Incubating domestic hens placed in physical contact with chicks increased their brooding activities, deserted their nests and experienced a decline in prolactin concentrations. Hens that were only exposed to visual or auditory stimuli did not abandon their nests, suggesting that the tactile stimulus of brooding chicks is partially responsible for the decline of prolactin in the domestic hen (Richard-Yris et al. 1998).

Experimental evidence indicates that prolactin mediates incubation behavior. Prolactin administered directly to the brain of turkey hens induced and maintained incubation (El Halawani et al. 1986; Youngren et al. 1991). Prolactin implants increased the amount of anti-predator behavior exhibited by willow ptarmigan (*Lagopus l. lagopus*) around their offspring (Pedersen 1989).

Correlative studies show that prolactin levels correspond to the amount of incubation performed. Female prolactin concentrations are several times higher than those of males in species where females exclusively incubate, such as the cooperatively breeding Florida scrub-jay (Schoech et al. 1996b) and Harris' hawk (Vleck et al. 1991) and the non-cooperatively breeding white-crowned sparrow (*Zonotrichia leucophrys*, Hiatt et al. 1987), dark-eyed junco (*Junco hyemalis*; Ketterson et al. 1990), gentoo penguin (*Pysoscelis papua*; Mauget et al. 1995), and cockatiel (*Nymphicus hollandicus*; Myers et al. 1989). In species exhibiting sex-role reversal in which males are the exclusive incubators, males have higher prolactin concentrations than females, as in the red-necked phalarope (*Phalaropus lobatus*, Gratto-Trevor et al. 1990), and Wilson's phalarope (*Phalaropus tricolor*; Oring et al. 1988). Males and females have equivalent prolactin concentrations in species with equal incubation by the sexes, such as the black swan (*Cygnus atratus*; Goldsmith 1982), three species of *Diomedea* albatrosses (Hector and Goldsmith 1985), Cape gannet (*Sula capensis*; Hall 1986), and the semipalmated sandpiper (*Caladris pusilla*; Gratto-Trevor et al. 1990).

Feeding behavior (hyperphagia), parental provisioning and helper provisioning of

nestlings may all be mediated by prolactin. Hyperphagia increases when prolactin is administered intra-cranially in the ring dove (Hnasko and Buntin 1993). Direct effects of prolactin on parental feeding behavior have been demonstrated in the ring dove, in which increasing prolactin results in crop sac formation and crop-milk production (Cheng 1979; Goldsmith et al. 1981; Buntin and Tesch 1985) and nonbreeding adults injected intra-cranially with prolactin were observed feeding 7-day old foster squabs (Buntin et al. 1991). Evidence linking prolactin and parental feeding behavior is less clear in correlative studies in other species. Prolactin concentrations and contributions to nestling provisioning did not exhibit a one to one relationship among breeding Florida scrub-jays (Schoech et al. 1996b) or female dark-eyed juncos (Ketterson et al. 1990). Correlative studies indicate that alloparental feeding behavior may be mediated by prolactin. Feeding scores positively correlated with high prolactin concentration in Florida scrub-jay helpers (Schoech et al. 1996b). Prolactin concentrations rose significantly in Harris' Hawk adult male helpers during the nestling stage, the same time at which these helpers provide more food for nestlings than do breeders (Vleck et al. 1991).

The relationship between prolactin, external stimuli and parental behavior is not straightforward (Buntin 1996). Evidence linking prolactin with stimuli from eggs and incubation behavior is fairly strong. However the link between prolactin and nestling feeding behavior in species that do not produce crop-milk is less clear. Our current knowledge suggests that the relationship between prolactin, external stimuli and parental behavior is best described in terms of positive feedback loops and not cause and effect. For example, high prolactin concentration during the breeding season may increase the probability of an individual expressing parental behavior, and the additional stimulus of eggs/nestlings may cause further elevation of plasma prolactin concentration.

Examining the physiological bases of alloparental behavior may resolve the controversy of whether helping is a non-adaptive trait that is maintained as a by-product of selection on parental behavior (Jamieson and Craig 1987; Jamieson 1989) or is an adaptive trait maintained by fitness benefits (Emlen et al. 1991a). The non-adaptive hypothesis states that helping is misplaced parental behavior triggered by the stimulus of eggs or begging young in the nest (Jamieson 1989). Therefore, the non-adaptive hypothesis predicts that the physiological bases of alloparental behavior will be identical to that of parental behavior. The adaptive hypothesis proposes that the physiological mechanisms underlying parental and alloparental behavior initially were identical. However, as natural selection maintains the expression of alloparental behavior, the rise in prolactin associated with alloparental behavior may uncouple from the previous rise in prolactin associated with other breeding cycle behaviors, such as nest building and incubation. In these cases, the physiological bases of alloparental behavior will have diverged from that of parental behavior. In sum, the adaptive hypothesis predicts that the physiological bases of alloparental behavior may or may not be identical to that of parental behavior. Therefore, support for the adaptive hypothesis must be drawn from both physiological and fitness benefit studies.

Results from studies of the physiological bases of helping in three cooperatively breeding species suggest that alloparental behavior has differentiated from parental behavior and hence is adaptive. In the Florida scrub-jay, the pattern of prolactin secretion in nonbreeding helpers is similar to that of breeders, with prolactin concentrations increasing in helpers prior to their

contact with nest stimuli. Therefore, helpers, like breeders, are hormonally primed to perform parental-like behavior. Interestingly, a correlation between prolactin and feeding rate was evident among nonbreeders, but not among breeders. These results suggest that although the physiological bases of helping is similar to parental behavior, it has been modified so that prolactin concentration and the expression of feeding behavior are more tightly linked in Florida scrub-jay helpers than breeders.

Further support for the adaptive hypothesis is provided by the Harris' hawk, in which nonbreeding adult males exhibited increasing prolactin concentrations after the eggs hatch, while breeder prolactin concentrations declines (Vleck et al. 1991). It is at this time that male nonbreeders begin to express alloparental behavior, by provisioning nestlings. This observation suggests that the elevation in prolactin associated with care of young by adult male helpers can be uncoupled from the earlier prolactin elevation associated with nest building and incubation in breeders. The temporal difference in prolactin concentration in the Harris' hawk helpers suggests that the rise in prolactin functions to facilitate provisioning of nestlings and fledglings in Harris' hawk helpers, which differs from the mechanism maintaining parental behavior in breeders.

Recently, a comparative study showed that the relative prolactin concentration in the cooperatively breeding Mexican jay were higher than those of the non-cooperatively breeding western scrub-jay (*Aphelocoma californicus*; Brown and Vleck 1998). It is likely that this difference is related to the expression of alloparental behavior by Mexican jays and not phylogenetic history or environment, because the two species are congeneric and sympatric. Brown and Vleck (1998) propose that selection favoring helping by nonbreeders has elevated prolactin concentrations in the species as a whole.

In Chapter 4, I examine the seasonal pattern of plasma prolactin concentrations in female breeder, male breeder and male helper red-cockaded woodpeckers. I also examine whether prolactin concentrations correlate with photoperiod, the number of eggs/nestlings, nestling age and feeding rate to determine if external stimuli mediate prolactin secretion in this species. Finally, I discuss my findings in the context of the controversy over whether helping behavior is an adaptive or non-adaptive trait.

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Table 1.1: Adaptive hypotheses to explain the evolution of cooperative breeding adapted from Emlen and Wrege 1989 .

BENEFIT	HYPOTHESIS	SOURCE
1.3.1 Current Indirect Benefit		
<i>Increased inclusive fitness</i>	Helper increases the survival probability of the recipient nestlings.	Hamilton 1964a; b
1.3.2 Future Indirect Benefit		
<i>Increased inclusive fitness</i>	Helper increases the annual survival probability of the breeder by (1) group size effects and/or (2) reducing breeder workload, thereby increasing the probability of the breeder producing young in subsequent years.	Mumme et al. 1989
1.3.3 Future Direct Benefit		
<i>Improved probability of surviving to breed</i>	Helpers increase group size by increasing the production of young. Helpers enjoy improved survival through group size effects, such as, increased foraging efficiency and enhanced predator detection.	Brown 1987 Stacey and Ligon 1987
	Breeder demands help in return for tolerance of helper, who gains access to critical resources (pay-to-stay hypothesis).	Gaston 1978b
<i>Increased future reproductive success</i>	Helping experience increases reproductive success when the helper becomes a breeder (skills hypothesis).	Brown 1987
	Original recipients of help may assist the helper once he attains breeding status (reciprocity hypothesis).	Ligon and Ligon 1978 ; Wiley and Rabenold 1984
<i>Increased future probability of breeding</i>	Original recipients of helper may assist helper in acquiring a breeding position through territorial budding.	Woolfenden and Fitzpatrick 1978
	Original recipients of help may disperse with helper and assist in competition for a territory.	Ligon and Ligon 1978
	Helping may increase an individual's access to mates by (1) mating with the breeder of the opposite sex or (2) breeding with the resident female when the breeder dies.	Reyer 1980

Table 1.2: Studies that have measured helper effects on breeder reproductive success.

Species	Increased production of fledglings	Source
White-fronted bee-eaters	0.17 to 0.25 offspring equivalents	Emlen and Wrege 1991
Acorn woodpecker ^a	0.18 offspring equivalents ^a	Koenig and Stacey 1990
Stripe-backed wren	0.20 offspring equivalents	Rabenold et al. 1990
Bell miner	0.38 more fledglings ^b	Clarke 1989
Red-cockaded woodpecker ^a	0.39 fledglings/helper	Heppell et al. 1994
Toucan barbet	0.6 fledglings/nest	Restrepo and Mondragon 1998
Pied kingfisher	0.65 offspring equivalents over two years	Reyer 1990
Seychelles warbler	0.78 fledglings/year	Komdeur 1994
Bicolored wren	0.86 fledglings/nest	Austad and Rabenold 1985
Galapagos mockingbird	0.90 fledglings/nest	Kinnaird and Grant 1982
White-throated magpie jay	0.98 offspring/helper	Langen and Vehrencamp 1999
Florida scrub-jay ^a	1.06 fledglings/nest	Mumme 1992
Western bluebird	1.12 fledglings/nest	Dickinson et al. 1996
Chestnut-bellied starling	1.15 fledglings/nest	Wilkinson 1982
Brown treecreeper	1.56 fledglings/nest	Noske 1991
Galapagos hawk	2X more fledglings per year	Faaborg and Bednarz 1990
Hoatzin	Number of fledglings increase with increasing group size	Strahl and Schmitz 1990
White-browed sparrow weaver	Number of fledglings increases with increasing group size	Lewis 1982
Arabian babbler	Brood size increases linearly with group size	Wright 1998
Grey-capped social weavers	Improved nestling survival	Bennun 1994
Small Green bee-eater	Increased	Sridhar and Karanth 1993
White-winged chough	Nests more likely to succeed	Heinsohn 1991
Noisy miners	Nests more likely to succeed with helpers	Dow and Whitmore 1990
Greater rhea	No effect	Condenotti and Alvarez 1997
Green woodhoopoe	No effect	Du Plessis 1991
Harris' hawks	No effect	Bednarz 1987
Jungle babbler	No effect	Gaston 1978a
Pinyon jay	No effect	Marzluff and Balda 1990
Pygmy nuthatch	No effect	Sydeman 1991
Riflemen	No effect	Sherley 1990
Splendid fairy-wren	No effect	Rowley and Russell 1997
White-browed scrub-wren	No effect	Magrath and Yezerinac 1997

^a Offspring equivalents are the units of indirect fitness that a helper gains by improving the reproductive success of breeders, devalued by the helper's coefficient of relatedness to the offspring.

^b Mean difference in the number of offspring produced by pairs with helpers and pairs without helpers.

Table 1.3: Evidence that helpers are closely related to the recipients of their aid.

Species	Helpers related to breeding pair	
Acorn woodpecker ^a	Protein electrophoresis	Mumme et al. 1985
Arabian babbler	Helpers are offspring of breeders.	Wright 1998
Bell miner	DNA fingerprinting	Conrad et al. 1998
Florida scrub-jay ^a	DNA fingerprinting	Quinn et al. 1999
Galapagos mockingbird	Preferentially aid close kin	Curry 1988
Grey-capped social weavers	Preferentially aid close kin	Bennun 1994
Noisy miners	DNA fingerprinting	Poldmaa et al. 1995
Pied kingfisher	Primary helpers are offspring of breeders	Reyer 1980
Red-cockaded woodpecker ^a	DNA fingerprinting	Haig et al. 1994
Seychelles warbler	Helpers are offspring of breeders	Komdeur 1994
Toucan barbet	Helpers are offspring of breeders	Restrepo and Mondragon 1998
Western bluebird	Helpers are offspring of breeders	Dickinson et al. 1996
White-fronted bee-eater	Preferentially aid close kin	Emlen and Wrege 1988
White-throated magpie jay	Helpers are offspring of breeders	Langen 1996
White-winged chough	Helpers are offspring of breeders	Heinsohn et al. 1987

^a Territory quality, breeder age and experience controlled

Table 1.4: Results of studies that have analyzed total feeding rates and individual feeding contributions in group with and without helpers.

	Total provisioning	Breeder workload	Breeder survivorship		Source
			Males	Females	
Acorn woodpecker	Increased	No effect	Increased	No effect	Mumme and de Querioz 1985; Koenig and Mumme 1987
Bell miner	Increased	N/A	N/A	N/A	Clarke 1984
Grey-capped social weaver	Increased	No effect	N/A	N/A	Bennun 1994
Pygmy nuthatch	No effect	N/A	N/A	N/A	Sydeman 1991
Pied kingfisher	Increased ^b	Females reduce	No effect	Increased	Reyer 1984
Splendid fairy-wren	No effect	Females reduce	No effect	Increased	Rowley and Russell 1990
					Russell and Rowley 1988
White-browed sparrow weaver	Increased	Females reduce	No effect	Increased	Lewis 1982
Galapagos mockingbird	Increased	Males reduce	No effect	No effect ^c	Kinnaird and Grant 1982
Rifleman	No effect	Males reduce	No effect	Increased	Sherley 1990
White-fronted bee-eater	Increased	No effect	No effect	No effect	Emlen and Wrege 1989
					Emlen and Wrege 1991
Chestnut-bellied starling	Increased	N/A	N/A	N/A	Wilkinson and Brown 1984
Florida scrub-jay ^a	Increased	No effect	No effect	No effect ^d	McGowan and Woolfenden 1990; Mumme 1992
Small green bee-eater	Increased	No effect	N/A	N/A	Sridhar and Karanth 1993
Arabian babblers	Increased	Breeders reduce	N/A	N/A	Wright 1997
Bushtit	N/A	Breeders reduce	N/A	N/A	Sloane 1996
Greater rheas	N/A	Breeders reduce	N/A	N/A	Condenotti and Alvarez 1997
Green woodhoopoe	No effect	Breeders reduce	N/A	N/A	Du Plessis 1991
Grey-crowned babbler	No effect	Breeders reduce	N/A	N/A	Brown et al. 1978
Purple gallinule	Increased	Breeders reduce	N/A	N/A	Hunter 1987
Western bluebird	Increased	Breeders reduce	No effect	No effect	Dickinson et al. 1996
Toucan barbet	No effect	N/A	N/A	N/A	Restrepo and Mondragon 1998
Bicolored wren	No effect	Reduced, esp. female	Increased	Increased	Austad and Rabenold 1985
					Rabenold 1990
White-throated magpie jay	N/A	Breeders reduce	N/A	N/A	Langen and Vehrencamp 1998
Stripe-backed wren	No effect	Reduced, esp. male	No effect	No effect	Rabenold 1984

N/A No data available

^a Experimental removal by non-breeders

^b Helpers have an effect on feeding rates at Lake Victoria but not at Lake Naivasha, indicating that breeders adjust their effort according to need.

^c Curry and Grant (1990) demonstrate that female survival increased from 59% to 83% in one-year, but the average increase in survival (59% unaided versus 63% aided) was not significant over the five year study.

^d Breeder survival in groups with non-breeders removed (96.8%) was not different from controls groups in which non-breeders were present (95.2%; Mumme 1992).

Table 1.5: Results from studies that have examined enhanced helper survivorship as a function of group size.

Species	Survival	Source
Acorn woodpecker ^a	No effect	Koenig and Mumme 1987
Bicolored wren	No effect	Rabenold 1990
Florida scrub-jay	Increased	Woolfenden and Fitzpatrick 1984
Pinyon jay	No effect	Marzluff and Balda 1992
Red-cockaded woodpecker ^a	Decreased	Khan, see Chapter 2
Splendid fairy-wren	Increased	Rowley and Russell 1990
Stripe-backed wren	Increased ^b	Rabenold 1985
White-fronted bee-eater ^a	No effect	Emlen and Wrege 1989

^a Territory quality controlled

^b Female helpers only

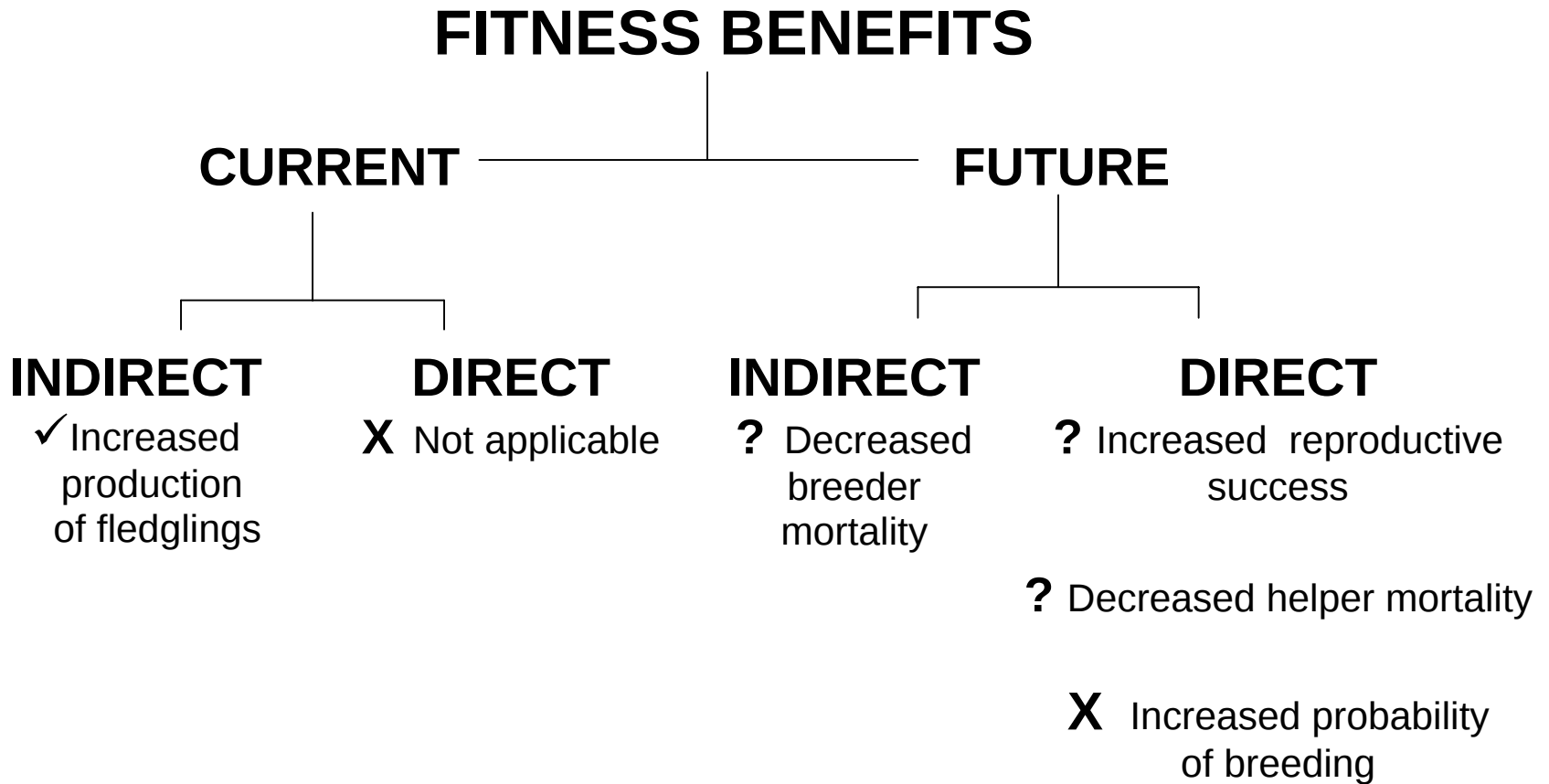


Fig. 1.1: Flow chart summarizing hypotheses to explain the evolution and maintenance of helping behavior in the red-cockaded woodpecker that have previously been demonstrated (✓) , have not been examined (?), or are not applicable to this study species (X).

