

Delayed Breeding Affects Lifetime Reproductive Success Differently in Male and Female Green Woodhoopoes

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Summary

In cooperatively breeding species, many individuals only start breeding long after reaching physiological maturity [1], and this delay is expected to reduce lifetime reproductive success (LRS) [1–3]. Although many studies have investigated how nonbreeding helpers might mitigate the assumed cost of delayed breeding (reviewed in [3]), few have directly quantified the cost itself [4, 5] (but see [6, 7]). Moreover, although life-history tradeoffs frequently influence the sexes in profoundly different ways [8, 9], it has been generally assumed that males and females are similarly affected by a delayed start to breeding [7]. Here, we use 24 years of data to investigate the sex-specific cost of delayed breeding in the cooperatively breeding green woodhoopoe (*Phoeniculus purpureus*) and show that age at first breeding is related to LRS differently in males and females. As is traditionally expected, males that started to breed earlier in life had greater LRS than those that started later. However, females showed the opposite pattern: Those individuals that started to breed later in life actually had greater LRS than those that started earlier. In both sexes, the association between age at first breeding and LRS was driven by differences in breeding-career length, rather than per-season productivity. We hypothesize that the high mortality rate of young female breeders, and thus their short breeding careers, is related to a reduced ability to deal with the high physiological costs of reproduction in this species. These results demonstrate the importance of considering sex-specific reproductive costs when estimating the payoffs of life-history decisions and bring into question the long-held assumption that delayed breeding is necessarily costly.

Results

Age at First Breeding and Reproductive Success

Green woodhoopoes live in year-round residential groups of 2–12 individuals; within each group, only one

pair breeds per season [10]. Consequently, although both males and females reach reproductive maturity at one year of age, individuals might not start breeding for several years [11]. Individuals of both sexes can attain a breeding position either in their natal group (58% of breeders), when one member of the breeding pair dies, or by dispersing to fill a breeding vacancy in another group (42% of breeders). Using a linear mixed model (LMM) to investigate the effects of age at first breeding, sex, territory quality, study site, group size, and prebreeding dispersal, we found that an individual's lifetime reproductive success (LRS, measured as the total number of fledglings produced in its breeding career) was significantly affected by its age at first breeding. However, this effect differed between the sexes ("age at first breeding \times sex" interaction term, Table 1A): Although age at first breeding was negatively associated with LRS in males, females that started breeding later actually had a higher LRS than earlier starters (Figure 1A). The association between age at first breeding and LRS does not appear to be driven by differences in per-season productivity; after controlling for significant effects of group size and the interaction between territory quality and study site, we found no significant effect of age at first breeding on the mean number of fledglings produced per breeding attempt (Table 1B, Figure 1B). Instead, differences in breeding-career length seem to be important. Age at first breeding significantly influenced the number of breeding seasons an individual experienced, but again, this effect differed depending on the sex of the breeder (Table 1C): Although age at first breeding was negatively associated with breeding-career length in males, females that started breeding later in life actually had longer breeding careers than earlier starters (Figure 1C).

Age at First Breeding and Mortality

The mortality rate of males once they commenced breeding was significantly lower for early starters (1–3 years old at their first breeding attempt) than for late starters (4–6 years old at their first breeding attempt; Kaplan-Meier estimate: $\chi^2 = 6.08$, $df = 1$, $p = 0.014$; Figure 2A). There was no significant difference between early-starting and late-starting males in the quality of their breeding territories (chi-square test: $\chi^2 = 4.30$, $df = 2$, $p = 0.117$), the mean group size in which they bred (two-sample t test: $t = 1.46$, $df = 60$, $p = 0.149$), or their lifespan (two-sample t test: $t = 1.67$, $df = 60$, $p = 0.101$).

