



Variance-Sensitive Green Woodhoopoes: A New Explanation for Sex Differences in Foraging?

Jonathan Wright* & Andrew N. Radford†,¹

* Department of Biology, NTNU, Trondheim, Norway

† Department of Zoology, University of Cambridge, Cambridge, UK

Correspondence

Jonathan Wright, Institute of Biology, NTNU, Trondheim, 7491 Norway.

E-mail: jonathan.wright@bio.ntnu.no

¹School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK.

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Abstract

Studies of cooperatively breeding birds rarely benefit from the extensive research on adaptive foraging behaviour, despite the potential for concepts such as state-dependent foraging to explain many aspects of behaviour in social groups. For example, sex differences in preferred foraging techniques used by green woodhoopoes, *Phoeniculus purpureus*, have previously been explained by sexual dimorphism in bill length and the benefits afforded by foraging specialization and niche differentiation within cooperative groups. Contrary to this argument, there were no sex differences in mean foraging success and/or prey size captured when males and females used the same foraging techniques. Subordinates of both sexes did experience lower and more varied foraging success compared with dominants, but probably only as a consequence of competition or inexperience. However, dominant males experienced greater variance in individual foraging success compared with dominant females, and dominant males also experienced greater variances in prey size when using their preferred foraging techniques. Dominant males therefore appeared to specialize in foraging techniques that provided more variable rewards, whilst dominant females consistently chose to minimize variation in reward. Dominant females also experienced less variance in foraging returns when using the same techniques as males, suggesting a possible link with sexual dimorphism in bill length. Partitioning of foraging niches in dominant green woodhoopoes therefore appears to be better explained by sex differences in variance (risk) sensitivity to foraging rewards. We suggest that this kind of detailed analysis of state-dependent foraging has the potential to explain many of the crucial age and sex differences in behaviour within cooperative groups.

Introduction

It has already been established that many subtle aspects of individual foraging behaviour are state-dependent and have evolved for the strategic management of time and/or energy budgets (see Cuthill & Houston 1997; Kacelnik & Bateson 1997; McNamara & Houston 1999; Stephens et al. 2007). Within social groups, such state-dependent behaviours may,

in turn, reflect contrasting sex- and dominance-specific strategies (e.g. Cuthill et al. 1997; Lange & Leimar 2004). However, studies of cooperatively breeding birds rarely include such detailed examinations of individual foraging behaviour (see Stacey & Koenig 1990; Koenig & Dickenson 2004). Even when foraging is quantified in cooperative breeders, it is usually from the perspective of population ecology and how particular types or distributions of food

resources may promote cooperative breeding systems (see Brown 1987). Our understanding of cooperative breeding systems could benefit substantially from a more sophisticated state-dependent approach to foraging and other behaviours. For example, recent investigations considering variation in individual energetic state have elucidated to a remarkable extent the potentially complex issue of collective group vigilance in the form of sentinel behaviour (Wright et al. 2001; Hollén et al. 2008; Bell et al. 2010).

One potentially fruitful area of research with regard to explaining individual behaviour because of short-term changes in state concerns risk-sensitivity theory (Stephens 1981; Real & Caraco 1985; Ydenberg 1994; Kacelnik & Bateson 1997; Stephens et al. 2007), now more correctly being referred to as variance-sensitivity theory (see Ydenberg 2008). The basic idea here is that foraging behaviour that provides a greater variance in rewards may allow individuals to gamble for greater energetic returns than might be expected based solely upon the average reward. The risk is that the more variable returns are just as likely to provide much poorer rewards than the average. Variance-sensitivity theory therefore considers when individual state makes such gambling or variance-prone behaviour adaptive, as opposed to more conservative variance-averse behaviour (e.g. Caraco et al. 1990). Different individuals (e.g. males vs. females, dominants vs. subordinates) may differ in the size of their daily energy requirements, and more specifically the non-linearity of the fitness gain (or utility) function from their foraging intake (see Fig. 1). A consequence of this will be that some members of a cooperative group might benefit from being variance-prone, while others might benefit from being variance-averse, and the most profitable tactic for individuals might differ according to seasonal or diurnal variation in individual energetic state (e.g. fat reserves).

