

Age-Related Changes in Nestling Diet of the Cooperatively Breeding Green Woodhoopoe

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Abstract

In many socially monogamous bird species, parents of altricial young respond to the increasing demands of growing nestlings by increasing their feeding rate and the size of prey items delivered and by altering the types of prey provided. In some cooperatively breeding species, similar changes in feeding rate and prey size have been documented. However, potential changes in the types of prey delivered, both as nestlings age and by different group members, remain largely unexplored. Moreover, studies rarely compare the diet fed to nestlings with that eaten by the provisioning adults themselves. Here, I show that green woodhoopoe (*Phoeniculus purpureus*) nestlings receive a smaller proportion of spiders and larger proportions of caterpillars and centipedes as they grow older. Both male and female adults delivered a higher proportion of spiders to young nestlings than they ate while self-feeding, probably in response to particular nutritional requirements of the chicks. However, only males altered the proportions of caterpillars and centipedes delivered, providing smaller proportions to young nestlings than eaten themselves. These prey items may be too large for young nestlings to handle, and males may make a greater adjustment in provisioning diet than females because they collect more caterpillars and centipedes than do females. Although there were sex differences in provisioning diet, there were no differences between same-sex breeders and helpers in terms of the overall proportions of prey delivered or the changes with nestling age. Hence, individuals of different reproductive status may be following the same provisioning rules, at least in terms of prey type.

Introduction

For altricial birds, the quantity and quality of food brought to nestlings can have a substantial influence on their growth, survival and condition at fledging (Martin 1987) and, consequently, their fitness (Naef-Daenzer & Keller 1999). Many studies of socially monogamous species have shown that the increasing food demands of older nestlings may be met by parental adjustments in the frequency of feeding visits (Johnson & Best 1982; Goodbred & Holmes 1996), the size of food items delivered (Eybert & Constant 1998; Krupa 2004) and/or the types

of prey brought to the nest (Grundel & Dahlsten 1991; Krupa 2004). Furthermore, differences in the way male and female parents respond to changes in nestling demands have sometimes been observed (Biermann & Sealy 1982; Goodbred & Holmes 1996).

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). Among these cooperatively breeding species, one of the most conspicuous and quantifiable types of help is the feeding of nestlings. Several studies of cooperative breeders have examined how whole groups (Hunter 1987; Fraga 1991;

Woxvold et al. 2006) and individual group members (Wright 1998; MacColl & Hatchwell 2003; Woxvold et al. 2006) change their feeding rate and the size of prey delivered as nestlings grow older. However, potential changes in the types of prey delivered at different nestling ages and by individuals of different sex and reproductive status remain largely unexplored (but, see Wright 1998).

The green woodhoopoe (*Phoeniculus purpureus*) provides an ideal opportunity to examine potential diet changes with increasing nestling age in a cooperatively breeding species. First, all adult group members (in South Africa, that is a breeding pair and up to six male and female helpers) provision young throughout the nestling period (du Plessis 1991), allowing a comparison of individuals of different sex and reproductive status. Second, because groups in South Africa only breed once a year (Radford 2004a), all individuals focus their helping behaviour at the nest; there are no fledglings from previous breeding attempts requiring care. Third, helping behaviour is unrelated to natal philopatry, putative relatedness or prior association with breeders (du Plessis 1993). Finally, green woodhoopoes are single-prey loaders and each invertebrate prey item can be categorised when the provisioning individual arrives at the nest (Radford & du Plessis 2003).

Here I consider four main questions. Does the diet provided to nestling green woodhoopoes change as they age? Given that adult males and females have different preferred foraging techniques (Radford & du Plessis 2003), is there a sex difference in the diet provided to nestlings as they grow older? Does the provisioning diet of breeders and helpers change in the same way with increasing nestling age? Does the diet provided to nestlings match that eaten by adults when self-feeding?

