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Incubation feeding by helpers influences female nest attendance in the green woodhoopoe, *Phoeniculus purpureus*

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Abstract In many bird species, the female alone incubates the eggs, but the male provides her with some food during the incubation period. In cooperatively breeding species, helpers might be expected to assist the breeding male in provisioning the female, but their contribution has been generally ignored. Here, I show that in the green woodhoopoe, *Phoeniculus purpureus*, the breeding male and helpers of both sexes bring food to the incubating female. The helpers did not increase the overall amount of provisioning the female received: groups of all sizes delivered a similar amount of food per hour. Helpers did, however, reduce the workload of the breeding male. Male and female helpers provisioned incubating females equally, as expected in a species where both sexes are likely to derive equal benefits from their helping behaviours. Female nest attendance was positively related to the level of group provisioning, but only in the short term. Thus, the female-nutrition hypothesis, which suggests that incubation feeding can provide an important source of energy to the breeding female, is supported in the green woodhoopoe.

Keywords Cooperatively breeding · Female-nutrition hypothesis · Helper contributions · Load-lightening

Introduction

In many species of bird in which only the female incubates the eggs, the male feeds his mate during the incubation period (Ricklefs 1974). In hornbills and some raptors, females are wholly dependent on males for food during this stage (Lack 1968; Kemp 1995). More often, males feed incubating females who also spend some time off the nest foraging for themselves, a strategy termed assisted gynaeparental incubation (Williams 1996). Re-warming of the eggs after these self-feeding bouts is likely to be costly (Biebach 1979; Vleck 1981). Moreover, avian embryos can suffer costs, such as increased mortality and reduced developmental rate, with decreasing nest attendance (the percentage of time that a parent sits on the nest) during incubation (White and Kinney 1974).

It is now generally accepted that, in addition to any possible role in mate assessment (Nisbet 1973, 1977) or pair-bonding (Lack 1940; Kluijver 1950), incubation feeding can be an important source of energy for the female (Royama 1966; Niebuhr 1981). Several intraspecific studies have shown that greater incubation feeding by males can improve female condition and/or reduce the time she spends foraging for herself, hence allowing increased female nest attendance (Lyon and Montgomerie 1985; Lifjeld and Slagsvold 1986, 1989; Halupka 1994). The benefits of incubation feeding therefore include a reduced risk of lethal chilling of the eggs and/or a decrease in the length of the incubation period (Lyon and Montgomerie 1985; Nilsson and Smith 1988).

In cooperatively breeding species, helpers may gain indirect fitness benefits if they increase the production of non-descendant kin (Hamilton 1964). Indirect fitness benefits may be gained during the current breeding season if a helper increases the production of offspring by related breeders, or in future breeding seasons if a helper increases the probability that related breeders will survive to reproduce again (Mumme et al. 1989; Crick 1992). There are therefore two main ways in which helpers may be of assistance during incubation feeding. First, they may

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reduce the workload of the breeding male ('load-lightening', sensu Brown 1987), by feeding the breeding female on some occasions. Second, they may increase the number of feeding visits to an incubating female, thus increasing her nest attendance. These two possibilities are not mutually exclusive. Helpers may also gain direct benefits from helping, such as direct access to parentage or the enhancement of social circumstances (see Cockburn 1998 for review).

I examined the contribution of helpers to incubation feeding in the cooperatively breeding green (or red-billed) woodhoopoe, *Phoeniculus purpureus*. In this species, a breeding pair are assisted in all group activities, including the provisioning of nestlings, territory defence and predator detection, by up to ten non-breeding helpers (Ligon and Ligon 1978). Woodhoopoes of both sexes frequently remain on their natal territory as non-breeders for several years. Most non-breeders in a group are therefore related to at least one of the breeders. However, non-breeders occasionally leave to join another group in which no breeding vacancy exists, and thus help in the raising of unrelated or only distantly related individuals (du Plessis 1989; Ligon and Ligon 1990). Unrelated immigrants feed and interact with nestlings and fledglings as frequently as do related helpers (Ligon and Ligon 1982).