Chapter 2

Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*).

Abstract

Helpers may gain future indirect fitness benefits by increasing the survival of breeders who produce offspring related to the helper. Helping may augment group size, through the helper's presence and by increasing the production of fledglings. Breeders may then experience enhanced survivorship because of the benefits of living in large groups. Helping may also reduce the workload of the breeder, which in turn may increase the likelihood that the breeder will survive to breed again. We used Cox's proportional hazards model to examine whether breeders' survival in the red-cockaded woodpecker (*Picoides borealis*) was enhanced when group size is increased because of the presence of (1) the helper itself or (2) 'extra' fledglings. We found that the presence of helpers reduces the risk of a breeder dying by 21%-42% for males and 14% for female breeders in the Sandhills. The presence of 'extra' fledglings reduces the risk of a breeder dying by 16%-42% in males and by 26%-43% in females. Furthermore, breeders reduce their workload in the presence of a helper by decreasing time spent incubating and provisioning nestlings. These results are consistent with the hypothesis that helpers gain future indirect benefits by reducing breeder mortality.

Key words red-cockaded woodpecker, *Picoides borealis*, cooperative breeding, breeder survival

Red-cockaded woodpeckers (*Picoides borealis*) occur in groups that consist of a pair of breeders and 0-4 non-breeding adult helpers (Ligon 1970; Lennartz et al. 1987; Walters et al. 1988; Walters 1990; Haig et al. 1994). Not all breeding groups have helpers and most groups that do have only a single helper (Walters et al. 1992). Helpers are usually previous male offspring of either the breeding male or both breeders, but helpers sometimes assist older siblings or other male relatives that have inherited the natal territory and occasionally aid unrelated breeders. Helpers participate in territory defense, constructing and maintaining nest and roost cavities, incubating eggs, feeding and brooding nestlings, removing fecal sacs from the nest cavity and feeding fledglings. Helpers acquire breeding status either through inheritance of the natal territory or by filling neighboring breeding vacancies (Walters et al. 1988).

Historically, helping behavior has posed an evolutionary paradox, because helpers seem to enhance the fitness of other individuals at their own expense. This paradox is addressed by considering how helping behavior might enhance a helper's own fitness. Helpers may gain indirect fitness benefits if they increase the production of non-descendent kin (Hamilton 1964). Indirect fitness benefits may be gained during the current breeding season if a helper increases the production of offspring by related breeders, or in future breeding seasons, if a helper increases the probability that related breeders will survive to reproduce again (Mumme et al. 1989). Previous work has shown that red-cockaded woodpecker helpers gain current indirect fitness benefits by improving the reproductive success of the breeding pair (Heppell et al. 1994), to which they usually are related (Haig et al. 1993; 1994). Here, we test the hypothesis that helpers gain future indirect fitness benefits by enhancing the survival of related breeders.

Two mechanisms for enhanced breeder survival have been proposed, decreased breeder workload (Brown 1974, 1978; Ricklefs 1975; Brown et al. 1978, Ligon and Ligon 1978) and benefits of group living. Breeders may profit in several ways if they expend less effort on current reproduction in the presence of a helper. Helpers will receive fitness benefits if breeders whose workload is reduced are more likely to survive to breed again or produce more offspring in subsequent years. We sampled incubation and nestling provisioning of pairs with and without a helper to determine if breeders incubated and fed nestlings less when assisted by a helper.

Breeders may experience enhanced survivorship because of the benefits of group living, such as decreased predation and increased foraging efficiency (Pulliam and Caraco 1984). The helper increases the group's size both by their own presence and by augmenting the number of fledglings produced by the breeding pair. To test for this possibility we examined the survival of breeders as a function of group size. Territory quality may confound analyses of mortality as a function of group size, if group size correlates with the quality of the site. We present three analyses of the data, to demonstrate and control for the effects of territory quality on survival in the red-cockaded woodpecker.

METHODS

Study areas

Red-cockaded woodpeckers are endemic to pine forests of the southeastern US. The study population of red-cockaded woodpeckers is located in the Sandhills region of south-central North Carolina, occupying the Fort Bragg Military Reservation, the Sandhills Gamelands and the resort towns of Southern Pines and Pinehurst. The Sandhills study area is dominated by second-growth longleaf pine (*Pinus palustris*) with scattered old-growth trees, a midstory of oaks (*Quercus spp.*) and a diverse ground cover dominated by wire grass (*Aristida stricta*). Riparian zones contain dense stands of deciduous and evergreen shrubs and pond pine (*P. serotina*) in the overstory. Loblolly pine (*P. taeda*) occurs as second growth on some old field sites. Red-cockaded woodpecker cavities are primarily in longleaf pine, but occasionally occur in loblolly and pond pine. Detailed descriptions of the study area are provided in Carter et al. (1983) and Walters et al. (1988).

The Coastal Plain study area, located along the southeastern coast of North Carolina, includes Camp LeJeune Marine Base and Croatan National Forest. Camp LeJeune encompasses 34,425 ha and consists of high pocosin wetlands, pond pine woodlands, pine savannas and wet and mesic pine flatwoods (Schafale and Weakley 1990). Both longleaf and loblolly pine occur in the savannas and flatwoods. Within the 63,907 ha of Croatan National Forest, red-cockaded woodpeckers are concentrated in pine flatwoods and pine/scrub oak communities in both longleaf and loblolly pine (Walters et al. 1995). Much of Croatan National Forest is comprised of high and low pocosin wetlands that are not used as nesting habitat.

Demographic data

Demographic data were collected for 17 years (1980-1997) from the Sandhills population, and 10 years from Camp LeJeune and Croatan National Forest, respectively. The western half of the Sandhills population (approximately 220 groups on 110,000 ha) and the entire Coastal Plain population (approximately 100 groups) were completely marked and monitored. A complete description of monitoring methods can be found in Walters et al. (1988). Briefly, censuses were conducted annually during the breeding season to identify all members of each group of red-cockaded woodpeckers. Annual survival was estimated by the proportion of birds identified in the annual census that were not seen in subsequent censuses (Walters et al. 1988). Censuses were conducted once a year, so detailed analyses of the timing of death (during the breeding season, after the breeding season) were not possible.

During each breeding season censuses, all unbanded immigrants and nestlings were marked with a uniquely numbered aluminum USFWS band and a unique color band combination. Adults were identified during repeated visits to each occupied territory. If a bird's identity was uncertain, the group was followed or the bird was captured to verify its identification. Walters et al. (1988) estimated that 94% of the birds were censused each year. The status (e.g. helper, breeder, floater) of each individual was determined based on several

criteria which are described in detail in Walters et al. (1988). The breeding system is monogamous, even in groups with unrelated male helpers (Haig et al. 1994). Most females and many male fledglings disperse and search for a breeding vacancy. Some of these individuals become breeders, and other become floaters. Some males and a few females remain on the natal territory as helpers at age one. They may remain as helpers for 1-7 years, until they disperse or inherit breeding status on the natal territory (Walters et al. 1992).

Reproduction was monitored by visiting the cavity trees of each group every 9-14 days during the breeding season, which begins in April and ends in mid-July. Nestlings are altricial and were banded between 6-10 days after hatch. Fledging occurs 26-29 days after hatch and fledglings were identified by following groups after the projected fledgling date. Fledglings were sexed by the presence (male) or absence (female) of a red crown patch. Pairs normally produce only one brood a year, but will re-nest if nest failure occurs early in the breeding season (Jackson 1994).

Traditional analysis of mortality: Logistic regression

We used logistic regression (PROC LOGISTIC, SAS 6.12) to examine mortality as a function of group size. We include this analysis for comparative purposes, both with the numerous other studies that have used logistic regression examine mortality and our own analyses using Cox's proportional hazards model (see below). We used the following model:

$$\text{logit (probability of breeder dying)} = \beta_0 + \beta_1 \text{ ADULTS} + \beta_2 \text{ FLEDGLINGS}$$

where, β_0 represents that log odds risk of death for a breeder with a standard set of independent variables, and β_1 represents the fraction by which the risk of death increases for every unit change in the independent variable, ADULTS, measured as the number of adults in the group the year the breeder died, and β_2 represents the fraction by which the risk of death increases for every unit change in the variable, FLEDGLINGS, measured as the number of fledglings in the group the year the breeder died. We did not control for either territory quality or breeder age in this model.

We controlled for age-dependent mortality using a second model,

$$\text{logit (probability of breeder dying)} = \beta_0 + \beta_1 \text{ ADULTS} + \beta_2 \text{ FLEDGLINGS} + \beta_3 \text{ AGE}$$

that included a third term, β_3 , which represents the fraction by which a breeder's risk of death increases for every unit change in the AGE of the breeder in the year it died.

Analyses without controlling for territory quality

We analyzed breeder survival, in terms of life-span of an individual, using PROC PHREG (SAS 6.12). The PHREG procedure is a semi-parametric method that uses Cox's

proportional odds model to estimate how particular variables influence the survival time of a subject. Although these methods are called survival analyses, the model actually estimates rates of death or hazards. The model is expressed as follows:

$$\log h_i(t) = \alpha(t) + \beta_1 \text{ADULTS} + \beta_2 \text{FLEDGLINGS}$$

where the log hazard function (h) for individual i at time t (measured as an individual's age at death, or life-span) is a function of the baseline hazard function, $\alpha(t)$, and the independent variables ADULTS and FLEDGLINGS. The baseline hazard function ($\alpha(t)$) is left unspecified in PHREG. The regression coefficients, β_1 and β_2 , reflect the degree to which each variable in the model increases the probability of mortality before a given time. We used two measures of group size the year the breeder died to discriminate between the effect of the presence of the helper(s) itself and the helper's augmentation of group size through the production of fledglings.

We included only birds of known age in the analysis. The last year of observation was 1997, so all breeders observed in 1997 were labeled as censored (not dead by the end of the study period). Breeders not observed in 1997 were presumed dead. Male breeders rarely disperse (Walters et al. 1988, Daniels 1997), so presuming they were dead rather than having dispersed is reasonable. About 10% of breeding females disperse per year, but most move only short distances (Daniels and Walters in press), and thus would not leave the study area (Walters et al. 1988). We assumed that the few instances of undetected dispersal of breeding females out of the study area was independent of group size.

We modeled ties in the data using the DISCRETE option, which assumes that when two or more events appear to happen simultaneously, there is no underlying order. This assumption is reasonable because our census methods are discrete; the age of death for an individual can only be an integer value expressed in years. The odds that individual i dies at time t is $O_{it} = P_{it} / (1 - P_{it})$, where P_{it} is the conditional probability that individual i dies at time t , given that individual i has not died already. The model assumes that the ratio of the odds for any two individuals O_{it}/O_{jt} does not depend on time. The DISCRETE option for ties in PHREG estimates regression coefficients using methods of partial likelihood. PROC PHREG uses the Wald statistic, which has a χ^2 distribution, to determine if estimated regression coefficients are significantly different from zero. Details for calculating the Wald statistic are presented in Allison (1995). PHREG calculates a hazard ratio which is the ratio of the rate of death when a single variable is increased by a single unit ($x + 1$), to the rate of death when the variable is equal to x , holding all other variables constant. The hazard ratio is more easily interpreted by calculating the percent change in the rate of death ($\% \Delta = (\text{hazard ratio} - 1) * 100$). When $\% \Delta$ is negative, a one unit increase in a single variable, holding all other variables constant, results in a $\% \Delta$ decrease in the rate of death.

We assessed model fit by using the likelihood ratio to determine if the alternative model containing k regression coefficients ($\beta_1, \dots, \beta_k$, likelihood = l_k) explains the observed data more accurately than the null model, in which no variable influences survivorship ($\beta_1, \dots, \beta_k = 0$; likelihood = l_0). Under the hypothesis of no difference between the two models, the likelihood ratio (l_0/l_k) has a χ^2 distribution with degrees of freedom $df = k$ (Allison 1995).

Analyses controlling for territory quality

To control for territory quality, we included an extra term in our survival analysis model:

$$\log h_i(t) = \alpha(t) + \beta_1 D_{\text{adults}} + \beta_2 D_{\text{fledge}} + \beta_3 T_{\text{avg}}$$

where the life-span of an individual was a function of the baseline hazard function, the number of adults on the territory relative to the territory average (D_{adults}), the number of fledglings relative to the territory average (D_{fledge}) and an index of territory quality (T_{avg}), the average group size on a territory over the time period that the territory has been in the monitoring study, including the year the breeder died. D_{adults} was calculated as the difference between the number of adults (i.e. breeding pair and helpers) residing on the territory in the year a breeder died and the mean number of adults on the territory over the entire study period. D_{fledge} was calculated as the difference between the number of fledglings residing on the territory in the year a breeder died and the mean number of fledglings produced per year on the territory for the entire study period. Our index of territory quality, and representation of group size as deviations from the territory average, was justified because group size, habitat quality measures (Walters and Daniels, unpublished data) and fledgling production are highly correlated (Walters 1990).

Breeder workload

We conducted one-hour nest watches in the morning (0600-1200) and afternoon (1201-1800) to determine incubation effort of 8 unassisted pairs and of 5 pairs with one male helper in the Sandhills during the 1996 breeding season. We measured incubation effort as the proportion of the observation period during which the nest was incubated.

In 1994, we observed each nest for 1.5 hours to measure the nestling provisioning behavior of 6 pairs assisted by a helper. In 1996, we conducted 2.0 hour observations on 11 assisted and 14 unassisted pairs. Total feeding rates between years did not differ (morning samples: $n = 31$, $df = 29$, $t = -0.05$, $p = 0.96$; afternoon samples: $t = 0.71$, $p = 0.48$), so we combined the data. We measured feeding effort as the number of feedings per nestling per hour (f/n/hr) because feeding rates increase linearly with brood size both in the morning ($F_{1,29} = 20.54$, $p < 0.0001$) and afternoon ($F_{1,29} = 25.99$, $p < 0.0001$; Fig. 1). Mean brood size of unassisted pairs (2.64 ± 0.17) was equal to that of assisted pairs (2.71 ± 0.21 , $df = 29$, $t = -0.23$, $p = 0.82$). We conducted observations when nestlings were 10-16 days old. Over this span of ages, the total feeding rate (f/n/hr) was unaffected by nestling age ($n=63$, morning: $F_{1,61} = 0.07$, $p = 0.80$; afternoon: $F_{1,61} = 1.35$, $p = 0.25$).

We used Kolmogorov-Smirnov tests of normality to determine whether to use parametric or non-parametric statistical tests. We analyzed the influence of time of day on incubation effort and feeding rate with a t-test or Wilcoxon signed rank test on the paired differences between morning and afternoon observations of the same individual. We conducted one-tailed tests for differences between incubation and feeding rates of breeders in groups with a helper and those without a helper using a two-sample t-test or Mann-Whitney test.

RESULTS

Traditional analysis of mortality: Logistic regression

In the Sandhills population, male breeder mortality significantly increased as the number of adults on the territory increased (Fig. 1) and significantly decreased (Fig 2) as the number of fledglings on the territory increased (Table 1). These relationships remained significant after we included the age of the male breeder in the model. In the Coastal Plain population, we found no significant relationship between male breeder mortality and the number of adults (Fig. 1) or the number fledglings (Fig. 2) on the territory whether or not we included the age of the male breeder in the model (Table 1).

Among female breeders in the Sandhills, mortality significantly increased as the number of adults on the territory increased (Fig. 1), but this relationship disappeared when the age of the female breeder was included in the model (Fig. 2; Table 2). However, the number of fledglings on the female breeder's territory, which previously had no effect, had a negative effect on mortality when age was included in the model (Table 2). In the Coastal Plain population, no effect of the number of adults on female breeder mortality was observed in either model (Fig. 1). Again, as we observed in the Sandhills, inclusion of age in the model altered the relationship between female breeder mortality and the number of fledglings from insignificant to a marginally significant, negative relationship (Fig. 2; Table 2).

Risk analyses excluding territory quality

The risk of male breeder mortality decreased with increasing numbers of adults and fledglings on the territory, in the Sandhills (pseudo- $r^2 = 0.14$, $\chi^2 = 35.68$ df = 2, $p = 0.001$) and the Coastal Plain (pseudo- $r^2 = 0.25$, $\chi^2 = 19.74$, df = 2, $p = 0.0001$) populations (Table 3). In the Sandhills, female breeder mortality also declined as both measures of group size increased (pseudo- $r^2 = 0.15$, $\chi^2 = 62.75$, df = 2, $p = 0.0001$) (Table 4). In the Coastal Plain population, female breeder mortality decreased as the number of fledglings on the territory increased (pseudo- $r^2 = 0.28$, $\chi^2 = 21.39$, df = 2, $p = 0.001$), but the number of adults on the territory had no effect (Table 4).

Risk analyses including territory quality

Male and female breeder mortality significantly decreased as the index of territory quality (T_{avg}) increased in both the Sandhills and Coastal Plain populations (Tables 5 and 6). Inclusion of an index of territory quality did not change the major findings from the previous model.

Male breeder mortality in the Sandhills and Coastal Plain populations decreased significantly with increasing number of adults and fledglings, relative to the territory average (Table 5). In the Sandhills, female breeder mortality decreased with increasing number of adults and fledglings relative to the territory average (Table 6). However, only the number of fledglings relative to the

territory average resulted in a significant decrease in female breeder mortality in the Coastal Plain population (Table 6). Among females in the Sandhills and Coastal Plain, controlling for territory quality increased the magnitude of the negative effect of the number of adults and fledglings on mortality. Among male breeders in the Sandhills and Coastal Plain, controlling for territory quality decreased the negative effect of the number of adults on mortality, and increased the negative effect of the number of fledglings.

Breeder workload

Time of day had no effect on incubation effort ($n = 14$, $t = -1.69$, $p = 0.11$). The total incubation time of pairs assisted by a helper (94% of observation time), although higher, was not statistically different than that of pairs without a helper (90%; $df = 11$, $t = -1.44$, $p = 0.090$). However, male and female breeders significantly reduced their incubation effort in the presence of helpers (Fig. 4: Male breeder: $t = 3.7$, $p = 0.005$; Female breeder, Mann-Whitney $W = 72$, $p = 0.011$).

Time of day significantly influenced feeding rates of pairs (Fig. 5; Wilcoxon signed ranks test: $D = 419.5$, $p < 0.001$). The mean feeding rate of pairs with a helper (AM, 7.79 ± 2.12 ; PM, 6.02 ± 1.71) was not statistically different from that of pairs without a helper (AM, 6.36 ± 2.17 , $p = 0.088$; PM, 5.62 ± 1.32 , $p = 0.085$), although the trend was for pairs with a helper to feed more (Fig. 5). During the morning hours, feeding rates of breeding males and females were no different in groups with or without helpers. During the afternoon hours, however, the feeding rate of male and female breeders declined significantly in the presence of a helper (Male: $t = 3.58$, $p = 0.001$; Female: $t = -1.76$, $p = 0.048$; Fig. 5).

DISCUSSION

Our results indicate that red-cockaded woodpecker helpers gain indirect fitness benefits by enhancing the survival of related breeders, and that both the helper itself and the additional fledglings they enable the breeders to raise contribute to this effect. Enhanced breeder survival might result from benefits of group living or, in the case of the effect of the helper itself, from the reduction in parental effort in the presence of a helper demonstrated by our data. In addition, our results demonstrate the importance of including effects of territory quality and age-dependent mortality in analyses of survival.

