THE IMPORTANCE OF A DOUBLE STANDARD: INTER-SEXUAL DIFFERENCES AND COOPERATIVE BREEDING IN THE GREEN WOODHOOPOE

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DECLARATION

This thesis represents original work undertaken towards a M.Sc. degree at the Percy FitzPatrick Institute, University of Cape Town and has not been submitted in any form towards a degree at any other university. I submit it as my own work and have acknowledged all assistance I received while producing it.

Amanda T. Hawn

CITATION

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Acknowledgements

When a rainy afternoon hits and a large body of water separates you from home, one often finds they'd like nothing better than to be 'back on the other side of the pond' for a bit. During my last eighteen months in Cape Town, it was in moments like this that I found myself turning to John Steinbeck's wonderful rough-hewn descriptions of America and Americans for temporary transportation across the Atlantic. I remember thinking as I read from *Log from the Sea of Cortez* on one such afternoon, that I was damn lucky to have Morné du Plessis as an advisor.

Prior to setting sail, Steinbeck's log records the reasons he and Ed Ricketts have for setting forth on their exploration of the Sea of Cortez. Specifically, the author writes of his friend's desire to break free from the kind of science that reduces the study of a fish to that which can be measured when it sits, pickled, on a laboratory shelf. Seen through a glass jar, Steinbeck observes, questions concerning the nature of the fish may be objectively answered and duly recorded. And yet, because they relate nothing of the world in which the fish moved, nothing of its fight or color as it fell to the deck of a boat wet from the sea, the writer declared these answers are as utterly false as they are correct.

Confined to Cape Town and a computer because of my teaching schedule, I might easily have become the scientist staring at a pickled fish, jotting down tiny truths and recording huge lies and ... I would have gone mad. Morné's measured criticism, constant enthusiasm and love of 'fishing' for answers in the real world not only kept me from insanity, but also made this dissertation fascinating from start to finish. For allowing me to work with a database that represents a lifetime's worth of early mornings in the forest and for becoming a mentor as well as an advisor, I extend great gratitude to him.

Thanks also are due to the landowners in the Eastern Cape, South Africa who allowed Morné and others free access to their farms throughout the past two decades. I am grateful to Dr. Melvin Swanson for his assistance in the statistical analysis in the first chapter and to Tom Martin for reminding to think again about juvenile reef fish.

Many people within the Fitz made going to the office a pleasant proposition on a daily basis. In particular, Hilary Buchanan was a reassuring and helpful port of call whenever things little and big went awry. Chris Tobler dealt with me during the inevitable computer meltdown in his usual efficient, friendly style. Marta, Odette, Conrad, David, Amy and Rita – I will miss you all and look forward to the crossing of our paths again in the future.

Lara du Plessis and Nate Larsen proved cheerful help in the field and stiff competition in numerous games of crazy 8's. For the good company and peanut butter pancakes, I thank 'em. Last but not least, I'd like to give a nod to my parents and older brother for the childhood I wish I might throw on repeat, as well as for their patience while listening to me talk about woodhoopoes.

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CONTENTS

Abstract

Life-history theory predicts that long-lived species probably realize optimal lifetime reproductive success by maximizing the number of times they breed during their life (Clutton-Brock 1988, Stearns 1992). Framed against this idea, delayed reproduction on the part of non-breeding helpers in cooperative species seemingly represents a sub-optimal strategy (see Emlen 1994 for review). Given their relevance to the evolution of sociality and dominance in kinship systems, the mechanisms driving cooperative breeding have fascinated behavioral ecologists for almost forty years.

Despite the seemingly high cost of cooperative breeding to non-breeders, the relative rarity of the system (approximately 3% of bird species, Sibley & Monroe 1990) suggests that it is not the normative condition of group living and thus may have adaptive value in some contexts. While a great deal of work on the subject has identified many of these contexts, situating them within a cohesive framework remains a central goal of avian ecology (Arnold & Owens 1999, Heinsohn & Legge 1999, Hatchwell & Komdeur 2000, Clutton-Brock 2002, Cockburn in press). Ironically, recent reviews suggest that such cohesion eventually may result from clarifying inter-specific and intra-specific differences, rather than similarities, in individual reasons for cooperating (Arnold & Owens 1999, Hatchwell & Komdeur 2000, Heinsohn & Legge 1999, Clutton-Brock 2002, Dickinson & Koenig 2003, Cockburn in press).

Following from this logic, this study examines the idea that males and females in the cooperatively-breeding green woodhoopoe (*Phoeniculus purpureus*) differ in life-history pattern and behavior. Despite the assumption inherent in classic models of dispersal strategy that there is a reproductive cost of delayed breeding, few studies have quantified this cost in terms of lifetime reproductive success (Emlen 1994, Komdeur 1996). In the first chapter I use complete life-history data on 125 breeders to demonstrate that green woodhoopoe females delaying reproduction *increase* lifetime reproductive success, while males delaying reproduction *decrease* lifetime reproductive success. This observation suggests that females should seek to ensure survival, rather than increase inclusive fitness

when young. Males, on the other hand, likely experience significant selective pressure to disperse and breed as soon as possible.

Subsequent analysis of the data supported predictions that were based on the idea that females use the natal territory as a refuge, while males use it to make the best of a bad situation when constrained from independent breeding. Specifically, the results showed that, (1) the timing of dispersal and reproduction varied significantly with levels of breeder saturation among males but not females, and (2), contrary to previous hypotheses (Cockburn 1998), related male helpers increased reproductive success more than related female helpers in the study species (Chapters 2 & 3).

The findings of this study support several ideas relevant to the interpretation of evolutionary patterns among cooperative species. First, the reproductive costs of delaying reproduction may not be as high as previously assumed in some cooperative species if, as in females of this species, birds delaying breeding tend to live longer than birds reproducing at maturity. Second, as demonstrated by inter-sexual differences in the reaction of birds to varied levels of breeder saturation, behavioral responses to ecological constraints may depend on life-history pattern. And finally, helpers may regulate levels of care in context dependent ways such that temporal and/or spatial changes in the immediate costs and benefits of providing help should not be overlooked in models of dispersal strategy.

When taken together, the three chapters of this study suggest that life history patterns, ecological constraints, and benefits of philopatry co-evolve to maintain cooperative breeding in the green woodhoopoe.

Introduction

Both breeding and non-breeding adults provide parental care to the young of a single nest in approximately three percent of extant bird species (Sibley & Monroe 1990, Arnold & Owens 1998). This general condition, termed cooperative breeding, has a number of variations (ranging from singular to plural, to polygamous breeding systems) and is facultative in some instances, but obligate in others (Brown 1987). Given their relevance to the evolution of sociality and dominance in kinship systems, the mechanisms driving cooperative breeding have fascinated behavioral ecologists for almost forty years.

Until a decade ago, evolutionary explanations of cooperative breeding were split between two camps. Historically, one school of thought contended that delayed dispersal and helping evolves in populations when habitat saturation limits the number of available territories able to support successful breeding attempts (e.g. Koenig & Pitelka 1981, Emlen 1982); the other argued that juveniles delay dispersal because they seek benefits associated with group living and breeding on the natal territory (e.g. Stacey & Ligon 1987, 1991).

General consensus now holds that historical conceptions of cooperative breeding represent two sides of a semantic coin (*sensu* Emlen 1991, 1994, 1997, Koenig et al 1992, but see Ligon 1999). This reconciliation hinges, largely, on the concept of territory quality (Koenig et. al 1992, Emlen 1994). Contemporary authors suggest that where one school of thought pointed to costs associated with dispersing into low quality habitat (extrinsic constraints), the other pointed to the benefits of group living/breeding (intrinsic benefits) on high quality territory. The difference is one of emphasis rather than substance.

Stemming from this idea, several game theory models of dispersal choice have been developed (sensu Koenig et al 1992, Stacey & Ligon 1991). Their approach finds strong support in Komdeur's (1992) conclusion that a cost-benefit analysis of lifetime fitness options based on territory quality successfully predicted juvenile dispersal in the

Seychelles warbler. The same logic falters as an evolutionary explanation, however, when confronted with the contention of Kokko & Lundberg (2001) that, while natal philopatry is more likely on high-quality territories, variation in territory quality alone rarely leads to delayed dispersal. Given that critical resources in most habitats naturally change over time (e.g. du Plessis 1995, McClaren et al. 2002), the assumption that relative territory quality within a population remains constant also may be dubious. Further investigation of the ubiquity and strength of territory quality's influence on intra-specific dispersal patterns remains worthwhile.

Following from the observation that reproductive opportunities on high quality territories often are as limited in many non-cooperative species as in cooperative species (*sensu* Koenig & Pitelka 1981, Stacey & Ligon 1991), the idea that territory quality gradients drive cooperative breeding has been challenged at the inter-specific level as well (see Hatchwell & Komdeur 2000 for review). The inability of classic dispersal models to account for inter-specific patterns of cooperative breeding may be due to the fact that, until recently, most authors were concerned with the maintenance rather than the evolution of cooperative breeding (*sensu* Koenig et al. 1992, Stacey & Ligon 1991, Emlen 1994, but see Kokko & Lundberg 2001, Kokko & Ekman 2002, Cant & Reeve 2002, Härdling et al. 2003).

The evolution of cooperative breeding has taken place across time, space and phylogeny, leaving demographic and phylogenetic record of its process. In particular, the notable clustering of cooperatively breeding species in South Africa (approximately 7% of non-marine species, du Plessis et al. 1995) and Australia (approximately 10% of all species, Brown 1987), suggests that either ecological or phylogenetic trends in these areas have impacted the evolution of cooperative breeding (*sensu* Hatchwell & Komdeur 2000). Taking a comparative approach to this record, a number of studies have sought evidence of cooperative breeding's probable evolutionary route (Arnold & Owens 1998, 1999, Cockburn 1996, du Plessis et al. 1995, Edwards & Naeem 1993, Ford et al. 1988, Poiani & Pagel 1997).

To date, the challenges associated with uncertain phylogeny, patchy data-sets and the tautological interpretations to which historical studies are prone, have led to conflicting conclusions concerning the evolution of cooperative breeding. Important advances have been made nonetheless. Comparative study has revealed, for instance, that cooperative breeding represents an ancestral state in some lineages, but is recently evolved in others (Arnold & Owens 1999). Distributions of obligate and facultative cooperative breeders in South Africa may have ecological correlates (du Plessis et al. 1995). And there is worthwhile speculation that life-history traits act in concert with ecological constraints to drive the evolution of cooperative breeding (Arnold & Owens 1998, Hatchwell & Komdeur 2000). Further research clearly is needed to sort out the frustrating challenges and promising leads surrounding the evolution of cooperative behavior (Clutton-Brock 2002, Dickinson & Koenig 2003).

Generally speaking, recent reviews have advocated two approaches that might help situate the diversity of mechanisms maintaining cooperative breeding within a larger evolutionary framework. The first entails thinking more specifically about why different types of non-breeding helpers provide care within cooperative systems (*sensu* Emlen 1998, Heinsohn & Legge 1999, Clutton-Brock 2002, Dickinson & Koenig 2003, Cockburn 2003). The second entails thinking more broadly about similarities in life-history pattern and ecology across cooperative systems (*sensu* Arnold & Owens 1998, 1999, Martin et al. 2000, Hatchwell & Komdeur 2000). This dissertation aims to apply logic from each of these approaches to analysis of two decades of data on the green woodhoopoe (*Phoeniculus purpureus*), a cooperatively-breeding species found throughout much of Sub-Saharan Africa.

The higher survival and slower life history patterns of tropical and south temperate species have been documented well (Gaston 1978, Rowley & Russel 1991, Arnold & Owens 1998). The demographic concentration of cooperative breeding in these areas is interesting when coupled with the finding of Arnold & Owens (1998) that low adult mortality plays an important role in predisposing a lineage to cooperative breeding. Low adult mortality might well ease the pressure to breed as soon as it is possible, suggesting that the cost of delayed reproduction may be lower in some cooperative breeders than previously thought.

Despite the assumption inherent in classic models of dispersal strategy that there is a reproductive cost of delayed breeding, few studies have quantified this cost in terms of lifetime reproductive success (Emlen 1994, Komdeur 1996). In the first chapter I use complete life-history data on 125 breeders to investigate male and female patterns of age-related reproductive success in the study species. I then consider the implications of these patterns for the maintenance of delayed reproduction in each sex.

In the second chapter I utilize an inter-sexual divide in life history pattern, as well as comparison between study sites, to evaluate evidence for the idea that slower life history patterns may act in concert with ecological constraints to facilitate the evolution of cooperative breeding. Specifically, I test the idea that, in light of their respective life-history patterns, green woodhoopoe females should use the natal territory as a refuge even when constraints on independent breeding are relaxed, whereas non-breeding males should aim to disperse and breed as soon as they are able.

Finally, in the third chapter, I examine the impact of gender on the contributions of related helpers to the reproductive success of breeders. Analyzing patterns within and between populations, I seek support for the idea that related juvenile helpers in this species regulate helping behavior based on calculations of fecundity and survival that follow logically from the life history pattern of their sex.

Each of the chapters is presented as a manuscript in its entirety, with separate abstract, introduction, methods, results and discussion sections. While this format is conducive to the efficient communication of results, it necessitates some repetition of logic and method. I apologize, forthwith, to the reader for any redundancy that follows.