I asked three key questions. (1) Does the presence of helpers reduce the workload of the breeding male during incubation feeding? (2) Do male and female helpers assist equally? (3) Does provisioning of the female during incubation serve an energetic function and permit her to spend more time incubating?

Methods

Data collection

I studied a colour-banded population of green woodhoopoes near Morgan's Bay (32°43'S, 28°19'E), Eastern Cape Province, South Africa. In this population, there is only one breeding attempt per season (du Plessis 1989). All helpers are therefore from the previous breeding season or before and are classified as adults. The breeding female alone incubates the clutch, for c. 18 days, and she is fed at the nest by other group members (Ligon and Ligon 1978). Study groups ranged in size from two to five adults (mean±SE=3.1±0.2).

Data on the feeding of incubating females were collected in 1999-2000 (8 nests) and 2000-2001 (14 nests). No group featured in both years and no breeding males or females switched groups between years. Nest sites were located by following birds returning with food or by listening for the food-solicitation calls that are given by breeding females in the vicinity of the nest (Rowan 1970; Ligon and Ligon 1978). Nest watches were conducted from 20 to 35 m away using binoculars. Groups usually resumed normal activities around the nest within 10-15 min of the observer's arrival. Nests were watched between 0500 and 1100 hours and between 1500 and 1900 hours, as this was when the birds were most active (personal observation). For analysis, these periods were divided into 2-h segments. The length of nest watches varied because a fixed period would have biased observations towards short incubation and foraging bouts: I therefore observed nests until three incubation bouts had been completed. Nest watches on the same group were separated by at least 2 days. The aim was to

observe incubation behaviour at each nest on at least three separate occasions spread across the incubation period, but nest predation prevented this for some of the groups.

During a nest watch, I recorded the times at which an incubating female entered and left the nest, and all visits by other group members to feed this female. The incubating female usually came to the entrance of the nest cavity to be fed. Occasionally, she would leave the cavity completely to collect food from another group member. If she stayed outside the nest cavity for less than 30 s, this time was not subtracted from the period of nest attendance, and the period was classified as a single incubation bout. Each time a group member returned with food, I noted the time, the individual's identity and the size of the prey item. Prey size was expressed as the ratio of prey length to bill length of a female woodhoopoe (taken as 46 mm; Radford and du Plessis 2003). Prey biomass was calculated from the formula of Rogers et al. (1976):

$$B = (0.0305L)^{2.62}$$

where B is the dry biomass in g and L is the body length in mm. A distinction was made between 'feeding frequency' (the number of visits to a nest per hour) and 'provisioning rate' (the total biomass of prey delivered per hour).

As a result of the strict queuing system operating in this species, breeders tend to be those individuals of each sex that have been in the group the longest (unpublished data). When this information was not known, breeding status was established by watching copulation attempts (preliminary paternity analysis has confirmed that only the dominant pair breed; M.A. du Plessis, unpublished data) and displacement activity during group foraging (when breeding individuals dominate non-breeding helpers; Radford and du Plessis 2003). Here, the incubating female and the breeding male are referred to as 'breeders', while 'helper' encompasses all other adult group members.

Statistical analysis

When using nests as independent data points to analyse the provisioning of incubating females, I used only those groups which had been observed on at least three separate occasions (and thus included at least nine incubation bouts). Consequently, only 18 nests were included in these analyses (mean±SE observation time per nest = 523±50 min), as the remaining 4 were depredated before this threshold was achieved. These analyses used group means in ANOVA and regressions. In analyses using observation periods as independent samples, a total of 80 (mean±SE duration = 125±22 min, $n=22$ nests) were available for inclusion.

When considering the influence of group provisioning rate on female nest attendance, I used a REML analysis to control for the random factor 'group'. All proportions were arcsine square-root transformed prior to parametric analysis. Statistical tests were two-tailed and summary statistics are presented as mean±SE.

