BEHAVIOURAL ECOLOGY OF THE REDBILLED WOODHOOPOE *PHOENICULUS PURPUREUS* IN SOUTH AFRICA

by

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Dedicated to my parents, A.S. and Mienkie, for a stable natal territory

And the 'Hlekabafazi' for sharing the best times of my life

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ABSTRACT

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A study was made of two Redbilled (Green) Woodhoopoe *Phoeniculus purpureus* populations spanning an eight year period (1981-1988) and 258 'flock-years', in the eastern Cape Province of South Africa. The main objectives of the study were to investigate (1) why woodhoopoes live in groups; (2) why nonbreeders do not breed; and, (3) why nonbreeders provision young that are not their own?

Ecological and demographic data were gathered in addition to detailed behavioural observations of 54 woodhoopoe flocks. The following experimental manipulations were performed: (1) breeders were removed from flocks to (a) monitor dispersal patterns and restructuring of flocks; and, (b) observe behavioural reactions by remaining birds; (2) cavity availability was (a) decreased, to enable quantification of availability; and, (b) increased, by addition of nest/roost boxes to an area which supported no permanent woodhoopoe territories; and, (3) stimuli, associated with the food provisioning response of adult birds, were manipulated to investigate the evolutionary basis of allofeeding behaviour

Variability in social and reproductive behaviour reflects environmental selection pressures, in the form of roost-cavity availability, with a reduction in cavity availability leading to increased group size. The group-territorial social system and high level of inbreeding of Redbilled Woodhoopoes have evolved primarily in response to environmental constraints on dispersal, rather than by particular benefits that arise from group living. Therefore, the habitat-saturation hypothesis best explains group living of woodhoopoes. Behavioural dominance hierarchies ensure that dominance relationships are well-defined among potential competitors (for breeding status), and thereby minimize disruption to flock cohesion upon the death (or removal) of a breeder. If competition for a breeding vacancy arose at the time of the breeder's death, the resultant delay in occupancy of the breeding vacancy would increase the likelihood of competition from unrelated birds. The establishment of such hierarchies is therefore adaptive in the context of the direct component of kin selection. The presence of nonbreeding helpers do not increase fledgling success, breeding frequency, survivorship (of any age, sex or social class), or number of breeder-offspring produced. Because no unambiguous indirect fitness benefits could be shown to result from helping behaviour (specifically allofeeding), I propose that the unselected (misdirected parental care) hypothesis is a viable alternative to the 'functional hypotheses.' This hypothesis is supported by observations/manipulations of misdirected food provisioning by both breeders and helpers.

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GENERAL INTRODUCTION

Cooperative or communal breeding as a social system is defined primarily by the regular involvement of nonbreeding helpers in the feeding and care of young that are not their own (Brown 1978). An important characteristic of cooperative breeding behaviour in many species is the deferral of breeding to the age of two or more years. Consequently, the evolution of cooperative breeding behaviour can only be understood if the motive(s) for group living, and alloparental behaviour as exhibited by nonbreeding helpers, are identified. However, these two concepts cannot be separated entirely, since non-dispersal and group living are obligate prerequisites for subsequent helping behaviour by nonbreeders (Koenig & Mumme 1987). Thus, the fitness consequences of helping behaviour must be taken into consideration when examining the phenomena of non-dispersal and group living.

The most popular current explanation for group living is one of 'habitat saturation' or 'ecological constraints' (Selander 1964; Brown 1974, 1987; Stacey 1979; Koenig 1981a, 1981b; Koenig & Pitelka 1981; Emlen 1982a). The important feature of this explanation is that nonbreeders are forced to remain in their natal groups as a result of either space- or resource-related constraints. Nonbreeders are making the best of a situation although they would improve their fitness by breeding independently if they were able to overcome the constraint that prevents them from doing so. Stacey & Ligon (1987) presented an alternative hypothesis, stressing that the benefits of philopatry, rather than costs of dispersal, may have influenced the evolution of group living. A third hypothesis proposes that the young of cooperative breeders delay breeding and remain in their natal groups because they have not yet the skill to breed independently (Brown 1987).