Results from the first logistic model suggested that male and female breeder mortality in the Sandhills increases as the number of adults on a territory increases. This pattern suggests competition among adults, but it might also result from older breeders living in larger groups on high quality territories, if older breeders have higher mortality. Our results support the latter possibility. When we included breeder age as an additional independent variable in a logistic model, the number of adults on a territory no longer influenced female breeder mortality. This is consistent with a previous study (Reed and Walters 1996), in which no effect of the number of

adults in a group on breeder mortality was found. When we employed survival analysis, which allows for non-linear effects of age on mortality, we found a negative rather than positive effect of number of adults on breeder mortality. We believe this to be an accurate result, as effects of age on mortality in red-cockaded woodpeckers are known to be non-linear. Specifically mortality is higher in very young and very old adults (Walters et al. 1992; Walters, unpublished data). The difference between results from logistic and survival analyses demonstrates the pitfalls of simplistic analyses of mortality rates, and the importance of adequately addressing age effects.

While confounding by age-dependent mortality produced counter-intuitive relationships between breeder mortality and group size, confounding by territory quality is more difficult to identify. Walters (1990) previously demonstrated that fledgling production and territory quality are positively correlated. Therefore, the observed inverse relationship between the number of fledglings and male and female breeder mortality in the Sandhills and Coastal Plain populations is certainly confounded by territory quality. Confounding by territory quality, as well as inadequate treatment of age effects (see above), might account for the erroneous results obtained using logistic regression. However, analogous survival analyses models with and without a territory quality index produced similar results. This finding may be interpreted in three ways, (1) the territory quality index is an inadequate indicator of territory quality, (2) territory quality does not matter as much as age-dependent mortality, or (3) the unspecified baseline hazard function for an individual, $\alpha(t)$, accounts for territory quality.

The precise manner in which fledglings might enhance breeder survival is unclear. One possible benefit related to enhanced group size (Pulliam and Caraco 1984) is that breeders have increased foraging efficiency in large groups with many fledglings. However, adults are unlikely to gain useful information about food from fledglings because fledglings continue to be fed by adults for many weeks (Jackson 1994). More likely explanations are dilution effects (i.e. safety in numbers) and enhanced predator detection when more fledglings are present. An alternative interpretation of the relationship between the number of fledglings and breeder mortality is that breeders that produce many fledglings are high quality individuals that are naturally long lived.

Red-cockaded woodpecker helpers might enhance breeder survival by increasing breeder foraging efficiency as well as enhancing predator detection (Pulliam and Caraco 1984). Group members may observe where other animals are feeding and use this information to find food themselves. Individuals in red-cockaded woodpecker groups travel and forage together throughout the day (Walters 1990). Males and females exhibit strong sexual differentiation in their foraging niches (Ligon 1970), in that males forage more on branches and twigs and females forage more on the lower portion of the trunk. One would expect the effect of helpers on foraging efficiency to be more pronounced for male breeders than for female breeders because males forage in closer proximity to each other. Consistent with this expectation is the result that a single unit increase in the number of adults on a breeding male's territory reduces the hazard of death by 20% and 42% in the Sandhills and Coastal Plain populations respectively, whereas helper presence has a smaller effect on the hazard of death of female breeders in the Sandhills (16% reduction) and no effect in the Coastal Plain population.

Red-cockaded woodpeckers give warning calls when aerial predators are near (Ligon 1970). The woodpeckers stop their activities, cease vocalizing and freeze when these calls are given. Whether larger groups are quicker to identify predators than smaller groups is unknown, although it seems likely. However, in cases where effects of group size on predator detection have been demonstrated (Lima 1995; Creel and Creel 1995; Kildaw 1995), the group sizes were much greater than those observed in the red-cockaded woodpecker.

The effects of group size on breeder survival have been examined in several other cooperatively breeding species (Table 7). Group size may affect survival of members of a breeding pair or, alternatively, only one member of the pair. These data clearly demonstrate that the benefits of group living are not unilateral and survivorship must be examined for each group member. For example, future indirect benefits due to positive effects of helpers on survival of the male breeder, but not the female breeder, are estimated to contribute 1/3 of the fitness benefits of helping among acorn woodpeckers (Koenig and Stacey 1990).

Another mechanism by which helpers may reduce breeder mortality is by reducing the breeders' workload. Here we provide evidence that red-cockaded woodpeckers breeders reduce incubation and nestling feeding in the presence of helpers. The effects of helpers on breeder workloads in other species are mixed (Table 7). Since helpers assist with provisioning, if the total provisioning rate of groups with helpers is statistically equivalent to that of groups without helpers, then one or both breeders must be adjusting their effort to the presence of helpers. In several species, breeders adjust their workload in the presence of helpers so that the total provisioning rate is unchanged. In others, total provisioning significantly increases in the presence of a helper, yet one or both breeders reduces it workload. Breeders reduce their workload in 15 of the 24 species studied, including the red-cockaded woodpecker, suggesting that this is a common effect of helpers.

Only six studies, including this one, have documented an increase in breeder survival with a concomitant decrease in the breeder's workload: white-browed sparrow weaver (*Plocepasser mahali*; Lewis 1982), splendid fairy-wren (*Malurus splendens*; Rowley and Russell 1997), bicolor wren (*Campylorhynchus griseus*; Austad and Rabenold 1985), pied kingfisher (*Ceryle rudis*; Reyer 1984) and rifleman (*Ancanthisitta chloris*; Sherley 1990). Effects of reduced breeder workload on breeder survivorship are difficult to demonstrate because nestling provisioning may not be an accurate measurement of a breeder's total energy budget. If breeders spend time gained from reduced parental effort on other energetically demanding activities, no effect on survival is expected, but other benefits may be derived from these activities. For example, red-cockaded woodpecker breeders, in addition to tending eggs and young, forage, excavate cavities, defend their territories and rest. Excavation of cavities is most frequent during the summer months, so pairs with helpers may spend their 'extra' time and energy excavating cavities. Because the birds tend to use their newest cavity for nesting (Conner et al. 1998), and years of work are required to complete a cavity (Conner and Rudolph 1995; Harding 1997), having time to excavate a cavity could enhance future reproduction by the breeder.

We conclude that future indirect fitness benefits resulting from reduced breeder mortality contribute to the maintenance of helping behavior in the red-cockaded woodpecker. Helping behavior reduces breeder mortality by augmenting the production of fledglings, thereby

increasing group size. Helping behavior also reduces a breeder's workload, but whether breeder survival is enhanced because of this effect, or because of the presence of an extra adult, is not clear from our results. These two mechanisms are not mutually exclusive, and both may operate to reduce breeder mortality. Other possible benefits of helping behavior by red-cockaded woodpeckers not yet examined include (1) benefits through production of young that assist non-descendant kin of the helper in a subsequent season (Reyer 1984; Rabenold 1985) and (2) benefits through aid provided to the helper by former recipients of help, once the helper inherits the natal territory and becomes a breeder (Connor 1986; Emlen and Wrege 1989). That helpers benefit directly through improved reproductive ability due to helping experience has previously been ruled out for this species (Khan and Walters 1997). The only demonstrated benefit of helping, besides those examined here, is the indirect benefit resulting from increased production of non-descendent kin (Walters et al. 1992).

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TABLE 2.1: Male breeder mortality in the Sandhills and Coastal Plain populations analyzed with logistic regression. First, we modeled male breeder mortality as a function of the number of ADULTS and the number of FLEDGLINGS in the group the year the male breeder died. In a second model, we included a third variable in the model, AGE of the breeder in the year of death, to control for age-dependent mortality rates. In neither model did we control for territory quality.

Population	n	Parameter	Estimate	Wald χ^2	p	Model fit	
						χ^2	P
Sandhills	554	ADULTS	0.286	9.226	0.001***	16.469	<0.001***
		FLEDGLINGS	-0.153	12.262	0.002**		
		AGE	0.050	4.356	0.037*	20.369	<0.001***
		ADULTS	0.232	7.388	0.007**		
		FLEDGLINGS	-0.162	10.083	0.002**		
Coastal Plain	137	ADULTS	-0.087	0.149	0.699	2.968	0.227
		FLEDGLINGS	-0.200	2.172	0.141		
		AGE	0.0485	0.446	0.504	3.406	0.333
		ADULTS	-0.136	0.327	0.567		
		FLEDGLINGS	-0.216	2.477	0.116		

* Significance at 0.05 alpha level

** Significance at 0.01 alpha level

*** Significance at 0.001 alpha level

TABLE 2.2: Female breeder mortality in the Sandhills and Coastal Plain populations analyzed with logistic regression. First, we modeled male breeder mortality as a function of the number of ADULTS and the number of FLEDGLINGS in the group the year the male breeder died. Second, we included a third variable in the model, AGE of the breeder in the year of death, to control for age-dependent mortality rates. In neither model did we control for territory quality.

Population	n	Parameter	Estimate	-		Model fit	
				Wald χ^2	p	χ^2	P
Sandhills	747	ADULTS	0.143	3.756	0.053*	4.391	0.111
		FLEDGLINGS	-0.058	1.758	0.185		
		AGE	0.071	7.216	0.007**		
		ADULTS	0.118	2.513	0.113		
		FLEDGLINGS	-0.087	3.748	0.053*		
Coastal Plain	173	ADULTS	-0.024	0.022	0.882	6.927	0.031*
		FLEDGLINGS	-0.273	6.062	0.014*		
		AGE	-0.422	3.053	0.081		
		ADULTS	0.022	0.018	0.894		
		FLEDGLINGS	-0.220	3.642	0.056*		

* Significance at 0.05 alpha level

** Significance at 0.01 alpha level

*** Significance at 0.001 alpha level

TABLE 2.3: Male breeder mortality as a function of the number of ADULTS and FLEDGLINGS on their territory in the Sandhills and Coastal Plain populations. The Wald chi-square test statistic is used to determine if the parameter estimate is significantly different from zero. % Δ is the percent change in the rate of death when a single independent variable is increased by one unit and all other variables are held constant. For example, a one unit increase in the relative number of adults on a territory results in a 27.3% decrease in the mortality rate for a male breeder in the Sandhills population.

Population	n	Parameter	Estimate	Wald χ^2	p	% Δ
Sandhills	554	ADULTS	-0.32	16.71	0.0001	-27.3
		FLEDGLINGS	-0.16	10.72	0.0011	-15.1
Coastal Plain	137	ADULTS	-0.57	5.31	0.0212	-43.5
		FLEDGLINGS	-0.37	6.92	0.0085	-31.1

TABLE 2.4: Female breeder mortality as a function of the number of ADULTS and FLEDGLINGS on their territory in the Sandhills and Coastal Plain populations. The Wald chi-square test statistic is used to determine if the parameter estimate is significantly different from zero. % Δ is the percent change in the rate of death when a single independent variable is increased by one unit and the other variables are held constant. For example, a one unit increase in the number of adults on a territory results in a 13.8% decrease in the mortality rate for a female breeder in the Sandhills population.

Population	n	Parameter	Estimate	Wald χ^2	p	$\Delta\%$
Sandhills	747	ADULTS	-0.15	4.22	0.0399	-13.8
		FLEDGLINGS	-0.28	42.10	0.0001	-24.4
Coastal Plain	173	ADULTS	-0.24	2.42	0.1202	
		FLEDGLINGS	-0.45	16.10	0.0001	-36.1

TABLE 2.5: Male breeder mortality is significantly reduced as the average number of adults on a territory increases (T_{avg}), and the number of adults (D_{adults}) and the number of fledglings (D_{fledge}) relative to their respective territory averages increases, in the Sandhills and Coastal Plain populations. The Wald chi-square test statistic is used to determine if the parameter estimate is significantly different from zero. $\% \Delta$ is the percent change in the rate of death when a single independent variable is increased by one unit and all other variables are held constant. For example, a one unit increase in the relative number of adults on a territory results in a 20.8% decrease in the mortality rate for a male breeder in the Sandhills population.

Population	n	Parameter	Estimate	Wald χ^2	p	$\% \Delta$
Sandhills	554	T_{avg}	-0.77	24.17	0.0001	-56.4
		D_{adults}	-0.23	7.42	0.0064	-20.8
		D_{fledge}	-0.17	9.72	0.0018	-15.6
Coastal Plain	137	T_{avg}	-0.89	7.29	0.0069	-59.7
		D_{adults}	-0.55	3.99	0.0458	-42.3
		D_{fledge}	-0.54	9.60	0.0019	-41.8

TABLE 2.6: Female breeder mortality as a function of the average number of adults on a territory (T_{avg}), and the number of adults (D_{adults}) and the number of fledglings (D_{fledge}) relative to their respective territory averages, in the Sandhills and Coastal Plain populations. The Wald chi-square test statistic is used to determine if the parameter estimate is significantly different from zero. $\Delta\%$ is the percent change in the rate of death when a single independent variable is increased by one unit and the other variables are held constant. For example, a one unit increase in the relative number of adults on a territory results in a 15.3% decrease in the mortality rate for a female breeder in the Sandhills population.

Population	n	Parameter	Estimate	Wald χ^2	p	$\Delta\%$
Sandhills	747	T_{avg}	-0.32	6.04	0.0142	-27.3
		D_{adults}	-0.17	3.96	0.0473	-15.3
		D_{fledge}	-0.30	39.58	0.0001	-26.0
Coastal Plain	173	T_{avg}	-1.33	20.88	0.0001	-73.5
		D_{adults}	0.09	0.23	0.6291	
		D_{fledge}	-0.55	17.78	0.0001	-42.5

Table 2.7: Results of studies that have analyzed helper effects on total feeding rates, individual feeding contributions and/or breeder survival. The absence of an effect of helpers is denoted by a 0, while positive and negative effects are denoted by + and - , respectively. If no information is available then N/A is noted. If only one sex of the breeding pair reduces their workload in the presence of a helper, then that sex is noted.

	Total provisioning	Breeder workload	Breeder survivorship		Source
			Males	Females	
Arabian babblers	+	-	N/A	N/A	Wright 1997
Long-tailed tit	+	-	N/A	N/A	Hatchwell and Russell 1996
Purple gallinule	+	-	N/A	N/A	Hunter 1987
Western bluebird	+	-	0	0	Dickinson et al. 1996
Green woodhoopoe	0	-	N/A	N/A	Du Plessis 1991
Grey-crowned babbler	0	-	N/A	N/A	Brown et al. 1978
Bushtit	N/A	-	N/A	N/A	Sloane 1996
Greater rheas	N/A	-	N/A	N/A	Condenotti and Alvarez 1997
White-throated magpie jay	N/A	-	N/A	N/A	Langen and Vehrencamp 1999
Bicolored wren	0	- esp. female ^d	+	+	Austad and Rabenold 1985; Rabenold 1990
Stripe-backed wren	0	- esp. male	0	0	Rabenold 1984
White-browed sparrow weaver	+	- females	0	+	Lewis 1982
Pied kingfisher	+ ^b	- females	0	+	Reyer 1984
Splendid fairy-wren	0	- females	0	+	Russell and Rowley 1988
Galapagos mockingbird	+	- males	0	0 ^c	Kinnaird and Grant 1982; Curry and Grant 1990
Rifleman	0	- males	0	+	Sherley 1990
Acorn woodpecker	+	0	+	0	Mumme and de Querioz 1985; Koenig and Mumme 1987
Florida scrub Jay ^a	+	0	0	0 ^a	McGowan and Woolfenden 1990; Mumme 1992
Grey-capped social weaver	+	0	N/A	N/A	Bennun 1994
Small green bee-eater	+	0	N/A	N/A	Sridhar and Karanth 1993
White-browed scrub wren	+	0	0	0	Magrath and Vezerinac 1997
White-fronted bee-eater	+	0	0	0	Emlen and Wrege 1989; Emlen and Wrege 1991
Bell miner	+	N/A	N/A	N/A	Clarke 1984
Chestnut-bellied starling	+	N/A	N/A	N/A	Wilkinson and Brown 1984
White-winged chough	+	N/A	N/A	N/A	Heinsohn 1995
Pygmy nuthatch	0	N/A	N/A	N/A	Sydeman 1991
Toucan barbet	0	N/A	N/A	N/A	Restrepo and Mondragon 1998

^a Experimental removal of non-breeders

^b Helpers have an effect on feeding rates at Lake Victoria but not at Lake Naivasha, indicating that breeders adjust their effort according to need.

^c Curry and Grant (1990) demonstrate that female survival increased from 59% to 83% in one-year, but the average increase in survival (59% unaided versus 63% aided) was not significant over the five year study.

^d Both sexes reduce their workload, but the reduction by female is greater.

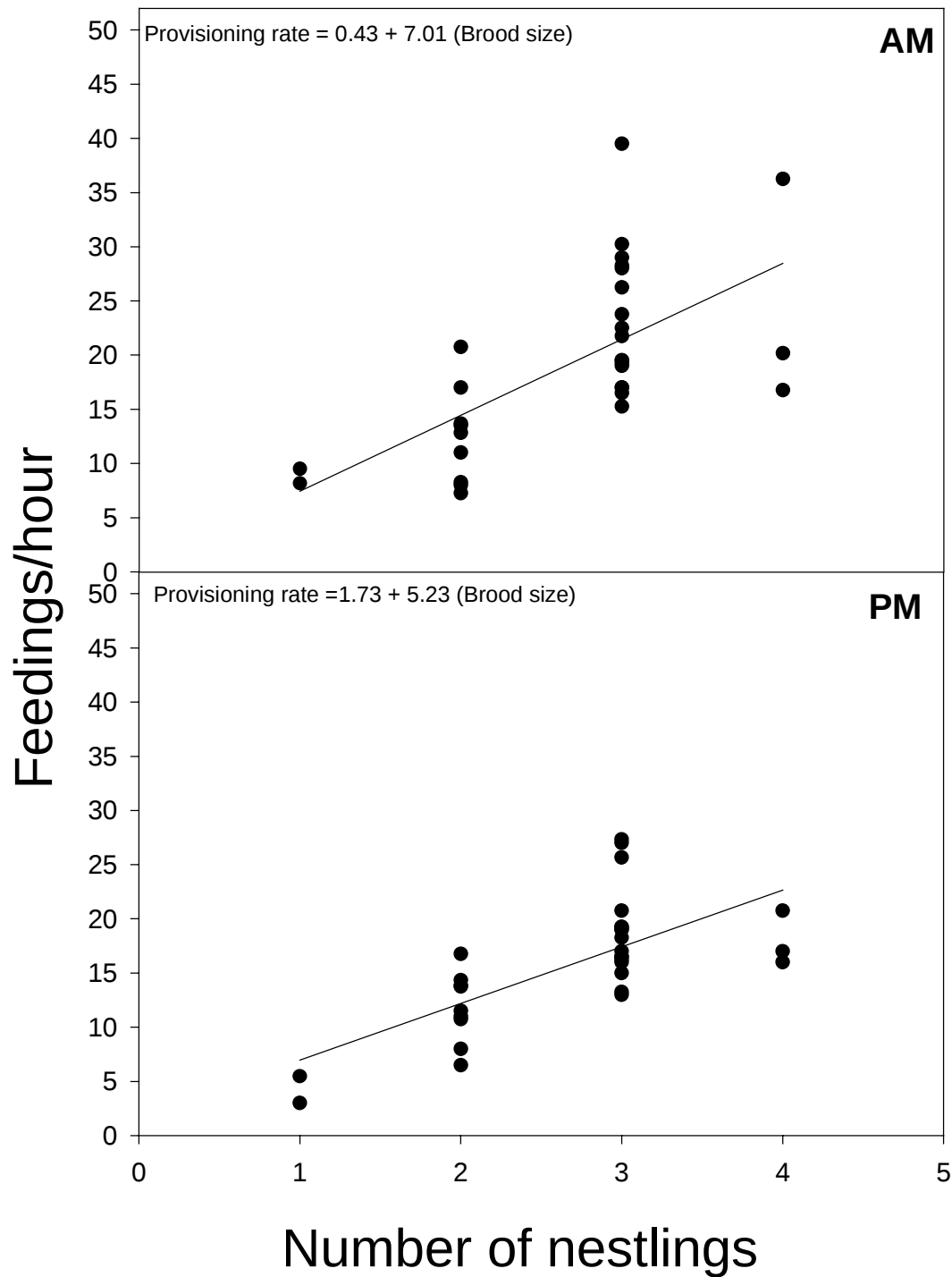


Fig. 2.1: Feeding rate increases linearly with brood size when nestlings are 10-16 days old during morning (AM: 0600-1200) and afternoon (PM: 1201-1800) observations. Each symbol represents the average total feeding rate for each nest that was observed. Linear regression lines and parameter estimates are shown.