Results

Contribution of helpers

There was no significant effect of year (ANOVA, feeding frequency: $F_{1,56}=1.48$, $P=0.228$; provisioning rate: $F_{1,56}=0.23$, $P=0.636$), day of the incubation period (feeding frequency: $F_{11,56}=0.72$, $P=0.717$; provisioning rate: $F_{11,56}=1.04$, $P=0.424$) or time of day (feeding frequency: $F_{4,56}=0.89$, $P=0.476$; provisioning rate: $F_{4,56}=0.34$, $P=0.852$) on either the group visit rate or the provisioning rate to the incubating female. Thus, data were pooled from each nest in subsequent analyses.

The mean number of feeding visits per hour to the incubating female (feeding frequency) did not vary significantly with group size (ANOVA: $F_{3,14}=0.72$, $P=0.554$). Taking prey biomass into account, there was no significant difference in the rate at which groups of different size provisioned the incubating female ($F_{3,14}=1.81$, $P=0.192$; Fig. 1). All subsequent analyses use the provisioning rate, to eliminate the confounding factor of different quantities of food delivered per visit.

The contribution of the breeding male to provisioning of the incubating female decreased significantly with increasing group size (ANOVA: $F_{3,14}=48.92$, $P<0.001$; Fig. 2): breeding males in groups of two had significantly higher provisioning rates than those in groups of all other sizes (Tukey's post-hoc test: all $P<0.001$), and breeding males in groups of three provisioned at a significantly higher rate than those in groups of five ($P<0.05$). However, all breeding males still provisioned at a higher rate than individual helpers within their group (paired t -test: $t=11.63$, $df=10$, $P<0.001$; Fig. 2).

Individual helpers provisioned at a lower rate in larger groups (ANOVA: $F_{2,8}=10.62$, $P=0.006$; all Tukey's post-hoc tests: $P<0.05$; Fig. 2). Considering groups where there was at least one helper of each sex, male and female helpers did not differ significantly in their provisioning rates (Wilcoxon test comparing the provisioning rate of male helpers with that expected from the relative number of helpers of each sex if they assist equally: $W=10.5$, $n=5$, $P=0.50$).

Effect of provisioning on the behaviour of the incubating female

The mean length of incubation bouts was 26.7 ± 1.1 min ($n=18$ nests with at least nine bouts observed), and the mean length of foraging bouts was 15.0 ± 1.0 min ($n=18$). The lengths of incubation and foraging bouts were positively correlated (regression: $r_s=0.36$, $F_{1,16}=8.98$, $P=0.009$; Fig. 3). The proportion of total time that females spent incubating ('nest attendance') varied among nests ($64.4\pm 1.2\%$, $n=18$, range= 52.8 – 73.1%).

Provisioning by other group members might allow breeding females to spend more time incubating by reducing the duration of foraging bouts and/or increasing the duration of incubation bouts. Female incubation behaviour was not significantly correlated with the mean provisioning rate of the group across the incubation period (mean duration of incubation bout: $r_s=0.03$, $F_{1,16}=0.51$, $P=0.486$; nest attendance: $r_s=0.01$, $F_{1,16}=0.07$, $P=0.789$). The length of female foraging bouts decreased, though not significantly with an increased provisioning rate by the rest of the group ($r_s=0.19$, $F_{1,16}=3.63$, $P=0.075$).

Adjustment of incubation behaviour by females in response to group provisioning rates may occur over a short time frame, rather than over the entire incubation period. Instead of using nests as independent data, I therefore investigated incubation behaviour using obser-