Here, we present an analysis of data from the green woodhoopoe, *Phoeniculus purpureus*, one of the few cooperatively breeding bird species to have been subjected to detailed observations of individual foraging, and one in which intriguing within-group differences in foraging behaviour have already been revealed (see Radford & du Plessis 2003). Green woodhoopoes possess extreme sexual dimorphism in bill length (adult males have 36% longer bills than females), which does not appear to be the result of sexual selection or reproductive role division, but rather seems to have evolved in association with sex differences in foraging (see Radford & du Plessis

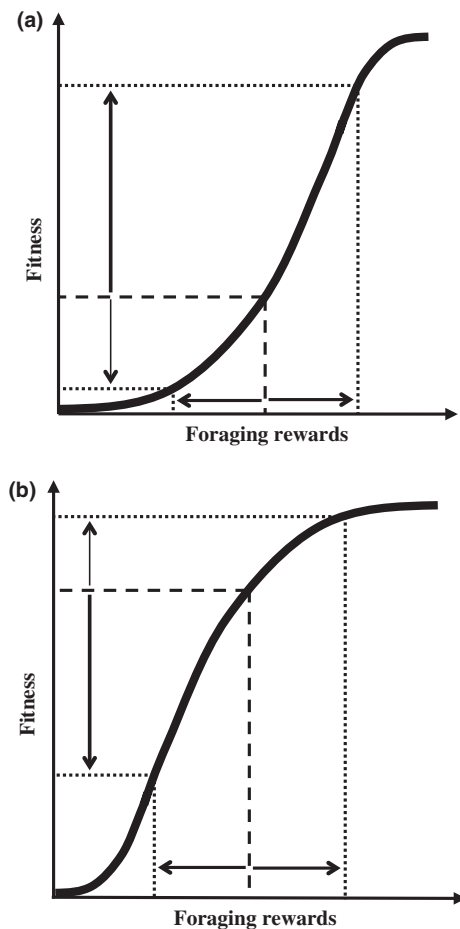


Fig. 1: The graphical logic of variance-sensitivity applied to foraging in green woodhoopoes and possible differences between: (a) males, where accelerating fitness returns from a largely concave-up utility function (solid line) would convert symmetrical (random) variation (dotted lines) either side of mean foraging rewards (dashed line) into beneficial asymmetrical variation in fitness – variance in foraging returns on average increases male fitness; and (b) females, where diminishing fitness returns from a largely concave-down utility function (solid line) converts symmetrical (random) variation (dotted lines) either side of mean foraging rewards (dashed line) into detrimental asymmetrical variation in fitness – variance in foraging returns on average decreases female fitness. See Krebs & Kacelnik (1991) for similar arguments, and text for details.

2004). This species has a very varied arboreal foraging niche, acquiring a wide range of invertebrate prey by (1) probing into the ends of broken branches; (2) probing into existing holes; (3) scaling off loose bark; (4) pecking at bark; and (5) gleaning from the surfaces of leaves and tree trunks (Radford & du Plessis 2003). Adult males end-probe and scale more often than females, perhaps because their longer bills make it easier to perform these particular foraging techniques. In contrast, females attempt to

peck for prey much more often than males, perhaps because their shorter bills are better adapted to pecking than are the longer, more unwieldy bills of males. Green woodhoopoe groups spend the majority of their time foraging as a close-knit unit, often in the same tree and with access to the full range of foraging microhabitats. As all group members therefore have the opportunity to forage using all five techniques (1–5 above), they are assumed to benefit from this niche separation (e.g. Selander 1966; Aulén & Lundberg 1991) because of reduced foraging competition it affords between the sexes (Radford & du Plessis 2003).

Given the sex differences in preferred foraging techniques observed by Radford & du Plessis (2003), and the matching dimorphism in bill length, one would expect clear sex-specific patterns in relative foraging success (i.e. prey capture per attempt and/or prey size captured). However, individuals of both sexes appear to experience similar levels of success when using the same foraging technique (Radford & du Plessis 2003). How can we explain this lack of a sex difference in foraging returns, especially with such a large sex difference in preference for foraging techniques? More specifically, why are females not more successful at pecking with their shorter bills, and why are males not more successful at end-probing and scaling with their longer bills?

Radford & du Plessis (2003) suggest that green woodhoopoes may employ less preferred foraging techniques (for females: (1) end-probing, (2) hole-probing and (3) scaling; for males: (4) pecking and (5) gleaning;) only when the individual rewards are especially high. This would tend to iron-out any differences in average success rates and prey sizes recorded. If true, individual birds should switch to their less preferred foraging techniques only when the benefits match or better the average success rate obtained when using their preferred technique. As a result, we might predict that individuals of both sexes should experience much greater variance in foraging success when using preferred foraging techniques, because non-preferred techniques will be employed in only a subset of situations when the individual rewards are especially high and therefore much less variable.