Methods

Study Site and Species

Data were collected on a colour-ringed population of green woodhoopoes near Morgan's Bay (32°43'S, 28°19'E), Eastern Cape Province, South Africa. Throughout the c. 28-d nestling period, all group members collect food for the young and enter the nest to provision them directly. However, in the first 2 wk, the breeding female intercepts many prey items brought by other group members, and either eats them or takes them into the nest herself (Ligon & Ligon 1978). All provisioning individuals had fledged in the previous breeding season 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 vocalisations (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). The identity of the breeding female was confirmed during incubation, because she is the only group member to incubate the eggs (Radford 2004a). Extra-pair paternity in the study 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 Collection

Data on nestling provisioning were collected from six groups in 1999/2000 and from 12 groups in 2000/2001 ($\bar{x} \pm \text{SE}$ group size = 3.0 ± 0.3 , range: 2–5). No group or individual featured in both years. All nests were active between late November and early February. Nest sites were located during incubation by following birds returning with food for the breeding female (Radford 2004a) or by listening for the food-solicitation calls given by breeding females in the vicinity of the nest (Ligon & Ligon 1978). Nest watches were conducted from 20 to 35 m away using binoculars, between 0500 and 1100 hours and between 1500 and 1900 hours. Groups usually resumed normal activities around the nest within 10–15 min of the observer's arrival. Nest watches lasted for an hour following the first feed and those on the same group were separated by at least 2 d. The number of watches varied per nest because of predation and differences in accessibility ($\bar{x} \pm \text{SE}$ watches per nest = 11.9 ± 0.9 , range: 7–16, $n = 18$ nests). Whenever an adult returned to the nest with food, I recorded the individual's identity, the type of prey and whether the food was taken into the nest by the provisioning adult or intercepted by the breeding female. In the latter case, I noted whether the breeding female ate the prey item or took it into the nest herself. Invertebrate prey items (which make up 98.8% of delivered prey) were assigned to seven categories: spiders (Araneae), caterpillars (Lepidoptera), centipedes (Chilopoda), cockroaches (Blattodea), termites (Isoptera), bugs (Hemiptera) and 'other', which encompassed prey types not readily identifiable in the other groups (see Radford & du Plessis 2003).

Hatching date was established from a change in behaviour of the breeding female: once nestlings are

present, she begins taking food delivered by other group members into the nest, rather than consuming it all herself outside the cavity (Ligon & Ligon 1978, pers. obs.). Nests could not be checked directly because green woodhoopoes desert when disturbed during incubation (M. A. du Plessis, pers. comm.). Because hatching dates may therefore be inaccurate by a day or two, nestlings were assigned to two discrete age categories ('young' nestlings were those that had hatched within 12 d of the nominal hatch date, and 'old' nestlings were those in the final 12 d before fledging; data from the few days in between were not analysed), rather than using day as a continuous variable in the analyses. The risk of desertion and the relative inaccessibility of nests (usually in deep tree cavities) prevented the collection of brood-size data in this study (in a population in Kenya, mean brood size was two, range: 1–4; Ligon & Ligon 1978). This is a potential issue, because brood size has previously been shown to influence the trade-off between food quantity and quality (Wright et al. 1998), although within-nest comparisons (see below) minimise the problem to some extent.

Data on self-feeding were collected from the same groups as those on chick feeding, between late November and early February in 1999/2000 and in 2000/2001 (i.e. during the same periods that nests were active in the study population). Foraging individuals were monitored continuously from when they were first seen until they vanished from sight ($\bar{x} \pm \text{SE}$ focal watches per individual = 14.3 ± 1.9 , range: 8–20, $n = 47$ individuals; $\bar{x} \pm \text{SE}$ length of focal watch = 39 ± 9 s, range: 13–86 s). Observations were made during clear weather between 0500 and 1100 hours and between 1500 and 1900 hours. Each time an individual ate an invertebrate prey item, the prey was assigned to one of the seven categories (see above).

Statistical Analysis

To investigate the factors affecting each prey type delivered at the two nestling ages and eaten when self-feeding, I used separate Linear Mixed Models (LMMs) with a normal error distribution. I used LMMs because they allow the inclusion of both fixed and random terms, and can thus take account of repeated measures of the same individual and group. 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. The significance of eliminated terms was derived by adding them individually to the minimal model. All models were conducted in GenStat (10th edition, Lawes Agricultural Trust, Rothamsted, Harpenden, UK).

The 0.9% (range: 0.5–1.4%, $n = 1443$ prey items, 18 groups) of prey items delivered by other group members and then eaten by the breeding female outside the nest cavity were discarded from the analyses. Because there was no significant difference in the proportions of different prey items that were taken directly into the nest by other group members and those that were intercepted by the breeding female and then taken into the nest ($\chi^2 = 6.98$, $df = 7$, $p = 0.323$), these values were combined and assumed to represent the nestling diet. Only individuals that delivered or ate at least 10 prey items were included in the analyses.

