Selective Prey Delivery to Incubating Females by Dominant Males, but not Helpers, in the Cooperatively Breeding Green Woodhoopoe

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Abstract

In cooperatively breeding bird species, one of the most conspicuous helping behaviours is the provisioning of food. Many studies have considered the feeding of nestlings, but far fewer have examined feeding of incubating females, and none have looked at the types of prey delivered at this stage. Here I show that green woodhoopoe (*Phoeniculus purpureus*) group members selectively feed incubating females with certain prey items: the diet delivered to incubating females contains a higher proportion of caterpillars, centipedes and cockroaches than that eaten by the provisioning adults themselves. The prey items selectively delivered are the largest in the diet and so might be provided in an effort to enhance the breeding female's condition, thus minimizing the time that she spends off the nest and so increasing hatching success. Intriguingly, it is only breeding males that show this adjustment in provisioning diet; helpers of both sexes simply provide the incubating female with the same proportions of different prey items that they eat when self-feeding. My results therefore offer the first evidence that members of cooperative groups may not all follow the same provisioning rules, and they also emphasize the need for studies to consider the incubation stage in just as much detail as the nestling phase if we are to understand fully the complexities of cooperative societies.

Introduction

In about 9% of bird species, breeding pairs are assisted by non-breeding helpers, which contribute to the rearing of young that are not their own (Cockburn 2006). Helpers in these cooperatively breeding avian societies can assist in the incubation of eggs (Legge 2000), the provisioning of food at various stages (Zack 1986; Wright 1998; Langen 2000), the recruitment of young to valuable resources (Radford & Ridley 2006), the defence of the territory (Radford 2003) and the protection of young from predators (Arnold 2000; Hollén et al. 2008). Perhaps the most widely studied of these helping behaviours is the feeding of nestlings, because it takes places at

a fixed location and is relatively easy to quantify. Many researchers have therefore examined how provisioning by helpers at this stage can enhance the amount of food received by chicks and/or reduce the workload of the parents (see Hatchwell 1999). Moreover, several studies have investigated differences between individual group members in their feeding rates, and the size and types of prey delivered to the nestlings (Wright 1998; MacColl & Hatchwell 2003; Woxvold et al. 2006; Radford 2008).

In some cooperatively breeding bird species, the breeding female conducts all the incubation and the helpers feed her at this stage of the reproductive cycle (Reyer 1986; Zack 1986; Poiani 1992; Radford

2004a). The more food received by an incubating female, the more time she can spend on the nest (Hatchwell et al. 1999; Radford 2004a), which may in turn decrease the length of the incubation period and/or increase hatching success (Royama 1966; Webb 1987). Moreover, provisioning by helpers during incubation can lighten the workload of the breeding male (Radford 2004a). Incubation feeding can therefore play an important role in avian cooperative societies, and it should be just as easy to quantify as the feeding of nestlings. However, the relative contributions of different group members to incubation feeding have only rarely been considered (Zack 1986; Radford 2004a), and never in terms of the types of prey delivered.

The green woodhoopoe (*Phoeniculus purpureus*) provides an ideal opportunity to investigate prey delivery to incubating females in a cooperatively breeding bird species. First, although groups in South Africa include a breeding pair and up to six male and female helpers, it is the breeding female alone who tends the clutch throughout the c. 18 d incubation period (Radford 2004a). Second, because all other adult group members provision her throughout this time (Radford 2004a), it is possible to compare the contributions to incubation feeding of individuals of different sex and reproductive status. Male and female helpers bring food to incubating females at equal rates, and groups of all sizes deliver a similar amount of food; helpers do not increase the overall amount of provisioning, but lighten the load of the breeding male (Radford 2004a). Third, because groups in South Africa only breed once a year (Radford 2004a), all group members focus their helping behaviour at the nest; there are no youngsters from previous breeding attempts requiring care. Fourth, helping behaviour is not related to natal philopatry, kinship or prior association with breeders (Du Plessis 1993). Finally, green woodhoopoes are single prey-loaders, so each invertebrate prey item can be easily categorized and scored when the provisioning individual arrives at the nest (Radford & du Plessis 2003; Radford 2008).