In contrast to that of males, the mortality rate of females once they commenced breeding was significantly higher for early starters (1–3 years old at their first breeding attempt) than for late starters (4–6 years old at their first breeding attempt; Kaplan-Meier estimate: $\chi^2 = 6.33$, $df = 1$, $p = 0.012$; Figure 2B). There was no significant difference in the territory qualities (chi-square test: $\chi^2 = 3.02$, $df = 2$, $p = 0.221$) or mean breeding-group sizes (two-sample t test: $t = 0.66$, $df = 57$, $p = 0.514$) of late-starting and early-starting females. However,

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Table 1. Terms Affecting Green Woodhoopoe Breeding Parameters

Full Model	df	(A)		(B)		(C)	
		χ^2	p	χ^2	p	χ^2	p
Age at first breeding × sex	1	7.02	<u>0.008</u>			9.12	<u>0.003</u>
Mean breeding-group size	1	2.20	0.138	19.85	<u><0.001</u>	0.38	0.540
Territory quality	2	2.83	0.243			1.27	0.530
Study site	1	1.17	0.279			2.03	0.154
Prebreeding dispersal	1	0.01	0.931	0.68	0.410	0.01	0.958
Territory quality × study site	2			6.24	<u>0.002</u>		
Sex	1			0.21	0.647		
Age at first breeding	1			0.20	0.56		
Minimal Model		Effect	SE	Effect	SE	Effect	SE
Constant		1.434	0.158	1.333	0.043	1.913	0.092
Age at first breeding × sex		0.402	0.152			0.233	0.079
Age at first breeding		0.245	0.090			0.112	0.046
Sex: female		0	0			0	0
Sex: male		0.018	0.188			-0.067	0.012
Mean breeding-group size				0.201	0.033		
Territory quality × study site				0.362	0.136		

(A) LRS—the total number of fledglings produced in an individual’s breeding career, (B) mean number of fledglings produced per breeding attempt, and (C) breeding-career length. Results from linear mixed models (LMMs) were based on a sample of 121 green woodhoopoes from 44 groups with dates of first breeding in 18 different years. The year of first breeding was included as a random term in all three models ($p < 0.05$). The total number of fledglings and breeding-career length were square-root transformed, and the mean number of fledglings was square-root (+1) transformed prior to analysis. Significant results ($p < 0.05$) are underlined. Standard error (SE) is shown.

late-starting females had significantly longer lifespans than early starters (two-sample t test: $t = 6.26$, $df = 57$, $p < 0.001$).

Discussion

Our results suggest that the costs of delayed breeding differ for male and female green woodhoopoes. Males met the expectation that delayed breeding entails a long-term reproductive cost; males that were older at first breeding had a lower LRS than earlier starters. In contrast, and counter to the assumption that delayed breeding is costly, females that started breeding later in life actually had a higher LRS than those that began breeding earlier. Only two previous studies have attempted to quantify the potential cost of delayed breeding in cooperatively breeding species. A study of Siberian jays (*Perisoreus infaustus*) found that individuals that delayed breeding had a higher LRS than those that bred in their first season, but only males were considered in the analysis [6]. Research on Seychelles warblers (*Acrocephalus sechellensis*) considered both males and females but found no difference between them in their age-related reproductive patterns; in both sexes, individuals that started breeding at a young age produced more fledglings in their lifetime than those that delayed breeding [7].

Green woodhoopoe males that started breeding at different ages produced a similar number of fledglings per breeding attempt, but males that started breeding later had shorter breeding careers than those that started earlier. The variation in male LRS appears, therefore, to be driven by interindividual differences in breeding-career length rather than per-season productivity. Later starters had a higher mortality rate than early starters once they commenced breeding, but this was not due to differences in territory quality or mean group