Adaptive variance-sensitive foraging provides an alternative explanation for the apparently paradoxical observation of sex differences in foraging technique preferences with no sex differences in mean foraging success in green woodhoopoes. This is because variance-sensitivity can generate preferences based solely on contrasting variances in success

between alternative foraging options, with no differences being required in mean foraging rewards. For example, one might speculate that adult male green woodhoopoes may experience greater daily foraging requirements than females, because of their larger body size (5–8% difference in most linear measures: Radford & du Plessis 2003) and a greater intensity of competitive interactions with other individuals (Radford 2002). Males might therefore be predicted to experience accelerating (exponentially increasing) fitness returns from an increased likelihood of winning physical contests and the dominance that results from any increase in energy gain (see Radford 2002; Radford & du Plessis 2003), and to thus forage adaptively in a largely variance-prone manner by using techniques that provide more variable foraging rewards (Fig. 1a). Females, in contrast, might perhaps be expected to be more variance-averse, preferentially using less variable foraging techniques, because they may experience the more usual decelerating (diminishing returns) utility function most of the time (Fig. 1b). Reasons for this might include females having lower daily energy requirements and the fact that their reproductive fitness is probably limited more by the help they receive from the rest of the group than by their personal foraging intake and body condition (Ligon & Ligon 1990; Du Plessis 1991; Radford 2004a, 2008).

Here, we reanalyse the data presented in Radford & du Plessis (2003) to examine for the first time the variances in natural individual foraging rewards for different green woodhoopoe group members, with the aim of distinguishing between these two potential explanations as to why adult males and females exhibit different preferred foraging techniques despite there being no detectable sex differences in mean foraging rewards when using the same foraging techniques. If individuals only use non-preferred foraging techniques in limited circumstances, we predict reduced variation in foraging rewards for all group members when using their non-preferred techniques. However, if adaptive variance-sensitive foraging is driving these foraging technique preferences, we predict that males should more often use techniques that lead to more variable foraging rewards, while females might benefit from minimizing variation in foraging rewards much of the time. This study therefore also provides a first step in testing the prediction that there could be sex differences in the shapes of utility functions, as suggested in Fig. 1. In addition to this primary aim of explaining sex differences in woodhoopoe foraging preferences, we also test for any associated influences of

individual bill length, group size and dominance rank.

Methods

Data Collection

Foraging data were collected as part of another study (Radford & du Plessis 2003) at Morgan's Bay in the Eastern Cape Province of South Africa (32°43'S, 28°19'E) from Jan. to May 2001 and from Jan. to Mar. 2002. These periods included parts of both the non-breeding and breeding seasons, but data were not collected from a group when it had an active nesting attempt. Data were accumulated from 55 individually colour-ringed adult (>12 mo) green woodhoopoes in 22 different wild groups (mean ± SE group size: 3.51 ± 1.03 , range 2–5). Groups consist of a dominant breeding pair and subordinate non-breeding helpers of both sexes (Hawn et al. 2007), with a total of six male and six female subordinates in this dataset. As a result of the strict queuing system operating in this species, dominant 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 (where breeding individuals dominate non-breeding helpers; Radford & du Plessis 2003). Adults could be sexed on the basis of sexual dimorphism in both bill length (Radford & du Plessis 2003) and vocalizations (Radford 2004b).

Individuals were watched only once during any 1 d (0500–1000 h or 1500–1900 h), for a continuous observation period of foraging no shorter than 10 s (the length of time usually required to record sufficient foraging attempts and prey captures to avoid an excess of zero values). These focal watches lasted for as long as constant visual contact could be maintained in this arboreal and visually cluttered habitat (mean ± SE observation time = 34 ± 8 s, range 11–94 s, $n = 1174$). Observations recorded each foraging attempt and the technique used (i.e. an end-probe, a hole-probe, a scale, a peck or a glean), along with any success and the size of prey captured. Prey size was estimated in relation to the bill length of the bird. In females, this was expressed as the ratio of prey length to the average bill length of 46 mm. In males, this ratio was multiplied by a factor of 1.3 to take account of their longer bills. Prey biomass (g)

was calculated from prey length using the formula of Rogers et al. (1976; see Radford & du Plessis [2003] for more details). Differences in prey length and therefore estimated prey biomass were largely the result of differences in prey type (i.e. invertebrate taxa). This was especially true for differences in mean prey biomass associated with the different foraging techniques, because of the different prey found in different microhabitat locations. However, accurate prey type identification was not possible for enough of the prey capture events for this variable to be included in any of the analyses presented here.