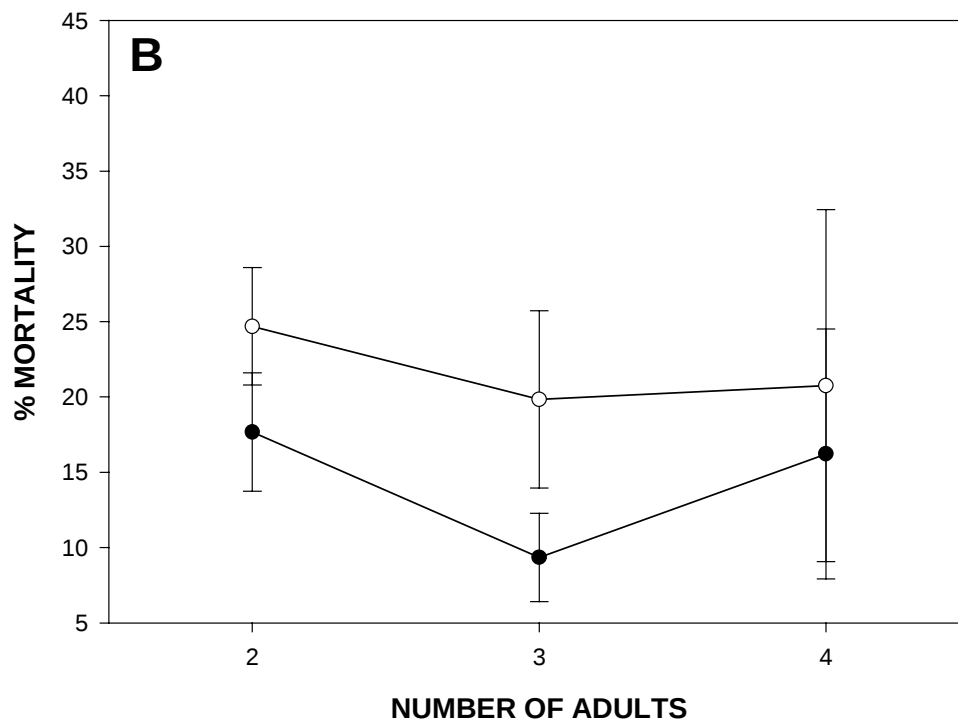
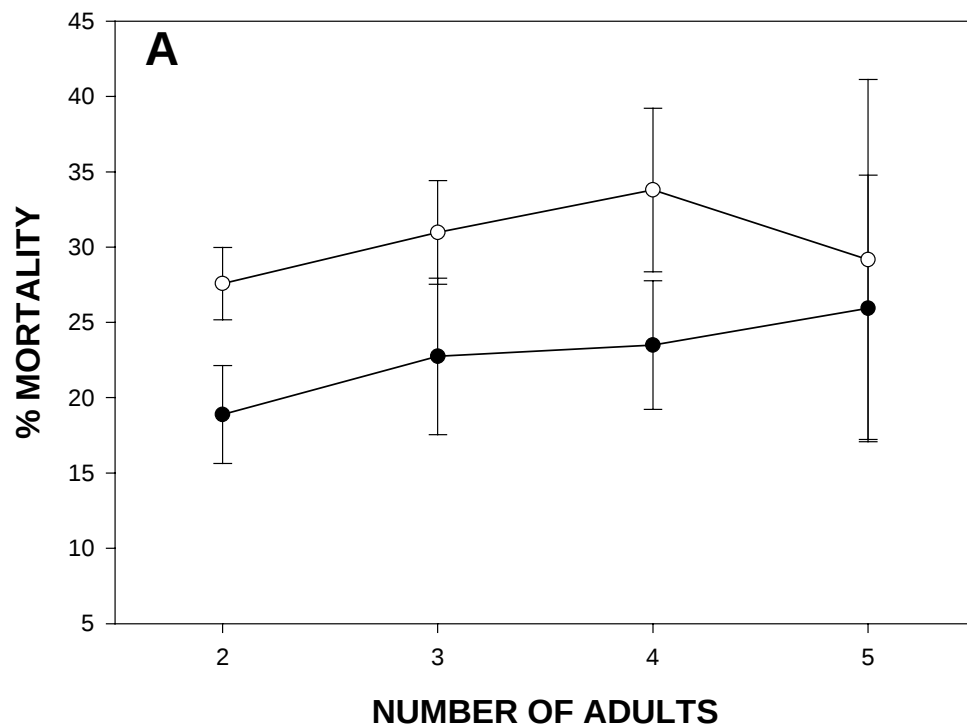


Fig. 2.2: Mean mortality ($\pm$ SE) of male (closed circle) and female (open circle) breeders in the Sandhills (A) and Coastal Plain (B) populations as a function of the number of adults on the territory the year the breeder died. This analysis did not control for territory quality or breeder age.

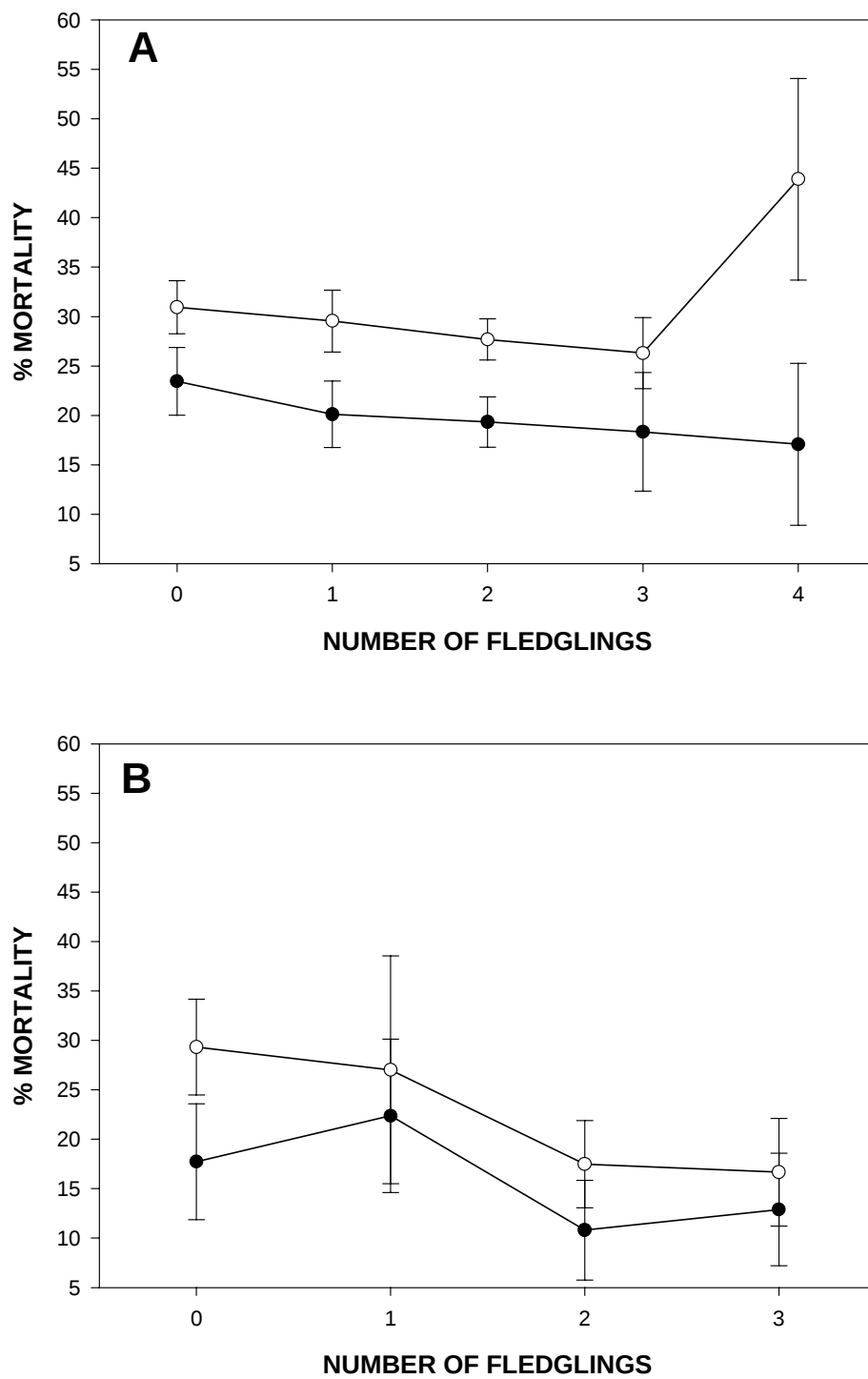


Fig. 2.3: Mean mortality ($\pm$ SE) of male (closed circle) and female (open circle) breeders in the Sandhills (A) and Coastal Plain (B) populations as a function of the number of fledglings on the territory the year the breeder died. This analysis does not control for territory quality or breeder age.

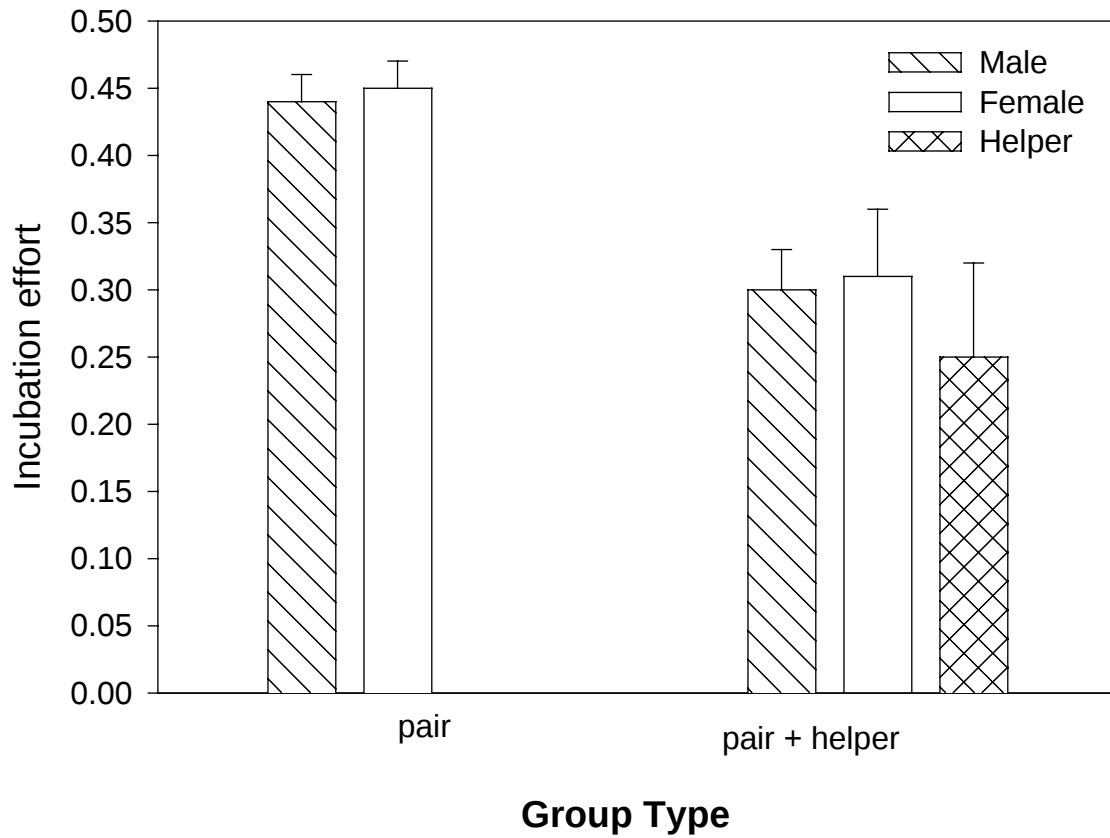


Fig. 2.4: Incubation effort (+ 1SE) by female breeders, male breeders and male helpers. Unassisted pairs (n = 8) and pairs assisted by a single helper (n = 5) were observed during the 1996 breeding seasons.

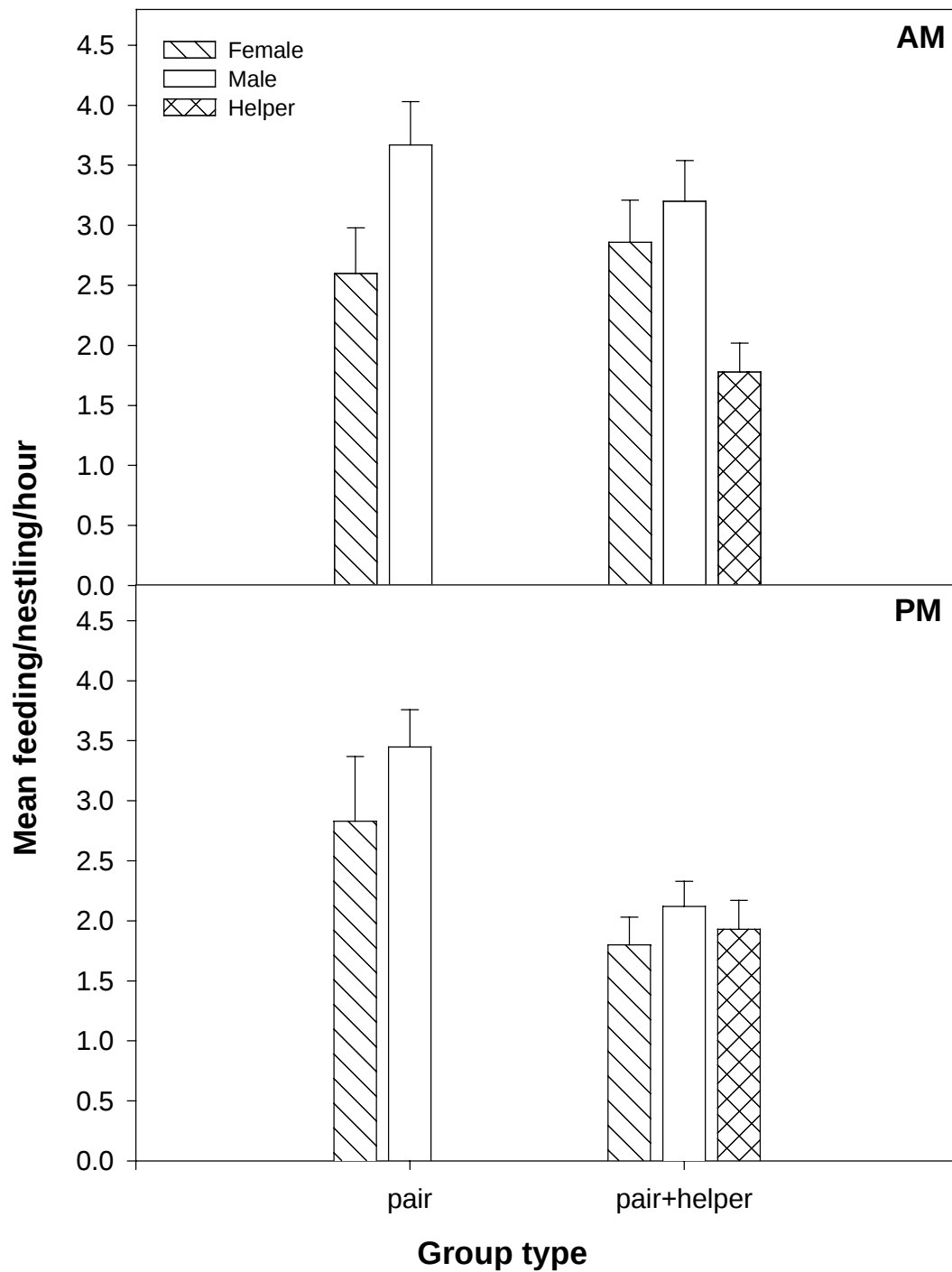


Fig. 2.5: Feeding effort (+ 1SE) by female breeders, male breeders and males helpers during morning and afternoon observation periods. Unassisted pairs (n = 13) and pairs assisted by a single helper (n = 18) were observed during the 1994 and 1996 breeding season.

Chapter 3

An analysis of reciprocal exchange of helping behavior in the red-cockaded woodpecker.

Abstract

We examine the frequency of reciprocal exchanges of helping behavior in three red-cockaded woodpecker populations to determine if such exchanges might constitute a significant fitness benefit of helping. Specifically we determine how often helpers, once they become breeders, are assisted by young they previously helped raise. The expected frequencies of reciprocal exchange of helping based on survival and status transition probabilities are low (2%). Observed instances of reciprocity occur significantly more often than expected in two of the three populations studied. High rates of retention of young males as helpers on high quality territories or preferential helping of kin, as well as preferential helping of former care-givers, might explain this result. When the analysis is restricted to helpers unrelated to the young they help raise, which controls for preferential helping of kin and largely eliminates effects of territory quality, reciprocity occurs no more often than expected. We conclude that young males do not preferentially help former care-givers and that reciprocal exchange of help is not an important factor in the evolution of helping behavior in the red-cockaded woodpecker. In the red-cockaded woodpecker, all known benefits of helping behavior are indirect (i.e., derived through kin selection) rather than direct. We discuss the occurrence of unrelated helpers in this context.

Key words: red-cockaded woodpecker, *Picoides borealis*, reciprocity, helping behavior

Cooperative breeding is a social system in which adult birds help raise offspring that are not their own. This social system occurs in 222 avian species from 24 orders and has evolved independently many times (Brown 1987). In the most common variant of this system, such as occurs in the red-cockaded woodpecker (*Picoides borealis*), most helpers are nonbreeding individuals that have remained on their natal territory. In these systems, the evolution of cooperative breeding involves two distinct adaptive traits: (1) young remain on their natal territory, rather than dispersing and (2) young help breeders on the natal territory raise offspring (Brown 1987; Emlen 1982a, b). The evolution of delayed dispersal is well understood in many species (Stacey and Ligon 1987; Komdeur 1992; Walters et al. 1992a), whereas the evolution of helping behavior is poorly understood.

One difficulty in resolving the issue of the evolution of helping behavior is that individuals of different species may help for different reasons. As a consequence, generalities have been elusive. For example, helping behavior has probably evolved in the white-fronted bee-eater (*Merops bullockoides*) because helpers gain substantial indirect inclusive fitness benefits by increasing the production of non-descendant kin by their groups (Emlen 1992). In contrast, helping behavior by males unrelated to the breeders in the pied kingfisher (*Ceryle rudis*) has probably evolved because these helpers gain direct fitness benefits by increasing the probability of future mating with the female they helped (Reyer 1984).

Current research on the evolution and maintenance of helping behavior strives to determine the relative importance of the various possible fitness benefits of helping in a variety of species (Brown 1987; Emlen 1991; Cockburn 1998). Direct benefits accrue when the helper's survival or eventual production of descendant kin is enhanced. Indirect benefits accrue when helping behavior results in increased production of non-descendant kin. Both immediate and delayed benefits of each type have been proposed (Koenig and Mumme 1990).

We are examining a variety of possible benefits of helping behavior by male red-cockaded woodpeckers. Previous work showed that helpers gain indirect benefits by increasing the reproductive output of relatives (Heppell et al. 1994). Helpers also accrue future indirect benefits by promoting the survival of related breeders (Khan and Walters, in prep). Here, we examine the possibility that helpers gain a future direct benefit by enhancing the production of young that will eventually assist the helper once he becomes a breeder (reciprocity hypothesis, Ligon and Ligon 1978; Wiley and Rabenold 1984).