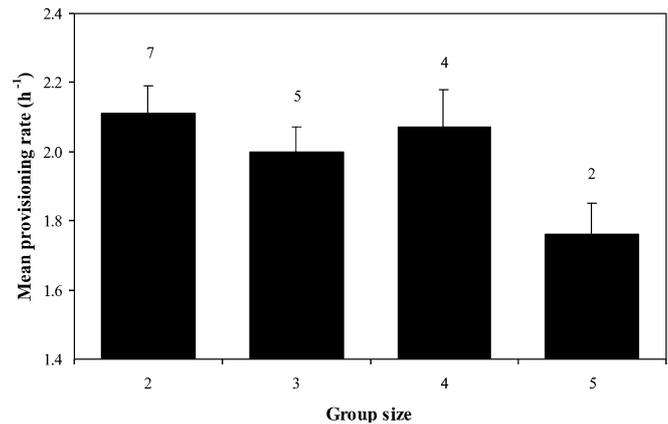


Fig. 1 Relationship between group size and provisioning rate (total prey biomass delivered per hour) of the whole group to incubating female green woodhoopoes, *Phoeniculus purpureus*. Shown are means+SE for the number of groups indicated above the bars

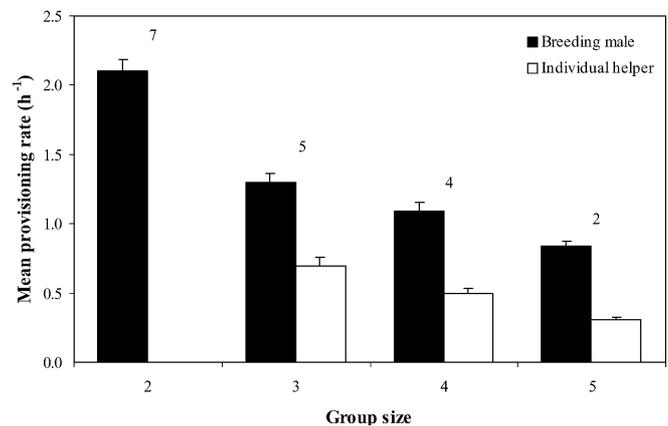


Fig. 2 Relationship between group size and provisioning rate (total prey biomass delivered per hour) of breeding males and individual helpers to incubating female green woodhoopoes. Shown are means+SE for the number of groups indicated above the bars

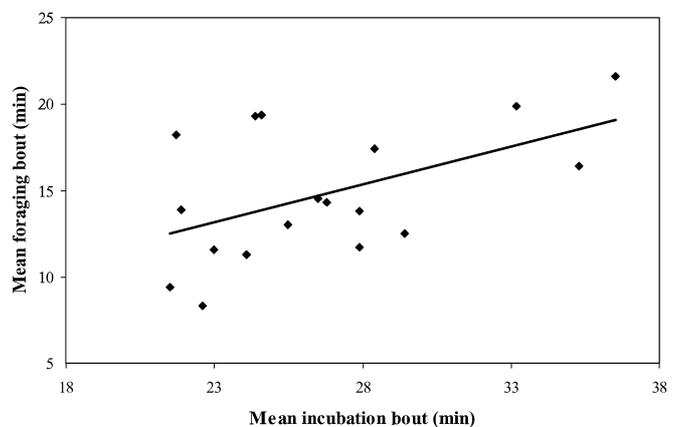


Fig. 3 Relationship between the mean duration of foraging bouts and the mean duration of incubation bouts in female green woodhoopoes. Shown are mean values per female and a least-squares regression line ($y=0.44x+3.16$)

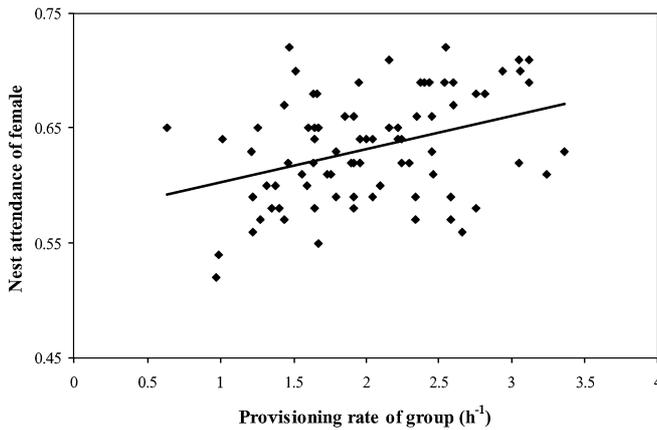


Fig. 4 Relationship between the provisioning rate of a green woodhoopoe group and the nest attendance (proportion of total time spent on nest) of the incubating female. Shown are 80 separate observation periods from 22 groups and a least-squares regression line ($y=0.03x+0.57$)