Woodhoopoes were caught using nets placed over roost holes before dawn. Bill length (the chord between the tip of the bill and the anterior edge of the cere) was measured to the nearest 0.1 mm with dial callipers. The bill measurement from the first occasion a particular individual was caught as an adult was used in the analyses.

Analysis

Foraging success was measured as the mean proportion of attempts that resulted in prey capture (arcsine square-root transformed prior to analysis) and as estimated prey biomass values per capture. Data for each individual (mean ± SE observation periods = 21 ± 4 ; range = 8–37) were collated into a mean and coefficient of variation (CV) for each of the five foraging techniques. All variables were analysed using parametric repeated-measures ANOVA, because they conformed to homogeneity of variance and normality requirements. Five different repeated-measures ANOVA models were run on (1) mean foraging success, (2) mean biomass per prey item, (3) mean total foraging rewards (success × biomass), (4) variance in foraging success and (5) variance in biomass per prey. Each model assessed the importance of the within-subject factor 'foraging technique' (end-probing, hole-probing, scaling, pecking, surface gleaning), and the between-subject factors 'dominance status' (dominant, subordinate), 'sex', 'group size' and the covariate 'individual bill length'. The latter two models (4 and 5) concerning variance were run a second time excluding data from all subordinates to assess more clearly the results for experienced foragers only. Group identity had no significant effect here (all p -values > 0.20) and no effect on the main results presented, and so to simplify the analyses this variable was dropped from all models. All analyses were carried out using SPSS v.11.0 (SPSS Inc., Chicago, IL, USA) and two-tailed p -values are used throughout.

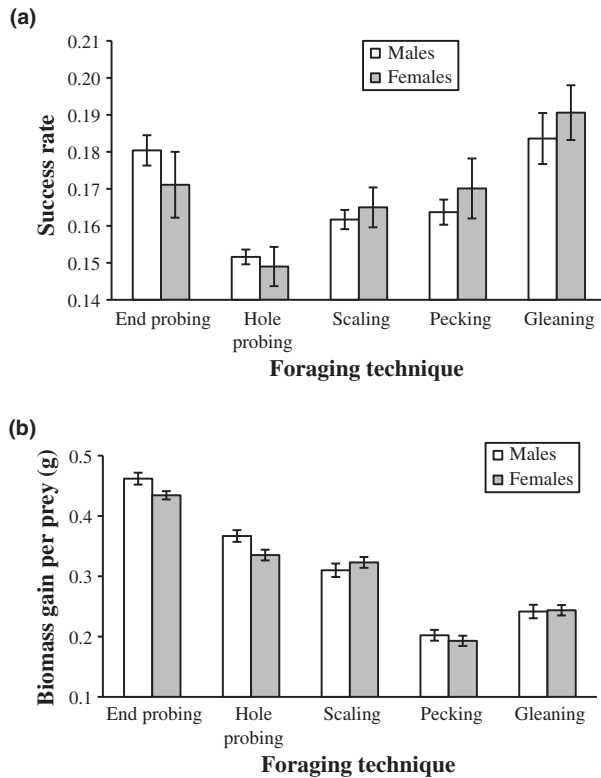


Fig. 2: Foraging rewards (mean \pm SE) of adult male and female green woodhoopoes, which did not differ significantly when using different foraging techniques, measured as: (a) success rate (per attempt); and (b) prey size (biomass per prey captured).

Results

Mean Foraging Success

Using the data set from Radford & du Plessis (2003), there was a significant overall effect of foraging technique on mean individual success rate ($F_{4,200} = 3.01$, $p = 0.019$), with end-probing and gleaning being the most profitable techniques (Fig. 2a). There was also a significant effect of individual dominance status ($F_{1,50} = 17.04$, $p < 0.001$; Fig. 3), and a minor interaction between foraging technique and dominance status ($F_{4,200} = 2.56$, $p = 0.040$). There were no significant effects of sex, group size or individual bill length (when controlling for obvious sex differences), nor any significant interactions involving these variables (all p -values > 0.25). Therefore, mean foraging success differed only in that dominants were more successful than subordinates, especially when end-probing, hole-probing and scaling (Fig. 3).