Here I consider three main questions. (1) Does the diet provided to incubating females differ from that eaten by the provisioning adults themselves? Given that adults selectively bring certain prey types to nestlings (Radford 2008), there is the possibility that they also choose to feed particular prey items to incubating females. (2) Is there a sex difference in the diet provided to incubating females? Given that adult male and female green woodhoopoes have different preferred foraging techniques (Radford & du Plessis 2003), I predict that the composition of the diet that they deliver will be different. (3) Do male breeders and male helpers deliver the same proportions of different prey types? Given that same-sex individuals of different reproductive status use the same preferred foraging techniques (Radford & du Plessis 2003), I predict that there will be no difference between male breeders and helpers in the prey delivered to incubating females.

Methods

Data Collection

The study was conducted on a colour-ringed population of green woodhoopoes near Morgan's Bay (32°43′S, 28°19′E), Eastern Cape Province, South Africa. All provisioning individuals had fledged in the previous year or before and were classified as adults. Adults were sexed on the basis of sexual dimorphism in both bill length (Radford & du Plessis 2003) and vocalizations (Radford 2004b). Reproductive status was established by watching group foraging, when breeders (the putative breeding pair) consistently displace non-breeding helpers of the same sex (Radford & du Plessis 2003). Extra-pair paternity in this population is likely to be very low, as no extra-pair young were identified in the breeding attempts of 16 groups (M.A. du Plessis, unpubl. data).

Data on the feeding of incubating females were collected between Nov. and Jan., from eight groups in 1999/2000 and from 14 groups in 2000/2001 ($\bar{x} \pm$ SE group size = 3.1 ± 0.2, range: 2–5). No group or individual featured in both years. Nest sites were located by following birds returning with food or by listening for the food-solicitation calls given by breeding females in the vicinity of the nest (Ligon & Ligon 1978). The end of the incubation period was signalled by a change in behaviour of the breeding female: once nestlings are present, she begins taking food delivered by others into the nest, rather than consuming it all herself outside the cavity (Ligon & Ligon 1978; Radford 2008). Nest watches were conducted from 20 to 35 m away using binoculars, between 05.00 and 11.00 hours and between 15.00 and 19.00 hours, and those on the same group were separated by at least 2 d. Groups usually resumed normal activities around the nest within 10–15 min of the observer's arrival. The length of nest watches varied ($\bar{x} \pm$ SE duration = 125 ± 22 min, range: 92–174 min, n = 80 watches) because of another study (Radford 2004a), and the number of watches per

nest varied ($\bar{x} \pm$ SE watches per nest = 3.6 $\pm$ 0.3, range: 1–6, n = 22 nests) because of predation and differences in accessibility.

Whenever an adult arrived at the nest, its identity and the size and type of prey it delivered were recorded. Prey length was estimated as a fraction of the female's bill length and then converted to a biomass score using mean female bill length (see Radford & du Plessis 2003). Invertebrate prey items (which make up 98.8% of delivered prey) were assigned to seven categories: spiders (Araneae), centipedes (Chilopoda), cockroaches (Blattodea), termites (Isoptera), bugs (Hemiptera), caterpillars (Lepidoptera) and 'unknown', which encompassed prey types not readily identifiable in the other groups (see Radford & du Plessis 2003; Radford 2008).

Data on self-feeding were collected from the same groups as those on the provisioning of incubating females, between Nov. and Jan. 1999/2000 and 2000/2001 (i.e. during the same periods that eggs were being incubated in the study population). Foraging individuals were monitored continuously from when they were first seen until they vanished from sight ($\bar{x} \pm$ SE focal watches per individual = 12.5 $\pm$ 1.6, range: 6–18, n = 46 individuals; $\bar{x} \pm$ SE length of focal watch = 41 $\pm$ 10 s, range: 15–89 s, n = 575 watches). Observations were made during clear weather between 05.00 and 11.00 hours and between 15.00 and 19.00 hours. Each time an individual ate an invertebrate prey item, the prey type and its size in relation to the forager's bill length were recorded (as above). Mean bill lengths of females and males were then used to calculate a biomass score for each prey item.