vation periods as independent samples. The number of watches conducted on each nest varied (3.64 ± 0.28 watches, range 1–6, $n=22$ nests), so to avoid the problem of pseudoreplication I performed a REML analysis, controlling for group identity. There was a significant positive relationship between provisioning rate and female nest attendance in a particular observation period ($\chi^2=13.40$, $df=1$, $P<0.001$; Fig. 4).

Discussion

Helper contributions

I found no difference in the feeding frequency or the provisioning rate of green woodhoopoe groups of different size when providing food for the incubating female. Studies of many cooperatively breeding species, including green woodhoopoes (du Plessis 1991), have found no significant variation in the rate of chick provisioning with the number of helpers (Brown et al. 1978; Brown and Brown 1981; Raitt et al. 1984; Russell and Rowley 1988; Woolfenden and Fitzpatrick 1990; Langen and Vehrencamp 1999). However, although some researchers have considered the contribution of helpers to incubation itself (e.g. Heinsohn and Cockburn 1994; Komdeur 1994; Legge 2000), only Zack (1986), in a study of grey-backed fiscal shrikes, *Lanius excubitorius*, has examined helper feeding of the incubating female in any detail. This is somewhat surprising, since the incubation period may last for a period of weeks, during which time a male would have to provision on a regular basis if he was the sole provider. He might therefore be expected to incur large energetic costs during this time. The reason for the paucity of studies on incubation feeding in cooperative breeders may be that helpers do not usually assist in this way (e.g. Marzluff and Balda 1990), that they are prevented from helping by the dominant male (e.g.

Stallcup and Woolfenden 1978), or that helpers are not present at this stage of the breeding cycle (e.g. Hatchwell et al. 1999). However, in species in which helpers do contribute to incubation feeding (e.g. bushy-crested jay, *Cyanocorax melanocyanea*, Hardy 1976; pied kingfisher, *Ceryle rudis*, Reyer 1986; bell miner, *Manorina melanophrys*, Poiani 1992), the potential for load-lightening at this stage should be considered more regularly than it has been to date.

Although incubating female woodhoopoes did not receive extra food in groups of larger size, the contribution of helpers did appear to reduce the input of the breeding male. Alternatively, helpers may have been compensating for the lower effort of some breeding males. Fogden and Fogden (1979) noted that the decline in protein and fat reserves in males of two passerine species coincided with peaks in food transfer to females, suggesting that the behaviour was associated with a significant cost to males (see also Røskoft 1985; Lifjeld and Slagsvold 1986). Thus, male woodhoopoes in larger groups may benefit because they can afford to work less hard during incubation. As with the provisioning of nestlings (du Plessis 1991), though, all breeding males contributed more than individual helpers in terms of the absolute amount of food delivered.

The reduced energy expenditure by breeding males in larger groups might theoretically enhance their survival. Koenig and Mumme (1987) suggested for acorn woodpeckers, *Melanerpes formicivorus*, that a major portion of the indirect fitness accruing to non-breeders comes not from direct aid to younger siblings, but from increased survivorship of male breeders. However, although helping by non-breeders lightens the workload of woodhoopoe breeders at various stages of the breeding cycle (Ligon and Ligon 1978; du Plessis 1991; this study), the saving does not apparently result in fitness benefits as measured by survivorship (du Plessis 1991).