There was a highly significant effect of foraging technique on biomass gained per prey item

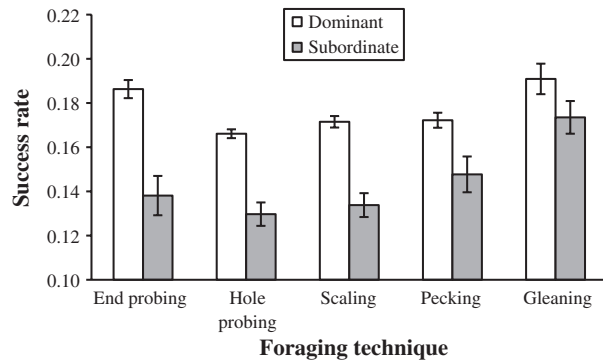


Fig. 3: Foraging success (mean prey items per attempt \pm SE) of dominant and subordinate adult green woodhoopoes, which differed significantly when using different foraging techniques.

($F_{4,136} = 13.43$, $p < 0.001$; Fig. 2b), but no significant effects of sex, dominance status, group size or individual bill length, nor any significant interactions (all p -values > 0.20). Thus, the size of prey obtained was strongly related to foraging technique, with end-probing, hole-probing and scaling providing the largest mean prey sizes. Importantly, however, all individuals appeared to obtain similarly sized prey, on average, when foraging using the same technique.

To ensure that there really were no sex differences in overall foraging rewards, we examined the effect of mean success rate multiplied by mean prey size. This measure of total biomass gained per attempt from all foraging techniques combined still showed the significant effect of dominance status ($F_{1,38} = 15.10$, $p < 0.001$), but with no significant effects of sex, group size, individual bill length nor any interactions (all p -values > 0.15). Likewise, total biomass gained from all foraging techniques combined, per time observed, showed the same significant effect of dominance status ($F_{1,38} = 17.64$, $p < 0.001$), but no significant effects of sex, group size, individual bill length or any interactions (all p -values > 0.17). Therefore, whichever way one looks at these data, dominants were more successful than subordinates, but males and females experienced similar foraging rewards (per attempt and per time interval), despite foraging using largely different techniques and with bills of different lengths.

Variations In Foraging Success – All Group Members

There were significant differences in the CV in individual success rates for the five different foraging techniques ($F_{4,136} = 6.79$, $p < 0.001$): end-probing,

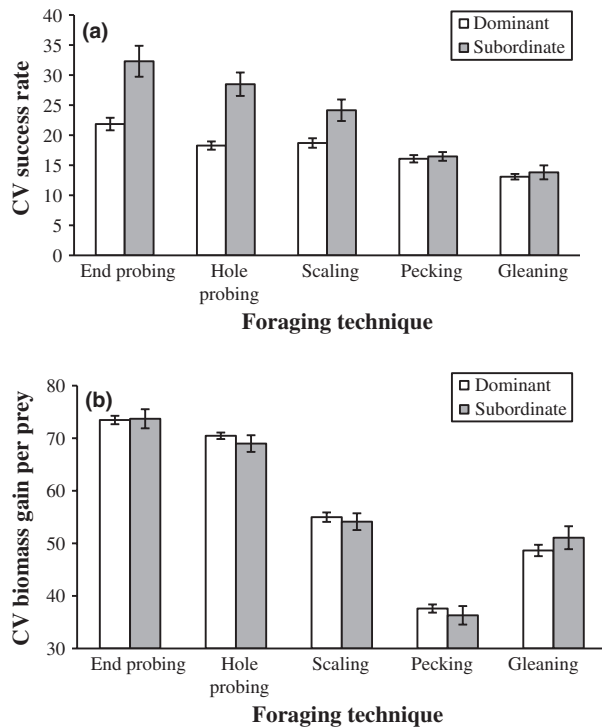


Fig. 4: Variance in foraging rewards (mean \pm SE) for dominant and subordinate adult green woodhoopoes using different foraging techniques, measured as: (a) coefficient of variation (CV) in success rate (per attempt); and (b) CV in prey size (biomass per prey captured). Note that the significant difference between dominants and subordinates and the significant interaction of dominance status with foraging technique in (a) was not the case in (b) – see text for details.

hole-probing and scaling varied much more than pecking and gleaning in the number of prey captures per attempt (Fig. 4a). There was a significant effect of dominance status ($F_{1,34} = 25.54$, $p < 0.001$) and a significant interaction between foraging technique and dominance ($F_{4,136} = 9.61$, $p < 0.001$). There were, however, no significant effects of sex, group size, individual bill length or any interactions involving these variables (all p -values > 0.15). The CV in individual foraging success was not correlated with mean success rates when using the five different foraging techniques (Pearson's $r = -0.48$, $n = 5$, $p = 0.473$), suggesting that more profitable techniques did not always provide all individuals with greater variance in the probability of success. In summary, therefore, subordinates experienced much greater variation in foraging success, especially when using the foraging techniques of probing and scaling that provided the highest variance in success rate.