The hypothesis that selection acts on individuals to increase their inclusive fitness (Hamilton 1964; Maynard Smith 1964), and thus that aid rendered to non-descendant kin (*sensu* Brown 1987) can be as selectively advantageous as that rendered to descendant offspring, has become one of the most important concepts in behavioural ecology (reviewed by Brown 1987). However, kin selection, and more specifically the indirect component of inclusive fitness (*sensu* Brown 1987), frequently has been uncritically invoked in explaining cooperative breeding, leading several authors to emphasize alternatives (e.g. Woolfenden & Fitzpatrick 1978, 1984; Ligon & Ligon 1978a, 1983; Ligon 1983; Koenig & Pitelka 1981; Koenig & Mumme 1987).

Trivers (1971) was the first to stress the potential for aid-giving behaviour to evolve when altruistic acts can be repaid in kind. Such reciprocity has been considered important in some cooperative breeding systems (Ligon & Ligon 1978a, 1983; Brown & Brown 1980; Ligon 1983; Craig 1984; Wiley & Rabenold 1984).

A number of hypotheses, grouped under the concept of individual fitness, suggest that the apparent altruism in cooperatively-breeding societies is deceptive and instead serves primarily to promote the donor's direct fitness. These hypotheses include (1) a helper may gain experience and hence improve its later reproductive success (Rowley 1977; Brown 1987); (2) by feeding begging chicks a helper reduces audible cues to potential predators (Caraco & Brown 1986); (3) a helper may be more likely to acquire a mate (Reyer 1980; Woolfenden & Fitzpatrick 1984; Emlen *et al.* 1986); and, (4) helping may serve to advertise or improve dominance status of an individual within the group (Zahavi 1976; Carlisle & Zahavi 1986).

More recently, it has been suggested that helping *per se* may have no adaptive value (Woolfenden & Fitzpatrick 1984; Ligon 1985; Jamieson 1986, 1989; Jamieson & Craig 1987; Koenig & Mumme 1987), but is a response to begging stimuli from chicks, thus representing misdirected parental care (*sensu* Price *et al.* 1983).

The fact that the social structure of most cooperative breeders is based on family units makes the importance of kin selection in the evolution of group behaviours intuitively undeniable (Koenig & Mumme 1987). Thus, a major aim of this dissertation is an analysis aimed at determining the relative importance of the direct and indirect fitness components of helping behaviour.

Redbilled (Green) Woodhoopoes *Phoeniculus purpureus* (Aves: Coraciiformes: Phoeniculidae) were studied in the field over an eight year period to answer three broad key questions: (1) Why live in groups? (2) why do nonbreeders not breed? (3) why do nonbreeders feed young that are not their own? The findings are compared with studies of other cooperatively-breeding vertebrate species and interpreted within the framework of the hypotheses outlined above.

Approach and Organization of the Study

Redbilled Woodhoopoes are singular breeding (only one pair breeds per flock), group-territorial birds, inhabiting a broad range of woodland types over a wide Afrotropical range. The family Phoeniculidae is a small group of eight species restricted to sub-Saharan Africa (Fry 1978). In the southern African subregion three species are recognized in the genus *Phoeniculus* (White 1965; Davidson 1976; Fry 1978), namely *purpureus*, *damarensis*, and *cyanomelas*. Redbilled Woodhoopoes *Phoeniculus purpureus* are known to be cooperative breeders (Rowan 1970; Grimes 1976; Ligon & Ligon 1978b). Violet Woodhoopoes *P. damarensis* have been little studied, but are known to live in groups of two to 12 (Ligon & Davidson 1988), and almost certainly are cooperative breeders. Scimitarbilled Woodhoopoes *P. cyanomelas*, on the other hand, live and breed in pairs (Hoesch 1933).

Several features of woodhoopoe biology render them suitable study subjects to address the above questions. Flock and individual histories can be followed as woodhoopoes defend group territories of which the boundaries rarely change, and dispersal takes place only over short distances. Comparisons between aided and unaided pairs are possible, because a relatively large proportion of birds live and breed successfully as unaided pairs. Demographic analyses are simplified because woodhoopoes in the South African study areas breed only once a year, sexes are dimorphic from the nestling stage, and individuals can be reliably separated into three age classes. Additionally, woodhoopoes are, because of their noisy behavioural displays, relatively easy to follow and observe. To control (to some extent) for environmental influences on social behaviour, two study sites were selected which differ widely in vegetation characteristics and rainfall.