size. Instead, mortality may simply increase with age, irrespective of breeding status: Early- and late-starting males showed no differences in their mean lifespan. These results suggest that the best strategy as a male is to begin breeding as soon as possible. However, male green woodhoopoes do help raise the offspring of others, and this behavior may arise for two reasons. First, a male’s strategy might also be influenced by its phenotypic quality if there is competition for breeding positions: Good-quality males might be better able to bear the costs of competition when they are young, whereas poor-quality males might make the “best of a bad job” and avoid breeding until they are older. Unfortunately, we do not have reliable phenotypic data to test this idea, but it is unlikely to be an explanation for helping behavior in green woodhoopoes because competition for breeding positions appears to be scarce (A.N.R. and M.A.d.P., unpublished data). Second, because breeding positions arise only rarely in the study population [12], males might help raise the offspring of others to gain indirect fitness benefits [3], and group size did have a significant positive influence on mean fledgling production per season.

The variation in female green woodhoopoe LRS with age at first breeding also appears to be driven by inter-individual differences in breeding-career length; later-starting females had longer breeding careers than earlier starters. Females that started breeding earlier in life suffered a higher mortality rate than those that started breeding later (although more than 60% of females that started breeding when they were 1–3 years old died after one or two breeding seasons, less than 30% of females that started breeding when they were 4–6 years old suffered this fate) and had shorter lifespans. The difference in mortality between early- and late-starting breeders might arise in several ways. First, individuals that start breeding later might have access to higher-quality

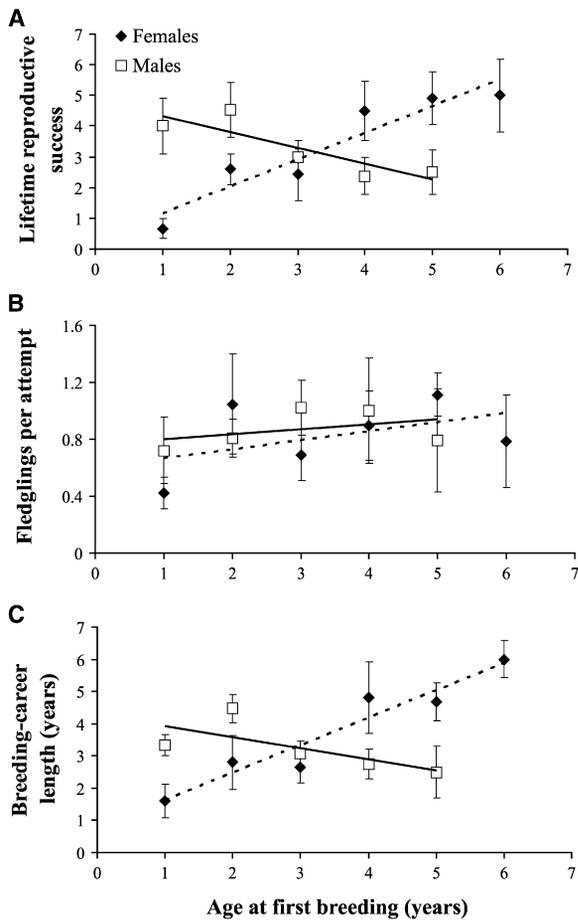


Figure 1. Intersexual Variation in Breeding Parameters with Age at First Breeding

Means \pm SE and least-squares regression lines for (A) LRS—the total number of fledglings produced in an individual's breeding career, (B) mean number of fledglings produced per breeding attempt, and (C) breeding-career length. The solid line signifies males ($n = 62$) and the dotted line signifies females ($n = 59$).

territories, which could increase their survival chances because of, for example, increased prey availability or decreased predation risk [13, 14]. However, early- and late-starting female green woodhoopoes did not breed on territories of different quality, and territory quality was not a significant predictor of breeding-career length. Second, later-starting individuals might breed in larger groups, which could increase their survival chances because of a reduced workload during breeding [15] and/or direct group-size benefits, such as reduced predation [16]. However, early- and late-starting females did not breed in groups of different mean size, and group size was not a significant predictor of breeding-career length in the green woodhoopoe. Furthermore, although previous studies of green woodhoopoes have shown a load-lightening effect of helpers on breeder effort, there is no evidence that this translates into an increased likelihood of breeder survival [17].