The nature of the interaction between a helper and a previous recipient of help as well as its influence on the evolution of helping is of theoretical interest. Exchanges of help may represent by-product mutualism (both helper and recipient benefit from their interaction; Vehrencamp 1979) or reciprocal altruism (the recipient benefits and the helper suffers a cost from their interaction; Trivers 1971) depending on whether the helper bears a fitness cost for helping (Brown and Brown 1981; Koenig 1988). The distinction between by-product mutualism and reciprocal altruism is important for understanding the evolutionary basis of behavior. However, the initial step in examining the reciprocity hypothesis, which we undertake here, is to determine if reciprocal exchanges occur at sufficient frequencies to potentially constitute an

important direct benefit. We examine reciprocal exchanges of helping in three red-cockaded woodpecker populations located in North Carolina.

The red-cockaded woodpecker is endemic to the pine forests of the southeastern United States. Red-cockaded woodpeckers typically live in groups that consist of one monogamously breeding pair and 0-4 helpers (Lennartz and Harlow 1979), the majority of which are male offspring from previous breeding seasons (Walters et al. 1988). Helpers unrelated to the breeders occur occasionally. Males are sufficiently long-lived to provide ample opportunity for reciprocal interactions. In the North Carolina Sandhills, male breeders have lived to age 17 (Walters et al. unpublished data). On the other hand, not all fledgling males remain as helpers and not all helpers become breeders on their natal territory. Some fledgling males disperse in their first year to search for a breeding vacancy, and some helpers disperse to neighboring territories to fill breeding vacancies (Walters et al. 1988). Thus, the likely frequency of reciprocal exchanges of helping behavior in the red-cockaded woodpecker is not obvious.

Methods

The Sandhills (SH) study area is located in south-central North Carolina, and contains approximately 250 groups of marked red-cockaded woodpeckers. This study area encompasses approximately 110,000 ha and is described in detail in Carter et al. (1983) and Walters et al. (1988). The other two populations are located along the southeastern coast of North Carolina. The population on Camp LeJeune Marine Base (CL) inhabits 34,425 ha, and that on Croatan National Forest (CNF) 63,907 ha. Combined, these two populations contain approximately 100 groups of marked red-cockaded woodpeckers. Complete descriptions of the habitats associated with Coastal Plain populations are in Zwicker (1995).

All three populations inhabit longleaf pine (*Pinus palustris*) communities of various types, with diverse ground cover and sparse hardwood midstory. Demographic data were collected for 16 years (1980-1996) from the Sandhills population, and 9 (1987-1996) and 11 (1985-1996) years from Camp LeJeune and Croatan National Forest, respectively. A complete description of monitoring methods is in Walters et al. (1988). Most individuals were marked with color bands as nestlings and their life histories were followed thereafter. During annual breeding season censuses we determined the identity and status (e.g. breeder, helper) of each member of each group. We also determined the number and identity of all fledglings produced by each group. From these data we calculated annual survival rates, status transition probabilities (e.g. fledgling to helper, helper to breeder) and the coefficient of relatedness between helpers and the offspring they help raise.

We examined reciprocal exchanges of helping between males because males are more often helpers, more often become breeders on their natal territories and have lower mortality rates compared to females (Walters et al. 1988; Daniels 1997). Therefore, exchanges between males will be much more common than exchanges involving females. We used transition

probabilities between male life stages (Table 1) to compute expected probabilities of reciprocation in each of the three populations. For a male's help to be reciprocated, the following must occur: (1) a helper must raise at least one male fledgling, (2) the helper must inherit the breeding position on the territory on which he helped and (3) the male fledgling must stay and help the new breeder. A male fledgling has three possible fates other than remaining as a helper: he may (1) die, (2) disperse or (3) inherit the natal territory and become a breeder in his first year as an adult (Walters et al. 1988). Similarly, a helper may (1) die, (2) disperse or (3) remain for another year as a helper rather than inherit the breeding position (Walters et al. 1988). We assume there is no possibility of reciprocation for helpers that disperse because non-natal helpers are rare (Walters 1990).

If the helper does not inherit the natal territory after one year of helping, but instead stays and helps again in the following year, he may raise yet another male helper. To determine the overall probability of reciprocation, all the possible permutations by which reciprocation may occur must be summed. For example, a fledgling male raised when the helper is age one might assist the helper when he becomes a breeder at age two, or one raised when the helper is age three might assist him when he becomes a breeder at age six. We calculated all possible permutations for helpers through age eight: we have observed no males that helped beyond age eight (Walters et al., unpublished data). To calculate the expected probability of reciprocation (R) based on population-specific transition probabilities we employed the following expression:

$$\hat{R} = \sum_{x=1}^9 I_x H^{(x-1)} \left(B_x \frac{1 - H^{(x-1)}}{1 - H_x} \right)$$

where I is the annual probability that a helper inherits breeding status; H is the annual probability that a helper will remain a helper for an additional year and B is the annual probability that the helper will raise a male fledgling that will stay and help in the following year. B is calculated as the product of the increase in reproductive success attributable to a helper (0.39 fledglings; Heppell et al. 1994), the nestling sex ratio (0.5; Walters 1990) and the probability that a male fledgling will stay on the natal territory and help at age one (Table 1).

The calculated value represents the expected probability of reciprocation based on population-specific transition probabilities. We calculated the observed probability of reciprocal exchanges as the number of reciprocity events divided by the number of helpers in the population over the time period of the study. To examine the possibility that individuals preferentially assist those who helped raise them, we used a one-tailed binomial test based on a Poisson distribution to compare the expected probability of reciprocation to the observed proportion of reciprocation in each of the three study populations (Zar 1984).

Reciprocal exchanges of help might occur more often than expected because of effects of confounding variables. Specifically, high rates of retention of young males on high quality territories or preferential helping of kin might explain such a result. To examine the effects of kinship, we divided helper-offspring pairs into four relatedness categories depending on the value of the coefficient of relatedness between them (r): closely related ($r \geq 0.5$), moderately related ($0.49 \geq r \geq 0.25$), distantly related ($0.24 \geq r \geq 0.01$) and unrelated ($r = 0$). We used only Sandhills data for the analysis of kin effects on observed levels of reciprocity, because only for this population were sample sizes in each relatedness category sufficient. We used a chi-square test to determine if reciprocity occurs independently of relatedness. Also, we compared the expected frequency of reciprocal exchange of helping to the observed frequency among unrelated helper-offspring pairs using a binomial test based on a Poisson distribution.

Results

The expected probability of reciprocation was approximately 2% for Camp LeJeune, Croatan National Forest and the Sandhills (Table 2). The observed incidence of reciprocity was significantly higher than expected at Camp LeJeune ($n = 196$; reciprocal exchanges = 9; $p = 0.005$) and the Sandhills ($n = 1251$; reciprocal exchanges = 73; $p < 0.0001$; Fig. 1). For Croatan National Forest, the observed incidence of reciprocity was no different from that expected ($n = 103$; reciprocal exchanges = 1; $p = 0.906$).

If reciprocity is an important factor contributing to the decision of young male fledglings to help, we expect reciprocity to occur equally among relatedness classes. On the contrary, the frequency of reciprocity is dependent on the degree of relatedness between the helpers and the male offspring they help raise ($\chi^2 = 8.31$, $df = 3$, $p = 0.04$). Reciprocity was more common than expected among the most closely related males (Table 3). The strongest test of preferential assistance to former care-givers is to compare the observed and expected incidence of reciprocated assistance by males unrelated to helpers who helped raise them. In this circumstance, reciprocity does not occur more often than expected ($n=60$; $p(x \geq 2)=0.387$).

Discussion

Our results indicate that reciprocal exchanges of helping behavior do not occur sufficiently often to constitute an important benefit of helping behavior. Still, the observed frequency of reciprocation was significantly higher than expected from survival and status transition probabilities in the Camp LeJeune and Sandhills populations. Does this mean that males preferentially assisted those who had raised them? We think it is more likely that reciprocity is an incidental by-product of other processes governing helping behavior. Males may preferentially assist relatives due to the indirect fitness benefits derived from helping kin

(Walters et al. 1992b; Heppell et al. 1994), and those who helped raise them usually are kin (Walters 1990). The lack of reciprocity in unrelated helper male-offspring pairs supports this assertion.

Territory quality may be a confounding factor as well. Fledglings may be more likely to stay and help, and helpers to remain to inherit breeding status, on high quality territories, regardless of aid received as nestlings. If helping is concentrated in a subset of territories, rather than being distributed randomly among territories, then reciprocal exchanges will occur more often than expected from the population-wide status transition probabilities. Confounding by territory quality might explain why reciprocity is observed more often than expected in the Sandhills and Camp LeJeune populations, but not on Croatan National Forest. Croatan appears to contain relatively little high quality habitat. Much of the Croatan is comprised of high and low pocosin wetlands that are not used as nesting habitat (Walters et al. 1995) and, unlike in the other two areas, management has been focused on timber production rather than maintaining high quality longleaf habitat.

We conclude that reciprocal exchanges of helping provide no selective advantage to promote helping behavior in red-cockaded woodpeckers. Is this benefit important in other species? Benefits resulting from aid by previous recipients of help have been demonstrated only in the green woodhoopoe (*Phoeniculus purpureus*). In this species, non-breeding adults become helpers whether or not they are related to nestlings, suggesting that indirect benefits are not a sufficient explanation for helping behavior. Green woodhoopoe breeders receive aid in acquiring territories and raising young from subordinate birds with whom they formed alliances when they were helpers (Ligon and Ligon 1978; 1983). Reciprocity may also be important in the white-winged cough (*Corcorax melanorhampos*), but definitive results remain to be published. In this species, helpers are a necessity for successful reproduction, and occasionally, young are kidnapped from other groups. Heinsohn (1991) speculated that older helpers form relationships with kidnapped young to increase the chances of future help.

In two studies, reciprocity was rejected as an explanation of helping despite a high incidence of reciprocity compared to our paper. Stripe-backed wren (*Campylorhynchus nuchalis*) breeders receive aid from 17% of the young they helped raise while helpers. Rabenold (1985) nevertheless rejected the reciprocity hypothesis because breeders reliably received aid from younger non-breeders whether or not that particular breeder helped raise the younger non-breeder. Galapagos mockingbirds (*Nesomimus parvulus*) are flexible helpers, meaning that an individual can simultaneously be a breeder in one group and a helper in another during the same breeding season. If reciprocity was an important direct benefit in this species, one would expect to observe an exchange of helping between helpers and adult breeders as well as between helpers and offspring they had helped raise. Curry and Grant (1990) concluded that reciprocity was not an important benefit of helping because it never occurred between helpers and adult breeders and because the 15% probability of reciprocity observed between helpers and offspring they helped raise was confounded by relatedness.

The hypothesis that helpers gain benefits from future assistance by the young they help

raise has been rejected for most cooperatively breeding birds in which it has been studied because of a low incidence of reciprocity. For example, pinyon jays (*Gymnorhinus cyanocephalus*) receive aid from those they help raise only 1.1% of the time (Marzluff and Balda 1990). White-fronted bee-eater breeders (*Merops bullockoides*) who had been helpers for at least one year had no higher probability of being aided than breeders who had never helped (Emlen and Wrege 1989). This hypothesis also has been rejected for Arabian babblers (*Turdoides squamiceps*; Zahavi 1990), hoatzin (*Opisthocomus hoazin*; Strahl and Schmitz 1990) and gray-breasted jays (*Aphelocoma ultramarina*; Brown 1987).

Cumulative evidence suggests that red-cockaded woodpeckers may derive no direct fitness benefits from helping behavior. Helpers do not gain reproductive benefits through improved reproductive skills (Khan and Walters 1997), or future reproductive benefits through increased access to mates (Haig et al. 1994). Helpers do, however, gain indirect fitness benefits from helping (Heppell et al. 1994; Khan and Walters, in prep).

If helpers gain only indirect benefits from helping behavior, what explains the occurrence of unrelated helpers in red-cockaded woodpecker populations? Perhaps helping unrelated breeders is a by-product of natural selection favoring helping behavior between kin. Unrelated helpers likely join groups as a means to obtain a high quality territory. Subsequent helping behavior by unrelated males in this context may represent a mistake. Given selection for helping relatives, and perhaps an initial predilection toward parental behavior (Jamieson and Craig 1987), the frequency of unrelated helpers and the costs of helping may be insufficient to produce discrimination among potential recipients of help based on kinship.

One adaptive explanation for helping behavior by unrelated birds is the pay-to-stay hypothesis (Gaston 1978). This hypothesis assumes that breeders bear a cost of sharing their territory with additional adults and helpers assist with reproduction to defray this cost. The pay-to-stay hypothesis predicts that breeders will evict any adult that does not help. This hypothesis is difficult to test in the absence of adults that do not help.

One factor correlated with the presence of unrelated helpers is the age of the male breeder. Unrelated helpers occur at higher proportions in groups with one and two year old breeders (Table 4; $\chi^2 = 38.89$, $df = 4$, $p < 0.05$). Perhaps young breeders are more likely to have unrelated helpers because they do not have any offspring that could assist in excluding immigrant males, or are less able to exclude them themselves. That unrelated helpers join groups with young male breeders because young breeders are vulnerable to cuckoldry is ruled out by the finding that helpers, whether related to the breeders or not, do not sire offspring (Haig et al. 1994). We suggest that the existence of unrelated helpers in these populations may be explained by either the adaptive pay-to-stay hypothesis or a non-adaptive hypothesis, but further work is necessary to discriminate between these possibilities.

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Table 3.1: Annual transition probabilities used to calculate the probability of reciprocation in three populations of Red-cockaded Woodpecker, Sandhills (SH), Camp LeJeune (CL) and Croatan National Forest (CNF).

	Symbol	SH	CL	CNF
Fledgling stays and helps ^a		0.31	0.39	0.29
Helpers stays and helps again	<i>H</i>	0.5	0.51	0.6
Helper inherits natal territory	<i>I</i>	0.14	0.08	0.11

^a The probability that a fledglings stays on the natal territory and helps at age one is multiplied by the increase in reproductive success attributable to a helper (0.39 fledglings; Heppell et al. 1994) and the nestling sex ratio (0.5; Walters 1990) to determine *B* in the expression used to calculate the probability of reciprocation.

Table 3.2: Expected probabilities of reciprocation based on survival and status transition probabilities for three populations of red-cockaded woodpecker, Sandhills (SH), Camp LeJeune (CL) and Croatan National Forest (CNF). Values represent the probability that a helper will inherit breeding status at the age indicated and subsequently be assisted by a male he helped raise. The summed values represent the overall probability that a helper will be assisted as a breeder by a male he helped raise.

Age	SH	CL	CNF
2	0.0088	0.0061	0.0062
3	0.0063	0.0047	0.0059
4	0.0036	0.0028	0.0043
5	0.0018	0.0015	0.0028
6	0.0009	0.0008	0.0018
7	0.0005	0.0004	0.0011
8	0.0002	0.0002	0.0007
9	0.0001	0.0001	0.0004
SUM	0.0222	0.0166	0.0232

Table 3.3: Kinship effects on reciprocity in the Sandhills population. Values are number of helper male-offspring pairs in which male offspring reared by the helper did (Reciprocated) or did not (Unreciprocated) assist the helper when the helper became a breeder. Expected values are shown in parentheses.

Coefficient of relatedness	$r \geq 0.50$	$0.49 \geq r \geq 0.25$	$0.24 \geq r \geq 0.01$	$r = 0$
Unreciprocated helpers	537 (547.6)	384 (374.5)	135 (135.5)	58 (56.5)
Reciprocated helpers	45 (34.4)	14 (23.5)	9 (8.5)	2 (3.6)

Table 3.4: Effect of breeder age in years on the occurrence of unrelated and related helpers in the Sandhills population. Expected values are shown in parentheses.

Breeder age	Unrelated Helper	Related Helper
1-2	13 (3.0)	39 (49.0)
3	5 (5.5)	92 (91.5)
4	7 (9.1)	152 (150.0)
5	5 (8.4)	142 (138.7)
6-13	17 (21.1)	353 (348.9)

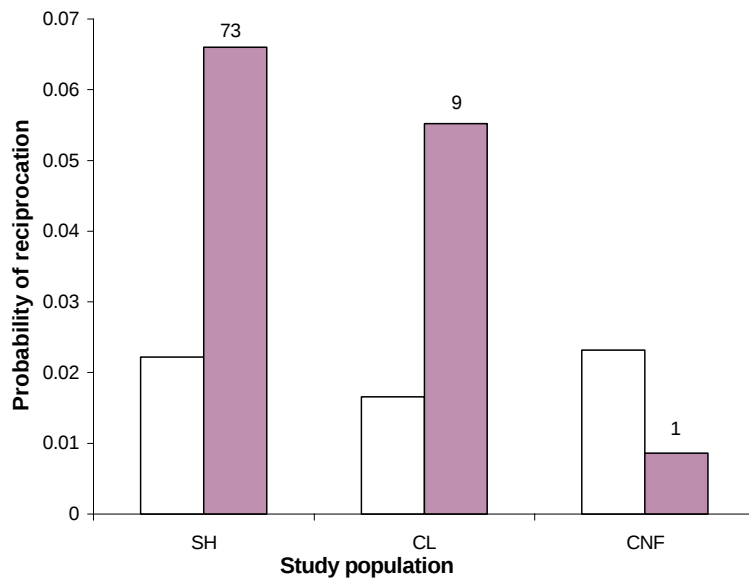


Fig. 3.1: Expected (clear bars) and observed (hatched bars) probability of reciprocation of helping among male helpers in three red-cockaded woodpecker populations in North Carolina, Sandhills (SH), Camp LeJeune (CL) and Croatan National Forest (CNF). Number of incidences of reciprocal exchange of helping are indicated above the hatched bars.

Chapter 4

Patterns of testosterone and prolactin concentrations and reproductive behavior of helpers and breeders in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*).

ABSTRACT

We examined the proximate causes of delayed breeding and alloparental behavior in the cooperatively breeding red-cockaded woodpecker by measuring plasma concentrations of testosterone (T) and prolactin (PRL) in female breeders, male breeders, and male helpers during different stages of the reproductive cycle. Male breeders and helpers have low T during the prebreeding period, highest T during copulation, and low concentrations of T during the egg-laying/incubation and nestling provisioning stages. Helpers appear physiologically capable of reproducing; their T concentrations equal that of male breeders. Helpers unrelated to the breeding female have higher T than helpers sharing a territory with their mother. Sexual inactivity by male helpers is best explained by behavioral suppression through the male helper's interactions with the breeding pair, which differ in accordance with his relatedness to the breeding female. Female breeder, male breeder, and male helper PRL did not differ and increased from the prebreeding stage through the copulation and egg-laying/incubation stages. During the nestling provisioning stage, male breeder and helper PRL declined, while female PRL continued to increase. Based on these results, we conclude that the physiological bases of alloparental behavior have not diverged from those that mediate parental behavior in this species.

Key words: testosterone, prolactin, delayed breeding, helping behavior, red-cockaded woodpecker, *Picoides borealis*

In many cooperative breeding systems among birds and mammals “helpers” delay breeding while they help raise young that are not their offspring (Emlen and Vehrencamp 1983; Brown 1987). Although the ultimate causes for delayed breeding and alloparental behavior in such species have been closely examined (Brown 1987; Koenig and Mumme 1990; Emlen 1991; Cockburn 1998), the proximate mechanisms underlying cooperative breeding behavior have not been thoroughly evaluated in many species. Reproductive behaviors in males of most avian and mammalian species are strongly correlated with elevated plasma testosterone concentrations (Wingfield and Farner 1993) while low concentrations of reproductive hormones appear to be the proximate bases of sexual inactivity in mammalian (Creel, Creel, Wildt, and Monfort 1992; Roberts, Zullo, Gustafson and Carter 1996) and some avian cooperatively breeding species (Reyer, Dittami, and Hall 1986; Mays, Vleck, and Dawson 1991; Schmidt, Bradshaw, and Follett 1991; Schoech, Mumme, and Moore 1991; Wingfield, Hegner, and Lewis 1991; Schoech, Mumme, and Wingfield 1996a; Poiani and Fletcher 1994). Parental behavior in mammals, birds, and fish is correlated with elevated plasma prolactin concentrations (reviewed in de Vlaming 1979; Buntin 1996). Prolactin appears to play a role in the proximate control of alloparental behavior in cooperatively breeding species (Vleck, Mays, and Dawson 1991; Schoech, Mumme, and Wingfield 1996b; Brown and Vleck 1998). How these hormones are involved in the mediation of sexual behavior and alloparental behavior of helpers is an important question in cooperative breeding research.