Measurement Error

The calculation of prey biomass scores entails various estimations and conversions which might potentially result in a problematic propagation of measurement errors. For example, the visual estimation of prey length will have an error associated with it; there is variation in the bill lengths of individuals of the same sex (Radford & du Plessis 2004a) and measurement errors are possible when determining bill length; and estimated prey lengths are converted to a biomass score using a regression equation which itself will have an error component. However, there are a number of reasons why I believe that these potential errors do not fundamentally alter the main conclusions in this paper. First, bill-length measurements of the same individual are highly repeatable

(Radford & du Plessis 2004a). Second, qualitatively similar results are obtained throughout if estimated prey sizes are used in the analyses and thus any error arising from the conversion to biomass scores is eliminated. Third, and perhaps most crucially, differences are found in the prey sizes delivered by breeding and non-breeding males, despite no significant difference in the bill lengths of these two classes of individuals (Radford & du Plessis 2004a) and thus any systematic measurement errors being the same for both.

Statistical Analysis

Statistical tests were two-tailed and conducted in GenStat (10th edition, Lawes Agricultural Trust, Rothamsted, Harpenden, UK). Linear mixed models (LMMs) were used because these allow the inclusion of random as well as fixed terms and can thus take account of repeated measures of the same group and individual. In all models, variance components were estimated using the restricted maximum likelihood method, and random terms were retained unless the variance component was found to be zero (and hence their removal did not influence the findings reported). All fixed terms were initially entered into the LMM and then sequentially dropped until only terms whose elimination would have significantly reduced the explanatory power of the model remained (the minimal model). All two-way interactions were tested, but only those that were significant are presented in the Results section. The significance of eliminated terms was derived by adding them individually to the minimal model. The significance of fixed terms was determined using the Wald statistic, which approximates the chi-squared distribution.

Separate LMMs with a normal error distribution were used to investigate the factors affecting the proportion of each prey type delivered to incubating females and eaten when self-feeding. Proportions were arcsine square-root transformed prior to analysis. Each model was based on 92 proportions from 46 individuals (22 breeding males, 14 helper males, 10 helper females) in 22 groups (eight with only a breeding pair, 14 with at least one helper). Feeding period (incubation feeding, self-feeding), individual category (breeding male, helper male, helper female), group size, year and incubation start date (first week in Nov. = week 1) were included as fixed terms. The start of incubation could not be identified to the nearest day because green woodhoopoes desert if the nest is checked at this stage of breeding

(M.A. du Plessis, pers. comm.). A further LMM with a normal error distribution, based on 2051 prey items from 46 individuals in 22 groups, was used to investigate the factors affecting prey size. Prey type (spiders, centipedes, cockroaches, termites, bugs, caterpillars, unknown), feeding period, individual category, group size, year and incubation start date were included as fixed terms. In all LMMs, group identity and individual identity were included as random terms.

Results

Incubating female green woodhoopoes were provided with a significantly different diet of invertebrate prey to that eaten by the provisioning adults themselves (χ^2 = 30.17, df = 1, p < 0.001). Incubating females received a significantly greater proportion of caterpillars, centipedes and cockroaches and a significantly smaller proportion of unknown invertebrates than the provisioning adults ate when self-feeding (Fig. 1).

The proportions of caterpillars, centipedes, cockroaches and unknown invertebrates in the diet were each significantly influenced by the interaction term between individual category and feeding period (Table 1a–d): dominant males, but neither helper males nor helper females, delivered a higher proportion of caterpillars, centipedes and cockroaches and a lower proportion of unknown invertebrates to the incubating female than they ate themselves (Fig. 2a–d). There were no significant differences in the proportions of termites, spiders and bugs delivered to the incubating female compared to those consumed by the adults themselves (Table 1e–g). Breeding males and helper males delivered and ate signifi-

cantly fewer termites than did helper females (Table 1e), and there were fewer cockroaches (Table 1c) and more termites (Table 1e) in the diet in the second year of the study. There was no significant influence of group size or incubation start date on the proportions of any prey item (Table 1). All results remained qualitatively the same when considering only groups with at least one helper.

The size of prey items was significantly influenced by the prey type (Table 2): caterpillars, centipedes and cockroaches were significantly larger than termites, spiders, bugs and unknown invertebrates (Fig. 3a). Prey size was also significantly influenced by the interaction between individual category and feeding period (Table 2): helpers of both sexes delivered similar sized prey to those they ate, whereas breeding males delivered prey items of a larger size to breeding females than they ate themselves (Fig. 3b). However, there was no significant interaction between prey type and feeding period (LMM: Wald statistic = 13.72, df = 6, p = 0.160), so individuals were not bringing larger examples of the same prey items to incubating females as they found for themselves (Fig. 3a); the larger size of prey delivered to incubating females arose solely from a change in proportion of the different prey types delivered (see above). There was no significant influence of group size, year or incubation start date on the size of prey in the diet (Table 2). All results were again qualitatively the same when considering only groups with at least one helper.