Proportions were arcsine square-root transformed prior to analysis and, in all models, feeding period (young nestlings, old nestlings and self-feeding), adult sex, reproductive status (breeder, helper), group size, year and nominal hatch date (the number of days after 1st November) were included as fixed terms. Initial models were based on 128 proportions from 47 individuals (18 breeding males, 12 breeding female, 10 helper males and seven helper females) in 18 groups (eight with only a breeding pair, 10 with at least one helper), and included group and individual identity as random terms. To test explicitly for within-group differences, and thus minimise the influence of between-group variation, the models for each prey type were then re-run using individual proportions centred about the group mean. That is, the response variable was the proportion of a given prey type delivered by a particular individual subtracted from the mean proportion of that prey type delivered by all members of the particular individual's group. Because these centred proportions will sum to zero for each group, only individual identity was included as a random term.

Results

Young and old nestlings received significantly different diets in terms of the relative proportions of different prey types ($\chi^2 = 43.78$, $df = 7$, $p < 0.001$). Young nestlings received significantly fewer spiders and significantly more caterpillars and centipedes than older nestlings (Fig. 1).

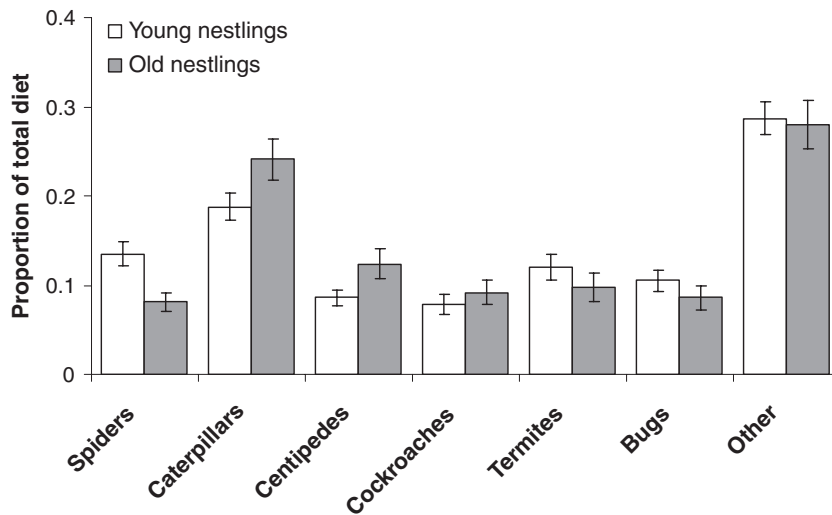


Fig. 1: Proportion of different prey types delivered to young and old nestlings by adult green woodhoopoes. Prey were either delivered directly by the provisioning adult or intercepted by the breeding female and then taken into the nest. Shown are $\bar{x} \pm SE$ proportions of the overall diet at each nestling age ($n = 18$ groups).

Feeding period significantly influenced the proportion of spiders in the diet, after controlling for a significant negative influence of group size (Table 1a): all adults delivered a significantly greater proportion of spiders to young nestlings compared with old nestlings, and the proportion delivered to old nestlings matched that collected when self-feeding (Fig. 2a). The interaction between feeding period and adult sex significantly influenced the proportion of both caterpillars and centipedes in the diet (Table 1b, c): females delivered similar proportions to nestlings of both ages as they ate themselves, whereas males delivered significantly more of both prey types to old nestlings compared with young nestlings, with the proportion delivered to old nestlings matching that found when self-feeding (Fig. 2b, c). Adult sex significantly influenced the proportions of cockroaches, termites and other invertebrates, but not bugs, in the diet (Table 1d–g): males delivered significantly more cockroaches and significantly fewer termites and other invertebrates than females. The proportions of these prey items did not change significantly with feeding period (Table 1d–g).

Reproductive status did not have a significant influence on the proportions of any of the prey types in the diet (Table 1). All results remained qualitatively the same when only groups containing at least one helper were analysed; same-sex individuals of different reproductive status did not differ significantly in the proportions of any prey items in the diet (all $p > 0.10$). Moreover, when within-group differences were explicitly tested, there was still no significant influence of reproductive status on the proportion of any prey type in the diet, either when considering the full data set (all $p > 0.30$) or only

groups that contained at least one helper (all $p > 0.10$).