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CHAPTER ONE

Age-related reproductive success in the cooperatively-breeding green woodhoopoe (*Phoeniculus purpureus*)

Abstract

Identifying the mechanisms driving the evolution of cooperative breeding has been a central goal of avian ecology for almost four decades. In particular, singular cooperative breeding - in which just one pair breeds per social group, but all birds help in the care of young - has intrigued researchers because it apparently entails the forfeiture of breeding opportunities on the part of reproductively mature individuals. Numerous studies have considered how non-breeding adults might mitigate this reproductive cost, alternately positing gains in inclusive fitness, survival, parenting skills and access to high quality territories as a result of delayed dispersal. Contrary to much of this thinking, our long-term study of a singular cooperative breeding species in South Africa (*Phoeniculus purpureus*) suggests that, (1) females delaying reproduction actually increase rather than decrease their lifetime reproductive success, and (2) this pattern may be explained better by physiological constraints in young birds than by age-related behaviors or territory quality gradients. Females that began breeding when over the age of three bred for more seasons, produced a greater number of young in their lifetime, had more offspring surviving to the age of one, and lived longer than females that began breeding at the age of 3 years or younger. In sharp contrast to these results, males that began breeding when 3 or older bred for fewer seasons in their lifetime and had fewer offspring surviving to the age of one, than males that began breeding in their first two years of life. Males that began breeding at ages as markedly different as one and five showed no significant difference in life span. Year-by-year analysis of reproductive success, group structure and breeder survival suggests that mortality patterns among female breeders can largely be attributed to a high cost of reproduction, but that male patterns are governed by age and intra-sexual competition. These results support the idea that the costs and benefits of delaying reproduction differ hugely between sexes and that reasons for delaying dispersal and engaging in helping behavior are likely different for males and females of the species.

Keywords: *Phoeniculus purpureus*, cooperative breeding, lifetime reproductive success, delayed reproduction, inter-sexual life history patterns.

Introduction

In at least 3% of extant bird species both breeding and non-breeding adults provide parental care to the young of a single nest (Sibley & Monroe 1990, Arnold & Owens 1998). This general condition, termed cooperative breeding, has a number of variations ranging from singular to plural to polygamous breeding systems. In particular, singular cooperative breeding - in which just one pair breeds per social group, but all birds help in the care of young - has intrigued researchers because it entails the forfeiture of breeding opportunities on the part of reproductively mature individuals. Despite the seemingly high cost of singular cooperative breeding to non-breeders, the relative rarity of the system suggests that it is not the normative condition of group living and thus may have adaptive value in some contexts. While a great deal of work on the subject has identified many of these contexts, situating them within a cohesive framework remains a central goal of avian ecology (Arnold & Owens 1999, Heinsohn & Legge 1999, Hatchwell & Komdeur 2000, Clutton-Brock 2002, Cockburn in press).

It is generally held that cooperative breeding systems evolve when offspring that remain with their parents manage to compensate for the cost of missed breeding opportunities (Emlen 1994). Consequently, much attention has been given to the various ways in which non-breeding adults might overcome the cost of delayed reproduction. Among the hypothesized benefits of delaying reproduction and providing help are gains in inclusive fitness, heightened chances of survival, the acquisition of parenting skills, and increased access to high quality territories later in life (see Emlen 1991, 1994, 1997, Koenig et al. 1992 for review). Recent reviews suggest that, perhaps to our detriment, much less time has been spent quantifying the costs accrued by helpers in cooperative systems (Heinsohn & Legge 1999, West et al. 2002, Heinsohn in press).

Any comprehensive understanding of the evolution of cooperative breeding ought to explain why it has evolved in one species or lineage, but not in others (*sensu* Smith 1990, Koenig et al. 1992). Several game theory models of dispersal choice, weighing benefits available on the natal territory against the cost of missed reproductive opportunities available elsewhere, have been developed (*sensu* Emlen 1994, 1997, Koenig et al 1992, Stacey & Ligon 1991). Such models find strong support in a number of intra-specific studies (see Hatchwell & Komdeur 2000 for review), but fail to explain inter-specific patterns of cooperative breeding when: (1) the limitation of reproductive opportunities in many non-cooperative species is as severe as that found in cooperative species (*sensu* Koenig & Pitelka 1981, Stacey & Ligon 1991), and (2) fitness benefits associated with helping are not always readily apparent (Cockburn 1998 for review, but see Emlen 1994).

Lacking evidence of uniformity in the inter-specific ecological determinants of cooperative breeding, researchers increasingly have recognized the need to qualify intra-specific explanations in order to accommodate phylogenetic distributions of cooperative breeders (*sensu* Russell 1989, Arnold & Owens 1999, Hatchwell & Komdeur 2000, e.g. Cant & Reeve 2002, Härdling et al. 2003). In particular, the notable clustering of cooperatively breeding species in Australia (10% of all species, Brown 1987) and South Africa (7% of non-marine species, du Plessis et al 1995) indicates that either ecological or phylogenetic trends in these areas influenced the evolution of cooperative behavior (*sensu* Hatchwell & Komdeur 2000).

The higher survival and slower life history patterns of tropical and south temperate species have been well documented (Gaston 1978, Rowley & Russel 1991, Arnold & Owens 1998). The demographic concentration of cooperative breeding in these areas is interesting when coupled with the finding of Arnold & Owens (1998) that low adult mortality plays an important role in predisposing a lineage to cooperative breeding. Low adult mortality rates might well ease the pressure to breed as soon as it is possible and suggest that the cost of delayed reproduction may be lower in some singular cooperative breeders than previously thought.

Despite the assumption inherent in current models of dispersal strategy that there is a reproductive cost of delayed breeding, few studies have quantified this cost in terms of lifetime reproductive success (Emlen 1994, Komdeur 1996). Collecting appropriate sample sizes to calculate lifetime reproductive success for long-lived birds dispersing across time and space is notoriously difficult. Komdeur (1996) reported that the lifetime fecundity of birds breeding on territories of equal quality decreased with age at first breeding. In their study of the Siberian jay, a species in which juveniles often delay dispersal but do not help on the natal territory, Ekman et al. (1999) compared 11 males that delayed dispersal with 15 that bred in their first year. The researchers concluded that delayed dispersal was associated with significant increases in lifetime reproductive success. Clearly the cost of delayed reproduction differs from species to species and should be carefully measured when considering the evolution and maintenance of cooperative breeding systems.

Using complete life histories taken from twenty years of data on the cooperatively breeding green woodhoopoe (*Phoeniculus purpureus*), we investigated the breeding strategy and lifetime reproductive success of 125 birds in two color-ringed populations in South Africa. Specifically, we tested the null hypotheses for each sex that: (i) there is no difference in lifetime reproductive success between birds that begin breeding at different ages; (ii) there is no difference in the number of juveniles surviving to one year of age between birds that begin breeding at different ages; (iii) there is no difference in the number of seasons spent breeding between birds that begin breeding at different ages; and (iv) there is no difference in life span between birds that begin breeding at different ages.

Regardless of whether or not birds delaying reproduction suffer a reproductive cost, they must run a survival risk while waiting to breed. In order to assess the degree of this risk we looked at the survival and reproductive patterns of males and females across age at each study site. And finally, noting inter-sexual differences in the life history patterns measured, we sought to elucidate them by identifying the respective costs of reproduction for male and female breeders.

Methods

Study species. The green woodhoopoe is a territorial, obligate cavity-roosting species found throughout the woodlands of Sub-Saharan Africa. Living in year-round residential groups of 2-12 individuals, both males and females reach reproductive maturity at one year, but may delay dispersal and/or breeding for up to seven years. All adults participate fully in the feeding and care of young, but only one pair breeds per group (Ligon & Ligon 1978, du Plessis 1993). Non-breeding group members are related to one or both of the breeders in approximately 90% of cases (du Plessis 1993). Helping behavior, however, is unrelated to nest-site specificity, kin discrimination or prior association with breeders (du Plessis 1993). Previous research on the species suggests that non-breeding adults reduce the food provisioning workload of the breeding pair, but do not increase either the number of young fledged or the survival of breeders (du Plessis 1991, 1993).

Study site. The study included two populations occupying distinctly different sites in the Eastern Cape Province, South Africa. Monitoring began at both sites in 1981. Data from the coastal site in Morgan's Bay (32°43'S, 28°19'E) is current through 2002. Census of the inland site in the Kubusi River Valley (32°32'S, 27°47'E) continued through 1997. The two sites vary considerably in vegetation, habitat and climate (du Plessis 1989). A maximum 32 breeding groups occupy the 33km² of the coastal site. Their territories, punctuating an open agricultural landscape, are stacked linearly along riverine forest belts running away from the Indian Ocean. In contrast, the 45km² inland site houses 26 groups whose territories center more randomly on small patches of riverine forest growing in the tributary valleys of the Kubusi River. At an elevation of 650 m, these inland tributaries snake through a landscape otherwise dominated by valley bushveld. On average, coastal territories cover 17.5 ha, 16.7 ha of which are riverine forest. Territories at the inland site are generally twice as large (35.1 ha), but contain just 2.3 ha of the riverine forest where the birds typically find roosting cavities. The number of available cavities per territory is thus greater at the coastal site than it is at the inland site (10.9 vs. 2.9) (du Plessis 1989). The coastal site is also wetter (1070 mm vs. 435 mm of precipitation) and warmer (min temp. 4° vs. -4°) than the inland site. Territory boundaries within both sites were stable throughout the study period regardless of environmental conditions or group size, suggesting that food availability may not be limiting for either population (Lepage & du Plessis unpubl. ms.).

Data Collection. Each bird was banded with a unique combination of three synthetic Darvic-color rings and a numbered metal ring (SAFRING) upon their first capture as juveniles. As birds bred annually and relatively synchronously (December through February), pre- and post-breeding censuses were performed in all but a few years when only a post-breeding census was completed. All juveniles observed in a group during a post-breeding census were considered to have hatched on the territory since dispersal is negligible during the first year (du Plessis 1993). Based on behavioral observations that were confirmed by preliminary genetic fingerprinting, the assumption also was made that putative parents were the genetic parents in all cases (D. Parkin & M. du Plessis unpubl. data). Relatedness between helpers and breeders thus was derived on the basis of pedigree. To ensure consistency, January 1 was considered the hatching date of all birds fledging in a given year. If a one month old juvenile appeared in November or December of a year, the bird was considered to be the product of the upcoming breeding season and its hatching date was listed as January 1 in the following year. Males and females were separated on the basis of bill length and vocal dimorphism as both traits are easily deciphered in the field (Ligon & Ligon 1978). In order to account for dispersal out of the system, the 5 km region around each study site was searched twice a year between 1981 and 1989 and irregular searches of up to 20 km were conducted.

Data Analysis. Total lifetime reproductive success was measured as the number of young fledged by a breeder during its lifetime and the number of these offspring that survived to at least one year of age was recorded. Age at first breeding was calculated using each bird's hatching date and the first year that it was clearly established as a breeder. The number of seasons each bird bred was counted. If a breeder dispersed from one breeding territory to another, the timing of its move was noted such that skipped breeding seasons were taken into account where appropriate. The number of young a breeder fledged in a season on average and the average number of juveniles a breeder had surviving per season were calculated simply by dividing the number of offspring fledged/surviving by the number of seasons a bird bred during its lifetime. Each bird's date of death was back-dated to January 1 of the year in which it last was seen and life span was calculated from hatching dates and death dates.

The 125 birds with complete life histories that attained breeding status in their lifetime were split between males (n=65) and females (n=60). Mann-Whitney U-tests were conducted to detect differences between the sexes in lifetime reproductive success, number of surviving offspring, number of seasons spent breeding, and life span. A Levene statistic was used to test for any inter-sexual differences in variance of the same traits.

Age-related reproductive success. Prior to conducting any statistical analysis concerning age-related reproductive success, I checked that other factors potentially impacting survival and reproductive patterns in each of the sexes either were controlled or non-significant. T-tests with no assumptions about variance were used to test for significant differences between study sites in life span or reproductive success. We then compared averages in these traits of breeders occupying core territories with those of breeders in peripheral territories to ensure that breeder mortality was not overestimated because of undetected dispersal out of the system. Previous research on the same system records that just 12 of 562 breeding individuals changed territories after their first breeding season, and less than 13% of all dispersal events within the study area occurred across groups separated by more than two territories (Lepage & du Plessis unpubl. ms.). It is unlikely, therefore, that breeders in the core territories of the study site dispersed out of the study area undetected.

In order to approximate equal sample size, birds of each sex were split between two groups, 'young starters' and 'old starters,' based on their age at first breeding. The final population breakdown was as follows: females 1 through 3 years old at first breeding (n=34) vs. females 4 through 7 years old at first breeding (n=26); males 1 or 2 years old at first breeding (n=23) vs. males 3 through 5 years old at first breeding (n=27). Mann-Whitney U-tests were used to compare groups within each sex in lifetime reproductive success, number of juveniles surviving to one year of age, number of seasons spent breeding, number of young fledged per season, number of juveniles surviving per season and lifespan.

In addition to the above univariate tests, multiple regression models were constructed for both sexes to elucidate the effects of dispersal history, territory quality and a continuous age at first breeding variable on the life history traits measured. Territory quality was assigned on the basis of a natality/mortality (N/M) index calculated from the birth rates and death rates in each of the territories from 1986 onwards (sensu Ligon & Ligon 1988). Given that birth rate and death rate were used to assign territory quality, the variable was not entered into the regression equations concerning number of young fledged or number of juveniles surviving to the age of one. All variables were entered initially and a backward exclusion process was used to remove any variables with probability ≥ 0.100. Thus, final models included only those variables that were significant predictors of lifetime reproductive success, number of juveniles surviving to one year of age, number of young fledged per season, number of juveniles surviving per season, number of seasons spent breeding, and life span.

Cost of reproduction. Four multiple linear regression models (two for each sex: males, n= 185 breeder years; females, n= 142 breeder years), were used to test the impacts of group structure, age, breeding history and reproductive success on (1) a breeder's probability of surviving to the next year, and (2) the number of years a breeder had until death. The following ten independent variables were entered into each of these models: a breeder's age, the number of seasons he/she had bred, the number of young he/she had fledged to date, the number of these juveniles that had survived to the age of one year, the number of young fledged in the current year, the number of juveniles surviving to one in the current year, the number of related female helpers, the number of unrelated female helpers, the number of related male helpers, and the number of unrelated male helpers. A backward exclusion process removing all variables with probability ≥ 0.100 was used to determine the ultimate components and significance of the final models. As a post-hoc measure, partial correlation coefficients were used to test the significance of relationships between each of the included variables and breeder survival when all other variables were controlled.