It seems unlikely that direct benefits are the driving force behind the incubation feeding provided by green woodhoopoe helpers. Theoretically, helping might result in access to parentage (Cockburn 1998). For example, male helpers might gain mating opportunities with the breeding female they feed. However, helpers of both sexes provision incubating female green woodhoopoes, suggesting that this is not the sole consideration. Furthermore, preliminary paternity analysis indicates that only the breeding male sires offspring in this species (M.A. du Plessis, unpublished data). An alternative theoretical benefit from helping is the enhancement of social circumstances within the group (Zahavi 1990). By helping, individuals might accelerate the attainment of a breeding position through the formation of dispersal coalitions. However, in the study population of woodhoopoes, individuals disperse alone (but see Ligon and Ligon 1990).

Ligon and Ligon (1978), studying a Kenyan population of green woodhoopoes, also found that helpers reduced the feeding visits of the male parent to the incubating female, although they did not correct for prey size. Both

their study and this one found no difference between helpers of different sex in their provisioning rate to incubating females. It has been suggested that helpers of the sex that more commonly remains and breeds in their natal group should contribute more assistance than those of the sex which tends to disperse to breed (Clutton-Brock et al. 2002). In green woodhoopoes, both sexes are likely to remain and gain breeding status on their natal territory (du Plessis 1992), perhaps explaining why they help equally. It was also noticeable in the current study that individual helpers in larger groups contributed less than those in smaller groups.

Behaviour of the incubating female

The female-nutrition hypothesis (Royama 1966) predicts that females should maintain better body condition and/or provide better incubation if provisioned at a high rate. I have no information on female condition during incubation, due to the difficulty of catching the birds, but incubation feeding did appear to influence the incubation behaviour of female green woodhoopoes. Female nest attendance increased as group provisioning increased. However, this relationship held only in the short-term, i.e. in analyses of individual watches, rather than for mean values per nest. This was also the case in a study of long-tailed tits, *Aegithalos caudatus* (Hatchwell et al. 1999). Zack (1986) found no relationship between the time that a female grey-backed fiscal shrike incubated and the number of times she was fed per hour, but he did not investigate the possibility of short-term benefits. Such short-term effects may be expected if environmental factors, such as food availability, vary from day to day. Previous studies have found that nest attendance was influenced by food availability. For example, in both wheatears, *Oenanthe oenanthe*, (Moreno 1989) and song sparrows, *Melospiza melodia*, (Arcese and Smith 1988), supplementary feeding increased female nest attendance by reducing the length of foraging bouts. There was some indication in the current study that increased provisioning led to a decrease in female foraging time, although the relationship was not statistically significant.

The fact that females responded to an increase in food supply by spending more time on the nest demonstrates that nest attendance is influenced by the females' energy demands. Increased nest attendance may increase fitness by decreasing the length of the incubation period and/or increasing hatching success (reviewed by Webb 1987). Thus, by supplying food, the male may directly enhance his fitness, while related helpers gain indirect fitness benefits. Unfortunately, it was not possible to assess hatching success in this species, since females are likely to desert if the nest is examined during the incubation phase. However, it is known that hatching failure is relatively common in the green woodhoopoe (Ligon and Ligon 1978), and its occurrence may be related to reduced female nest attendance. If females need to spend less time out of the nest foraging, they may also benefit from a

reduced predation risk. On the other hand, there may be a predation cost of more frequent visits to the nest, if they make the nest more conspicuous.

My analysis of the relationship between the provisioning rate of the group and the length of incubation is based exclusively on deliveries made to the incubating female at the nest. Any food deliveries during the female's self-foraging trips were impossible to follow in detail, since she was usually out of sight of the observer during these periods. However, this is likely to constitute a relatively small proportion (<5%) of the total food ingested by incubating females (unpublished data). Moreover, the benefits of group food deliveries should be greatest when the female is fed in the nest and no interruption of incubation is necessary (see Nilsson and Smith 1988).

In conclusion, helpers assist the breeding male in feeding incubating female green woodhoopoes. The amount of food provided by groups of different size does not vary, but breeding males in larger groups benefit from a reduced workload. Females respond to a higher rate of provisioning in the short term by increasing their nest attendance; thus, incubation feeding in this species appears to influence female energy budgets.

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