Discussion

Incubating female green woodhoopoes were provided with a greater proportion of caterpillars, centipedes and cockroaches, and a smaller proportion of unknown invertebrates, than provisioning adults ate themselves. Dietary choices may be influenced by such external factors as time of year and territory quality (Grundel & Dahlsten 1991; Smart et al. 2000). However, the difference between the diet provided to incubating females and that eaten by the provisioning adults was apparent in all groups, from different territories, in two consecutive years and with incubation times spread over a 2-mo period in each year. Moreover, only the breeding male delivered different proportions of prey to those usually eaten, despite all group members foraging together (Radford & du Plessis 2003). A more likely explanation for the selective prey delivery is that this increases the biomass of food provided to the incubating female, because caterpillars, centipedes and
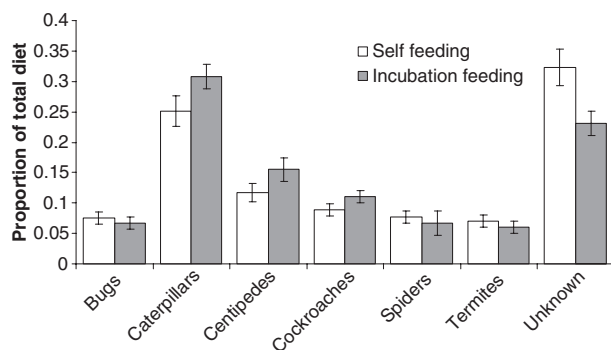

Fig. 1: Proportion of different prey types delivered to incubating females and eaten themselves by adult green woodhoopoes. Shown are $\bar{x} \pm$ SE proportion of the overall diet in each feeding period (n = 46 individuals in 22 groups).

Table 1: Terms influencing the proportion of (a) caterpillars, (b) centipedes, (c) cockroaches, (d) 'unknown' invertebrates, (e) termites, (f) spiders and (g) bugs delivered to incubating females and collected when self-feeding by green woodhoopoe adult group members

Full model	df	(a) Caterpillars		(b) Centipedes		(c) Cockroaches		(d) 'Unknown'[a]		(e) Termites		(f) Spiders		(g) Bugs	
		Wald[b]	p	Wald	p	Wald	p	Wald	p	Wald	p	Wald	p	Wald	p
Feeding period × individual category	2	10.49	0.009	19.19	<0.001	11.79	0.005	46.18	<0.001						
Group size	1	1.88	0.185	0.29	0.596	4.01	0.056	1.09	0.310	0.81	0.379	1.35	0.259	2.02	0.171
Year	1	0.50	0.492	3.49	0.111	12.80	0.001	3.35	0.078	12.50	0.001	0.09	0.765	2.84	0.107
Incubation start date[c]	1	0.01	0.981	1.33	0.278	0.81	0.382	3.05	0.100	2.13	0.152	2.02	0.171	0.06	0.809
Feeding period	1									1.95	0.170	0.01	0.928	1.11	0.299
Individual category	2									11.17	0.007	5.11	0.094	1.65	0.446
Minimal model		Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE
Fixed terms															
Constant		0.339	0.038	0.194	0.036	0.273	0.063	0.696	0.045	0.299	0.050	0.214	0.026	0.262	0.025
Feeding period															
Self-feeding		0	0	0	0	0	0	0	0						
Incubation feeding		0.035	0.040	0.069	0.035	0.062	0.056	-0.008	0.018						
Individual category															
Helper females		0	0	0	0	0	0	0	0	0	0				
Helper males		0.236	0.046	0.162	0.047	0.001	0.066	-0.051	0.044	-0.178	0.050				
Breeding males		0.312	0.053	0.274	0.053	0.101	0.081	-0.320	0.055	-0.183	0.063				
Feeding period × individual category		See Fig. 2a		See Fig. 2b		See Fig. 2c		See Fig. 2d							
Year															
1						0	0			0	0				
2						-0.196	0.055			0.164	0.046				
Random terms															
Individual identity		0.0124	0.0041	0.0157	0.0047	0.0189	0.0078	0.014	0.0046	0.0196	0.0047	0.0090	0.0046	0.0305	0.0088
Group identity		-0.0027	0.0015	-0.0036	0.0016	0.0055	0.0066	0.0036	0.0046	0.0001	0.0001	0.0061	0.0047	-0.0014	0.0051