Before hormonal data were available, various authors suggested several proximate causes of the sexual inactivity of helpers (Rowley 1965; Brown 1978). For example, it has been hypothesized that male helpers exhibit low testosterone concentrations and remain sexually inactive because they are: (1) reproductively immature (delayed maturation, Brown 1978), (2) in poor body condition (physiological suppression, Schoech, Mumme and Wingfield 1997; Wingfield et al. 1991) or (3) not receiving appropriate stimulation from females (Poiani and Fletcher 1994; Schoech et al. 1996a). Alternatively, helpers may be reproductively capable, but may be prevented from reproducing because of social interference (behavioral suppression, Brown 1978; Mumme, Koenig, and Pitelka 1983; Emlen and Wrege 1988). Endocrine studies of cooperatively breeding birds provide little support for the delayed maturation or physiological suppression hypotheses (Reyer et al. 1986; Mays et al. 1991; Schmidt et al. 1991; Schoech et al. 1991, 1997; Wingfield et al. 1991; Poiani and Fletcher 1994). Currently, the hypotheses that best explain the absence of sexual behavior by male helpers are behavioral suppression and absence of appropriate stimulation (Reyer et al. 1986; Mays et al. 1991; Poiani and Fletcher 1994; Schoech et al. 1996b).

The theoretical framework for research on the proximate causes of alloparental behavior is less complete than that for delayed breeding. The mediation of incubation and care of nestlings by prolactin involves complex interplay with steroid hormones and environmental stimuli (Buntin 1996). Work on other cooperatively breeding species indicates that prolactin concentrations of male helpers may rise prior to exposure to nestlings (Schoech et al. 1996b), or they may differ from those of breeders by only increasing after stimulation from observing eggs and/or nestlings (Vleck et al. 1991).

We measured plasma concentrations of testosterone and prolactin in female breeders, male breeders, and male helpers in the red-cockaded woodpecker (*Picoides borealis*) during

different stages of the reproductive cycle. Red-cockaded woodpeckers are both socially and genetically monogamous (Haig, Walters, and Plissner 1994). They live in groups consisting of a single breeding female, a dominant breeding male and 0-4 subordinate, nonbreeding helpers (Ligon 1970; Walters et al. 1988; Khan and Walters 1997). Seventy percent of breeding groups do not have helpers and of the 30% of groups with helpers, most have only a single helper (Walters et al. 1988; Walters, Doerr, and Carter 1992). Helpers are usually male offspring of the breeding pair that delay dispersal and remain on their natal territory (Walters 1990). Because turnover of breeding females is higher than that of breeding males (Walters et al. 1988), helpers often are related to the male breeder but unrelated to the female breeder. Occasionally they help breeders to which they are unrelated (5%). Helpers that inherit breeding status on their natal territory (14% per year Walters et al. 1992) will pair with the resident female only if she is unrelated to them (Walters et al. 1988; Daniels and Walters in press). The individuals in a group forage peaceably together and defend the same territory. Helpers participate in defending territories, constructing and maintaining nest and roost cavities, incubating eggs, feeding and brooding nestlings, removing fecal sacs from the nest cavity, and feeding fledglings (Walters 1990; Jackson 1994).

We compared plasma testosterone concentrations of male helpers to those of male breeders to determine if red-cockaded woodpecker helpers had low plasma testosterone concentrations. We measured variables that reflect body condition to determine if helpers were in poorer body condition than breeders. To assess the physiological bases of alloparental behavior, we compared plasma prolactin concentrations of breeders with those of male helpers and examined the correlation between prolactin concentration and contribution to nestling care by individual birds.

METHODS

Study area and study species

The study population of red-cockaded woodpeckers is located in the Sandhills region of south-central North Carolina and contains approximately 250 groups of birds. The study area encompasses roughly 110,000 ha and includes portions of Fort Bragg Military Reservation (FB), the Sandhills Gamelands (SGL), and the resort towns of Southern Pines and Pinehurst (SOP). The birds are color-banded and a census is conducted annually during the breeding season. Each year all unbanded immigrant adults and nestlings are caught and banded. Reproduction is monitored by visiting trees with nest cavities every 9-14 days during the breeding period. Detailed descriptions of the study area and monitoring methods are found in Carter, Stamps, and Doerr (1983) and Walters, Doerr, and Carter (1988).

Blood sampling and field measurements

We collected blood samples from female breeders, male breeders, and male helpers during the prebreeding, copulation, egg-laying/incubation, and nestling provisioning stages of the annual cycle in 1997 and 1998, and from the copulation stage in 1999 (Table 1). The status (i. e., helper or breeder) assigned to an individual was based on several criteria described in detail in Walters et al. (1988). These include previous status, age, kin relationships among males, dominance status, and interactions with the breeding female. The accuracy of the criteria used to distinguish helpers from breeding males within a group has been verified through genetic techniques (Haig et al. 1994). Prebreeding and copulation stages were determined from previous data from the Sandhills red-cockaded woodpecker population. Prebreeding is assigned to any sample collected greater than 5 weeks prior to egg-laying. Copulation typically begins 5-6 weeks prior to egg-laying (Jackson 1994) and egg-laying usually begins the third week (± 1 week) of April in the Sandhills population (Walters et al. 1988). The egg-laying/incubation and nestling provisioning stages were determined by locating nests and checking their contents every 9-14 days. We located nests by checking for birds flushing from tree cavities during the day. If a bird flushed, we climbed the tree and checked the cavity for the presence of eggs. Clutch size is 3-4 eggs (mean = 3.27 eggs, LaBranche and Walters 1994). The estimated date the first egg was laid was calculated by aging nestlings using the criteria in Ligon (1970). We assumed a single egg is laid each day and the eggs are incubated for 11 days following laying of the last egg (LaBranche and Walters 1994).

Birds were captured in their roosting cavities by placing a net attached to a telescoping pole over the cavity entrance and banging the trunk of the tree to flush the bird into the net. To avoid diel variation in hormone concentrations, all birds were sampled in the evening from dusk to 2200. Handling time was measured from the time the net was placed over the cavity entrance to the time a blood sample was collected: handling time was 11 ± 0.31 minutes (mean $\pm$ SE: n=171).

Blood samples (approximately 300 μ l) were collected in heparinized micro-hematocrit tubes from wing veins (vena ulnaris), punctured with a 26 gauge needle. Hematocrit tubes were sealed with S/P Miniseal (Baxter) and placed on ice in a cooler. Samples were centrifuged within 5 h of collection, the plasma was separated from the red blood cells and frozen in O-ring sealed vials. Frozen samples were transported to Virginia Tech and stored at -80°C until analysis. To assess body condition we measured wing-chord length (mm) and body mass (g). We noted the presence or absence of a brood patch because brood patch development is dependent on both circulating steroid hormones and prolactin in most avian species (Buntin 1996). We qualitatively correlate our observations of brood patches with observed seasonal patterns of plasma testosterone and prolactin concentration.

Hormone analyses

Plasma testosterone (T) concentrations were measured by radioimmunoassay (RIA) following extraction in diethyl ether, drying under nitrogen gas, reconstitution in 10% ethyl

acetate in iso-octane and chromatographic separation on diatomaceous earth/glycol/water micro-columns. Column chromatography was used to remove neutral lipids and separate steroid hormones (methods from Wingfield and Farner 1975; Ball and Wingfield 1987). Neutral lipids were removed in 1.5 ml 100% iso-octane, 5- α -dihydrotestosterone was removed in 2.0 ml 10% ethyl acetate in iso-octane and testosterone was collected in 2.7 ml 20% ethyl acetate in iso-octane. The testosterone fraction was dried under nitrogen gas and reconstituted in 500 μ l of buffer. To determine hormone recovery, 2000 cpm radiolabeled testosterone was placed in each sample prior to extraction and chromatography.

The reconstituted testosterone fraction was divided into duplicate samples in the RIA, and a 50 μ l aliquot was counted to measure recovery of testosterone. Testosterone concentrations determined in the RIA were then corrected for individual column recovery ($91.9\% \pm 0.52\%$, mean $\pm$ SE). The standard curves ranged from 0.02 ng/ml to 0.50 ng/ml. Sample plasma testosterone concentrations were measured in seven assay runs. Each assay run included four distilled water blanks and six replicates of the 0.10 ng/ml standard. If the water blanks were not equivalent to the standard without hormone in the RIA, the blank measurements were averaged and subtracted from each sample value before measurements were adjusted for recovery and sample volume. The inter- and intra-assay coefficients of variation for testosterone were 16.9% ($n = 7$ assay runs), and $12.8\% \pm 2.9\%$ (mean $\pm$ SE: $n = 7$ runs, six standard replicates within each run), respectively.

Radiolabeled testosterone was purchased from DuPont New England Nuclear (Wilmington, DE; T specific activity = 121 Ci/mmol). Acid-washed diatomaceous earth was purchased from Sigma (Celite D-5384). Testosterone standards were generously donated by MS Khan (St. Luke's Roosevelt Hospital, NY, NY). Goat antibody raised against rabbit testosterone was purchased from Wien Laboratories (Succasunna, NJ).

Plasma prolactin (PRL) was measured with a dove prolactin radioimmunoassay (P. J. Sharp and R. T. Talbot, unpublished). A cDNA encoding ring dove (*Streptopelia risoria*) prolactin (Howarth, Goldsmith, and Sharp 1994) was used to make recombinant-derived dove prolactin and to develop a radioimmunoassay as described by Talbot and Sharp (1994). The assay showed parallelism with three pools of woodpecker plasma selected for predicted high, intermediate and low concentrations of prolactin (Fig. 1). Woodpecker samples were run in duplicate. Individual sample volumes varied, but were brought up to a constant volume of 100 μ l with RIA buffer. The standards ranged between 0.06 - 125 ng/tube. All samples were run in a single assay with intra-assay variation of 6.2% ($n = 3$).

Nestling provisioning behavior

To examine the relationship between an individual's contribution to nestling care and its plasma prolactin concentration, nests with 10-16 day old young were observed for 2 hours on the afternoon (1200-1800) of the evening capture and sampling. We observed 13 nests in 1997 and 17 nests in 1998. Individuals were identified by their unique color band combination using a spotting scope from a distance of approximately 20m. The rate that an adult fed nestlings

(nestling provisioning rate) was measured as the number of times an individual fed nestlings per hour. A nest visit was tallied as a feeding event if the individual entered the nest cavity with food in its bill and left the cavity with an empty bill.

Statistics

Plasma hormone data were logarithm transformed as required to control for variance and to achieve an approximate normal distribution (Zar 1996). Seasonal testosterone and prolactin data were first analyzed with a three-factor ANOVA with year, reproductive stage, and status (i. e., helper male, breeder male, or breeder female) as factors. If main effects were found, multiple pair-wise comparisons were made with Tukey's post hoc test.

To assess the effects of handling time on plasma hormone concentration, we regressed plasma hormone concentration against handling time for each status during each of the reproductive stages. Residual analysis was used to assess the relationship between status and body condition. Residuals from a regression of body mass on wing chord were analyzed with an ANOVA using status as a class variable. Whether plasma testosterone concentrations of male helpers that lived in a group in which they were unrelated to the breeding female differed from those of male helpers that were in a group in which the breeding female was their mother was determined with a Mann-Whitney U-test because of small sample size.

The nestling provisioning rate for each adult was square-root transformed (Zar 1996) to meet the assumption of normally distributed data. A one-way ANOVA was used to examine whether the status of each adult influenced its nestling provisioning rate. We used Spearman's rank correlation to assess whether prolactin concentration was correlated with rate of nestling provisioning or with external stimuli (number of eggs/nestlings, nestling age) on the day of blood sampling.

Non-parametric statistics (Mann-Whitney U, Spearman rank correlation) were performed using Minitab 10.5; SAS 6.12 statistical software was used for all parametric tests (*t*-test, regression, ANOVA). Significance level for all tests was set at $p \leq 0.05$. Means are shown with standard errors unless otherwise noted.

RESULTS

Body condition

The linear regression model of body mass as a function of wing-chord length was significantly different from zero (mass = $0.272[\text{chord length}] + 16.22$; $F_{1,165} = 8.17$, $p = 0.005$). Body condition did not differ among male helpers, male breeders and female breeders ($F_{2,164} = 1.45$, $p = 0.24$).

Testosterone

Year, status, and reproductive stage significantly influenced plasma testosterone concentrations (Table 2). Female testosterone concentrations were significantly lower than those of male breeders and helpers (Tukey's, $p < 0.05$). Therefore, in subsequent tests, males and females were analyzed separately.

Males: Male breeders and male helpers had equivalent plasma concentrations of testosterone ($F_{1,100} = 1.19$, $p = 0.279$). Plasma testosterone concentrations were significantly influenced by year ($F_{2,100} = 6.69$, $p = 0.002$) and reproductive stage ($F_{3,100} = 16.32$, $p = 0.0001$; Fig. 2). Plasma testosterone concentrations were higher in 1997 than in 1998 and 1999 ($p < 0.05$, Tukey's). Among male breeders and male helpers plasma testosterone concentrations were significantly higher during the copulation stage than during the prebreeding, egg-laying/incubation, and nestling provisioning stages ($P < 0.05$, Tukey's). Interactions between status, stage, and year were not significant. Male helpers unrelated to the breeding female had higher plasma testosterone concentrations than helpers related to the breeding female ($U = 173.0$, $p = 0.03$; Fig. 3).

Females: Female plasma concentrations of testosterone did not vary across breeding season stages ($F_{3,42} = 1.85$, $p = 0.1526$) but varied between years ($F_{1,42} = 8.88$, $p = 0.0048$; Fig. 2). Concentrations in samples collected in 1997 were higher than those in samples collected in 1998 (Tukey's $p < 0.05$).

Annual variation in testosterone: Between-year differences in testosterone concentration were the results of a few high values from samples collected from male breeders and helpers during the copulation stage in 1997 (Fig. 2). Testosterone concentration might change in relation to the time of laying and birds were sampled closer to egg laying in 1997 than in 1998 and 1999 (Table 1). However, the data we collected in 1999 to test this idea do not support it. The highest testosterone concentration measured in 1997 occurred 20-25 days prior to egg-laying (Fig. 4). Samples collected 20-25 days prior to egg-laying in 1999 did not exhibit similarly high concentrations of testosterone.

Prolactin

Plasma prolactin concentrations did not vary between years, therefore, all subsequent analyses pooled samples from 1997 and 1998. Prolactin concentrations increased as the breeding season progressed (Table 3). Prolactin concentrations were lowest during the prebreeding stage and increased through the copulation and egg-laying/incubation stages (Tukey's test: prebreeding < copulate < lay/incubation, $p < 0.05$ for all comparisons; Fig. 5). During the nestling

provisioning stage, female prolactin concentration continued to increase, while the prolactin concentrations of male breeders and helpers declined (Fig. 5). Because the interaction between status and reproductive stage approached significance (Table 3), we conducted a post-hoc ANOVA of data from the nestling provisioning stage. This analysis revealed that females had significantly higher prolactin concentrations than either male breeders or helpers ($F_{2,31} = 10.61$, $p < 0.0001$; female breeders > male breeders = male helpers, Tukey's, $p < 0.05$).

Brood patch

Each member of a group developed a large brood-patch during the breeding season. During the copulation period, while prolactin concentrations were increasing and testosterone was peaking (in males); female breeders, male breeders, and male helpers were observed with completely defeathered and vascularized brood-patches that extended from the neck to the cloaca. The brood-patch was oedemous during the incubation stage when plasma prolactin concentrations were high and brood-patches of helpers appeared identical to those of breeders.

Prolactin and nestling provisioning behavior

Whether an individual was a breeder or helper significantly affected the rate at which an individual provisioned nestlings ($F_{2,86} = 6.73$, $p = 0.002$; Fig. 6). Male and female breeders fed nestlings at equivalent rates, whereas male helpers provisioned nestling at significantly lower rates than breeders of either sex (Tukey's, $p < 0.05$). During the nestling provisioning stage, when plasma prolactin concentrations are high in all group members, the rate that each adult fed nestlings did not correlate with its prolactin concentration (Fig. 7): female breeders (Spearman's $\rho = -0.540$, $n = 11$, $p > 0.05$), male breeders (Spearman's $\rho = -0.301$, $n = 9$, $p > 0.20$), and male helpers (Spearman's $\rho = 0.073$, $n = 11$, $p > 0.50$). In fact, the trend among breeders was toward less feeding by individuals with higher prolactin concentrations.

The number of nestlings did not correlate with prolactin concentration in female breeders (Spearman's $\rho = -0.473$, $n = 11$, $p > 0.10$), male breeders (Spearman's $\rho = 0.067$, $n = 9$, $p > 0.50$), or male helpers (Spearman's $\rho = 0.095$, $n = 11$, $p > 0.50$). However, nestling age was significantly correlated with prolactin concentration in female breeders (Spearman's $\rho = 0.647$, $n = 11$, $p < 0.05$) and tended to be in male breeders (Spearman's $\rho = 0.577$, $n = 9$, $p > 0.10$). No relationship between prolactin concentration and nestling age was evident among male helpers (Spearman's $\rho = 0.055$, $n = 11$, $p > 0.50$). Plasma prolactin concentration does not significantly correlate with the number of eggs in a clutch in female breeders (Spearman's $\rho = -0.257$, $n = 12$, $p > 0.20$), male breeders (Spearman's $\rho = -0.051$, $n = 13$, $p > 0.50$), or male helpers (Spearman's $\rho = -0.514$, $n = 12$, $p > 0.05$).

Hormone concentration and handling time

Handling time did not influence plasma hormone concentrations of male or female breeders during any stage of the reproductive cycle. However, plasma testosterone concentration showed small but significant decreases as handling time increased in male helpers sampled during the incubation stage ($\log T = -0.08[\text{handling time}] + 0.55$; $F_{1,13} = 5.70$, $p = 0.03$). Prolactin significantly increased with handling time in male helpers during the prebreeding stage ($\log PRL = 0.04[\text{handling time}] + 0.15$; $F_{1,8} = 5.94$, $p = 0.04$) and incubation stage ($\log PRL = (0.02[\text{handling time}] + 1.08$; $F_{1,11} = 8.01$, $p = 0.02$).

Handling time may influence our estimates of mean hormone concentration by increasing variability and biasing the mean. The most likely effect of handling time is to obscure our ability to detect differences between male breeders and male helpers because handling time increases variability around the mean. We argue that our overall interpretation of the hormone results are unchanged by the effect of handling time on plasma hormone concentrations in male helpers because male breeders and male helpers exhibit equivalent hormone concentrations during other reproductive stages, when no effects of handling time on hormone concentration were detected.

DISCUSSION

Behavioral suppression of reproduction by helpers

Because the delayed maturation, physiological suppression, and absence of stimulation hypotheses predict that helpers will exhibit testosterone concentrations lower than those of male breeders, our results are most consistent with the behavioral suppression hypothesis. Additionally, previous observations of helpers that assume a vacant breeding position and immediately reproduce are inconsistent with the delayed maturation and physiological suppression hypotheses (Walters et al. 1988). Observations of one-year old male red-cockaded woodpeckers successfully reproducing (Walters 1990) support the conclusion that delayed maturation does not explain the absence of sexual activity by helpers in this species. Our data also do not support the physiological suppression hypothesis because helper and breeder body conditions were equivalent. Our finding that unrelated male helpers have higher plasma testosterone concentrations than helpers that share a territory with their mothers suggest that this differences results from social interactions, either male-male interaction, male-female interaction, or a combination of the two (challenge hypothesis; Wingfield, Hegner, Dufty, and Ball 1990). Perhaps male helpers related to the breeding female exhibit lower testosterone concentrations because they are not involved, or are less involved in intra-group social interactions that are either sexually stimulating or agonistic (also see Schoech et al. 1996a). We propose that the mechanism that prevents inbreeding between female breeders and male helpers is that female breeders do not exhibit sexual behavior when they interact with related male helpers. The social context in which female breeders make dispersal decisions supports this hypothesis. For example, when a male helper inherits a territory, if the female breeder is unrelated to the male helper she stays, but if she is his mother then she disperses (Walters et al. 1988; Daniels and Walters in press).