Ligon & Ligon (1978a, 1978b, 1983, 1988; Ligon 1981, 1983) have studied Redbilled Woodhoopoes in Kenya. However, although many features of Redbilled Woodhoopoe biology are common to Kenyan and South African populations, there are several marked differences, which require a re-evaluation of the mechanisms invoked for the evolution of group living and cooperative breeding in this species.

All facets of the life history of an animal are so interwoven that a linear sequence of data presentation must be somewhat arbitrary (Woolfenden & Fitzpatrick 1984). For this reason, I have liberally cross-referred to earlier, and occasionally later, chapters of this dissertation. The results of this study are presented as a sequence of discrete papers. This approach allows the rapid communication of results, but inevitably results in some repetition, particularly in the presentation of the methods used. The synthesis (Chapter 9) summarizes the results of this study and discusses their contribution to a general theory explaining group living and alloparental behaviour in cooperatively-breeding vertebrate societies.

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SECTION 1

ECOLOGICAL CONSTRAINTS ON SOCIALITY

CHAPTER 1

THE INFLUENCE OF ROOST-CAVITY AVAILABILITY ON FLOCK SIZE

SUMMARY

The availability of roost cavities to Redbilled Woodhoopoes *Phoeniculus purpureus* was compared between two different populations in the eastern Cape Province of South Africa in order to identify the influence that this resource may have in promoting group living. Food availability and predatory pressure appeared to be similar at the two sites, but roost-cavity availability differed significantly. The latter was attributable to differences in the vegetation composition of territories at the different sites. Inland birds formed significantly larger flocks than coastal birds. The presence of marginal habitat (in terms of cavity availability) at the coastal site may have ensured an outlet for young birds from their natal territories, resulting in smaller flock sizes, whereas lack of such habitat at the inland site may have resulted in forced retention of young in their natal territories and hence larger flock sizes. It is suggested that variability in Redbilled Woodhoopoe social and reproductive behaviour reflects environmental selection pressures, in the form of roost-cavity availability, with a reduction in cavity availability leading to increased group size.

INTRODUCTION

Much interest has been shown recently in the evolution of communal or cooperative social systems in birds (Brown 1978, 1985; Koenig & Pitelka 1981; Emlen 1982, 1984; Woolfenden & FitzPatrick 1984). A central theme of explanations for group territoriality has been that each individual raised within the group is confronted by two possibilities in order to attain breeding status: either to remain within the group and to act as a nonbreeding helper until a breeding vacancy arises, or to disperse to an unoccupied territory or breeding vacancy. The potential costs and benefits to the individual's fitness, associated with these options, have been extensively considered (Brown 1978; Koenig 1981; Emlen 1982; Reyer 1984).

To understand the development of cooperative breeding it is necessary to isolate proximate factors that influence the presence, or number, of helpers within a group. Selander (1964) first suggested habitat saturation as a critical force favouring the development of cooperative breeding systems. Habitat saturation is associated with territorial defence and permanent residence, which may prevent nonbreeding birds from establishing territories locally. Cooperative breeding may result from such habitat restrictions through retention of offspring in the natal territory (Zack & Ligon 1985).

It has been suggested that the spacing pattern or social system of a population can be inferred from knowledge about the food resources it uses and about the predation to which it is exposed (Crook 1965; Lack 1968; Brown & Orians 1970). More recently, Alexander (1974), Hoogland & Sherman (1976) and Koenig & Pitelka (1981) pointed out that no automatic advantages are conferred by group living and that only three general classes of effects may provide the selective advantage necessary to counteract the inherent disadvantages of group behaviour: (1) defence against predators, (2) characteristics of the food supply, and (3) localization or limitation of some resource other than food.

Redbilled Woodhoopoes *Phoeniculus purpureus* are group-territorial birds which exhibit great variability in social organization from population to population. In the Kubusi River Valley (Figure 1.1) flocks are characterized by cooperative breeding, permanent residence in territories and frequent inter-flock territorial interactions. In contrast, at Morgan's Bay, fewer birds breed cooperatively, some territories are only occupied during some years (ephemeral territories) and fewer inter-flock interactions occur. Woodhoopoes in both study areas roost in either natural or woodpecker/barbet-excavated cavities each night (Ligon & Ligon 1978), and as many as 10 birds occasionally roost in the same hole. Sometimes false roosts are entered, before the birds move into the final roost site shortly before dark (Appendix 2), in the same way as Jungle Babblers *Turdoides striatus* and Southern Ground Hornbills *Bucorvus leadbeateri* (Gaston 1977; Kemp & Kemp 1980).