Mortality and reproduction versus age. The probability of surviving to a given age was calculated for males and females at each study site. Similarly, the probability of a bird breeding during its lifetime once it had survived to a given age was plotted for both sexes at both study sites. To control for underestimates of dispersal and/or overestimates of mortality, only those individuals that had been color-banded and were occupying a core territory at the time of their disappearance were included in this analysis (coastal males, n=122; coastal females, n=123; inland males, n=75; inland females, n=73).

Results

Males and females showed no significant differences in their lifetime reproductive success, the number of juveniles they had surviving to one year of age or the number of seasons they bred during their lifetime (Table 1). Life spans in the population varied between 2 and 13 years for the females and between 2 and 10 years for the males. While a ranked comparison of life span between the sexes showed no significant difference (Table 1), a Levene test suggested that longevity varied significantly more in females than in males (F = 11.45, p < 0.001; Figures 1 & 2).

Table 1. Univariate comparisons of four life history traits between male and female green woodhoopoes with complete life histories; significant differences determined by a Mann-Whitney U-test (n=125).

	Sex	*N*	Mean	S.D.	Min.	Max.	Z (Sig)
Lifetime reproductive success (total no. of young)	M	65	3.54	3.50	0	18	-.077
	F	60	3.50	3.37	0	13	(0.469)
Number of juveniles surviving to one year	M	65	1.91	2.07	0	9	-.514
	F	60	2.02	2.00	0	9	(0.302)
Number of seasons bred in lifetime	M	65	3.58	2.08	1	10	-.005
	F	60	3.73	2.45	1	11	(0.498)
Life span *	M	65	5.09	1.92	2	10	-.909
	F	60	5.85	3.00	2	13	(0.182)

Significance listed is 1-tailed; * indicates a significant difference in variance of the trait between the groups (p<0.001).

Figure 1.

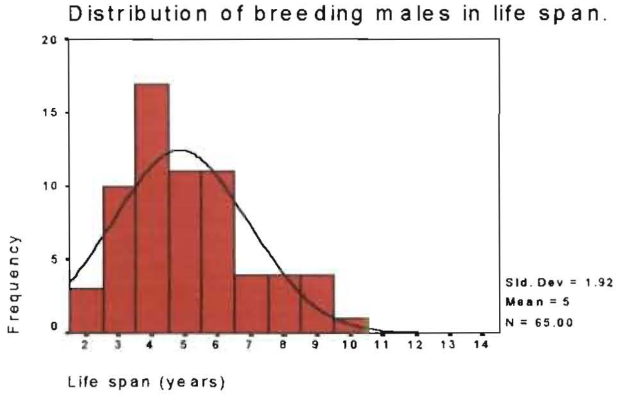
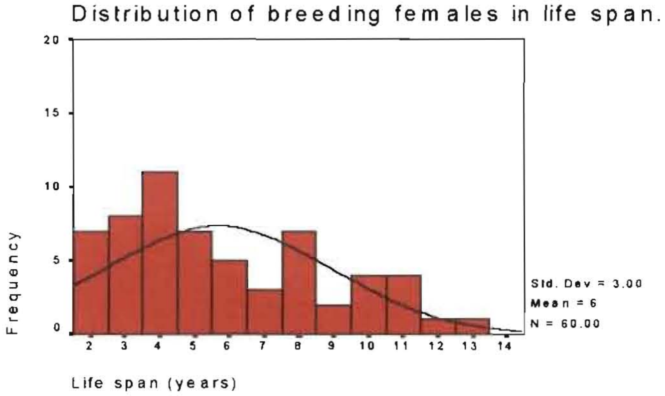


Figure 2.



Age-related reproductive success. Neither study site nor the location of a female in a core versus peripheral territory at the time of her disappearance showed a significant impact on the traits measured. Multiple linear regression showed age at first breeding to be the only significant predictor of life span in females ($\beta = 0.656$, $p < 0.001$) As the other variables had no significant bearing on a female breeder's longevity (dispersal history $\beta = 0.030$, $p = 0.794$; territory quality $\beta = 0.091$, $p = 0.402$), the final model ($r^2 = 0.430$, F (1, 54) = 40.76, $p < 0.001$) excluded territory quality and whether or not a bird had dispersed. Regression showed that dispersal history had no significant bearing on a female's lifetime reproductive success ($\beta = 0.080$, $p = 0.584$). Age at first breeding ($\beta = 2.387$, $p = 0.021$) was thus the only variable included in the final model predicting the number of young produced ($r^2 = 0.095$, F (1, 54) = 5.70, $p = 0.021$). Interestingly, a female breeder's dispersal history proved the strongest predictor of the number of offspring she had surviving to at least one year of age ($\beta = 0.285$, $p = 0.034$), with females that had dispersed realizing increased numbers of surviving offspring ($r^2 = 0.081$, F (1, 54) = 4.76, $p = 0.034$). Regression indicated that none of the variables was a significant predictor of the number of young a female fledged per season, the number of juveniles she had surviving per season, or the number of seasons she spent breeding.

When females were split between two groups based on their age at first breeding, univariate comparisons suggested that birds over three years of age at first breeding lived significantly longer than birds that began breeding in their first three years of life ($p < 0.001$). Birds that were older when initiating reproduction also bred for more seasons in their lifetime ($p < 0.05$), produced more fledglings per season ($p<0.05$), had greater lifetime reproductive success ($p < 0.01$), and had more juveniles surviving to the age of at least one year ($p < 0.05$) than birds that began breeding when relatively young. The two groups were not significantly different in the average number of juveniles they had surviving per season. (Table 2)

Table 2. Female averages (SD) in each trait measured in relation to age at first breeding. Significant differences determined by Mann-Whitney U test.

Trait	Age at first breeding: 1, 2 and 3 yr. (n=34)	Age at first breeding: 4 through 7yr. (n=26)	Z	Significance (one-tailed)
Lifetime reproductive success (total no. young)	2.59 (3.09)	4.70 (3.40)	-2.61	0.005**
Number of juveniles surviving to 1 year of age	1.41 (1.37)	2.81 (2.40)	-2.32	0.010*
Number of seasons bred in lifetime	3.18 (2.26)	4.46 (2.53)	-2.17	0.015*
Life span	4.35 (2.23)	7.81 (2.77)	-4.65	<0.001***
Number of young fledged per season	0.78 (0.87)	1.03 (0.64)	-2.05	0.021*
Number of juveniles surviving per season	0.47 (0.53)	0.58 (0.45)	-1.40	0.081 NS

NS= not significant. *Indicates significance at the <0.05 level; **at the <0.01 level; and *** at the <0.001 level.

In sharp contrast to the patterns shown by the females, males that began breeding when age 3 or older bred for fewer seasons in their lifetime ($p < 0.01$) than males that began breeding in their first two years of life. Males that delayed reproduction at least 2 years also tended toward significant decreases in lifetime reproductive success ($p = 0.06$) and had significantly fewer surviving offspring ($p < 0.05$). Males that began breeding at ages as markedly different as one and five showed no significant difference in life span, number of fledglings per season, or number of juveniles surviving per season. (Table 3) Regression models confirmed these results, showing that none of the variables was a significant predictor of lifespan (dispersal history $\beta = 0.186$, $p = 0.231$; territory quality β

= 0.016, p = 0.922; age at first breeding $\beta = 0.326$, p = 0.130). After backward removal, the final model predicting the number of seasons a male bred during his lifetime ($r^2 = 0.096$, F (1, 40) = 4.23, p = 0.046) included his age at first breeding ($\beta = -0.309$, p = 0.046), but excluded his dispersal history ($\beta = 0.149$, p = 0.327) and territory quality ($\beta = 0.069$, p = 0.661). Whether or not a male had dispersed to breed proved to be the best predictor of the number of juveniles he had surviving per season ($\beta = 0.295$, p = 0.058), but the final model was not significant ($r^2 = 0.087$, F (1, 40), p = 0.058). As in the females, males that had dispersed to breed tended to have more surviving offspring per season than males that bred on their natal territory. None of the variables successfully predicted a male's lifetime reproductive success, the total number of juveniles he had surviving to at least one year of age, or the number of young he fledged per season.

Table 3. Male averages (SD) in each trait measured in relation to age at first breeding. Significant differences determined by Mann-Whitney U test.

Trait		Age at first breeding: 1 and 2 yr. (n=23)	Age at first breeding: 3, 4 and 5 yr. (n=27)		Z	Significance (one-tailed)	
Lifetime reproductive success (total no. young)		5.26 (4.50)	3.18 (2.47)		-1.53	0.064 NS	
Number of juveniles surviving to 1 year of age		2.91 (2.47)	1.67 (1.71)		-1.83	0.034 *	
Number of seasons bred in lifetime		4.87 (2.30)	3.00 (1.52)		-3.02	<0.002 **	
Lifespan		5.39 (2.33)	5.08 (1.71)		-0.38	0.354 NS	
Number of young fledged per season		1.00 (0.65)	1.19 (1.09)		-0.17	0.434 NS	
Number of juveniles surviving per season		0.57 (0.39)	0.58 (0.56)		-0.25	0.403 NS	

NS= not significant. *Indicates significance at the <0.05 level; ** indicates significance at the <0.01 level.

While males from the study sites showed no significant differences in any of the traits measured, males that were last seen breeding in peripheral areas bred for significantly fewer breeding seasons than males that disappeared from core territories (t = -2.27, p = 0.016). Because we could not exclude the possibility that these differences resulted from undetected dispersal out of the system by peripheral breeders, we restricted the above analyses to the 50 males that were last seen in core territories.

Cost of reproduction. Multiple linear regression identified the number of fledglings a female breeder produced in a year, the number of fledglings she had produced to date, and the number of unrelated female helpers on her territory as significant predictors of her survival to the following year. The number of young a female had fledged to date ($\beta = -0.310$, $p < 0.001$) and the number of unrelated female helpers on her territory ($\beta = -0.171$, $p = 0.037$), were negatively correlated with her probability of survival to the next year. The number of young she had fledged in a given year was positively correlated with her probability of survival ($\beta = 0.186$, $p = 0.042$). The final model, including each of these variables, was highly significant ($r^2 = 0.101$, $F(3, 138) = 5.15$, $p = 0.002$).

Both the number of young a female had fledged to date and the number of unrelated female helpers on her territory in a given year were significant predictors of the number of years she had until death. Again, these variables were negatively correlated with a female breeder's probability of survival ($\beta = -0.242$, $p = 0.021$ and $\beta = -0.172$, $p = 0.024$, respectively). In addition, the number of seasons a female had bred ($\beta = -0.184$, $p = 0.061$) and the number of related male helpers on her territory ($\beta = -0.174$, $p = 0.034$) showed negative correlation with the number of years she had left to live. All other variables were excluded from the final model ($r^2 = 0.231$, $F(4, 137) = 10.32$, $p < 0.001$). Among the included variables, the number of young a female had fledged to date showed strongest correlation with the number of years she had until death. This relationship remained highly significant ($r = -0.27$, $p < 0.001$, 1-tailed) even when age, number of seasons bred and the number of unrelated female helpers on her territory were controlled. When the number of young a female breeder had fledged to date was controlled, only the number of unrelated female helpers on her territory retained significant negative correlation with the number of years she had until death ($r = -0.17$, $p < 0.05$, 1-tailed).

Age and the number of unrelated male helpers on a male breeder's territory were the most significant predictors of both his probability of surviving to the next year ($\beta = 0.240$,

$p < 0.001$ and $\beta = -0.334$, $p < 0.001$, respectively) and the number of years he had until death ($\beta = -0.384$, $p < 0.001$ and $\beta = -0.246$, $p < 0.001$, respectively). The number of related male helpers ($\beta = -0.127$, $p = 0.068$) was also included in the final model predicting a male breeder's survival to the next year ($r^2 = 0.198$, $F(3, 177) = 14.57$, $p < 0.001$). Age and the number of unrelated male helpers on the territory were the only variables included in the final model predicting the number of years a male breeder had until death ($r^2 = 0.222$, $F(2, 178) = 25.35$, $p < 0.001$).

Mortality and reproduction vs. age. Males and females suffered the highest mortality during their first two years of life at both the inland and coastal study sites. Mortality during this period impacted females at the inland site most severely, but did level off significantly among this population after the age of two. Just 34% of the females hatched at the inland site survived to the age of two, but 64% of these survivors lived to at least the age of five. In contrast, 47% percent of the males hatched at the inland site survived to the age of two, but just 40% of these birds survived to five years. Male and female patterns tracked each other more closely at the coastal site than at the inland site. In general, females at the coastal site suffered higher mortality to the age of five than males, while males suffered higher mortality thereafter (Figures 3 & 4).

Figure 3.