Instead, females that start breeding later in life might be better able to bear the costs of reproduction. Experiments have shown that the physiological cost of egg production has a significant negative influence on the

survival of female great tits (*Parus major*) [18]. In addition to egg laying, female woodhoopoe breeders conduct all the incubation of the eggs [19]. This means that as well as bearing the full cost of incubation (see [20]), they spend their nights alone while the rest of the group roosts communally, which might result in a thermoregulatory cost [12, 21]. Why might later-starting females be better able to bear these costs? First, if they have gained some relevant experience through helping in previous years [22], they might suffer lower costs than earlier starters when producing the same number of fledglings in a breeding attempt. However, green woodhoopoe helpers do not produce eggs or assist with incubation, so an increased level of experience is unlikely to explain the increased survival of later-starting breeders. Second, later starters might be in better physical condition when they begin breeding. This might arise if low-quality individuals start breeding at earlier ages [23], but there is no a priori reason to expect this [24]. Alternatively, late starters might have accumulated valuable physiological resources by the time they come to breed. Young female green woodhoopoes often fail to reach and maintain a body condition within two standard deviations of the mean of older adults [21]. If young females are battling to survive because of poor body condition, the added energetic burden of reproduction would create a steep tradeoff between current and future reproductive success, and this tradeoff might explain the disproportionately high cost of reproduction among young female breeders.

In theory, the increased LRS experienced by later-starting females might have resulted from an increase in per-season productivity. Individuals that start breeding later in life might, for example, invest more because their life expectancy is lower (the less-to-lose hypothesis [24, 25]). However, female green woodhoopoes that started breeding later were more likely to survive to the next breeding attempt, they bred for more seasons, and they had longer lifespans than earlier starters; therefore, their life expectancy was higher. Alternatively, later starters might have accumulated more parenting experience through helping and thus perform better than early starters once they started breeding (the skills hypothesis [24, 25], but see [26]). However, they did not raise a higher mean number of fledglings per season than early starters. Hence, the most likely explanation for the increase in the LRS of female green woodhoopoes with increased age at first breeding remains the higher mortality rate of early-starting breeders, and thus their shorter breeding careers compared to later starters.

Green woodhoopoe individuals help to raise the offspring of the dominant pair in their group while themselves waiting to breed [17]. Although a previous study indicated that the help provided by these nonbreeding adults did not increase the number of fledged young [10], our results (based on a much larger sample size) suggest that group size has a positive influence on per-season productivity. Because 90% of helpers are related to at least one of the breeders in the group [10], helpers might gain indirect fitness benefits while waiting to breed. Thus, the difference in inclusive fitness between late-starting and early-starting females may be even higher than suggested by our analysis of LRS as merely the total number of fledglings produced; if anything, we