The aim of this study was to investigate whether or not variation in flock size in a group-territorial bird was related to the availability of this localized and limited resource, given that suitable roost cavities are restricted to certain habitat types and are important to woodhoopoes on a daily basis.

METHODS

Observations were made at two study sites in the eastern Cape Province, South Africa, between July 1981 and July 1987 (Figure 1.1).

At Morgan's Bay (32°43'S 28°19'E) 27 Redbilled Woodhoopoe flocks were monitored in an area of 33 km^2 where riverine forest forms belts along river valleys. Canopy height varied between 8 and 15 m, with an average height of 9.6 m. Dominant tree species were *Harpephyllum caffrum*, *Erythrina caffra*, *Podocarpus latifolius*, *Zanthoxylum capense*, *Schotia latifolia*, *Diospyros natalensis*, *Cassine papillosa*, *Protorhus longifolia*, *Mimusops caffra*, *Vitellariopsis marginata*, *Sideroxylon inerme*, *Ekebergia capensis* and *Calodendrum capense*. On the dry northern and north

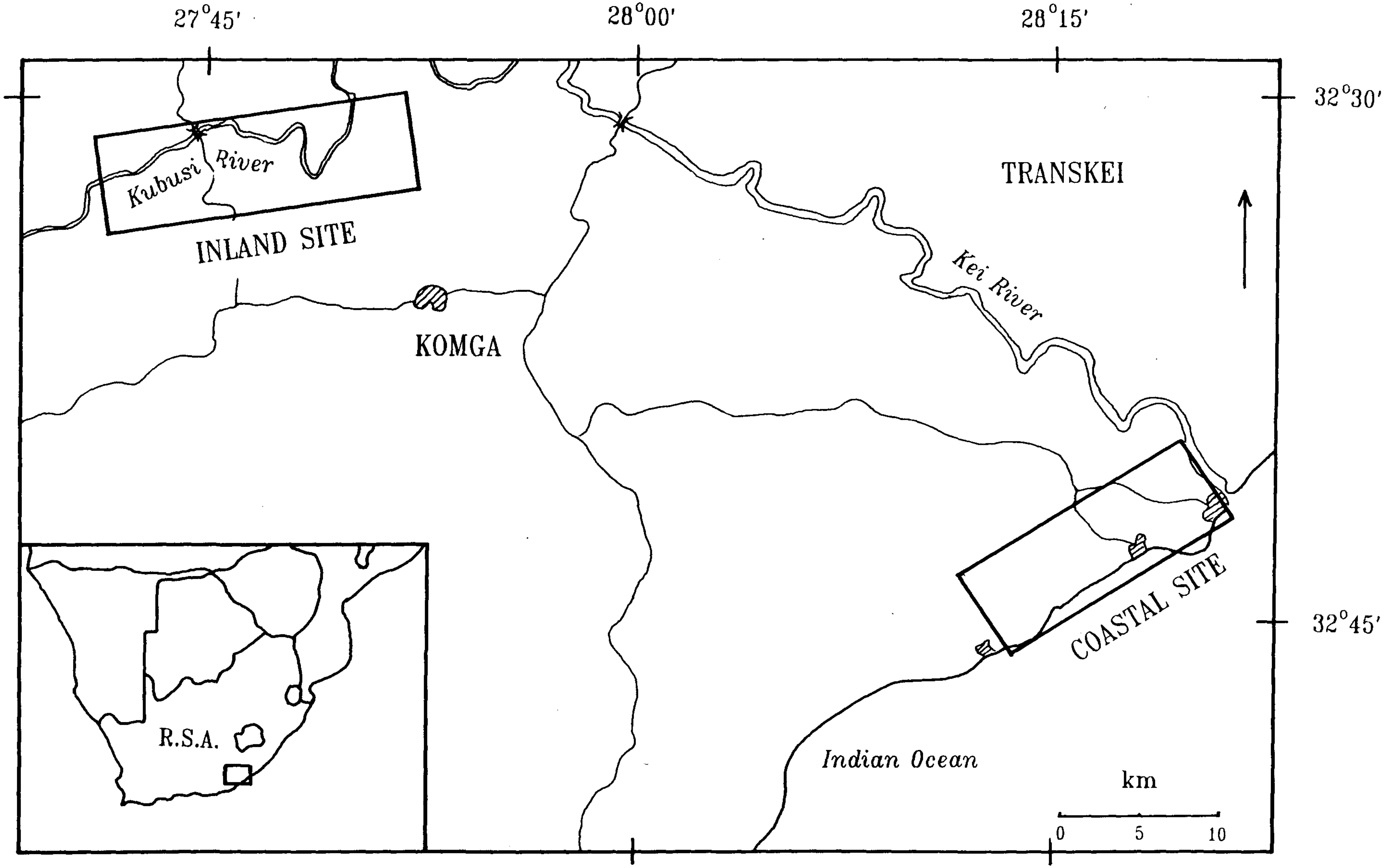

Figure 1.1. Location of the two Redbilled Woodhoopoe study areas.

western aspects, *Commiphora harveyi* and *Euphorbia triangularis* dominated, while *Phoenix reclinata* and *Strelitzia nicolai* were common in the cool moist areas. The mean annual rainfall (1973 - 1986) was 1 007 mm, with well-defined peaks in October and March.

In the Kubusi River Valley (32°32'S 27°47'E) 26 Redbilled Woodhoopoe flocks were monitored in an area of 45 km^2. Topographically the area comprises a central valley, *ca* 1 000 m wide and 350 m deep, with tributary valleys leading from it at irregular intervals, and relatively flat plateaus on either side. Most of the slopes were covered by valley bushveld dominated by *Olea africana*, *Rhus* spp., *Cussonia spicata*, *Euclea* spp., *Maytenus heterophylla*, *Plumbago capensis*, *Acacia karoo*, *Aloe ferox*, *Grewia robusta* and *Pappea capensis*, the most common species being the thorny creepers and shrubs. The upper slopes of the side valleys were dominated by tall *Euphorbia* spp. stands, occasionally with *Aloe bainesii*, which merged directly into forest species such as *Harpephyllum caffrum*, *Schotia afra*, *S. latifolia*, *Cussonia* spp., *Ptaeroxylon obliquum*, and, against the steep cliffs, *Urera tenax*. The plateau was covered almost exclusively by *Acacia karoo* ranging in height from 2 to 5 m, the average being 3.0 m. Mean total annual rainfall (1964 - 1985) for this area was 433 mm.