Results from separate linear mixed models were based on 92 proportions from 46 individuals (22 breeding males, 14 helper males and 10 helper females) in 22 groups (eight with only a breeding pair and 14 with at least one helper).

[a] Invertebrate prey which were not readily identifiable in the other categories.

[b] Significance of fixed terms was determined using the Wald statistic, which approximates the chi-squared distribution.

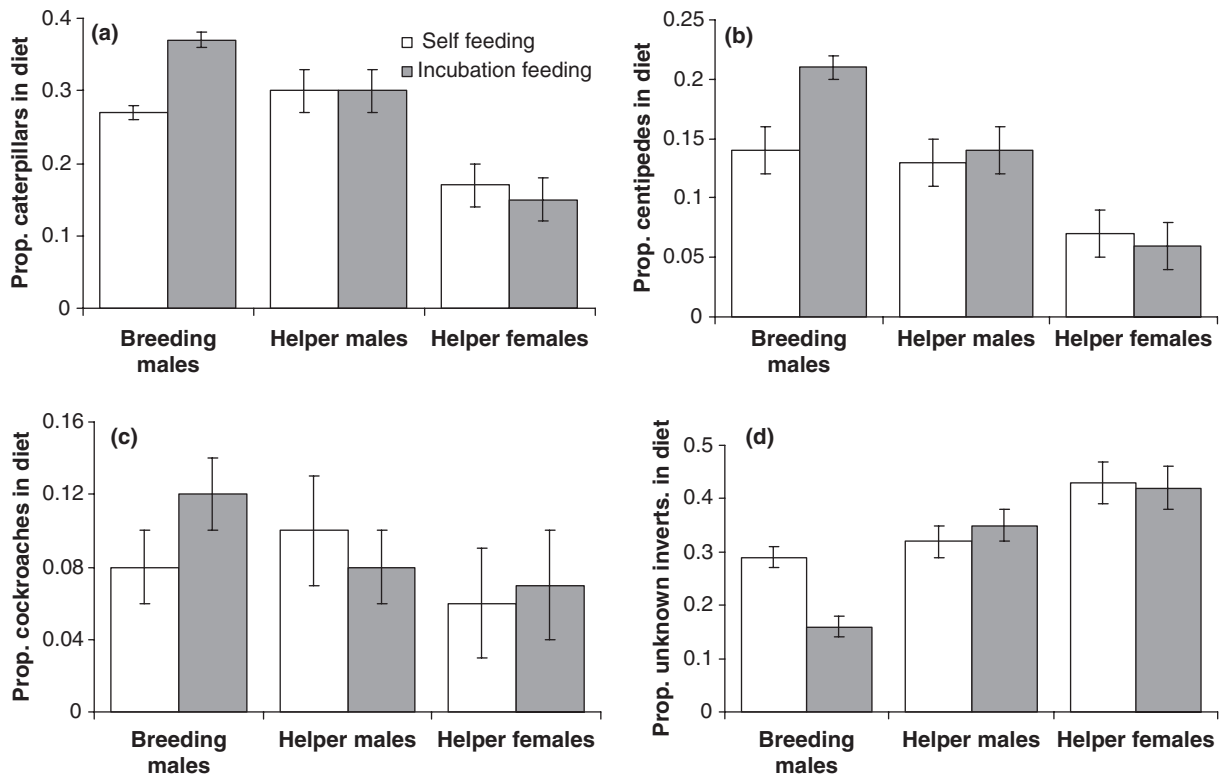[c] To the nearest week (week beginning 1 Nov. = 1).