Discussion

Changes in Diet with Nestling Age

The diet of young green woodhoopoe nestlings contained a larger proportion of spiders than that of older nestlings, which is a widespread trend among passerines (Royama 1970; Cowie & Hinsley 1988; Grundel & Dahlsten 1991; Naef-Daenzer et al. 2000; Arnold et al. 2007). There are a number of possible reasons for the change in spider provisioning. First, prey composition may be influenced by external factors, such as time of year and territory quality (Grundel & Dahlsten 1991; Smart et al. 2000). However, the trend in spider provisioning was the same in woodhoopoe groups from different territories and with hatching dates spread over a 3-mo period. Second, foraging skills may increase with age (Heinsohn 1991), which might lead to changes in the types of prey collected (Siikamäki 1996). However, skill levels are unlikely to improve greatly during the 1-mo nestling period of green woodhoopoes. Third, increasing nestling demands on parents might have a negative impact on spider predation rates (Cowie & Hinsley 1988; Grundel & Dahlsten 1991). However, adults provisioned older nestlings with a similar proportion of spiders as they found for themselves, implying that their predation rates were not negatively affected in the latter stages of the nestling period. Finally, and most likely, nestlings may have different nutritional requirements at different phases of their development and adults may

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

Full model	(a) Spiders		(b) Caterpillars		(c) Centipedes		(d) Cockroaches		(e) Termites		(f) Bugs		(g) Other		
	df	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value
Feeding period	2	20.18	<0.001					4.94	0.091	4.17	0.131	5.04	0.087	0.50	0.779
Group size	1	7.81	0.014	0.11	0.741	0.30	0.595	1.66	0.234	0.03	0.865	2.34	0.149	0.35	0.562
Adult sex	1	1.85	0.182					26.36	<0.001	24.06	<0.001	0.29	0.591	18.55	<0.001
Year	1	1.33	0.266	0.28	0.610	1.04	0.329	0.03	0.860	3.09	0.101	1.30	0.275	1.08	0.318
Hatch date ^a	1	1.22	0.292	0.01	0.964	4.26	0.085	0.37	0.563	0.09	0.770	0.01	0.966	0.01	0.991
Reproductive status ^b	1	0.20	0.654	0.10	0.751	0.07	0.787	0.21	0.648	0.27	0.608	0.03	0.855	1.37	0.250
Feeding period × sex	2			9.13	0.013	7.25	0.031								
Minimal model	Effect	SE		Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE	Effect	SE
Fixed terms															
Constant		0.328	0.025	0.346	0.037	0.148	0.037	0.092	0.026	0.380	0.036	0.697	0.030	0.459	0.032
Feeding period:															
Young nestlings	0	0	0	0	0	0	0								
Old nestlings	-0.116	0.027		-0.020	0.062	-0.034	0.041								
Self-feeding	-0.104	0.031		-0.002	0.021	-0.005	0.009								
Feeding period × sex				See Fig. 2b		See Fig. 2c									
Group size	-0.052	0.019													
Adult sex															
Female	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Male	0.094	0.048		0.135	0.047	0.191	0.037	0.037	0.037	-0.163	0.033			-0.134	0.031
Random terms															
Individual identity	0.0063	0.0033		0.0111	0.0043	0.0134	0.0045	0.0128	0.0043	0.0047	0.0030	0.0178	0.0058	0.0062	0.0026
Group identity	0.0018	0.0023		0.0011	0.0020	0.0001	0.0026	0.0022	0.0015	0.0090	0.0048	0.0015	0.0038	0.0043	0.0032

Results from separate Linear Mixed Models were based on 128 proportions from 47 individuals (18 breeding females, 12 breeding males, 10 helper males and seven helper females) in 18 groups (eight with only a breeding pair and 10 with at least one helper).

^a1st November = 1. ^bAdults were divided into breeders (the putative breeding pair) and helpers (all other adult group members).