There were also significant differences in the CV in individual prey biomass gained when using the

five different foraging techniques ($F_{4,140} = 20.19$, $p < 0.001$): end-probing, hole-probing and scaling provided the most varied prey sizes, and pecking resulted in the least variable prey sizes (Fig. 4b). However, there were no significant effects of sex, dominance status, group size, individual bill length or any interactions (all p -values > 0.10). Interestingly, CV in prey size was significantly positively correlated with mean prey biomass obtained when using the different foraging techniques ($r = 0.95$, $n = 5$, $p = 0.014$). Therefore, variation in prey size was similar for all group members, but it was heavily dependent upon foraging technique, with the techniques that resulted in the largest mean prey items (i.e. probing and scaling; Fig. 2b) also providing the most variable sizes of reward (Fig. 4b).

Variations In Foraging Success – Dominants Only

The large effects of dominance status (Figs 3 and 4) suggest that the inclusion of data from the 12 subordinate individuals may introduce an unnecessary amount of noise into the comparison of individual variances in foraging reward between the sexes. Therefore, a clearer examination of sex differences may be achieved by considering only data from the 43 dominant birds separately, because their foraging would have been less affected by lack of experience, competition and/or lack of access to foraging sites (see Radford & du Plessis 2003).

It is reassuring to note that qualitatively similar results were obtained for all tests on sex differences in mean foraging rewards when they were repeated on just this subset of dominant individuals (results not shown for reasons of brevity). Using only data from dominant individuals, the significant differences between CV in success rate remained when comparing the five different foraging techniques ($F_{4,116} = 15.06$, $p < 0.001$; Fig. 5a). However, here it became clear that dominant males experienced significantly greater variation in foraging success compared with dominant females ($F_{1,29} = 5.18$, $p = 0.030$; Fig. 5a), but there was no interaction between foraging technique and sex ($F_{4,116} = 1.64$, $p = 0.170$).

There were also significant differences in CV in prey biomass gained by dominant individuals when using the five different foraging techniques ($F_{4,120} = 269.05$, $p < 0.001$; Fig. 5b). Although there was no significant overall effect of sex ($F_{1,30} = 1.65$, $p = 0.207$), there was a strong interaction between foraging technique and sex ($F_{4,120} = 3.74$, $p = 0.007$). Dominant males experienced a greater variance in

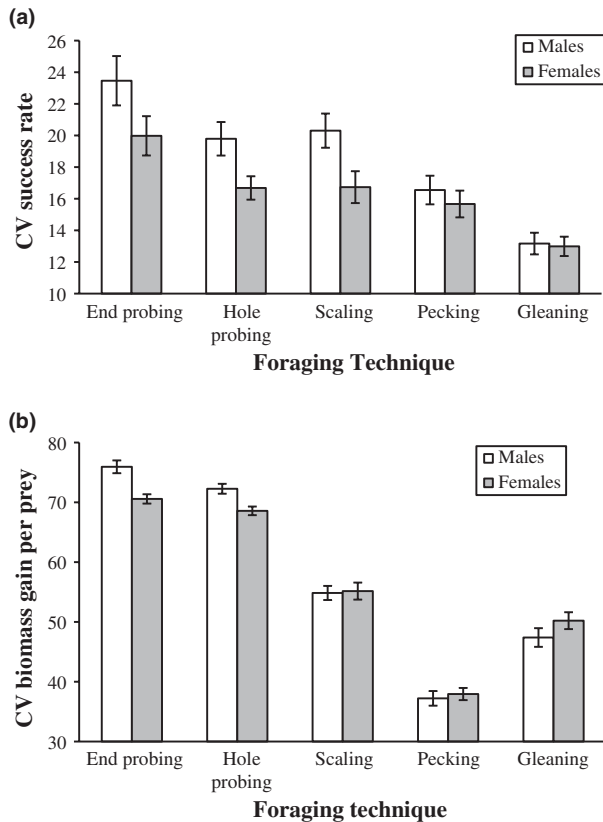


Fig. 5: Variance in foraging rewards (mean \pm SE) for dominant adult male and female green woodhoopoes using different foraging techniques, measured as: (a) coefficient of variation (CV) in success rate (per attempt); and (b) CV in prey size (biomass per prey captured).

prey biomass, especially when using the foraging techniques of end-probing and hole-probing.