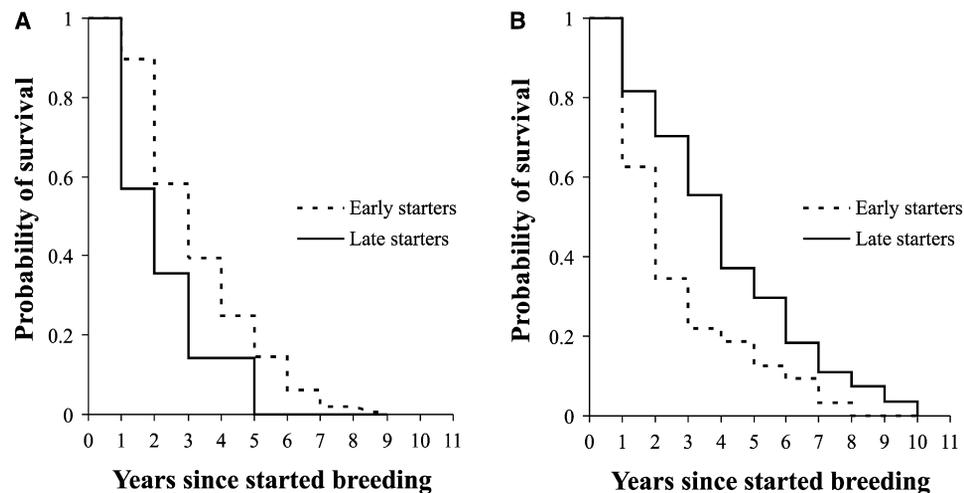


Figure 2. Kaplan-Meier Estimates of the Survival Function of Green Woodhoopoes Once They Commenced Breeding (A) Males and (B) females. Early-starting individuals were those that first bred at 1–3 years of age ($n = 48$ males, 32 females). Late-starting individuals were those that first bred at 4–6 years of age ($n = 14$ males, 27 females).

have been conservative in our estimate of the supposed benefit that females gain from delayed breeding. However, this does not mean that choosing to delay breeding is necessarily the best option available to a female green woodhoopoe and should be selected adaptively: The obvious risk of dying before obtaining a breeding position counteracts the benefits of waiting, especially because breeding vacancies only arise rarely in the study population [12]. Future studies need to establish whether it would pay for females to ignore breeding vacancies in some situations. In the meantime, it is clear that the assumption of reproductive costs associated with delayed breeding may not be as clear cut as once thought and that males and females of the same species may differ dramatically in the costs suffered.

Experimental Procedures

Study Species

The green woodhoopoe is a territorial, group-living, cavity-roosting species found throughout the woodlands of Sub-Saharan Africa [27]. All adults of both sexes participate in the provisioning of young, but only one pair breeds per group [10]. Nonbreeding group members are related to one or both of the breeders in approximately 90% of cases, but helping behavior is unrelated to natal philopatry, kinship, or prior association with breeders [10]. In South Africa, each group attempts to breed once every year, and a breeder's tenure is generally ended by death; very occasionally, breeders disperse to a breeding vacancy in another group (see below), but there is no evidence that breeders are ever usurped by other individuals (A.N.R. and M.A.d.P., unpublished data). Both males and females can attain a breeding position in their natal group (i.e., they do not need to disperse to breed), and they have an equal likelihood of doing so (58%, $n = 62$ males, 59 females; the other 42% of breeders of both sexes dispersed to fill a breeding vacancy in another group).

Data Collection

Data were collected from two color-ringed populations of green woodhoopoes in the Eastern Cape Province, South Africa. Each bird was ringed with three Darvic color rings and a metal ring (SAFRING) upon their first capture as a juvenile. At the "coastal" site near Morgan's Bay (32°43'S, 28°19'E), 32 groups were monitored from 1981 to 2005. Censuses of 28 groups at the "inland" site in the Kubusi River Valley (32°32'S, 27°47'E) were conducted between 1981 and 1997.

Because groups bred once each year and relatively synchronously (December to February), prebreeding (November) and postbreeding (March) censuses were performed in all but 4 years, when only a postbreeding census was completed. Prebreeding censuses provided a "breeding-group size" (i.e., number of adults present during breeding). If no prebreeding census had been conducted, the breeding-group size was assumed to be the number of adults present in the postbreeding census. All juveniles (identifiable from their predominantly black bills [27]) observed in a group during a postbreeding census were considered to have fledged on that territory because dispersal is negligible during the first year [10]. We have used the total number of fledglings produced in an individual's breeding career as a measure of LRS throughout (qualitatively, we obtained the same results when we used the total number of fledglings surviving to 1 year of age). Breeders were identified during incubation (only breeding females incubate the eggs [19]) and group foraging (when breeders of both sexes consistently displace nonbreeding helpers of the same sex [28]). Preliminary genetic fingerprinting indicated that the putative breeding male and female in a group were the genetic parents in all cases (D. Parkin and M.A.d.P., unpublished data). Adult males and females were distinguished on the basis of sexual dimorphism in both bill length [28] and vocalizations [29].