The following details were recorded for all known roost cavities: tree species; tree height; tree diameter at breast height (1.50 m) (DBH); diameter at cavity entrance height (DEH); cavity entrance height above ground; entrance height and width; cavity depth and inner diameter; aspect of the cavity entrance and origin of the cavity. An index of permanence was given in terms of the estimated life-span of a cavity: a value of 1 = cavity-bearing tree with more than 60% dead material; 2 = trees with some dead material, but less than 60%; and 3 = trees without dead material.

Some information was gathered on cavity availability independent of woodhoopoes in both study areas, by counting all trees with DBH > 0.08 m, in randomly chosen 100 m^2 quadrats, and searching them for potentially suitable roost cavities. In addition, the woodhoopoes themselves were used as indicators of effective cavity availability. Roost-cavity availability was manipulated in seven woodhoopoe territories at both inland and permanent coastal territories, and in a further two ephemeral coastal territories. This was done by closing up known roost cavities within these territories. The birds were thus forced to use alternative roost sites available to them. This manipulation was continued until two cavities, with entrance dimensions (height x width) outside the 95% confidence limits of cavities used under undisturbed conditions, were used on consecutive nights. The number of cavities falling within the normal range was then regarded as the effective number of cavities available to woodhoopoes in a given territory.

Properties of cavities in which other bird and mammal species roosted were also recorded and entrance dimensions compared to those of woodhoopoe roost cavities, in order to assess the degree of overlap between species.

RESULTS

Flock size, food and predators

Mean flock sizes recorded between 1981 and 1987 differed significantly between sites, with smaller flocks occurring at the coastal site (mean= 3.41 ± 1.38; n= 123) than at the inland site (mean= 4.74 ± 1.87; n= 93) (Mann-Whitney U: z= 5.48; P< 0.001) (Figure 1.2). Pair flocks were the most frequently encountered units at the coastal site (38.2%), but comprised only 12.7% of flocks at the inland site. On the other hand, flocks comprised five or more birds in 49.4% of instances at the inland site, but in only 19.5% of instances at the coastal site.