The absence of sexual activity by male helpers that are unrelated to the breeding female also might result from male-male interactions and/or because the breeding female is not receptive to copulation attempts by the male helper. That male-male interactions may inhibit reproductive activity by helpers is supported by the observation that breeding males tend to follow helper males during the copulation stage and the two males sometimes interact aggressively (Lape 1990). Female breeders also appear to be unreceptive to approaches by unrelated helpers during the copulation period. For example, Lape (1990) observed a subordinate male helper approach a female breeder and 'nudge her rump'. In response, the female became noisy and moved away. The effectiveness of the mechanism, which is still unknown, that prevents subordinate male red-cockaded woodpecker helpers from reproducing suggests female involvement rather than behavioral suppression through male-male interaction alone. Although numerous copulations between breeders have been observed (Lape 1990), helpers have never been observed to copulate with a female breeder (in contrast to copulation of breeders, see below), despite extensive observational sampling (Lape 1990; Walters 1990). Further, genetic studies confirm the lack of extra-pair paternity in this species (Haig, Belthoff, and Allen 1993; Haig et al. 1994).

Testosterone appears to mediate the expression of male sexual behavior in the other cooperatively breeding species in which plasma testosterone concentrations have been examined. For example, sexually active male breeders have testosterone concentrations that are consistently higher than those of reproductively inactive male helpers in the bell miner (Poiani and Fletcher 1994), Florida scrub-jay (*Aphelocoma coerulescens*, Schoech et al. 1991; 1996a), and white-browed sparrow weaver (*Plocepasser mahali*, Wingfield et al. 1991). In contrast, presumably sexually active male helpers exhibit plasma concentrations equivalent to those of male breeders in the pied kingfisher (Reyer et al. 1986), Harris' hawk (Mays et al. 1991), and Australian magpie (Schmidt et al. 1991). In the Harris' hawk, subordinate male helpers unrelated to the breeding female have been observed to copulate, unsuccessfully, with the breeding female (Mays et al. 1991). In the pied kingfisher, helper males that are unrelated to the breeding female are chased out of the territory by the breeding male when the female breeder is fertile (Reyer et al. 1986). This suggests that unrelated helper males will mate with the breeding female if given a chance. Red-cockaded woodpecker helpers are unique in that they exhibit a combination of high plasma testosterone concentrations but no evidence of sexual activity.

Seasonal and annual patterns of testosterone concentration

In breeder and helper male red-cockaded woodpeckers, the seasonal profile of testosterone concentration (see Fig. 2) is similar to that of other monogamously breeding species in which males exhibit parental care (Wingfield and Farner 1993; Beletsky 1995; Buntin 1996). These results suggest that male helpers, regardless of their relatedness to the breeding female, respond to environmental cues (e.g., photoperiod). These cues initiate an endocrine cascade resulting in gonadal recrudescence and an initial increase of testosterone concentration comparable to that of male breeders. The seasonal pattern of testosterone secretion also resembles that of year-round territory holders such that the absolute increase in testosterone during the breeding season is of lower magnitude than in seasonal migrants. Seasonal migrants establish and defend new territories each year, resulting in high levels of male-male interactions

and resulting in high plasma concentrations of testosterone (Wingfield et al. 1990; Wingfield and Hahn 1994).

The annual variation observed may be a result of the idiosyncrasies of the particular individuals sampled in 1997. Three of the four samples that had atypically high concentrations of testosterone (a breeder, a related helper and an unrelated helper, Fig. 2) were collected from the same group (SGL E04). The birds in this group may have experienced some event that triggered increased production of testosterone just prior to sampling; perhaps intra-group or inter-group conflict or the wild-fire that burned part of their territory that day! It is interesting to note that the oldest unrelated helper ($T = 8.00$ ng/ml) was observed intruding in a neighboring group during the breeding season in 1997.

Prolactin, parental behavior, and alloparental behavior

Our results are consistent with the hypothesis that proximate control of alloparental behavior of red-cockaded woodpecker helpers is mediated by the same factor(s) that control parental behavior of breeders. Like male breeders, male helpers exhibit parental behavior after a decline in testosterone, and an increase in prolactin, a pattern that matches the classic avian reproductive cycle paradigm first described in detail in the ring dove (Cheng 1979). Helpers, like breeders, develop brood patches and brood patch development in male helpers is likely to be dependent on both prolactin and sex steroids, as it is in most breeding birds (Buntin 1996). Helpers also incubate eggs and incubation bouts are divided equally among group members (Khan and Walters, unpublished data). During egg-laying/incubation, male helpers have concentrations of prolactin equivalent to those of male and female breeders. This is consistent with studies on other species that demonstrate that prolactin concentrations correspond to the amount of incubation performed (*Cygnus atratus*, Goldsmith 1982; *Diomedea* spp., Hector and Goldsmith 1985; *Sula capensis*, Hall 1986; *Calidris pusilla*, Gratto-Trevor, Oring, Fivizzani, El Halawani and Cooke 1990). As with breeders, the rate of nestling provisioning by helper males was not directly related to prolactin concentration. Despite the lack of a one-to-one relationship between prolactin and parental or alloparental behavior, one cannot rule out the possibility that these behaviors occur whenever an individual whose prolactin has reached a threshold concentration is exposed to the appropriate stimuli (i. e. eggs, young or both).

In birds, interactions between members of a breeding pair are usually important in synchronizing reproductive activities (Wingfield and Moore 1987). The expression of alloparental behavior by male helpers may be synchronized with the breeding cycle of the breeders because helpers observe the behavioral interactions of the breeding pair. Copulation in the red-cockaded woodpecker is conspicuous, prolonged and frequent, and occurs for several weeks prior to egg-laying (Lape 1990). Females appear to initiate copulation by calling to the male (Jackson 1994). Frequent copulation for a month prior to egg-laying may function to strengthen the pair bond and synchronize the activities of the breeders, while concomitantly providing information to the helpers. Since group members travel together throughout the day, helpers witness nearly every copulation.

Evolution of alloparental behavior

Evolutionarily, helping behavior is a derivation of parental behavior (Brown 1987). Cooperative breeding is thought to be a derived trait in red-cockaded woodpeckers because helping behavior is not obligatory (Walters 1990) and cooperative breeding is only represented by this single species within the genus *Picoides*. Therefore, the results of our study may more accurately reflect the original physiological bases of alloparental behavior, prior to modification by natural selection, than studies of other cooperatively breeding species, in which helping behavior has existed within the species' lineage for a longer period of time. The finding that the physiological bases of parental behavior and alloparental behavior are the same is especially relevant to the debate over whether alloparental behavior is a non-adaptive trait maintained as a by-product of selection on parental behavior (Jamieson and Craig 1987; Jamieson 1989) or is an adaptive trait maintained by fitness benefits (Emlen 1991). If helping behavior is a non-adaptive trait then the physiological bases of alloparental behavior will not have diverged from that of parental behavior. However, if helping behavior is an adaptive trait, then the physiological bases of parental behavior are expected to be modified by natural selection to facilitate the expression of alloparental behavior (Vleck et al. 1991).

In some cooperatively breeding species, the physiological bases of alloparental behavior may have diverged from that of parental behavior. For example, plasma prolactin concentration was positively correlated with provisioning rate among Florida scrub-jay helpers, but no relationship was evident among breeders (Schoech et al. 1996b). Vleck et al. (1991) observed that the prolactin concentration of Harris' hawk male and female breeders declined after hatch despite continued expression of parental behavior, while prolactin concentrations increased in male helpers during the nestling provisioning stage. These results suggest that natural selection had modified the physiological basis of parental behavior in helpers. If the origin of alloparental behavior is correctly represented by the proximate mechanism we observe in the red-cockaded woodpecker, and the mechanisms observed in Florida scrub-jays (Schoech et al. 1996) and Harris' hawks (Vleck et al. 1991) are derived from these origins, then alloparental behavior has been retained despite decoupling from other elements of the proximate control of reproductive behavior. This suggests that helping behavior is adaptive.

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TABLE 4.1: Date and mean number of days (mean $\pm$ SD) before/after clutch initiation for each sampling stage. Blood samples were collected during the following stages: (1) prebreeding, when no breeding activity was evident; (2) copulation, the 5-6 weeks preceding clutch initiation (Jackson 1994); (3) incubation, time period between clutch initiation and hatching, and (4) nestling provisioning, 10-16 days after hatching.

Stage		1997	1998	1999
Prebreeding	Dates	17–22 February	9-12 February	
	Days before clutch initiation	-65 ± 7	-76 ± 10	
Copulation	Dates	14-25 April	24-28 March	31 March-5 April
	Days before clutch initiation	-11 ± 8	-30 ± 5	-30 ± 7
Lay/Incubation	Dates	26 April –8 May	23 April- 6 May	
	Days after clutch initiation	9 ± 4	6 ± 3	
Nestling provisioning	Dates	8-21 May	6-20 May	
	Days after clutch initiation	26 ± 2	26 ± 2	

TABLE 4.2: Relationship between plasma testosterone and status (female breeder, male breeder, male helper), year, and reproductive stage (prebreeding, copulation, lay/incubation, nestling provisioning) evaluated by ANOVA.

	df	F	P
STATUS	2	4.17	0.0176*
YEAR	1	17.41	0.0001*
STAGE	3	18.77	0.0001*
STATUS*YEAR	2	0.37	0.6906
STATUS*STAGE	6	2.69	0.0171*
YEAR*STAGE	3	2.56	0.0580
STATUS*YEAR*STAGE	3	0.80	0.5724

df is numerator degrees of freedom.

Asterisks signify statistical significance at 0.05 alpha level

TABLE 4.3: Relationship between plasma prolactin concentration and status (female breeder, male breeder, male helper), year, and reproductive stage (prebreeding, copulation, lay/incubation, nestling provisioning) evaluated by ANOVA.

	df	F	P
STATUS	2	1.13	0.3278
YEAR	1	0.01	0.9049
STAGE	3	102.78	0.0001*
STATUS*YEAR	2	0.52	0.5964
STATUS*STAGE	6	2.18	0.0502 ^a
YEAR*STAGE	3	1.62	0.1896
STATUS*YEAR*STAGE	6	1.34	0.2393

df is numerator degrees of freedom

Asterisks signify statistical significance at 0.05 alpha level

^a Approaching significance

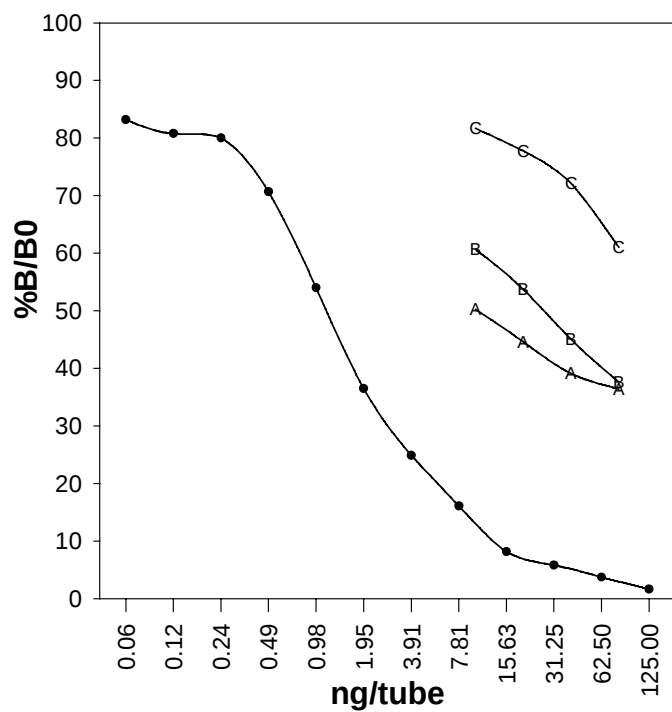


Fig. 4.1: Prolactin standard curve using recombinant chicken prolactin antibody and parallelism with dilution series of three red-cockaded woodpecker plasma pools with high (A), intermediate (B) and low (C) concentrations of prolactin.

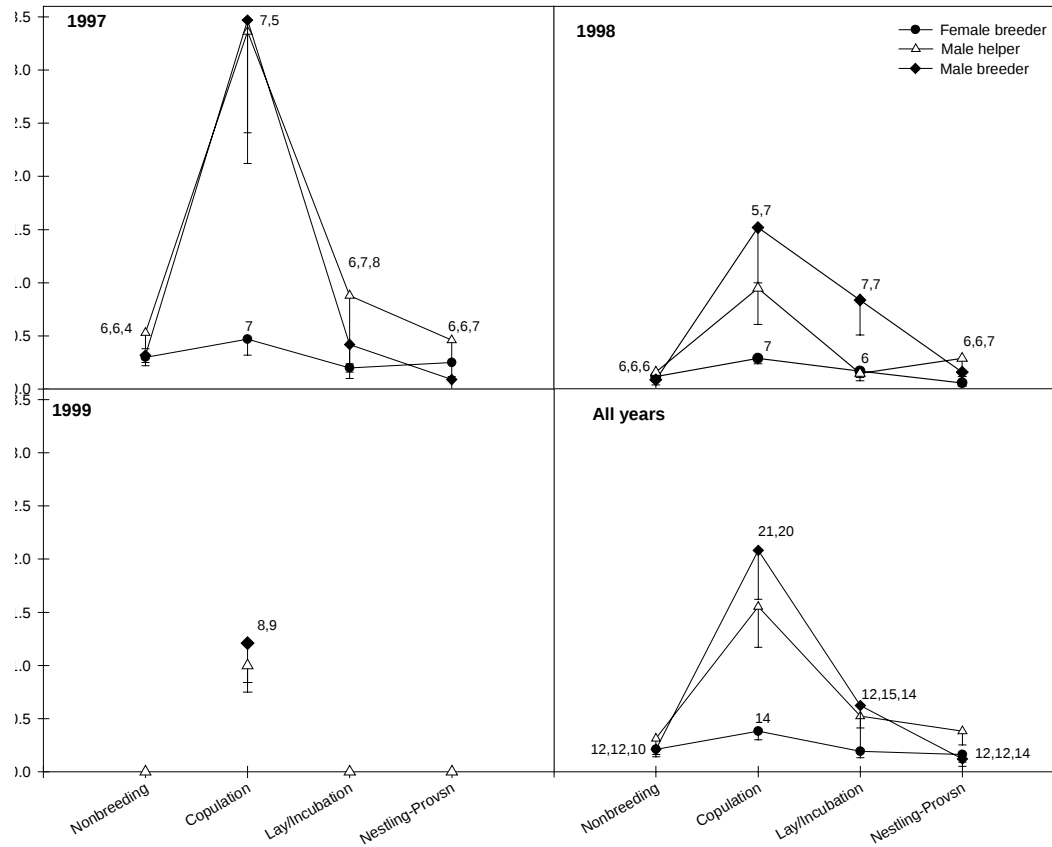


Fig. 4.2: Plasma testosterone concentrations (mean $\pm$ SE) of female breeders, male breeders and male helpers in 1997, 1998, 1999 and all years combined. Sample sizes are indicated on the plots; where means are too close to distinguish visually, sample sizes are listed in the following sequence: female breeder, male breeder, male helper; e.g. 6, 6, 4 during 1997 prebreeding stage represents 6 female breeders, 6 male breeders and 4 male helpers. Note: only males were sampled in 1999 during the copulation stage.

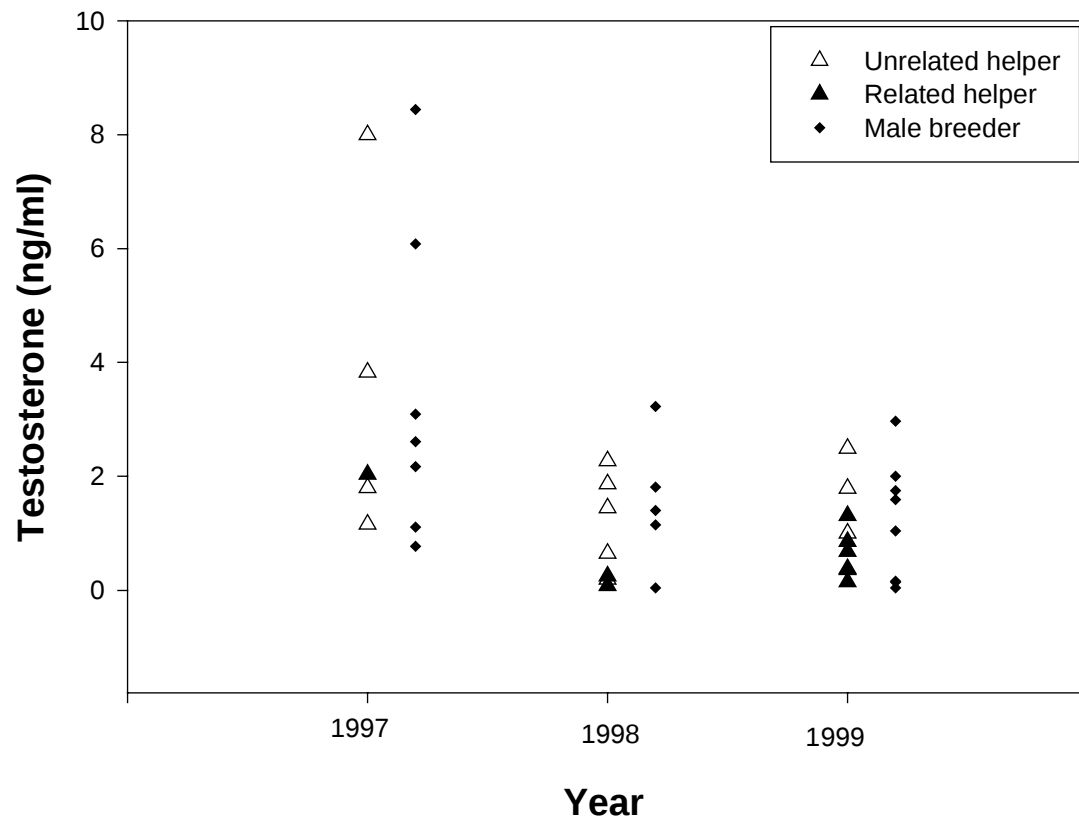


Fig. 4.3: During the copulation stage, plasma testosterone concentrations of helpers unrelated to the female breeder are higher than those of helpers related to the female breeder. Plasma testosterone values for male breeders are plotted to the right of the male helper values to indicate that all helpers have testosterone concentrations equivalent to those of male breeders. Each point represents an individual.