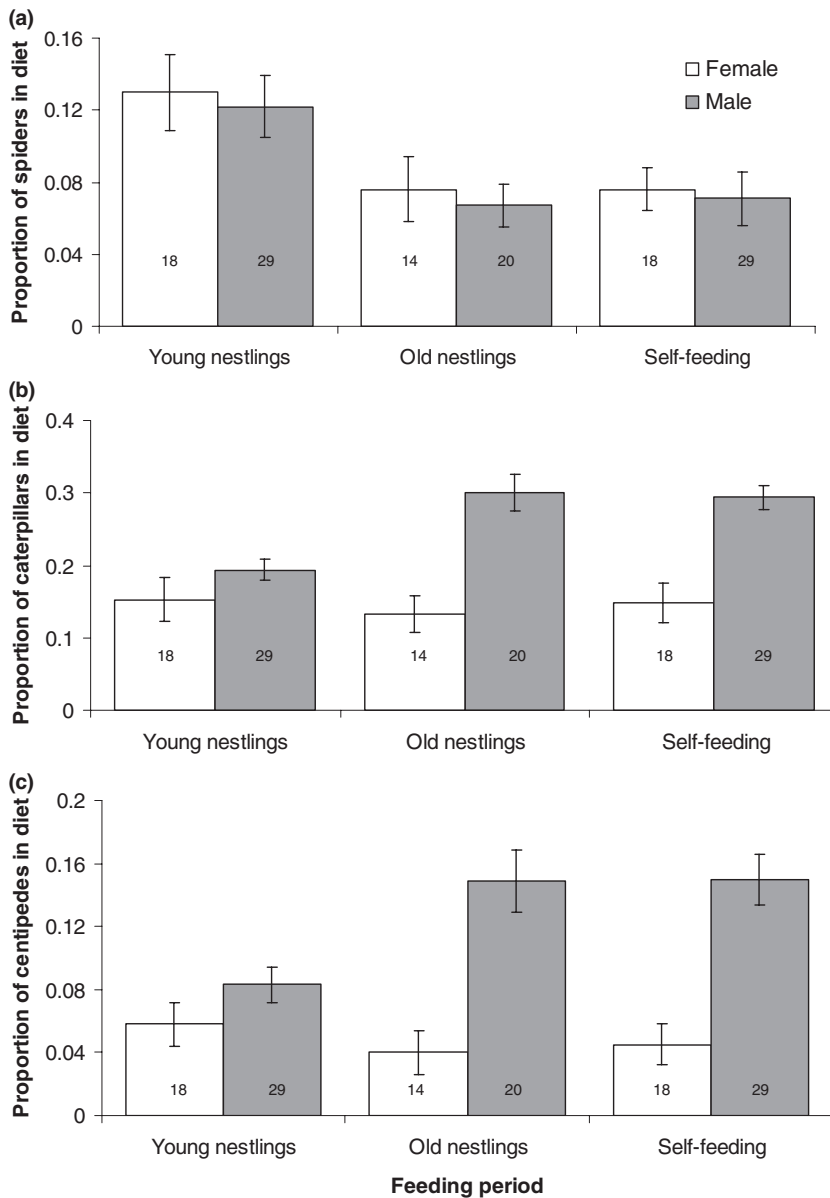


Fig. 2: Proportion of (a) spiders, (b) caterpillars and (c) centipedes in the diet provided to nestlings or eaten when self-feeding by adult green woodhoopoes. Items provided to nestlings were either delivered directly by the provisioning adult or intercepted by the breeding female and then taken into the nest. Shown are $\bar{x} \pm SE$ proportions of the overall diet at each stage for the number of different individuals indicated inside the bars.

adjust their provisioning accordingly (Krebs & Avery 1984). For example, spiders contain a lower level of chitin than many other prey types, making them more easily digestible by young chicks (Magrath et al. 2004). Moreover, spiders have a much higher taurine content than caterpillars (Ramsay & Houston 2003), and this protein is important to young nestlings for bile formation and the development of feathers and the central nervous system (Ramsay & Houston 2003), as well having downstream effects on foraging behaviour and competitive performance (Arnold et al. 2007).

Old green woodhoopoe nestlings received a greater proportion of caterpillars and centipedes

compared with young nestlings. This result contrasts with previous studies on other species, which have found either a decrease in caterpillar provisioning with increasing nestling age (Cowie & Hinsley 1988; Grundel & Dahlsten 1991) or no age-related change (Brickle & Harper 1999; Cummins & O'Halloran 2002). Provisioning woodhoopoe adults might selectively deliver a smaller proportion of caterpillars and centipedes to young chicks because they are generally the largest prey types (Radford & du Plessis 2003) and small chicks may be unable to handle them (Ramos et al. 1998). Unlike many other bird species, adult green woodhoopoes do not appear to break-up larger prey items to feed them piecemeal

to their young (pers. obs.). In support of the idea that fewer caterpillars and centipedes are delivered to young chicks because of their large size, it is noticeable that breeding females eat the largest prey items delivered by other group members in the first week of the nestling period (unpubl. data). Alternatively, breeding females may be consuming the most profitable prey items to minimise their own foraging requirements.