Fig. 2: Proportion of (a) caterpillars, (b) centipedes, (c) cockroaches and (d) unknown invertebrates in the diet provided to incubating females and eaten when self-feeding by adult green woodhoopoes of different sex and reproductive status. Shown are $\bar{x} \pm$ SE proportions of the overall diet in each feeding period for 22 breeding males, 14 helpers males and 10 helper females in 22 groups.

cockroaches are the largest prey items found by green woodhoopoes. It is also possible that at least some of these particular prey types, for example caterpillars, have a higher nutrient content than other dietary items or that they contain particularly useful nutrients (Ramsay & Houston 2003). As female woodhoopoes collect a relatively small proportion of caterpillars, centipedes and cockroaches themselves (Radford & du Plessis 2003), the delivery of these prey types by group members could be crucial.

By providing the incubating female with prey that are larger and/or of greater nutritional value, groupmates might improve her body condition. Such provisioning may be especially important in green woodhoopoes because breeding females spend the night alone in the nest cavity while the rest of the group roost together in another cavity elsewhere. Breeding females may therefore suffer a thermoregulatory cost and lose body condition overnight (Williams et al. 1991). Females that are better fed by groupmates, because of more regular provisioning (Radford 2004a) and/or the delivery of certain prey types (this study), will have to spend less time foraging themselves, so increasing the time that can be

spent on the nest (Lyon & Montgomerie 1985; Nilsson & Smith 1988; Radford 2004a). A greater proportion of time on the nest can, in turn, reduce the costs inherent in rewarming eggs (Vleck 1981), decrease mortality arising from lethal chilling of the eggs (White & Kinney 1974) and increase the developmental rate of eggs (Nilsson & Smith 1988), thus minimizing the length of the incubation period and the time that eggs are vulnerable to predation (Martin & Ghalambor 1999). Group members may therefore be able to enhance hatching success by changing the diet fed to incubating females, and the production of more young may result in indirect benefits from the raising of relatives (Hamilton 1964) and/or direct benefits from being part of a larger group (Kokko et al. 2001). Group augmentation could play a particularly important role in green woodhoopoes because intergroup interactions over territory space are common (Radford 2003) and the outcome is often dependent on the relative sizes of the two competing groups (Radford & du Plessis 2004b).

Despite the potential benefits, only breeding males appeared to selectively feed incubating females; other group members simply provided the same pro-

Table 2: Terms influencing the biomass (g) of individual prey items delivered to incubating females and collected when self-feeding by green woodhoopoe adults

Full model	Wald statistic	df	p-value
Prey type	451.23	6	<0.001
Feeding period × individual category	10.08	2	0.006
Incubation start date	2.29	1	0.158
Group size	1.12	1	0.303
Year	0.02	1	0.902

Minimal model	Effect	SE
Fixed terms		
Constant	0.199	0.076
Prey type		
Bugs	0	0
Caterpillars	0.533	0.077
Centipedes	1.301	0.084
Cockroaches	0.420	0.072
Spiders	−0.041	0.051
Termites	−0.056	0.059
Unknown invertebrates	0.053	0.053
Feeding period		
Self-feeding	0	0
Incubation feeding	0.061	0.065
Individual category		
Female helpers	0	0
Male helpers	0.014	0.062
Breeding males	0.121	0.081
Feeding period × individual category	See Fig. 3b	
Random terms		
Individual identity	0.0094	0.0065
Group identity	0.0027	0.0047

Fig. 3: Size of prey items delivered to incubating females and eaten when self-feeding by adult green woodhoopoes (n = 2051 items). Shown are $\bar{x} \pm$ SE biomass for each (a) prey type and (b) category of individual (n = 22 breeding males, 14 helpers males and 10 helper females in 22 groups).