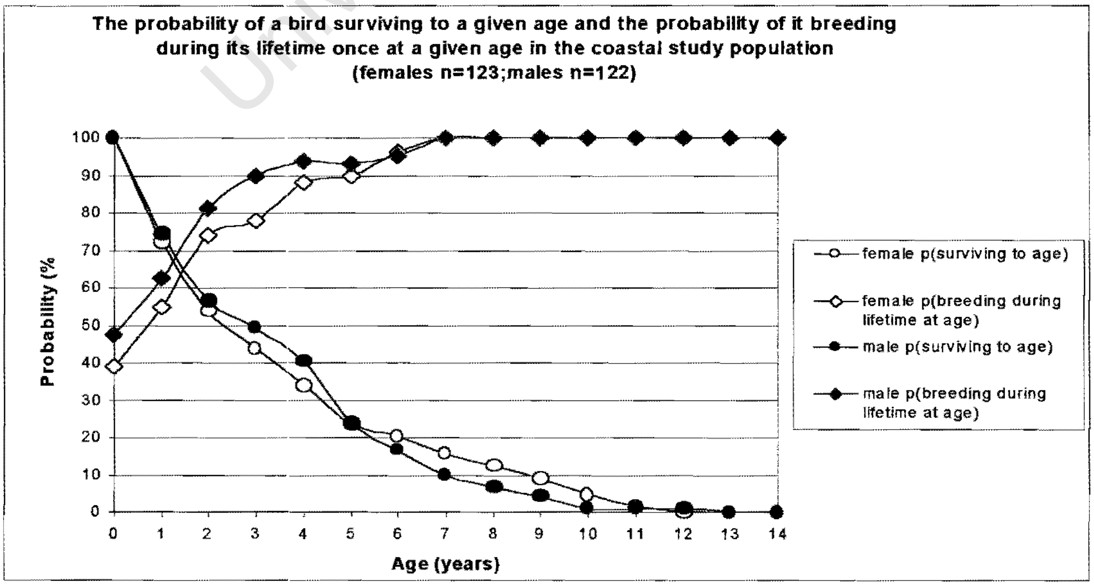
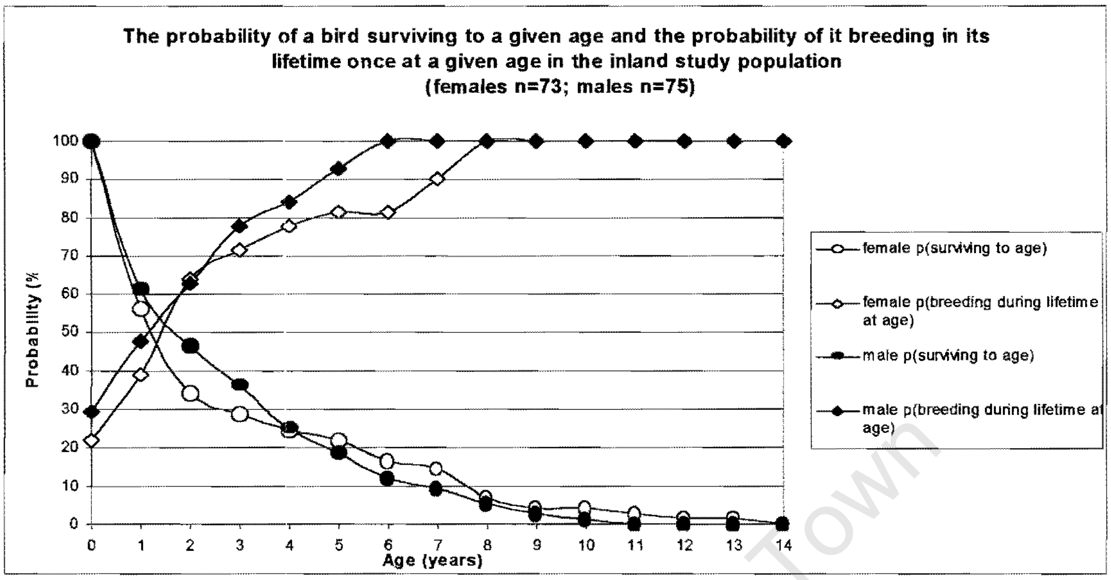


Figure 4.



Upon hatching, males had a higher probability than females of breeding during their lifetime at both study sites. The probability of breeding tended to increase more steeply with age for males than for females and this difference was more pronounced at the inland site than at the coastal site. All birds surviving to the age of seven at the coastal site became breeders within their lifetime; all males surviving to the age of six and all females surviving to the age of eight became breeders within their lifetime at the inland study site (Figures 3 & 4).

Discussion.

Female patterns. The results suggest that, counter to the long-standing assumption that non-breeding adults in cooperative systems forfeit breeding opportunities, females in the green woodhoopoe do not bear a reproductive cost to delayed reproduction. Females that delayed reproduction for at least three years actually bred for more seasons, had greater lifetime reproductive success and more surviving offspring than females that began breeding within two years of reproductive maturity.

Given the finding that mortality is highest among females during their first two years, one is tempted to explain the results by invoking differential survival through a juvenile mortality bottleneck. If this were the case, however, one would expect variance in each of the traits to narrow with age as lower quality individuals were selected out of the population. In fact, this study found the opposite pattern. Variance in the number of young fledged, the number of juveniles surviving to one, and the number of seasons a female bred all increased, rather than decreased, with age at first breeding.

Alternatively, three adaptive hypotheses might explain the female pattern in age-related reproductive success: (1) females that delay reproduction have access to higher quality territories when they eventually begin breeding (the territory-quality mechanism) (2) females that delay reproduction gain parenting skills as helpers such that they are better breeders than younger females when they begin breeding (the practice-makes-perfect mechanism), and (3) older females invest more heavily in the production of offspring than young females because their prospect of long-term survival is lower than that of the younger group (the less-to-lose mechanism) (see Forslund & Pärt 1995 for review).

The data from this study do not show strong support for any of these ideas. The territory-quality mechanism is undermined by the finding that females on territories of high and low quality did not differ significantly in age at first breeding. Models also indicated that a breeder's territory quality failed to explain variance in either her life span or the number of seasons she bred during her lifetime. In light of these observations, we find it unlikely that territory quality is the principal link between patterns of reproductive success and age at first breeding in the female population at hand.

Similarly, the practice-makes-perfect hypothesis falters when confronted with evidence suggesting that older females do not necessarily make better parents for juvenile birds. While females that began breeding after the age of three produced significantly more fledglings per season than females that began breeding at younger ages ($p<0.05$), the two groups showed no significant difference in the average number of these juveniles that survived to reproductive maturity. The latter result implies that the increased offspring survival of females delaying reproduction is merely a repercussion of their longer breeding career ($p<0.05$) and greater egg/fledgling production ($p<0.05$) and cannot be attributed to any increased parenting facilities they might possess.

Linear regression confirms this interpretation, indicating that a female's dispersal history, not her age at first breeding, was the best predictor of the number of offspring she had surviving to the age of one. While females in this population suffer no fecundity cost when they breed with relatives, a significantly smaller proportion of their inbred offspring survive to the age of one (M. du Plessis & A. Hawn unpubl. data). As females that disperse are much less likely to suffer inbreeding depression than females that remain on the natal territory, the finding that dispersal significantly impacts offspring survival, while interesting, is not surprising. Importantly, dispersal was not a significant predictor of a female's lifetime reproductive success, the number of seasons she spent breeding, or her life span. Thus dispersal, like territory quality and parenting experience, fails to explain the life history patterns at hand.

Finally, the premise of the less-to-lose mechanism falls apart when one considers that females delaying reproduction in this population lived significantly longer ($p<0.001$) and bred for more seasons ($p<0.05$) than females that began breeding when relatively young. The results of this study actually support the idea that older females have more-to-lose in terms of their own survival probabilities than younger females.

How, then, does one explain the data pattern at hand? As stated above, the results clearly demonstrate a connection between delayed reproduction and increased life span among females in the study population. The import of this finding does not lie in the long life span of birds delaying reproduction - one would expect this result given that a bird initiating reproduction at age five has already survived five years - but in the short life span of birds that begin breeding at reproductive maturity. The early mortality of the latter group points to a high cost of reproduction.

Why is the cost of reproduction highest among young females? Visser & Lessells (2001) concluded experimentally that the physiological cost of egg production significantly impacted patterns of female mortality in their study population of great tits. Similarly, year-by-year analysis of reproductive success, group structure and breeder survival in this study suggested that mortality patterns among female breeders can be attributed to a high physiological cost of egg production and/or incubation. While the number of young a female had produced to date was the strongest predictor of both her short-term and long-term survival, the number of these offspring that survived as juveniles showed no impact on her survival. Interestingly, the number of unrelated female helpers on a breeder's territory generally decreased her probability of surviving. The results suggest that (1) the physiological costs associated with producing young, but not necessarily caring for them, drive mortality patterns in female breeders, and (2) the energetic cost of maintaining status in the presence of unrelated females may contribute secondarily.

The number of young a female fledged in a given year was positively correlated with her probability of survival to the next year. In contrast to the prediction of the less-to-lose hypothesis, this result suggests that females invest more in reproduction when they themselves are most likely, rather than least likely, to survive. Survival patterns at both study sites indicate females experience intense mortality during their first two years of life, but enjoy comparative longevity thereafter. This age-specific mortality may be explained, in part, by the earlier observation of du Plessis & Williams (1994) that juvenile females in this system struggle to reach and maintain a body condition comparable to that of 95% of healthy adults.

The finding that females that delayed breeding several years produced more fledglings per season than females that began breeding while young, also suggests that the former may be better positioned to invest in reproduction. Clearly, if females are battling to survive because of poor body condition during the first two years of their life, the added burden of any energetic costs associated with bearing young will create a steep trade-off between current and future reproductive success. When I compared the mortality rates of helpers and breeders in core territories, I found that mortality was significantly higher among breeding females at all ages. Five (38.5%) of the 13 females breeding at the age of two died in their second year. In comparison, only eight (10.5%) of the 76 females that were non-breeding helpers at this age died. Even more interesting was the finding that, in sharp contrast to the almost 40% mortality rate of birds that began breeding at the age of two, just one of the 14 females (i.e. <10%) that began breeding when five or six died within a year of initiating reproduction.

The patterns of female fecundity and survival in this study suggest, first, that there is probably a significant physiological cost to egg-laying and/or incubation in this species, and secondly, that older females may better be able to bear this cost. Specifically, I posit that older females invest more in reproduction than young females, not because they have less-to-lose, but because they can better afford it physiologically. The distinction between this idea and those dismissed above arguably is minimal. If older females produce more fledglings because they invest more energy in egg production and/or incubation, then the practice-makes-perfect and less-to-lose mechanisms are at play, albeit for slightly different reasons. While the difference is one of emphasis rather than theory, it has the important implication that physiological limitations in young birds, rather than adaptive behaviors in older birds, may best explain age-related reproductive success among females in this species.

It should be noted, of course, that the results of this study also indicate that females delaying reproduction run a significant survival risk while waiting to breed. Consequently, it may be in the best interest of young females to breed when given the chance, despite a steep trade-off between fecundity and survival. In light of this observation we conclude that selection likely operates in both directions to determine the timing of reproduction among females in the green woodhoopoe.

Male patterns. In sharp relief to the patterns evidenced among females, males that began breeding when age three or older bred for fewer seasons in their lifetime and had fewer offspring surviving to the age of one, than males that began breeding in their first two years of life. Younger male breeders also tended toward a significant increase in their lifetime reproductive success. Males that began breeding at ages as markedly different as one and five showed no significant difference in life span. Taken together, the above results suggest that male patterns of age-related reproductive success in this species meet the expectation that delaying reproduction entails a forfeiture of reproductive opportunities.

The decrease in reproductive success with age at first breeding in males is not surprising on its own. When juxtaposing the result to patterns in females, however, one must ask why males delaying reproduction don't manifest more plasticity in their life span. At least part of the answer may rest in the observation that there seems to be minimal direct cost, but significant indirect cost, associated with reproduction in males. Neither the number of young a male fledged nor the number of these juveniles that survived affected his probability of survival. Instead, regression analyses suggested that intra-sexual competition drives male-survivorship. Given that males delaying reproduction suffer significant fitness costs, non-breeding males should be aggressive in the queue for breeding positions. Male breeders may pay substantial costs while defending status as a result. The finding that a male breeder's probability of surviving to the next year decreased significantly as the number of unrelated male helpers on his territory increased, offers indirect support for this idea.

In a review of social dominance and stress hormones, Creel (2001) points out that, in sharp contrast to non-cooperative species, dominants in cooperative breeding systems frequently show higher levels of glucocorticoid (GC) secretion over the long term than subordinates. High GC levels over more than a few days have been demonstrated to provoke a variety of pathologies including immune suppression, reduced reproduction, and an inability to battle short-term stressors such as behavioral challenges to rank (see Sapolsky 1992 for review).

The evidence at hand suggests that male breeders in the green woodhoopoe likely suffer more intra-sexual aggression than their female counterparts and that male survivorship, unlike that of females, is severely limited by age in combination with the degree of this aggression. Radford & du Plessis (2003), working on the same system, reported that inter-sexual aggression was rare during foraging, but that intra-sexual aggression among foraging males was comparatively common. In light of these findings and the synthesis of Creel (2001) concerning GC patterns in cooperative breeders, I strongly recommend further investigation of the idea that chronic stress might limit male longevity more than female longevity in this species.

Conclusions

The results of this study support the idea that the costs and benefits of delaying reproduction differ hugely between sexes and that reasons for delaying dispersal and engaging in helping behavior are likely different for males and females of the species. More specifically, the findings suggest that where female helpers likely use the natal territory as a refuge (seeking to ensure survival rather than mitigate reproductive costs while waiting to breed), male helpers probably use it as a launch pad. When constrained from breeding independently, however, male helpers may have more reason to seek inclusive fitness than female helpers. Further study concerning the impact of male and female helpers on the reproductive success of breeders in this population is clearly worthwhile.

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CHAPTER TWO

The mechanisms driving natal philopatry and delayed reproduction in the green woodhoopoe (*Phoeniculus purpureus*)

Abstract

Identifying the mechanisms driving cooperative breeding has broad implications for understanding the function of sociality and dominance hierarchy within the context of kinship. In particular, the evolution of cooperative breeding in avian species has taken place across space and lineage, leaving clear demographic and phylogenetic record of its process. Recent research suggests that adult mortality patterns may explain variation in a number of adaptive avian behaviors across latitudinal gradients. Given the notable clustering of cooperatively breeding species in south temperate areas, Hatchwell & Komdeur (2000) proposed that the slower life history patterns characterizing these areas may act in concert with ecological constraints to facilitate the evolution of cooperative breeding. Our long-term study evaluates evidence for this idea in a cooperatively-breeding species in South Africa (*Phoeniculus purpureus*), providing insight into interactions of life-history, habitat quality, and natal philopatry at the population level. Specifically, the results suggest that within the system at hand: (1) ecological constraints are the primary driver of delayed dispersal and delayed reproduction in males but not in females, and (2) juveniles use the natal territory in ways predicted by patterns of age-related reproductive success in their sex. This study supports the idea that life-history traits and ecological constraints act together to drive the evolution of cooperative breeding.

Key-words: *Phoeniculus purpureus*, cooperative breeding, evolution of life-history traits, ecological constraints, delayed reproduction, natal philopatry.