Provisioning by Individuals of Different Sex and Reproductive Status

Overall, males delivered more caterpillars, centipedes and cockroaches and fewer termites and other invertebrates than did females (see also Radford & du Plessis 2003). Although some previous studies on other species have also found differences between the sexes in provisioning diet (Gosler 1987; Suhonen & Kuitunen 1991), a sex difference in prey type is by no means commonplace (Cowie & Hinsley 1988; Grundel & Dahlsten 1991; Moreno et al. 1995). Sex differences are perhaps most likely in species exhibiting sexual dimorphism in body size and/or foraging niche. In green woodhoopoes, adult males and females differ in bill length by 38% and use different preferred foraging techniques, and these foraging techniques favour the capture of different prey items (Radford & du Plessis 2003). The sexual dimorphism in bill length reduces intra-group foraging competition when individuals are self-feeding (Radford & du Plessis 2003), but it remains to be investigated whether the dietary differences between provisioning adults have a positive impact on chick growth and fitness (see Gosler 1987).

In terms of age-related dietary changes, adults of both sexes increased the proportion of spiders delivered to young nestlings. This is probably because spider provisioning is driven by the nutrient needs of the nestlings (Ramsay & Houston 2003; Magrath et al. 2004; Arnold et al. 2007) and because males and females usually collect similar proportions of spiders for themselves. In contrast, only males altered the proportions of caterpillars and centipedes delivered; they brought more of these prey types as nestlings aged, eventually matching the proportions found when self-feeding. In other words, males are selectively delivering fewer of these prey items to young nestlings than they normally find, whereas females deliver similar proportions to those consumed when self-feeding. This sex difference in response to nestling age may arise because males typically collect a larger proportion of caterpillars

and centipedes than do females (Radford & du Plessis 2003; this study), and may therefore need to make a bigger adjustment to their provisioning diet when feeding young chicks that potentially cannot handle such large items.

Although there were strong dietary differences between provisioning adults of different sex, there were no apparent differences between breeders and helpers of the same sex, either in the overall proportions of different prey types delivered or in the changes with nestling age. Because of the relatively small sample size in this study, conclusions must be tentative. However, same-sexed breeders and helpers appear to be following the same provisioning rules in terms of prey type, at least with respect to the six types of invertebrate that could be reliably identified and which made up over 70% of the diet; differences might exist in the remainder of the diet. Arabian babbler (*Turdoides squamiceps*) breeders and helpers follow similar provisioning rules with respect to visit rate, prey size (Wright 1998) and the division of food between brood members (Ostreiher 1997), while long-tailed tit (*Aegithalos caudatus*) parents and helpers seem to adjust their provisioning rules similarly when additional helpers join the group (Hatchwell & Russell 1996). In green woodhoopoes, the strong sex differences in bill length and foraging technique (Radford & du Plessis 2003), and hence prey types found, may override any potentially small differences in diet between individuals of different reproductive status.

Conclusions

Several studies of monogamous species have shown adjustments in the types of prey delivered with increasing nestling age (e.g. Grundel & Dahlsten 1991; Krupa 2004). It has been argued that this change may arise because provisioning adults must trade-off visit rate with prey quality as nestling demand increases; parents may end up delivering increased quantities of food, but prey items of inferior quality, to older nestlings (Lifjeld 1989; Wright et al. 1998). In my study, the first to compare in detail the diet of adults and nestlings in a cooperative breeder, old nestlings were fed similar proportions of different prey types as eaten by the adults themselves. If the demands on individual foragers are reduced in cooperatively breeding species, because the provisioning load is shared among more individuals – there is load-lightening for green woodhoopoe parents in the presence of helpers (du Plessis 1991) – then each provisioning individual may be able to bring whatever it finds, rather than

facing a trade-off between quantity and quality. The dietary adjustments made therefore occur when feeding young nestlings, because these have specific nutritional requirements. For a fuller picture of provisioning rules in cooperative societies, future studies need to combine data on the visit rates, prey sizes and prey types delivered by different group members throughout the nestling period.

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