Discussion

Male vs. Female Foraging

The lack of sex differences in mean foraging rewards (measured here as either success rate, prey size or biomass gain) confirms the interesting anomaly first noted in a different type of statistical comparison by Radford & du Plessis (2003). One suggested explanation for the clear sex differences in foraging technique preferences despite this lack of differences in mean rewards was the opportunistic use of non-preferred techniques under restricted and particularly profitable conditions (Radford & du Plessis 2003). However, the pattern of variances in individual foraging rewards does not appear to support this idea. Although variation in dominant male foraging success and biomass of prey captured was lower for

less preferred foraging techniques, dominant females spent most of their time concentrating upon those foraging techniques that provided the least variable rewards.

Instead, the variances in dominant individual foraging rewards appear to match more closely the expectations from variance-sensitivity (see Introduction), and this hypothesis might therefore provide a much better explanation of inter-sexual niche partitioning in green woodhoopoes. Males and females may use contrasting foraging techniques specifically because this allows them to manage contrasting levels of foraging risk via differences in individual variation in success rates and prey sizes. The heavy use of pecking allowed dominant females to experience much lower variances in rewards than dominant males, but only as a result of this preferred usage, because males received similarly low variance in rewards when pecking. Dominant males preferentially used foraging techniques that produced consistently greater variation in their foraging rewards. Furthermore, variation in rewards (success rates and prey sizes obtained) was greater for dominant males than females when end-probing, hole-probing and scaling, suggesting an additional and possibly adaptive effect of the observed sexual dimorphism in bill length.

We therefore suggest that the extreme bill dimorphism seen in the green woodhoopoe does not lead to differential success in mean prey capture rates for males and females according to the particular foraging technique being employed. Instead, it may facilitate individual males and females achieving alternative optimum levels of variance in foraging rewards. Given the lack of evidence for sexual selection or reproductive role division in this system (see Radford & du Plessis 2004), the longer bills of males may well have evolved, and/or be maintained, via the benefits of increased variability of foraging returns, as evidenced by the fact that males experienced more variance than females in prey size even when using the same foraging techniques. So, males spend a greater proportion of their time receiving variable returns from probing and scaling, plus their longer bills appeared to be associated with even more variable rewards when foraging using these same techniques. In contrast, females concentrated upon the more consistent rewards from pecking, and their shorter bills may have evolved, and/or be maintained, via the need to limit the variability experienced in rewards whenever they had to use risky techniques like probing and scaling.

Variance-Sensitivity Within Social Groups

The key suggestion here is that different group members may have differently shaped foraging-fitness utility functions (see Introduction and Fig. 1) or that different individuals might occupy different places along the same utility function according to individual state (i.e. growth and/or energy reserves). In which case, ascendance in dominance rank would need to be associated with an increase with individual state (i.e. body condition), which is the common pattern found in groups of cooperative breeding birds (Wright et al. 2001; Hollén et al. 2008). The sigmoid curves for each different position within the social hierarchy would thus link together to form a single continuous and more complex utility function made up of a series of curved steps. All individuals within a dominance hierarchy would therefore move upwards on this complex utility function as they mature and/or increase in individual state (i.e. within daily and/or seasonal schedules). Kuznar & Fredrick (2003) have described just such a model with supporting evidence from human societies. As with the argument for Fig. 1 (see Introduction), they suggest that different parts of a sigmoid utility function favour either variance-averse or variance-prone behaviour, depending upon whether the curve is convex-up or concave-up (respectively) at that particular point. Variance-sensitivity would therefore differentially affect members within social groups according to their position on the utility curve, changing in its effects according to sex and dominance rank. For example, in wild groups of Siberian jays (*Perisoreus infaustus*) using experimental feeders, adult breeders show more variance-prone choices than non-breeding subordinates, because of the additional energy threshold (i.e. an extra convex-up part of the utility function) that breeders need to surmount prior to the breeding season (Ratikainen et al. 2010). Given the clear sex differences that always exist in the effects of individual state on fitness via sex-specific differences in reproductive potential, and the obvious permanent separation of individuals as either male or female, it seems reasonable to conceive of two separate utility functions within social groups: one for the males and one for the females.