Introduction

Avian cooperative breeding may broadly be defined as any system in which more than two adults provide care to the young of a single nest. As cooperative breeding apparently entails the forfeiture of reproduction on the part of non-breeding adults, identifying the mechanisms driving the system carries broad implications for understanding the function of sociality and dominance within the context of kinship. Despite the seemingly high cost of cooperative breeding to non-breeders, the relative rarity of the system (approximately 3 % of extant bird species) suggests that it is not the normative condition of group living and thus may have adaptive value in some contexts. While a great deal of work on the subject has identified many of these contexts, situating them within a cohesive evolutionary framework remains a central goal of avian ecology (Arnold & Owens 1999, Heinsohn & Legge 1999, Hatchwell & Komdeur 2000, Clutton-Brock 2002, Dickinson & Koenig 2003, Cockburn in press).

Any comprehensive understanding of the evolution of cooperative breeding ought to explain why it has evolved in one species or lineage, but not in others (*sensu* Smith 1990, Koenig et al. 1992). Lacking evidence of uniformity in the inter-specific ecological determinants of cooperative breeding, researchers increasingly have recognized the need to qualify intra-specific explanations of the system to accommodate the phylogenetic distribution of cooperative species (*sensu* Arnold & Owens 1999, Hatchwell & Komdeur 2000, e.g. Cant & Reeve 2002, Härdling et al. 2003). In particular, two hypotheses have shed light on how this might be done successfully.

The life-history hypothesis (*sensu* Russell 1989, Arnold & Owens 1999) proposes that the evolution of cooperative breeding involves a two-step process in which life-history traits pre-dispose a lineage to cooperative breeding and ecological constraints then facilitate the evolution of natal philopatry and helping in a subset of species. Support for this idea comes from Arnold & Owens' (1998) conclusion that low adult mortality pre-disposed a lineage to cooperative breeding in the taxonomically diverse database of their comparative study. In a thorough review of ecological constraints, life history traits and the evolution of cooperative breeding, Hatchwell & Komdeur (2000) suggested that life-history traits and ecological factors, rather than acting in turn, likely co-evolve to influence the evolution of cooperative breeding.

Both of these ideas are interesting given the notable clustering of cooperatively breeding species in Australia (10% of all species, Brown 1987) and South Africa (7% of non-marine species, du Plessis et al. 1995). The higher survival and slower life history patterns of south temperate species have been well documented (Gaston 1978, Rowley & Russel 1991, Arnold & Owens 1998) and recent research suggests that adult mortality patterns may well be driving a number of adaptive avian behaviors across latitudinal gradients (Russell 1989, Martin et al. 2000, Ghalambor & Martin 2001, 2002).

Unfortunately, elucidating the influence of life-history patterns and ecological factors on the evolution of cooperative breeding not only represents a vital avenue of research, but also a difficult proposition. Comparative analysis seeks correlation between evolutionary and environmental change but it cannot, by nature, corroborate potential benefits or causal relationships in the associations it identifies (*sensu* Arnold & Owens 1999). While a number of recent models have made important conceptual breakthroughs by incorporating the interaction of life-history patterns, ecological constraints, benefits of philopatry and dominance in their parameters (e.g. Cant 1998, Kokko & Ekman 2002, Härdling et al. 2003), any model necessarily simplifies the system it mirrors and consequently may be limited to those contexts giving rise to its assumptions (*sensu* Kokko & Lundberg 2001, Kokko & Ekman 2002). How, then, does one probe the mechanistic interactions between life-history and ecology when considering the evolution of cooperative breeding?

Using a database collected from two populations of the cooperatively-breeding green woodhoopoe (*Phoeniculus purpureus*) in South Africa, this study takes a novel approach to the problem. The study system at hand is uniquely situated to allow investigation of the relationship between life-history traits and ecological constraints in the evolution of cooperative breeding for two reasons. First, breeding opportunities are more ecologically constrained among males and females in one of the study populations. And second, while both sexes frequently delay reproduction and provide care to young other than their own, females show significantly more variability in life span and have lower mortality after the age of five than males (Chapter 1).

Earlier investigation of the same system revealed that females delaying reproduction tended to live significantly longer and realize greater lifetime reproductive success than females initiating reproduction at maturity. In sharp contrast, delayed reproduction in males showed no correlation with increased life span and was linked to decreased reproductive success. Given these findings, it stands that females should use the natal territory as a refuge during their first two years when mortality is heaviest, but that non-breeding males should aim to disperse and breed as soon as they are able. (Chapter 1)

If this reasoning is correct, one would expect three things. First, inter-sexual differences in age at first dispersal (AFD) and age at first breeding (AFB) should be most evident at the coastal site where relaxed ecological constraints on breeding allow a significant proportion of males to disperse as early as they choose. Second, variance in the timing of dispersal and delayed reproduction among males should be smaller than that among females in the coastal population where constraints on breeding are relaxed, but greater than that among females in the inland population where constraints on breeding are heightened. And third, average AFD and AFB should vary significantly with levels of ecological constraint on breeding opportunities among males, but not among females. Using over twenty years of life-history data, we tested each of these predictions in turn.

Methods

Study species. The green woodhoopoe is a territorial, obligate cavity-roosting species found throughout the woodlands of Sub-Saharan Africa. Living in year-round residential groups of 2-12 individuals, both males and females reach reproductive maturity at one year but may delay breeding for up to seven years. All adults participate fully in the feeding and care of young, but only one pair breeds per group (Ligon & Ligon 1978, du Plessis 1993). Non-breeding group members are related to one or both of the breeders in approximately 90% of cases (du Plessis 1993). Helping behavior, however, is unrelated to nest-site specificity, kin discrimination or prior association with breeders (du Plessis 1993). Previous research on the species suggests that non-breeding adults reduce the food provisioning workload of the breeding pair, but do not increase either the number of young fledged or the survival of breeders (du Plessis 1991, 1993).

Study site. The study included two populations occupying distinctly different sites in the Eastern Cape Province, South Africa. Monitoring began at both sites in 1981. Data from the coastal site in Morgan's Bay (32°43'S, 28°19'E) is current through 2002. Census of the inland site in the Kubusi River Valley (32°32'S, 27°47'E) continued through 1997. The two sites vary considerably in vegetation, habitat and climate (du Plessis 1989). A maximum 32 breeding groups occupy the 33km^2 of the coastal site. Their territories, punctuating an open agricultural landscape, are stacked linearly along riverine forest belts running away from the Indian Ocean. In contrast, the 45km^2 inland site houses 26 groups whose territories center more randomly on small patches of riverine forest growing in the tributary valleys of the Kubusi River. At an elevation of 650 m, these inland tributaries snake through a landscape otherwise dominated by valley bushveld.

On average, coastal territories cover 17.5 ha, 16.7 ha of which are riverine forest. Territories at the inland site are generally twice as large (35.1 ha), but contain just 2.3 ha of the riverine forest where the birds typically find roosting cavities. The number of available cavities per territory is thus greater at the coastal site than it is at the inland site (10.9 vs. 2.9) (du Plessis 1989). The coastal site is also wetter (1070 mm vs. 435 mm of precipitation), warmer (min temp. 4° vs. -4°), and has more territories in which natal rates generally exceed birth rates than the inland site (59.3% of territories vs. 49% of territories, A. Hawn & M. du Plessis unpubl. data). Approximately 48% of the males hatched at the coastal site bred within their lifetime. By comparison, only 30% of the males hatched at the inland site bred within their lifetime (Chapter 1). Territory boundaries within both sites were stable throughout the study period regardless of environmental conditions or group size, suggesting that food availability may not be limiting for either population (Lepage & du Plessis unpubl. ms).

Data Collection. Each bird was banded with a unique combination of three synthetic Darvic-color rings and a numbered metal ring (SAFRING) upon their first capture as juveniles. As birds bred annually and relatively synchronously (December through February), pre- and post-breeding censuses were performed in all but a few years when only a post-breeding census was completed. All juveniles observed in a group during a post-breeding census were considered to have hatched on the territory since dispersal is negligible during the first year (du Plessis 1993). Based on behavioral observations that were confirmed by preliminary genetic fingerprinting, the assumption also was made that putative parents were the genetic parents in all cases (D. Parkin & M. du Plessis unpubl. data). To ensure consistency, January 1 was considered the birth date of all birds fledging in a given year. If a one month old juvenile appeared in November or December of a year, the bird was considered to be the product of the upcoming breeding season and its birth date was listed as January 1 in the following year. Males and females were separated on the basis of bill length and vocal dimorphism as both traits are easily deciphered in the field (Ligon & Ligon 1978). In order to account for dispersal out of the system, the 5 km region around each study site was searched twice a year between 1981 and 1989 and irregular searches of up to 20 km were conducted.

Data Analysis. All birds that were born within one of the study populations and survived to breed and/or disperse were included in the analysis. Age at first breeding was calculated using each bird's hatching date and the first year that it was clearly established as a breeder. Similarly, age at first dispersal was calculated using each bird's hatching date and the date of its first dispersal. Individuals that began breeding prior to dispersing for the first time were not included in the latter analysis. As sample sizes were not equal across the sub-sets being compared but distributions were normal, T-tests with no assumptions about variance were used to test for (1) significant differences in each of the traits between males and females within a study population, and (2) significant differences between the populations within a sex.

A second sample population, including only those individuals that had been color-banded and were on a core territory at the time of their disappearance, was used to plot the percentage of surviving males and females at each study site breeding by a designated age (coastal males, n=121; coastal females, n=123; inland males, n=75; inland females, n=72). Previous research on the same system records that less than 13% of all dispersal events within the study area occurred across groups separated by more than two territories (Lepage & du Plessis unpubl. ms). It is unlikely, therefore, that birds in the core territories of the study site dispersed out of the study area undetected.

Results

Males from the two populations were significantly different in average age at first dispersal ($p<0.05$) and the trait's range among males in the coastal population (<12 mos. to 2 yrs.) was equal to just half that among males in the inland population (<12 mos. to 4 yrs.). Females from the two populations, by contrast, showed very similar variance and coastal females did not differ significantly from inland females in their average age at first dispersal. Males and females differed significantly in their timing of first dispersal in the coastal population ($p<0.01$), but not in the inland population (Table 1).

Table 1. Univariate comparisons of sexes and study populations in age at first dispersal.

	n	Mean AFD	S.D.	Min	Max		T-stat Sig. (1-tailed)
Comparisons btwn. sexes							
Coastal females vs.	21	1.95	1.26	0	4		3.07
Coastal males	31	1.03	0.71	0	2		0.002 **
Inland females vs.	15	2.47	1.13	1	4		1.35
Inland males	13	1.85	1.28	0	4		0.094 NS
Comparisons btwn. sites							
Coastal females vs.	21	1.95	1.26	0	4		-1.29
Inland females	15	2.47	1.13	1	4		0.102 NS
Coastal males vs.	31	1.03	0.71	0	2		2.16
Inland males	13	1.85	1.28	0	4		0.024 *

NS= not significant. * indicates significance at the $p<0.05$ level; ** at the $p<0.01$ level; ***at the $p<0.001$ level.

Coastal females, inland females, and inland males all ranged between 1 and 6 years in age at first breeding. Coastal males ranged between <12 months and 5 years in the same trait and, on average, were significantly younger than inland males ($p<0.01$) when they began breeding. There was no significant difference in average age at first breeding between females from the two populations or between males and females in the inland population. Coastal females did, however, tend to breed significantly later than coastal males ($p<0.001$, Table 2).

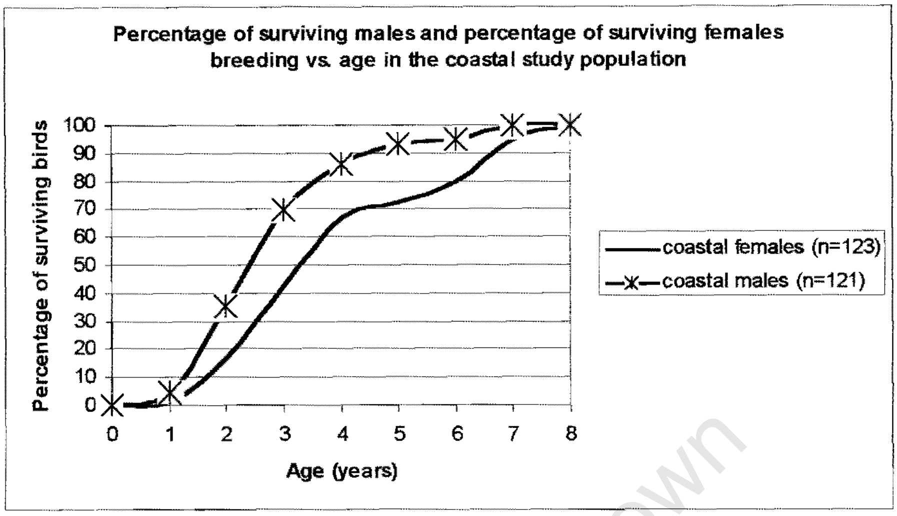
Table 2. Univariate comparisons of sexes and study populations in age at first breeding.

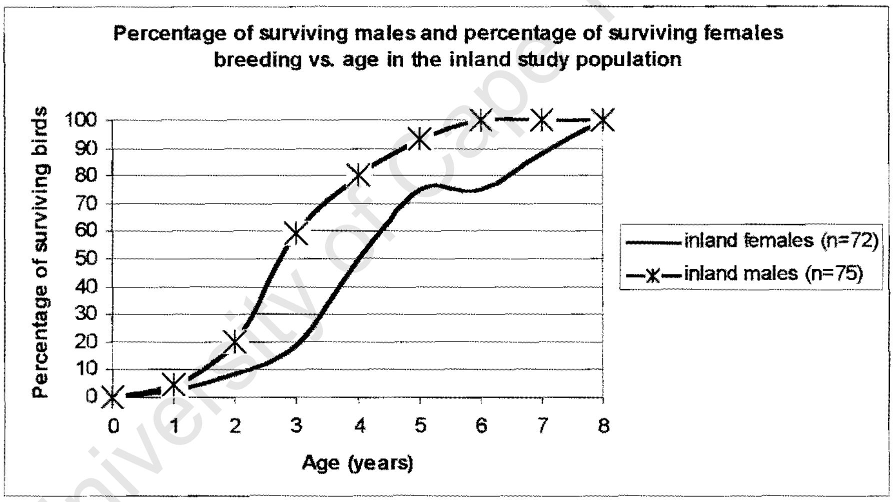
	n	Mean AFD	S.D.	Min	Max		T-stat Sig. (1-tailed)
Comparisons btwn. sexes							
Coastal females vs.	51	3.18	1.20	1	6		3.98
Coastal males	60	2.35	0.95	0	5		<0.001 ***
Inland females vs.	28	3.46	1.23	1	6		-1.46
Inland males	34	3.00	1.26	1	6		0.074 NS
Comparisons btwn. sites							
Coastal females vs.	51	3.18	1.20	1	6		1.00
Inland females	28	3.46	1.23	1	6		0.159 NS
Coastal males vs.	60	2.35	0.95	0	5		2.62
Inland males	34	3.00	1.26	1	6		0.006 **

NS= not significant. * indicates significance at the $p<0.05$ level; ** at the $p<0.01$ level;***at the $p<0.001$ level.