portions of different prey types as they ate themselves. Helper females find relatively few caterpillars, centipedes and cockroaches because of their particular foraging niche (Radford & du Plessis 2003), and so they might be constrained in the numbers of these items that they can provide; helper females also do not increase the proportion of caterpillars, centipedes and cockroaches provided to chicks compared to self-feeding (Radford 2008). The difference in diet provided by breeding and helper males is more intriguing, however, especially given that they forage using the same niche (Radford & du Plessis 2003) and find similar proportions of caterpillars, centipedes and cockroaches to one another when self-feeding (Radford 2008; this study). Hence, the difference in incubation diet is not the consequence of breeding males finding more of these larger prey items because they are, for example, more experienced foragers (see Wright 1998).
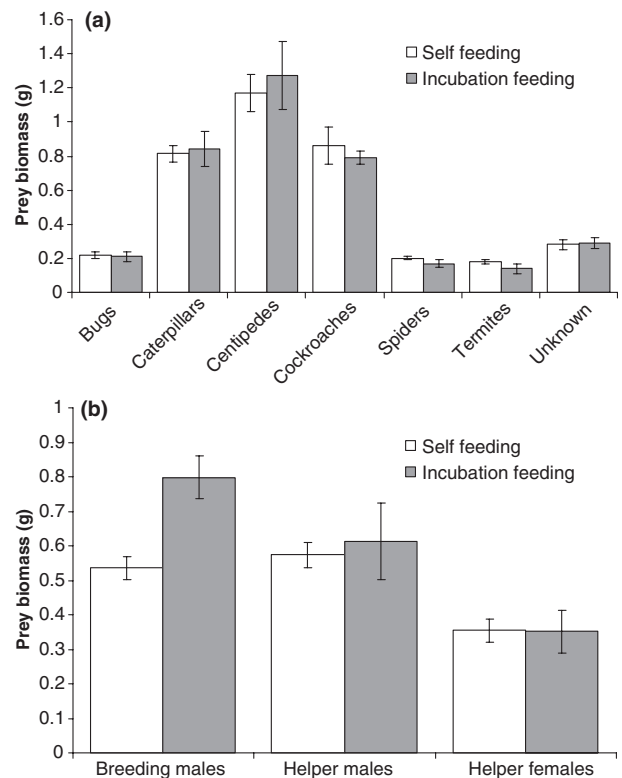
In some species, breeding males might bring particular dietary items because of a role in mate assessment (Nisbet 1973) or pair-bonding (Lack 1940); larger prey items, for example, may impress the female more. However, by the time incubation feeding takes place, female green woodhoopoes have clearly already mated and laid the eggs for the current breeding attempt, and there is no evidence of divorce in this species (breeding individuals almost invariably retain their position until death; Hawn et al. 2007). Instead, the difference between breeding males and helper males may arise because of a stronger selection pressure on the former to enhance the condition of the incubating female, and thus the likelihood of successful hatching. Breeding males appear to sire all the offspring in their nest (M.A. du Plessis, unpubl. data) and at least 10% of helper males are unrelated to either breeder (Ligon & Ligon 1990), so breeding males stand to gain more, on average, from any indirect fitness benefits that arise. Alternatively, if breeding males are in better condition than helper males (see Radford & du Plessis

2004a), and can also displace them from foraging patches (Radford & du Plessis 2003), breeding males may be better able than helper males to compensate nutritionally if they donate the largest prey items in their diet to incubating females.

Previous work on provisioning contributions in cooperatively breeding groups has suggested that all group members might behave similarly. For example, Arabian babbler (*Turdoides squamiceps*) breeders and helpers had the same provisioning rules with respect to visit rate, prey size (Wright 1998) and the division of food between the brood (Ostreiher 1997). Likewise, long-tailed tit (*Aegithalos caudatus*) parents and helpers responded in similar fashion when joined by additional group members (Hatchwell & Russell 1996). The current study therefore provides the first suggestion that cooperative group members of the same sex may differ in their provisioning rules, at least with respect to the types of prey delivered. Moreover, my work suggests that the relative provisioning rules of different group members may change between different stages of the breeding cycle; whereas breeding and helper males appear to differ in their provisioning rules when feeding incubating females (this study), they show the same rules when feeding nestlings (Radford 2004a).

Incubation behaviour in cooperatively breeding species has received far less attention than chick provisioning. In particular, although there have been a few studies investigating contributions by group members to incubation itself (e.g. Heinsohn & Cockburn 1994; Komdeur 1994; Legge 2000), rarely have helper contributions to the feeding of incubating females been considered (Zack 1986; Radford 2004a). This is surprising because data should be as readily available as during the nestling phase and, because incubation can last for a period of weeks, contributions at this stage could greatly affect the reproductive success of both the current breeding attempt (through influences on female nest attendance) and future attempts (through load lightening for the breeding male). Future studies should therefore consider the incubation period for a fuller picture of the provisioning rules of group members of different sex and reproductive status and of cooperative breeding societies in general.

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