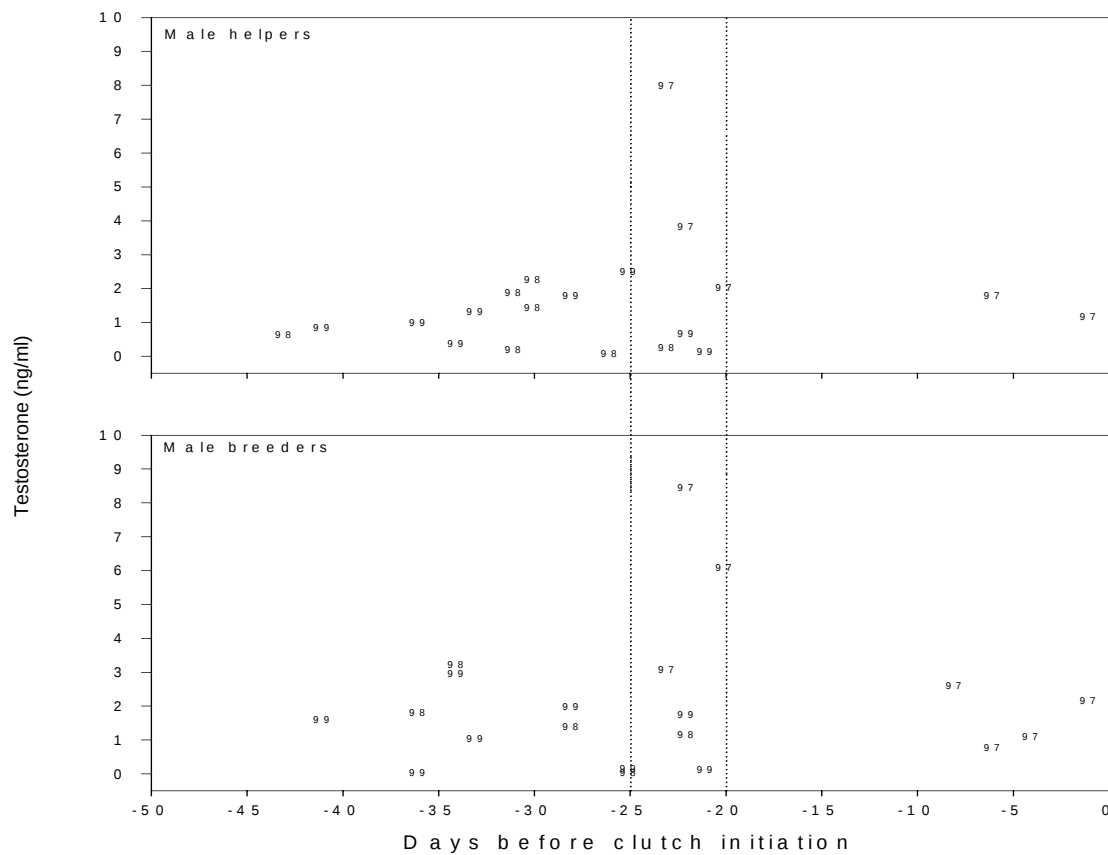


Fig. 4.4: Plasma testosterone concentrations of male breeders and male helpers plotted as a function of days before clutch initiation during the copulation stage. Symbols represent the year in which the sample was collected. The time period between 20-25 days before egg-laying is highlighted to illustrate that high testosterone concentrations measured at that time in 1997 were not duplicated in other years.

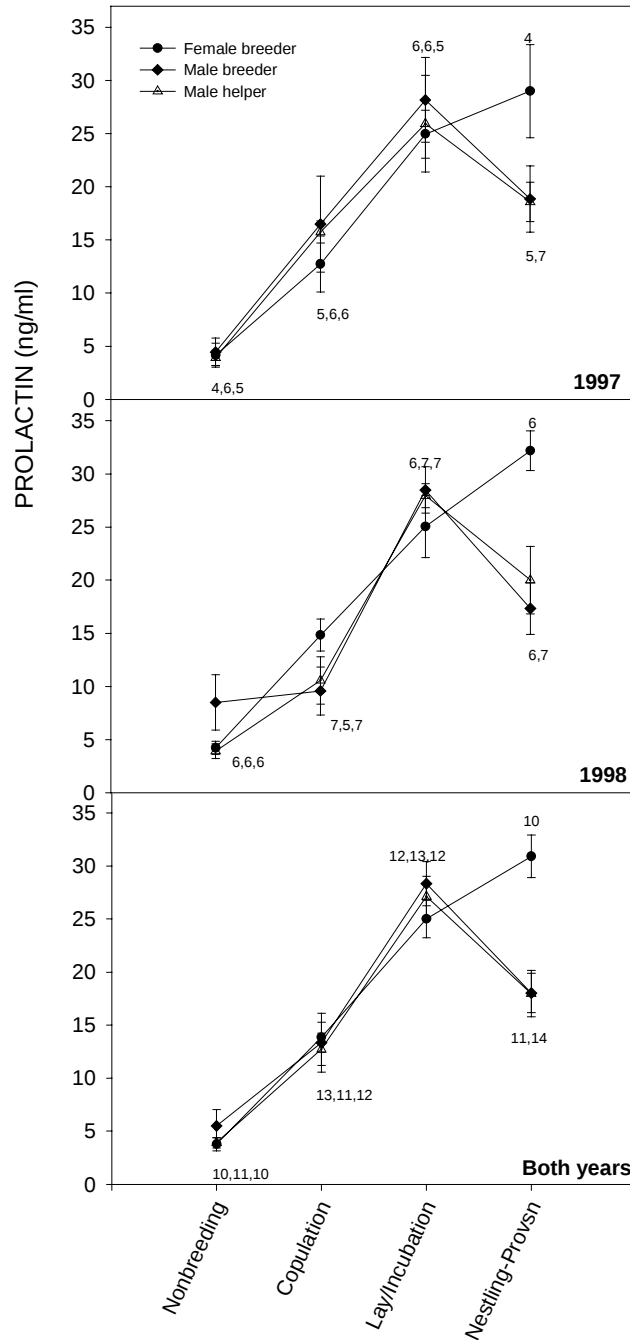


Fig. 4.5: Plasma prolactin concentrations (mean $\pm$ SE) of female breeders, male breeders and male helpers in 1997, 1998 and both years combined. Sample sizes are indicated on the plots; where means are too close to distinguish visually, sample sizes are listed in the following sequence: female breeder, male breeder, male helper; e.g. 4, 6, 5 during 1997 prebreeding stage represents 4 female breeders, 6 male breeders and 5 male helpers.

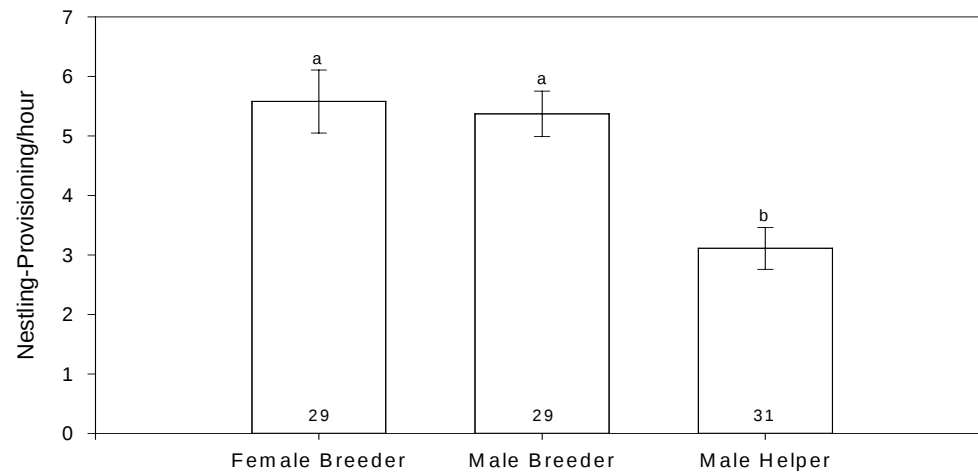


Fig. 4.6: Rates of nestling provisioning (mean $\pm$ SE) by female breeders, male breeders and male helpers in red-cockaded woodpeckers. Sample sizes are indicated at the bottom of each bar and small case letters indicate which comparisons were significantly different ($p < 0.05$).

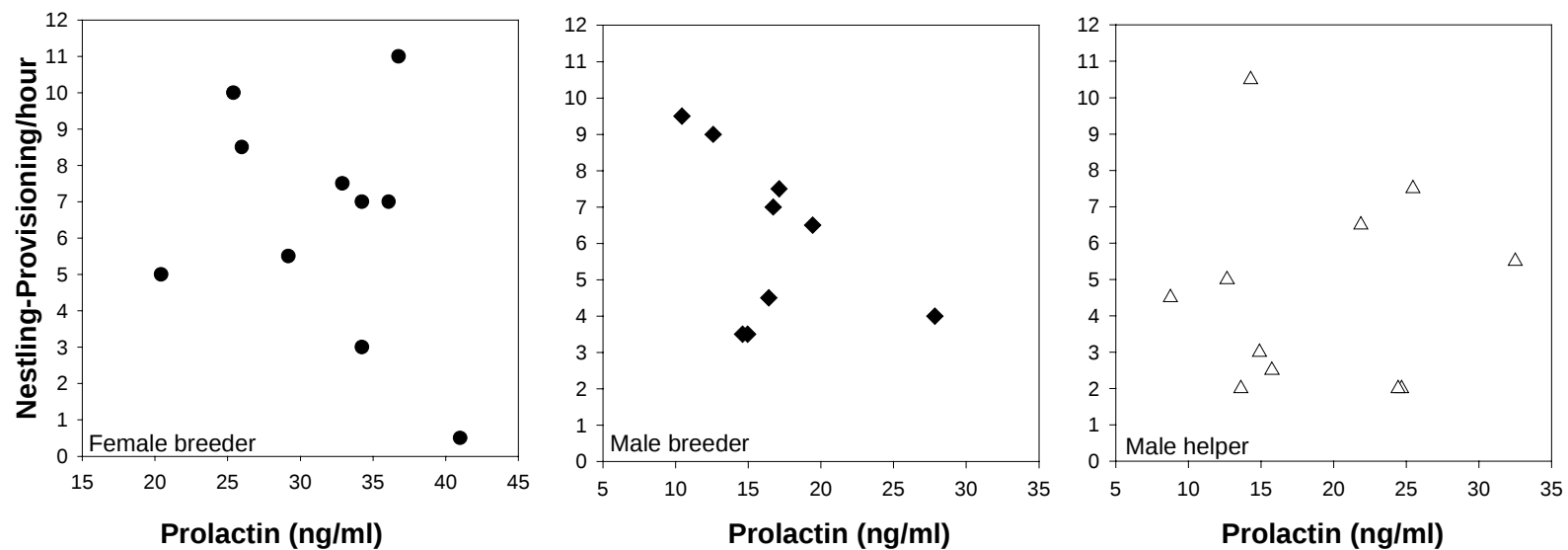


Fig. 4.7: Nestling provisioning rate of female breeders, male breeders and male helpers do not vary as function of plasma prolactin concentration. Symbols represent individual sample values.

Chapter 5

Summary and conclusions

My dissertation focuses on determining the factors that contribute to the maintenance of helping/alloparental behavior in cooperatively breeding birds. Although, cooperative breeding has been studied in the red-cockaded woodpecker for over twenty years, the ultimate and proximate factors that mediate helping behavior are not well understood. Below I summarize results from tests of two possible benefits of helping behavior, future indirect benefits through enhancement of breeder survival (Chapter 2) and future direct benefits through reciprocal exchange of helping (Chapter 3).

Although the ultimate hypotheses to explain delayed breeding/sexual inactivity and alloparental behavior have been well studied by myself and others in the red-cockaded woodpecker, the proximate mechanisms underlying these behaviors are poorly understood. In Chapter 4, I examine the proximate causes of delayed breeding and helping behavior by measuring testosterone and prolactin concentrations in the plasma of female breeders, male breeders and male helpers during different stages of the reproductive cycle. Below I summarize my results and conclusions from this work.

Helper effects on breeder survival

In Chapter 2, I determined two mechanisms by which helpers gain future indirect fitness by enhancing the survival of breeders who produce young related to the helper in subsequent breeding seasons. Helping behavior augments group size by increasing the production of fledglings (Heppell et al. 1994). It follows that breeders may have enhanced survival because of the benefit of living in large groups (e.g. enhanced predator detection, enhanced foraging efficiency, safety in numbers). In Chapter 2 I show that survival of breeders increases as the number of fledglings on the territory increases. The positive relationship between breeder survival and the number of fledglings is robust even when I controlled for territory quality. Therefore, I conclude that helping behavior reduces breeder mortality, through the general benefits of group living, by augmenting the production of fledglings and thereby increasing group size.

In addition, helpers increase group size through their own presence. I show that the survival of breeders increases as the number of adults on a territory increases. This survival benefit may be attributed to the benefits of group living and/or because breeders reduce their reproductive workload in the presence of a helper. Breeders who expend less energy during the reproductive season may be more likely to survive to reproduce again, or they may be more productive when they breed again. My data show that breeders reduce their workload in the presence of a helper by decreasing time spent incubating and provisioning nestlings. Whether survival of breeders is enhanced because of the presence of a helper (group living) or reduced workload is not clear from the results. These two mechanisms are not mutually exclusive and both may operate to reduce breeder mortality.

To date, no direct fitness benefits have been demonstrated to accrue to red-cockaded woodpecker helpers because of alloparental behavior. Helpers do not gain skills that improve their reproduction when they become breeders (Khan and Walters 1997). Nor do helpers receive preferential assistance from previous recipients of aid once they become breeders (Chapter 3). Furthermore, several future direct fitness benefits are not likely to be gained by red-cockaded woodpecker helpers, because the relevant events occur too rarely in the study population to provide a significant benefit. It is unlikely that helping behavior increases a helper's probability of breeding through territory acquisition, either through budding or joint dispersal, or his access to mates. The hypothesis that helping behavior is a payment to the breeder for access to limited resources remains to be examined.

Reciprocal exchange of helping

In Chapter 3, I determined that red-cockaded woodpecker helpers do not gain future direct fitness benefits by receiving assistance, once they become breeders, from young they helped raise. First, I determined the expected frequency of reciprocal exchange of helping based on population specific survival rates and status transition probabilities. In two of three populations studied, observed probabilities of reciprocal exchange of helping were higher than expected (2%). These results may be explained by (1) preferential helping of kin, (2) high rates of retention of young males as helpers on high quality territories or, (3) preferential aid of former care-givers. When I restricted the analysis to helpers unrelated to the young they help raise, which controls for preferential helping of kin and partially controls for territory quality, reciprocity occurred no more often than expected. Therefore, I found no support for helping being maintained via reciprocity in this species.

Behavioral suppression of reproduction by helpers

In Chapter 4, I conclude that sexual inactivity by red-cockaded woodpecker helpers is likely mediated by behavioral suppression and cannot be attributed to low testosterone concentrations. Male breeders and helpers have equal testosterone concentrations that are low during the nonbreeding stage, peak during copulation and decline during the egg-laying/incubation and nestling provisioning stages. Helpers unrelated to the breeding female have higher testosterone concentrations than helpers related to her. Sexual inactivity by male helpers is best explained by behavioral suppression through the helper's interactions with the breeding pair, which differ according to his relatedness to the breeding female. Male may be prevented from reproducing because the female is unreceptive to sexual advances by helpers, and/or because of agonistic interactions between the male helper and the dominant male breeder.

Prolactin likely mediates both parental and alloparental behavior in this species because prolactin concentrations were elevated during the reproductive stages when parental and alloparental behavior are expressed. I suggest that the proximate control of helping may be mediated by the same factor(s) that control parental behavior in breeders. Female breeder, male breeder and helper plasma prolactin concentrations were equal and increased from the

nonbreeding stage through the copulation and egg-laying/incubation stages. During the nestling provisioning stage, female prolactin remained elevated while male breeder and helper prolactin declined. Additional work is needed to determine how prolactin mediates parental and alloparental behavior during the nestling provisioning stage in the two sexes. Although prolactin increases the probability that parental and alloparental behavior will be performed, prolactin concentration and the amount of nestling-feeding behavior performed were not correlated when comparing individuals.

Why do red-cockaded woodpeckers help?

My dissertation research demonstrates that helping behavior is adaptive in the red-cockaded woodpecker. The most important benefits that contribute to the maintenance of helping behavior are current and future indirect benefits. Helpers increase the reproductive success of breeders (Heppell et al. 1994) and are closely related to the recipients of their aid (Haig et al. 1994) and thereby gain indirect fitness benefits. Helpers also gain future indirect benefits by enhancing the survival of related breeders, increasing the probability that they will survive and produce non-descendant kin in future breeding seasons.

The evolutionary origin of alloparental behavior is thought to be a derivation from parental behavior (Brown 1987). Natural selection modifies physiological traits, just as it does morphological or behavioral traits. Therefore, study of the physiological bases of parental and alloparental behavior is relevant to the debate over whether helping behavior is a non-adaptive trait maintained as a by-product of selection on parental behavior (Jamieson and Craig 1987; Jamieson 1989) or is an adaptive trait maintained by fitness benefits (Emlen 1991).

That is, the maintenance of helping despite evolution in its physiological bases indicates that helping behavior is adaptive. Cooperative breeding is thought to be a derived trait in red-cockaded woodpeckers because helping is not obligatory (Walters 1990) and cooperative breeding occurs only in this species within the genus *Picoides*. Red-cockaded woodpeckers exhibit a pattern of prolactin concentration in which helpers and breeders are equivalent. If the origin of helping behavior is correctly represented by the proximate mechanisms observed in the red-cockaded woodpecker, then deviations from this pattern (e.g. helpers have lower prolactin concentrations than breeders, or helpers exhibit a different temporal pattern), which have been observed in other cooperatively breeding species (Florida scrub-jay, Schoech et al. 1991, 1996b; Harris' hawk, Vleck et al. 1991) suggest that helping behavior is adaptive.

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- Vleck CM, Mays NA, Dawson JW, Goldsmith AR (1991) Hormonal correlates of parental and helping behavior in cooperatively breeding Harris' hawks (*Parabuteo unicinctus*). *Auk* 108:638-648
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Academic Degrees

SS 1995-FS 1999	Ph.D, Department of Biology, Virginia Tech
FS 1993- FS 1994	Enrolled toward a MS, Zoology, North Carolina State University, Fall 1993-Fall 1994, no degree conferred
SS 1992	BA, Biology, University of Chicago

Professional Experience

4/10/98 Little evidence for reciprocation as a direct benefit of helping behavior in the Red-cockaded Woodpecker. American Ornithological Union Annual Meeting in St. Louis, MO.
6/22/97 Survivorship effects of helping in the Red-cockaded Woodpecker. Animal Behavior Society Annual Meeting, College Park, MD
3/25/97 What are the benefits of helping behavior in the Red-cockaded Woodpecker. Departmental seminar.
9/15/95 Why do helpers help?: Lessons from the Red-cockaded Woodpecker. Poster at Interdepartmental Ecology Group Meeting.
8/17/95 Why do helpers help?: Lessons from the Red-cockaded Woodpecker. Poster at American Ornithologists' Union 113th Annual Meeting, Cincinnati, OH

Publications

Khan, M. Z. and Walters, J. R. 1998. An evaluation of future direct and indirect benefits of helping behavior in the Red-cockaded Woodpecker (*Picoides borealis*). Auk in review.
Khan, M. Z. and Walters, J. R. 1997. Is helping a beneficial learning experience for red-cockaded woodpecker (*Picoides borealis*) helpers? Behav. Ecol. and Sociobiol. 41: 69-73.

Teaching Experience

FS 1997	Teaching Assistant, General Biology Laboratory, Virginia Tech
SS 1994	Teaching Assistant, Cellular Techniques, North Carolina State University
FS 1993	Teaching Assistant, Vertebrate Zoology, North Carolina State University

RESEARCH EXPERIENCE

May 1995- present: I am currently examining hypotheses to explain why helpers help raise their siblings. Ultimate hypotheses for helping behavior are addressed by analyzing long-term demographic data collected from the third largest Red-cockaded Woodpecker population located in the Sandhills region of North Carolina. Proximate hypotheses to explain helping behavior are addressed by measuring behavioral and hormonal correlates.

May 1994-December 1994: Investigated the evolutionary question: Why do helpers help in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*)? Field research tried to determine if helper effort can be explained as a function of the helper's relatedness to the recipients of its help. Alternative explanations for helping were investigated using an extensive data set compiled on the Red-cockaded Woodpecker by Dr. Walters and his colleagues at NCSU.

January 1993-July 1993: Observed the Hawaiian crow (*Corvus hawaiiensis*) as a part of the Fish and Wildlife Service Hawaiian crow recovery project on the Big Island, Hawaii. Duties included extensive observations of wild pairs during the breeding season, predator trapping and monitoring non-breeding birds.

FELLOWSHIPS AND RESEARCH SUPPORT

- 1998 P. E. O. Scholarship, \$7,000
1998 Graduate Research Development Project, Virginia Tech, \$250
1997 American Ornithological Union, \$1349
1997 Sigma Xi, \$433
1993 Student Conservation Association, \$2700
1992 Friends of the National Zoo Internship, \$3400
1991 Lincoln Park Zoological Society, Dr. Scholl Fellowship, \$2500, "*Space Partitioning by Fifteen Species of Birds in a Captive Environment.*"
1990 University of Chicago, Richter Grant, \$800, "*Reintroduction of a juvenile female Colobus monkey (Colobus quereza) to her group.*"

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