Figures 1 & 2 indicate that the turnover of breeding positions was slower among females in both study populations. Only 20% of the surviving female population was breeding by the age of three at the inland study site. By comparison, over 60% of surviving males were breeding at this age in the same population. Breeder saturation was most severe among females at the inland study site and least severe among males at the coastal study site. In general, both males and females attained breeding status earlier in the coastal population than in the inland population.

Figures 1 & 2.





Discussion

Breeder saturation generally was higher among females than males, suggesting that the higher survival of females after the age of five likely slows the turnover of breeding vacancies in this sex. Females also tended to disperse and breed later than males in both populations. Consequently, one might identify differential constraints on breeding vacancies as the primary driver of inter-sexual differences in age at first dispersal and age at first breeding in the species. The patterns observed across populations, however, do not support this idea.

I report elsewhere (Chapter 1) that females hatched in the inland population have a 22% probability of becoming a breeder during their lifetime. By comparison, coastal females, at hatching, have a 39% chance of breeding during their lifetime. Part of this discrepancy may be attributed to higher juvenile mortality at the inland study site, but much of it is due to greater breeder saturation and/or high dispersal cost. The difference between the populations in the percentage of females that attained breeding positions was marked even when comparing females that had survived to adulthood. Coastal females had a 74% chance of breeding during their lifetime after surviving to the age of two, whereas inland females only had a 64% chance of becoming a breeder during their lifetime after surviving to the age of two (Chapter 1).

If females were adjusting their timing of dispersal and reproduction according to ecological constraints on breeding opportunity, then one would expect them to disperse and breed significantly later in the inland population than in the coastal population. Patterns in the results do not meet this expectation; inland females neither dispersed nor bred significantly later than coastal females ($p=0.102$ and $p=0.159$ 1-tailed, respectively). I thus find it unlikely that ecological constraints on breeding are the primary driver of natal philopatry and delayed reproduction among females in this species.

Instead, the patterns at hand match those predicted by the hypothesis that males use the natal territory as a launch-pad, while females use it as a refuge. As expected, inter-sexual differences in age at first dispersal and age at first breeding were highly significant in the coastal population where ecological constraints on breeding were relatively relaxed (AFD $p<0.01$, AFB $p<0.001$), but not in the inland population where ecological constraints on breeding were comparatively high (AFD $p=0.094$, AFB $p=0.074$). Variance in each of the measured traits was narrowest among coastal males (AFD 0.50; AFB 0.90) and widest among inland males (AFD 1.64; AFB 1.59), while female variance in both traits fell between these extremes. And finally, males from the two populations, unlike females, were significantly different in average age at first dispersal ($p<0.05$) and age at first breeding ($p<0.01$), with inland males dispersing and breeding later than coastal males.

Based on these results, we conclude that natal philopatry and delayed reproduction are maintained by different mechanisms in males and females of the green woodhoopoe. The timing of dispersal and reproduction in males of the species appears to be closely linked to ecological constraints on breeding opportunities. Females, on the other hand, seemingly delay dispersal and/or reproduction even when breeding constraints are relaxed. Given that males and females in this study occupied identical habitats, this difference carries important implications for the interpretation of evolutionary patterns among cooperative species. Specifically, the results suggest that inter-sexual differences in breeder saturation and regulation of natal philopatry observed in this study must be attributed to variation in life-history pattern rather than habitat.

Life-history theory predicts that long-lived species probably realize optimal lifetime reproductive success by maximizing the number of times they breed during their life (Clutton-Brock 1988, Stearns 1992). Framed against this idea, delayed reproduction on the part of non-breeding helpers in cooperative species seemingly represents a sub-optimal strategy (see Emlen 1994 for review). This notion seems to hold for males, but not for females in the green woodhoopoe. When comparing the complete life histories of birds that began breeding at different ages, previous study of this system revealed that males that begin breeding early breed for more seasons than males that begin breeding when older (Chapter 1). Females, on the other hand, seemingly maximize the number of times they breed by delaying reproduction (Chapter 1). How interesting, then, that males seem to disperse as soon as they are able, whereas females do not.

The finding that the respective response of males and females to levels of breeding constraint is best explained by inter-sexual differences in age-related reproductive success within the species, not only supports the idea that behavioral responses to ecological constraints depend on life-history pattern (*sensu* Arnold & Owens 1998, 1999, Hatchwell & Komdeur 2000), but also provides insight into how and why.

In particular, Arnold & Owens (1998) highlighted low adult mortality and low fecundity as life-history correlates of cooperative breeding in the taxa they studied. A number of authors have linked the idea of low adult mortality to cooperative breeding via a habitat saturation mechanism since breeder longevity likely slows the turn-over of breeding opportunities (*sensu* Hatchwell & Komdeur 2000, Heinsohn & Legge 1999). Perhaps because it does not echo the classic link between ecological constraint and delayed reproduction as clearly, the correlation between low-fecundity and cooperative breeding has not been given as much attention.

Returning to the idea that long-lived birds probably aim to maximize the number of breeding events in their lifetime (Clutton-Brock 1988, Stearns 1992), the link between cooperative breeding and low fecundity is, nonetheless, interesting. A number of authors have put forth the idea that juveniles should choose natal philopatry over dispersing to breed if breeding success comes at a prohibitively high cost in marginal habitat and delaying dispersal maximizes prospects of long-term survival (*sensu* Koenig et al. 1992, Ekman et al. 1999, Green & Cockburn 2001, Covas 2002). The logic at play, here, is that long-lived birds should prioritize investments in survival over reproduction when young since they can best maximize lifetime reproductive success by ensuring future breeding opportunities. Similarly, the lower fecundity of cooperative breeders suggests that long-lived individuals in cooperative societies may be swinging investment away from reproduction toward survival in order to maximize lifetime reproductive success.

Emlen (1990) reported that harsh conditions limited the number of breeding attempts in his study population of white-fronted bee-eaters. The author also noted that heightened costs of reproduction impacted young individuals most. Covas (2002) provides experimental evidence suggesting that birds decrease their age at first breeding in the sociable weaver when food is increased, indicating young birds may actively choose not to breed under normal conditions. Given these findings, it seems possible that differentially high costs of reproduction among young birds in long-lived species might predispose individuals to delayed reproduction, much like low quality habitat, by lowering the return on risking dispersal to breed.

There is evidence to support this idea in the green woodhoopoe, where the costs of reproduction appear to be disproportionately high among young birds. I report elsewhere that, in sharp contrast to the almost 40% mortality rate of birds that began breeding at the age of two, just one of the 14 females (i.e. <10%) that began breeding when five or six died within a year of initiating reproduction (Chapter 1). Furthermore, females that delayed reproduction at least three years realized increased lifetime reproductive success, bred for more seasons, and lived significantly longer than females that began breeding in their first three years. In light of these observations, the follow-up finding of this study that females do not differ significantly in their timing and dispersal between populations characterized by different levels of ecological constraint is interesting. Specifically, the results of this study support the idea that green woodhoopoe females may not actively seek to disperse and/or breed during the first several years of their life when mortality is high (Chapter 1) because the cost of reproduction at this stage is disproportionately large.

At the same time, it should be noted that mortality patterns in both study populations also indicate that females delaying reproduction run a significant survival risk while waiting to breed (Chapter 1). Consequently, it may be in the best interest of young females to breed if the opportunity presents itself, despite a steep trade-off between fecundity and survival. In light of this observation we posit that selection likely operates in both directions to determine the timing of reproduction among females in the green woodhoopoe (see Chapter 1).

Conclusions

The results of this study illustrate that life-history differences between males and females have important implications concerning the regulation of natal philopatry and delayed reproduction in the green woodhoopoe. The observation that males miss breeding opportunities when delaying reproduction and show little variance in life-span compared to females, fits well with the finding of this study that males disperse and breed significantly earlier in a population where ecological constraints on breeding are relaxed than they do in a population where ecological constraints on breeding are comparatively high. Perhaps more interesting, was the finding that females, as predicted by patterns of age-related reproductive success, tended to delay dispersal and reproduction regardless of a relaxation of breeding constraint. Importantly, this latter result implies that females in the study species are locked into an evolutionary feed-back loop in which delayed reproduction increases longevity, and longevity, in turn, decreases the costs of waiting to breed while increasing breeder saturation.

Taken together, patterns in the study species support the ideas that (1) life-history traits and ecological constraints co-evolve in the cooperative breeding system at hand, and (2) costs of reproduction, in addition to long life-spans, potentially play a role in predisposing a population, or sub-sets within it, to delayed reproduction (*sensu* Covas 2002).

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CHAPTER THREE

The investment strategies of related male and female helpers in the cooperatively-breeding green woodhoopoe (*Phoeniculus purpureus*)

Abstract

The evolution of helping behavior in birds is enigmatic as it seemingly entails the forfeiture of reproductive opportunities on the part of non-breeding adults. While numerous researchers have considered the various ways in which non-breeding adults might overcome the cost of delayed reproduction via long-term benefits associated with natal philopatry and inclusive fitness, recent reviews suggest that much less time has been spent considering the immediate costs and benefits of providing help (*sensu* Heinsohn & Legge 1999, Clutton-Brock 2002, West et al. 2003, Heinsohn in press, Cockburn in press). Utilizing over 20 years of data from a long-term study of two green woodhoopoe populations in South Africa, this study evaluates evidence for the idea that related male and female helpers in the species regulate helping behavior differently according to short-term calculations of fecundity and survival. The results indicate that male helpers in the species increase reproductive success on their natal territory more when constraints on independent breeding are high than when they are low. Female helpers, by contrast, have no net impact on juvenile survival and may regulate helping behavior according to calculations of survival rather than inclusive fitness. Taken together, the results of this study demonstrate the importance of the immediate costs and benefits of providing help in cooperative systems and that the trade-off between them might differ for males and females within a species.

Keywords: *Phoeniculus purpureus*, regulation of helping behavior, alloparental care, delayed reproduction, inclusive fitness, life-history evolution, cooperative breeding.

Introduction

In cooperatively breeding birds both breeding and non-breeding adults direct parental care toward the young of a single nest. It is generally held that cooperative breeding systems evolve when offspring acting as non-breeding 'helpers' on their natal territory manage to compensate for the cost of missed breeding opportunities elsewhere (Emlen 1994). Consequently, much attention has been given to the various ways in which non-breeding adults might overcome the cost of delayed reproduction. Among the hypothesized long-term benefits of delaying reproduction and providing help are gains in inclusive fitness, the acquisition of parenting skills, and increased access to high quality territories later in life (see Emlen 1991 & Wrege, Emlen 1994, 1997, Koenig et al. 1992 for review). Recent reviews suggest that much less time has been spent measuring the immediate costs and benefits of providing help and how the trade-off between them might differ for males and females within a species (*sensu* Cockburn 1998, Cockburn in press, Heinsohn & Legge 1999, Heinsohn in press, Clutton-Brock 2002, MacColl & Hatchwell 2002, Härdling et al. 2003).

Models of dispersal choice based on the long-term benefits derived from helping on high-quality territory have met with strong, though not universal, support at the intra-specific level (for review see Hatchwell & Komdeur 2000). Unfortunately, the same models generally fail to explain inter-specific patterns among cooperative breeders (*sensu* Arnold & Owens 1999, Hatchwell & Komdeur 2000). Lacking evidence of uniformity in the inter-specific determinants of cooperative breeding, researchers increasingly have recognized the need to qualify intra-specific explanations of the behavior's evolution in order to accommodate the phylogenetic distribution of cooperatively breeding species (*sensu* Russell 1989, Arnold & Owens 1999, Hatchwell & Komdeur 2000, e.g. Cant & Reeve 2002, Härdling et al. 2003).

The higher survival and slower life history patterns of tropical and south temperate species have been well documented (Gaston 1978, Rowley & Russel 1991, Arnold & Owens 1998). The demographic concentration of cooperative breeders in these areas is interesting when coupled with the finding of Arnold & Owens (1998) that low adult mortality plays an important role in predisposing a lineage to cooperative breeding. In their review concerning the cost of helping, Heinsohn and Legge (1999) underscore the notion that if longevity increases the likelihood of cooperative breeding, then helping behavior must be as likely a target for selection over an individual's lifetime as parental care itself.

A number of recent studies have shown that birds are capable of modifying parental behavior on remarkably fine scales. Ghalambor and Martin (2001) demonstrated that parents in species with low-adult mortality reduced mortality risk to themselves when predators were introduced at the nest, even when their offspring suffered as a result. In contrast, when parents in species with comparatively high adult mortality were placed in similar situations, they tended to reduce risk to their offspring, despite increased mortality risk to themselves. By experimentally manipulating brood size in collared flycatchers, Doligez et al. (2002) showed convincing evidence that potential breeders immigrated into areas when local offspring numbers were increased and emigrated from areas when local offspring quantity or quality were decreased. And finally, Hatchwell (1999) reviewed evidence in a number of cooperative species indicating that male breeders frequently reduce parental care when helpers are present, regardless of starvation risk among nestlings. Female breeders, on the other hand, usually maintain levels of care unless starvation risk in a species is minimal.