In addition to the obvious differences between the sexes of dominant individuals, data presented here concerning the foraging of subordinate group members may represent adaptive alternatives between variance-averse and variance-prone strategies according to subordinate maturity and/or

social status. Note that at no point did we detect any statistical interactions between sex and dominance rank. This suggests that subordinate group members were showing similar sex differences in foraging to those we recorded in dominant group members. Instead of simply preferring the less risky foraging techniques of dominant females (as did short-billed juveniles; Radford & du Plessis 2003), subordinate males with their longer bills appeared to be deliberately foraging by probing and scaling to obtain more variable rewards (Radford & du Plessis 2003). This could therefore represent variance-prone behaviour by male subordinates in response to being at a convex-up point on the utility function (rather than simply an inability to forage properly), and given the potentially complex shape of sex-specific utility functions then this convex-up region for subordinate males may not necessarily be the same region as that presumed for dominant males. Age- and sex-specific differences in bill length in the green woodhoopoe may thus have evolved in parallel, to facilitate adaptive responses to changes experienced by individuals in the shape of utility functions and hence their variance-sensitivity.

It should be noted that the precise shapes of the sex-specific utility functions shown in Fig. 1 represent mere speculation on our part. However, given the correspondence of our results to such speculations, these sex-specific shaped utility functions must now represent very real predictions for future research on this and other systems. The challenge being to demonstrate the aspects of green woodhoopoe life histories that might produce consistently diminishing fitness returns from food intake for variance-averse females and generally accelerating fitness returns for variance-prone males. The energetic requirements of egg production, incubation and brooding notwithstanding, dominant females within these cooperative groups do not seem to have very large daily energy budgets, even when reproducing, because other group members protect and provision the female and her young at the nest (Ligon & Ligon 1990; Du Plessis 1991; Radford 2004a, 2008). Thus, we might expect diminishing fitness returns and so variance-averse foraging most of the time in adult female green woodhoopoes. In the case of dominant males, our reasoning is perhaps a little more speculative. The effects of greater body mass in dominant males (Radford & du Plessis 2003) and the possible consequences of more intense male-male competitive interactions (Radford 2002) for dominant male daily energy routines, and specifically

foraging behaviour, still require confirmation. For example, overt aggression is rare in this system (vocalizations are used to minimize conflicts over foraging resources; Radford 2004c). However, dominant males might still be predicted to forage in a more variance-prone manner during periods of intense competition for breeding positions, or during periods of jostling for long-term positions within breeding queues. New and more suitable data are therefore required to test these suggestions properly. Nevertheless, perhaps we now have a clearer idea of the sorts of questions we should be asking regarding the ecology and sex differences in life history for green woodhoopoes, and other cooperatively breeding systems for which these types of foraging data are available.

Dominant vs. Subordinate Foraging

Although the mean size of prey captured did not differ between dominants and subordinates, there were clear differences in their foraging success rates. Dominants were always more successful when foraging whatever technique was used, although interestingly the differences were largest when end-probing, hole-probing and scaling. As reported by Radford & du Plessis (2003), these differences may reflect interference and/or exploitation competition within groups, with dominants constraining the foraging opportunities of subordinates. Success rates may also reflect age-related differences in experience and skill in foraging (e.g. white-winged cough, *Corcorax melanoramphos*: Heinsohn et al. 1988), or it may be that only the more skilled foragers were able to gain sufficient energy resources needed to survive, remain in the group and progress to the head of the breeding queue to become dominants.

The greater variation in subordinate foraging success shown here might also reflect the detrimental effects of competition, providing variable returns when using certain techniques in the company of dominants at specific and limited foraging locations. Similarly, lack of foraging experience could have resulted in more varied success for subordinates when using certain difficult techniques. Such passive effects on the variances experienced in subordinate foraging are supported by the fact that the most variable foraging techniques in terms of foraging success (end-probing, hole-probing and scaling) were also the ones in which subordinates showed the lowest success rates when compared with dominants. This suggests that any effects of dominance rank on variances in foraging success were most likely to be the

unavoidable consequence of competitive inability or inexperience in foraging by subordinates, rather than any adaptive strategy regarding variance-sensitive foraging.

Conclusions

Our analyses suggest that sex differences in variance-sensitivity in dominants may provide a better explanation for the foraging niche partitioning seen in green woodhoopoes by Radford & du Plessis (2003). Such a perspective also provides a window into potential sex-specific differences in life histories, utility function shapes and resultant activity budgets, all of which can now be investigated as the driving force behind these apparently contrasting foraging strategies of variance-prone males and variance-averse females. These results highlight an important role for the more detailed exploration of foraging behaviour within cooperatively breeding groups, given the success of state-dependent approaches in other areas of behavioural ecology (see Cuthill & Houston 1997; Stephens et al. 2007). We would therefore advocate the investigation of detailed foraging behaviour in other cooperative breeders to see whether this state-dependent approach is equally applicable.

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