Green woodhoopoes roost communally in tree cavities every night, a behavior that yields vital thermoregulatory benefits [21], and they nest in one of the same cavities that they use for roosting [11]. Cavities represent the critical resource for woodhoopoe survival and reproduction: Groups rapidly move into previously unoccupied areas of forest as soon as nestboxes are provided [12] and territories apparently contain a surplus of food [30]. Consequently, we assessed territory quality in terms of the cavities available. Both captive and free-living woodhoopoes roost preferentially in cavities that provide superior thermal insulation, and a positive relationship exists between the thickness of the roost-cavity wall and its thermal insulation capacity (M.A.d.P. and J.B. Williams, unpublished data). We therefore measured the cavity-wall thickness of all known roosts within each territory (mean \pm standard error [SE]: number of roosts per territory = 6.9 ± 2.9 , range = 2–14) and classified territory quality as "low" (0–50 mm), "medium" (51–150 mm), or "high" (>150 mm) depending on the mean wall thickness, and thus thermal-insulation capacity, of cavities available.

When calculating the LRS and breeding-career length of breeders, we assumed that individuals that disappeared from their group had died unless they were found in another group. One potential problem with this assumption is the underestimation of LRS and breeding-career length of any breeders that dispersed undetected. However, green woodhoopoe breeders are highly sedentary: We recorded a change in breeding territory only six times in 464 breeder years

(including twice-yearly searches of the 5 km region around each study site between 1981 and 1989). To avoid skewing our data set toward short-lived individuals, we excluded those that started breeding within 6 years of the end of our data collection (e.g., 1999 for the coastal site). Our data set of complete life-histories therefore contained 126 breeders that had been ringed as juveniles and whose age was known accurately.

Data Analysis

Age at First Breeding and Reproductive Success

To investigate the influence of age at first breeding on LRS, the mean number of fledglings per breeding attempt, and breeding-career length, we conducted three separate LMMs. LMMs allow the inclusion of both fixed and random terms, the latter making it possible to take account of repeated measures of group and year of first breeding. All data sets were normalized by transformation prior to analysis (see Table 1). Each LMM included data on 121 breeders (62 males, 59 females) from 44 groups. We excluded the five additional individuals (three males and two females) for which we had complete life histories but that definitely dispersed at least once after attaining breeding status and thus were known to have bred on more than one territory. The following fixed terms were included in all three models: age at first breeding, sex, study site (coastal, inland), territory quality (high, medium, low), dispersal status on attainment of a breeding position ("prebreeding dispersal": natal, dispersed), and mean breeding-group size. All fixed terms were initially entered into the model and then sequentially dropped until only those terms whose elimination would have significantly reduced the explanatory power of the minimal model remained. All two-way interactions were tested, but only those that were significant are presented in the Results. We derived the significance of eliminated terms by adding them individually to the minimal model. All statistical tests were two-tailed and conducted with GenStat (eighth edition, Lawes Agricultural Trust, Rothamsted, Harpenden, UK).

Age at First Breeding and Mortality

To investigate the influence of age at first breeding on mortality rate, we divided our data set into early starters (1–3 years old at their first breeding attempt) and late starters (4–6 years old at their first breeding attempt). We used the number of years since breeding started as the dependent variable in a Kaplan-Meier analysis and included age class at first breeding (early or late) as a categorical predictor variable. We used the number of years since breeding started, rather than absolute age, to control for the inherently greater age of later starters; late starters must have survived at least 4 years simply to belong to this category. In an effort to explain the differences in mortality rates that we found, we compared the territory qualities, breeding-group sizes, and lifespans of early- and late-starting breeders of each sex.

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