Helping constitutes a significant energetic investment and may reduce an individual's long-term survival in an array of species (Taborsky 1984, Reyer 1984, Heinsohn & Cockburn 1994, see Heinsohn & Legge 1999 for review). If birds are adjusting parental care so carefully, it follows that cooperative breeders should regulate helping behavior in context-dependent ways as well. In fact, there is mounting evidence to suggest that birds do adjust investment strategies when providing help on a territory (Reyer 1984, Emlen et al. 1998, Cockburn 1998, Russel & Hatchwell 2001, MacColl & Hatchwell 2002).

Reyer (1984) demonstrated that male helpers altered behavior depending on whether or not they were related to the female breeder in a group (see also Emlen & Wrege 1991, Baglione et. al 2003). Specifically, related male helpers fed nestlings while unrelated male helpers fed the female breeder. In an experimental study, Russell & Hatchwell (2001) similarly highlighted the importance of kinship to the expression of helping behavior in long-tailed tits, demonstrating that potential helpers helped at the nest of kin rather than non-kin virtually 100% of the time when given the choice. MacColl & Hatchwell (2002) reported that individuals in the same species switched from breeding to helping within a season according to the predictions of a model based on temporal differences in the fitness payoffs of the two strategies. And finally, the observation that males are most likely to provide help when paternity of a clutch is shared and/or uncertain (*sensu* Vehrencamp 1983, Emlen et al. 1998, for review see Johnstone 2000), provides inter-specific support for the idea that non-breeding adults adjust levels of help according to short-term calculations of fecundity and survival.

The concept of reproductive skew, however, fails to explain helping in singular cooperative breeders since helpers do not apparently gain direct reproductive fitness while helping on a territory. Singular cooperative breeding, in which all birds help in the care of young but only one pair breeds per group, thus represents a particularly important challenge to avian ecologists seeking to explain the evolution of helping behavior. Helping behavior in the green woodhoopoe, a singular cooperative breeder in Sub-Saharan Africa, is especially interesting because non-breeding helpers in the species have been shown to significantly increase the production of young in some populations, but not in others (du Plessis 1993, Lepage & du Plessis unpubl. ms).

Utilizing over 20 years of data from a long-term study of two green woodhoopoe populations in South Africa, this study evaluates evidence for the idea that helpers in the species may be regulating helping behavior in context-dependent ways. Previous investigation of the same system (Chapter 1) suggests that reasons for delaying dispersal and engaging in helping behavior are likely different for males and females of the species. Females delaying reproduction showed significant *increases* in lifetime reproductive success, while males delaying reproduction showed significant *decreases* in lifetime reproductive success. Given these patterns, one would expect females to use the natal territory as a refuge (seeking to ensure survival rather than mitigate reproductive costs while waiting to breed) and males to use it as a launch pad (seeking to disperse from it, or breed on it, as soon as they are able).

Assuming that helping is costly, the divide between males and females in their timing of dispersal and age-related reproductive success in the system at hand leads to two important predictions. (1) While females likely have more reason to delay dispersal than males, they may have less reason to seek inclusive fitness from helping on their natal territory; thus male helpers should impact breeder productivity more than female helpers. (2) If helping is a best-of-a-bad-job strategy for males, then male helpers should increase productivity on their natal territory most when ecological constraints on independent breeding are severe.

This study tests these predictions by comparing the impact of male and female helpers on breeding success in a coastal population where competition over breeding vacancies is relatively relaxed, as well as in an inland population where competition over breeding vacancies is comparatively fierce. If the above predictions hold, then one would expect two patterns to emerge from the results of this study. First, related male helpers should impact the production and survival of young more than related female helpers in both populations. Second, related male helpers should increase breeder fecundity and offspring survival more at the inland study site (where males tend to delay dispersal) than at the coastal study site (where males tend to disperse within a month or two of reproductive maturity) (Chapter 2).

Methods

Study species. The green woodhoopoe is a territorial, obligate cavity-roosting species found throughout the woodlands of Sub-Saharan Africa. Living in year-round residential groups of 2-12 individuals, both males and females reach reproductive maturity at one year but may delay breeding for up to seven years. All adults participate fully in the feeding and care of young, but only one pair breeds per group (Ligon & Ligon 1978, du Plessis 1993). Non-breeding group members are related to one or both of the breeders in approximately 90% of cases (du Plessis 1993). Helping behavior, however, is unrelated to nest-site specificity, kin discrimination or prior association with breeders (du Plessis 1993). Previous research on the species suggests that non-breeding adults reduce the food provisioning workload of the breeding pair, but do not increase either the number of young fledged or the survival of breeders (du Plessis 1991, 1993).

Study site. The study included two populations occupying distinctly different sites in the Eastern Cape Province, South Africa. Monitoring began at both sites in 1981 and continued at the coastal site in Morgan's Bay (32°43'S, 28°19'E) through 2002. Data collection at the inland site in the Kubusi River Valley (32°32'S, 27°47'E) is current through 1997. The two sites vary considerably in vegetation, habitat and climate (du Plessis 1989a). A maximum 32 breeding groups occupy the 33km² of the coastal site. Their territories, punctuating an open agricultural landscape, are stacked linearly along riverine forest belts running away from the Indian Ocean. In contrast, the 45km² inland site houses 26 groups whose territories center more randomly on small patches of riverine forest growing in the tributary valleys of the Kubusi River. At an elevation of 650 m, these inland tributaries snake through a landscape otherwise dominated by valley bushveld.

On average, coastal territories cover 17.5 ha, 16.7 ha of which are riverine forest. Territories at the inland site are generally twice as large (35.1 ha), but contain just 2.3 ha of the riverine forest where the birds typically find roosting cavities. The number of available cavities per territory is thus greater at the coastal site than it is at the inland site (10.9 vs. 2.9) (du Plessis 1989b). The coastal site is also wetter (1070 mm vs. 435 mm of precipitation), warmer (min temp. 4° vs. -4°), and has more territories in which natal rates generally exceed birth rates than the inland site (59.3% of territories vs. 49% of territories, A. Hawn & M. du Plessis unpubl. data). Approximately 48% of the males hatched at the coastal site bred within their lifetime. By comparison, only 30% of the males hatched at the inland site bred within their lifetime (Chapter 1).

Data Collection. Each bird was banded with a unique combination of three synthetic Darvic-color rings and a numbered metal ring (SAFRING) upon their first capture as juveniles. As birds bred annually and relatively synchronously (December through February), pre- and post-breeding censuses were performed in all but a few years when only a post-breeding census was completed. All juveniles observed in a group during a post-breeding census were considered to have hatched on the territory since dispersal is negligible during the first year (du Plessis 1993). Based on behavioral observations that were confirmed by preliminary genetic fingerprinting, the assumption also was made that putative parents were the genetic parents in all cases (D. Parkin & M. du Plessis unpubl. data). The relatedness of helpers to breeders was construed from the above pedigree assumptions and was adjusted from year to year if helpers or breeders on a territory changed. To ensure consistency, January 1 was considered the hatching date of all birds fledging in a given year. If a one month old juvenile appeared in November or December of a year, the bird was considered to be the product of the upcoming breeding season and its hatching date was listed as January 1 in the following year. Males and females were separated on the basis of bill length and vocal dimorphism as both traits are easily deciphered in the field (Ligon & Ligon 1978).

Data Analysis. 192 group years were analyzed at the coastal study site and 78 at the inland study site. Only those groups occupying core territories were included in the analysis to ensure that undetected dispersal out of the study area was negligible. Previous research on the same system records that less than 13% of all dispersal events within the study area occurred across groups separated by more than two territories (Lepage & du Plessis unpubl. ms.). It is unlikely, therefore, that juveniles in the core territories of the study site dispersed out of the study area undetected.

In order to maximize sample sizes, we divided the samples from each population between groups failing to fledge young in a year and groups successfully fledging young in a year. Mann-Whitney U-tests were used to test for significant differences between these categories in their number of related male helpers and related female helpers. In a subsequent analysis, the group-years were divided on the basis of whether or not they produced juveniles surviving through at least their first year. Again, Mann-Whitney U-tests were used to test for significant differences in the number of related male helpers and the number of related female helpers in successful versus unsuccessful groups. Partial correlation coefficients were used to determine whether or not helpers had a direct impact on the survival of juveniles once a group's production of fledglings was controlled.

Recent studies have underscored that the impact of any individual on the reproductive success of a group depends upon the efforts of other group members (*sensu* Härdling et al. 2003). In order to investigate the impact of related male and female helpers on reproductive success without the confounding variable of group size, groups of three adults in which only one related male (n=25) or female helper (n=34) was present were compared in terms of the average number of young they fledged and the average number of juveniles they produced that survived their first year. Partial correlation, controlling for the effect of study site, was used to test whether or not breeding success was correlated with the presence of a related male versus a related female helper.

Previous research on the same species highlighted the importance of relative territory quality to the dispersal and helping strategies of non-breeding adults (Ligon & Ligon 1988). To elucidate the role of territory quality in the system at hand, we split each study site between high quality and low quality territories (see below) and tested for significant differences in number of related male helpers and/or number of related female helpers. We also sought to clarify the impact of any interaction between helper number and territory quality on reproductive success by calculating correlation coefficients between bivariate measurements of territory quality, the presence of fledglings, the presence of surviving juveniles, the presence of related male helpers, and the presence of related female helpers.

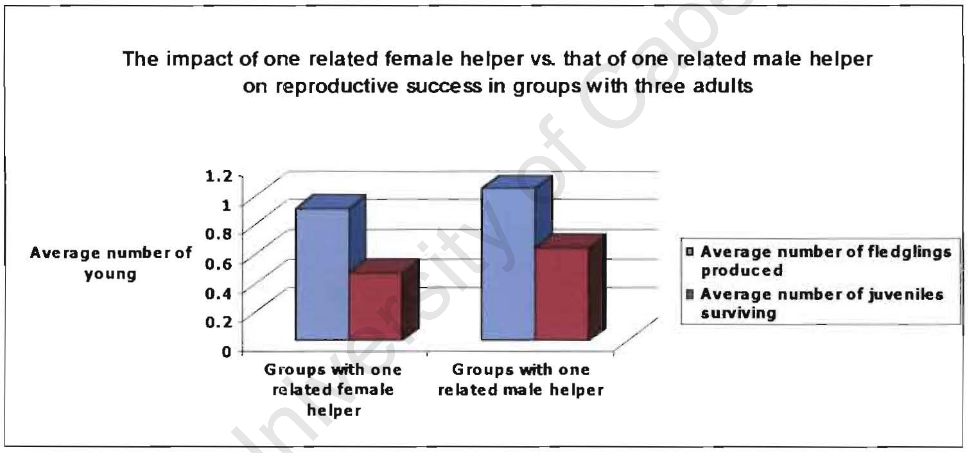
Territory quality was assigned on the basis of a natality/mortality (N/M) index calculated from the birth rates and death rates in each of the territories from 1986 onwards (*sensu*

Ligon & Ligon 1988). Explicitly, territories in which average birth rate exceeded average death rate were deemed high quality. Conversely, low quality territories were considered to be those in which average death rate exceeded average birth rate.

Results

Groups with one related male helper tended to produce more fledglings and had, on average, more juveniles surviving their first year, than groups with one related female helper (Figure 1). While these differences were not significant, the presence of a related male helper in place of a related female helper was significantly correlated with whether or not a group fledged young when study site was controlled ($r = 0.24$, $p = 0.038$ 1-tailed). Specifically, groups of three adults including one related male helper fledged young more often than groups of three adults including one related female helper.

Figure 1.



While, at both study sites, the number of related male helpers and related female helpers was greater among groups that fledged young in a year than among groups that did not, these differences were only significant at the inland site. When groups with and without juveniles surviving through their first year were compared at the coastal site, they did not differ significantly in their number of related male and female helpers. Similarly, the number of related female helpers in a group with juveniles surviving their first year in the inland population was not significantly different from that found in a group without juveniles surviving their first year. By contrast, the number of related male helpers at the inland study site was significantly larger on territories with juveniles surviving through their first year than on territories without surviving juveniles.

Table 1. Univariate comparisons between successful and unsuccessful breeding-years in the coastal study population. Significant differences determined by Mann-Whitney U-test.

Coastal population	N	Mean	S.D.	Min	Max		Z-stat Sig. (1-tailed)
Number of related male helpers in Groups failing to fledge young	81	0.31	0.61	0	3		-1.398
Number of related male helpers in Groups successfully fledging young	101	0.42	0.64	0	3		(0.081) NS
~~							
Number of related female helpers in groups failing to fledge young	81	0.43	0.61	0	3		-0.306
Number of related female helpers in Groups successfully fledging young	101	0.50	0.73	0	4		(0.380) NS
~~							
Number of related male helpers in groups w/out surviving juveniles	110	0.39	0.65	0	3		-0.416
Number of related male helpers in groups with surviving juveniles	72	0.33	0.58	0	3		(0.339) NS
~~							
Number of related female helpers in groups w/out surviving juveniles	110	0.49	0.73	0	4		-0.299
Number of related female helpers in groups with surviving juveniles	72	0.43	0.60	0	2		(0.383) NS

NS = not significant. *Indicates significance at the p<0.05 level; ** indicates significance at the p<0.01 level.

Table 2. Univariate comparisons between successful and unsuccessful breeding-years in the inland study population. Significant differences determined by Mann-Whitney U-test.

Inland population	N	Mean	S.D.	Min	Max		Z-stat Sig. (1-tailed)
Number of related male helpers in groups failing to fledge young	31	0.26	0.63	0	2		-2.901
Number of related male helpers in Groups successfully fledging young	47	0.64	0.67	0	2		(0.002)**
~~							
Number of related female helpers in groups failing to fledge young	29	0.41	0.63	0	2		-2.522
Number of related female helpers in Groups successfully fledging young	45	0.89	0.83	0	3		(0.006)**
~~							
Number of related male helpers in groups w/out surviving juveniles	44	0.36	0.61	0	2		-1.870
Number of related male helpers in groups with surviving juveniles	34	0.65	0.73	0	2		(0.031)*
~~							
Number of related female helpers in groups w/out surviving juveniles	40	0.63	0.36	0	3		-0.963
Number of related female helpers in groups with surviving juveniles	34	0.79	0.65	0	2		0.168

*Indicates significance at the p<0.05 level; ** indicates significance at the p<0.01 level.

When the fledging success of a group was controlled, neither the number of related male helpers nor the number of related female helpers was positively correlated with offspring survival through the first year. In fact, the number of related male helpers on a territory at the coastal study site was negatively correlated with the number of juveniles surviving through their first year ($p = 0.016$). Conversely, the number of related female helpers on a territory at the inland study site was negatively correlated with the number of surviving juveniles on a territory ($p = 0.024$).

At the coastal site, high quality and low quality territories showed no differences in either the number of related male helpers or the number of related female helpers they housed (2-tailed: $p = 0.493$ and $p = 0.828$, respectively). Similarly, the number of related female helpers was not significantly different between high and low quality territories at the inland study site ($p = 0.173$, 2-tailed). The number of related male helpers, however, was significantly greater on high quality territories than on low quality territories in the inland population ($p = 0.002$, 2-tailed).

Correlation calculations failed to identify any significant relationship between territory quality and the presence of fledglings, surviving juveniles, related male helpers or related female helpers in the coastal population. The presence of related male helpers only tended toward a significant positive relationship with the production of fledglings ($p = 0.074$); none of the other variables showed correlation with each other. At the inland study site, territory quality was not significantly correlated with the presence of fledglings ($p = 0.070$, 1-tailed), surviving juveniles ($p = 0.098$, 1-tailed) or related female helpers ($p = 0.153$, 1-tailed), but it was significantly correlated with the presence of related male helpers. Specifically, high quality territories tended to have related male helpers, while low quality territories did not ($r = 0.36$, $p < 0.001$, 1-tailed). The presence of related male helpers also showed significant correlation with the presence of fledglings ($r = 0.37$, $p < 0.001$, 1-tailed) and the presence of surviving juveniles ($r = 0.21$, $p = 0.033$, 1-tailed). The presence of related female helpers was positively correlated with the presence of fledglings in the inland population ($r = 0.27$, $p = 0.010$, 1-tailed), but showed no correlation with juvenile survival ($p = 0.239$, 1-tailed).

Discussion

Cockburn (1998) summarized experimental evidence indicating male and female helpers may be driven by different aims in cooperative systems. Specifically, he concluded that males usually seek direct benefits when helping, whereas female helpers generally seek inclusive fitness. While previous investigation of this system suggested helpers do not influence fledging success or breeder survival on the natal territory per se (du Plessis 1993), significant patterns may have been obscured by differences between male and female helpers in their provision of care (*sensu* Stoffberg unpubl. ms.). By confining sample sizes to related helpers and distinguishing between male and female helpers in our analysis, this study revealed important inter-sexual differences concerning the impact of helpers on fledging success and juvenile survival.

Prediction (1) The null hypothesis that there is no difference between related male and female helpers in their impact on the production and survival of young was proven false. As predicted, related males increased the probability of fledging young more than related females when group size and study site were controlled. In their recent study of the coastal population, Radford & du Plessis (2003) reported that male helpers brought significantly larger prey items to the nest than female helpers and delivered greater biomass overall. Ligon & Ligon (1978) concluded that, in a Kenyan population of green woodhoopoe, the presence of more than one male helper deterred potential predators and reduced the number of territory challenges from other breeding groups. One thus might expect that the number of related male helpers and the number of surviving juveniles would be positively correlated on a territory. Once the fledging success of a group was controlled, however, the number of related male helpers showed no correlation with the number of surviving juveniles on a territory at the inland study site and was negatively correlated with juvenile survival at the coastal study site.

Prediction (2) The expectation that related male helpers should increase breeder fecundity and juvenile survival more at the inland study site (where males tend to delay dispersal/reproduction) than at the coastal study site (where males tend to disperse/breed within a year of reproductive maturity) also was met by the results of this study. Strong evidence implicating a role for male helpers in fledging success was found in the inland population, but not in the coastal population. Some part of this pattern may result from the tendency of male helpers to bring large prey items to the nest (Radford & du Plessis 2003), since food contributions may translate into fledging success more at the sparse inland site than at the coastal site.

This last observation brings up the important possibility that the patterns across study sites may be due to the differential needs of breeders at the two study sites, rather than the differential investment levels of helpers. Indeed, Magrath (2001) suggested that group size effects on reproductive performance may be greater in poor conditions than in good conditions when comparing intra-specific populations. While this prediction matches patterns in the results at hand, previous findings also indicate male helpers disperse and breed significantly later in the inland population than in the coastal population (Chapter 2) and food may not be limiting for either population (Lepage & du Plessis unpubl. ms.). Consequently, it follows that behavior on the part of helpers, rather than need on the part of breeders, is most likely to change between the two populations. Nonetheless, I recommend further investigation of the idea that food delivery rates at the nest may be lower in the absence of helpers at the inland study site than at the coastal study site.

One also should bear in mind that the impact of any individual on the reproductive success of a group depends upon the efforts of other group members (*sensu* Härdling et al. 2003). Luck (2002) reported that rufous treecreeper breeders in fragmented landscapes tended to use the care of helpers as additive to their own, while breeders in continuous landscapes lowered their level of care in the presence of helpers. Based on these results, he posited that readily available food resources may mitigate the impact of helpers on reproductive success. As the inland site is patchier than the coastal site and foraging distances are smaller in the latter, an inter-site comparison of breeder and helper food delivery at the nest is an important program for future study in this species.

The impact of female helpers in the inland population. The presence of related female helpers contributed significantly to fledging success at the inland site. Groups with and without surviving juveniles, however, showed no significant differences in their number of related female helpers, and the number of related females was negatively correlated with the number of surviving juveniles once the fledging success of a group was controlled. This finding echoes the earlier observation of du Plessis (1989a) and Lepage & du Plessis (unpubl. ms.) that, while fledging success in the inland population was positively correlated with group size, the number of juveniles surviving to one year was not. Evidence indicating that the presence of related female helpers may drive this result is interesting, given life-history patterns suggesting females should prioritize their own survival over that of related juveniles.

I report elsewhere that females at the inland study site experienced heavier mortality during their first two years of life than either inland males or juveniles at the coastal study site (Chapter 1). Given the cold temperatures of the inland site and the difficulty young females have with thermoregulation (du Plessis & Williams 1993), it follows that related female helpers may represent a resource sink, rather than source, to juveniles in the inland population. This idea is further supported by the observation of Radford & du Plessis (2003) that all juveniles in this system feed like adult females since bills of juvenile males and females are the same length as those of adult females. Juveniles also were less successful than adults when foraging, perhaps because of an overlap in foraging niche between inexperienced juveniles and experienced adults (Radford & du Plessis 2003).

One might conclude that interference competition during foraging would negatively impact juvenile survival more at the inland study site than at the coastal study site where territory quality is comparatively good. Taken together, the above observations present the possibility that females in the inland population may help at the nest in order to avoid a net loss of inclusive fitness when subsequently foraging with related juveniles. Further investigation of this idea would be worthwhile (*sensu* West et. al. 2002). In addition, consideration should be given to the possibility that old related female helpers may contribute more than young related female helpers to reproductive success since mortality rates slow among females later in life, perhaps allowing them to shift resources from survival to juvenile care.

The link between territory quality and related male helpers. Komdeur (1996) found that helpers on high quality territories were predominantly female, whereas helpers on low quality territories were usually male. This study reports the opposite pattern. High quality territories in the inland population tended to have significantly more related male, not female, helpers than low quality territories. Interestingly, territory quality showed no correlation with the presence of either related male helpers or related female helpers in the coastal population. Taken together, these findings suggest that (1) territory quality may play a role in male dispersal decisions when ecological constraints are severe, but not when they are relaxed, and (2) females may not base dispersal decisions on calculations of inclusive fitness via territory quality at all.

Given the link between the presence of related male helpers and high quality territory, it could be argued that this study's definition of territory quality, rather than the contributions of male helpers, drove the differences between successful and unsuccessful breeding groups in male helper number. This interpretation of the data is undermined, however, by the finding that territory quality was not significantly correlated with the presence of fledglings or surviving juveniles at either study site. By contrast, the presence of related male helpers was significantly correlated with both the presence of fledglings and surviving juveniles in the inland population. I thus posit that while the presence of related male help and high territory quality may coincide because of male dispersal strategy, patterns of male help rather than territory quality gradients best explain the results evidenced in this study.

Conclusions. Contrary to previous hypotheses concerning inter-sexual patterns of helper care (*sensu* Cockburn 1998), the results of this study indicate green woodhoopoe males, rather than females, seek inclusive fitness through helping on the natal territory. Importantly, providing help on the natal territory seems to represent a best-of-a-bad-job strategy to males of this species, since evidence of increased breeding success in the presence of related male helpers is lacking in the coastal population where competition for breeding vacancies is relatively slight and high quality territory is fairly abundant. Furthermore, the results may indicate females regulate helping behavior according to calculations of survival rather than inclusive fitness, emphasizing their own survival over that of related young. This finding is interesting in light of the earlier observation that female green woodhoopoes increase lifetime reproductive success when they delay reproduction as long as they are able to survive the first two years of their life when mortality is high.

Taken together, the findings presented by this study demonstrate the importance of the immediate costs and benefits of providing help in cooperative systems and that the trade-off between them might differ for males and females within a species. In particular, we recommend further empirical study of the idea that male and female helpers pursue different investment strategies based on the life-history patterns and ecological constraints of their respective sex.

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Synthesis

Situating the mechanisms driving cooperative breeding within a cohesive evolutionary framework, remains a central goal of behavioral ecology. Ironically, recent reviews suggest that such cohesion eventually may result from clarifying inter-specific and intra-specific differences, rather than similarities, in individual reasons for cooperating (Arnold & Owens 1999, Hatchwell & Komdeur 2000, Heinsohn & Legge 1999, Heinsohn in press, Clutton-Brock 2002, Dickinson & Koenig 2003, Cockburn in press).

A number of authors have underscored the notion that different cooperative systems likely result from different selective pressures (Emlen 1998, Arnold & Owens 1999, Hatchwell & Komdeur 2000, Clutton-Brock 2002). Evidence indicating helpers probably seek different benefits depending on their sex and/or relatedness to a breeding pair also is mounting (Reyer 1984, Emlen & Wrege 1991, Cockburn 1998, for review see Cockburn in press). Specifically, authors increasingly have recognized that differences in helper type between and within systems will influence the reaction of individuals to forces such as kinship selection, direct benefits of philopatry, dispersal risk, and breeder saturation on high quality habitat (Arnold & Owens 1998, 1999, Hatchwell & Komdeur 2000, Kokko & Ekman 2002, Härdling et al. 2003).

Following this logic, I examined the idea that males and females in the cooperatively-breeding green woodhoopoe differ in life-history pattern and behavior. As hypothesized, I found that clarifying inter-sexual differences allowed insight into the mechanisms driving cooperative breeding in the study species.

My most important finding was that green woodhoopoe females delaying reproduction *increased* lifetime reproductive success, while males delaying reproduction *decreased* lifetime reproductive success. Interestingly, indirect evidence also suggested that physiological limitations in young birds, rather than adaptive behaviors in older birds, best explain female patterns of mortality and reproduction in this species. The subsequent findings of chapters two and three also indicated that, (1) the timing of dispersal and reproduction varied significantly with levels of breeder saturation among males but not females, and (2) related male helpers may contribute more to breeder productivity than related female helpers when breeding opportunities are scarce. Taken together, the three chapters presented here thus support the notion that young males use the natal territory as a launch pad when breeding constraints are relaxed and as a nursery when they are not. Young females, on the other hand, seem to use the natal territory as a refuge regardless of how saturated breeding opportunities are in a population.

The results of this study provide evidence for three main ideas relevant to the broader study of cooperative breeding. First, they highlight that the fitness costs of delaying reproduction may not be as high as previously assumed in some cooperative species if, as in females of this species, birds delaying breeding tend to live longer than birds reproducing at maturity. This idea is crucial because it has the power to explain why delayed dispersal might evolve in one communal species or lineage, but not in another. Specifically, when considering the evolution of cooperative breeding, researchers might better reconcile intra-specific explanations of the behavior with its inter-specific patterns by taking into account innate sources of variation in the cost of delayed reproduction.

Second, age-related patterns of female reproduction and mortality in this species indicate that variability in reproductive cost potentially plays a role in predisposing a population, or sub-sets within it, to delayed reproduction. Specifically, the finding that young females seemingly pay a disproportionately high cost of reproduction in the green woodhoopoe, provides support for the notion that high reproductive costs may help to explain the evolution of delayed breeding and/or dispersal. Arnold & Owens (1998) recorded that both low adult mortality and low fecundity were prominent life-history correlates of cooperative breeding in the taxa they studied. While the idea that longevity might lead to delayed reproduction via breeder saturation has been given much attention in the past decade (see Hatchwell & Komdeur 2000 for review), the idea that significant reproductive costs might lead individuals to adopt delayed breeding and/or low fecundity as a life-history strategy has not (*sensu* Covas 2002). The trends of this study clearly suggest that the latter idea merits further investigation.

And finally, the results presented heretofore provide evidence for a link between intra-specific variation in helper type and intra-specific variation in reproductive strategy. Male and female differences in age-related patterns of reproductive success in this species suggest that females should prioritize survival over reproduction while young, whereas males should aim to disperse and breed as soon as possible. As stated above, inter-sexual differences in the reaction of birds to varied levels of breeder saturation, as well as gender related patterns concerning helper impact, fit this prediction. The system at hand thus provides an elegant demonstration of how and why behavioral responses to ecological constraints may depend on life-history pattern.

Taken as a whole, the differences between male and female life-history strategies evident in this study suggest that life-history patterns, ecological constraints and benefits of philopatry co-evolve to maintain cooperative breeding in the green woodhoopoe. This conclusion is important, not least, because it reminds us that in order to understand the evolution of cooperative breeding on a broad scale, it is first necessary to consider the diversity of social, ecological, and physiological factors operating at the level of the individual.

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