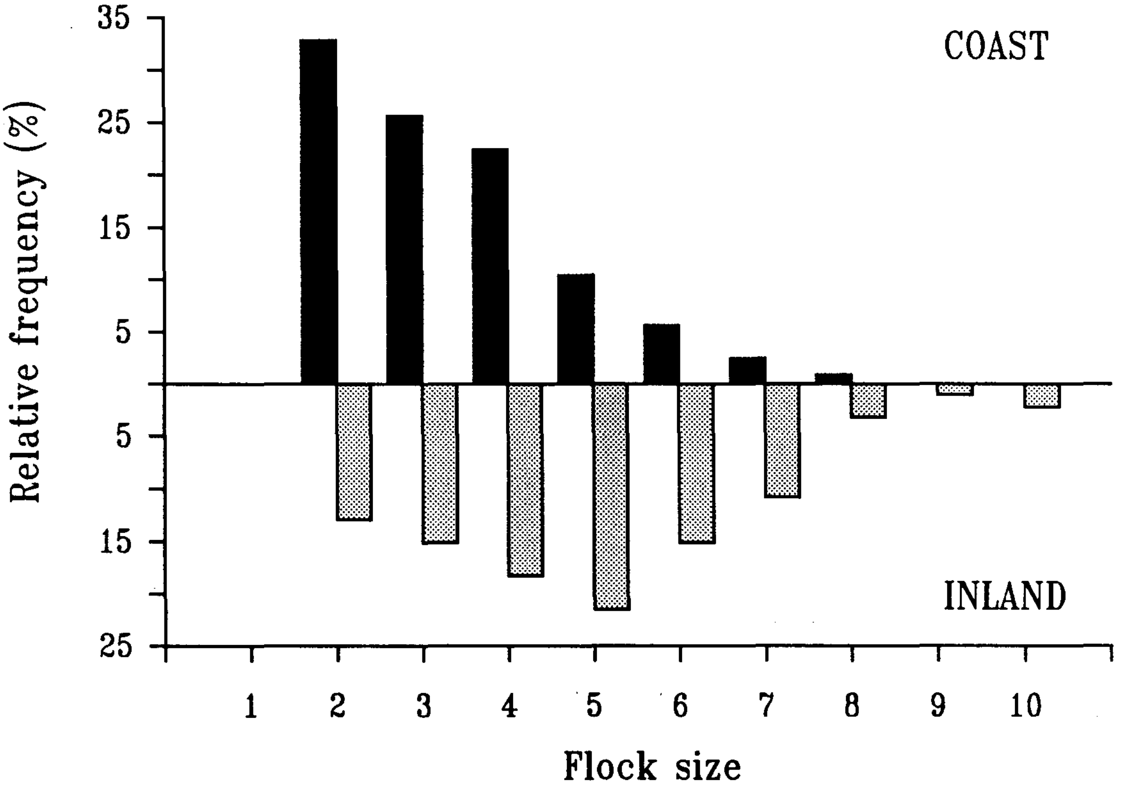

Figure 1.2. Comparative flock sizes of Redbilled Woodhoopoes at the coastal (n= 123) and inland sites (n= 93) (1981–1987).

Food availability to Redbilled Woodhoopoes was apparently similar in the two study areas, as observed feeding rates were much the same (unpubl. data). Although predatory pressure is difficult to quantify, it was assumed to be comparable in the two areas as predator species composition was virtually identical (Table 1.1).

Habitat

Permanent coastal Redbilled Woodhoopoe territories were significantly smaller than inland territories in total area (20.1 ha ± 2.2 *vs* 43.5 ha ± 6.1) and also differed in vegetation composition. Ephemeral coastal territories were significantly smaller than permanent territories (13.3 ha ± 3.2). Permanent coastal territories contained a mean of 16.7 ha (± 2.2) of riverine forest compared to a mean of 2.3 ha (± 0.7) at inland and 6.8 ha (± 0.4) at ephemeral coastal territories. *Acacia* thornveld covered a mean of 3.4 ha (± 2.0), 7.8 (± 1.8) and 20.0 ha (± 8.1) of permanent and ephemeral coastal, and inland territories respectively: only inland territories contained valley bushveld (mean = 21.3 ha ± 11.7) (Figure 1.3).

Cavity characteristics

Most roost cavities at the coastal site were in *Harpephyllum caffrum*, *Vitellariopsis marginata*, *Schotia latifolia* and *Ficus* spp.; at the inland site *Euphorbia* spp., *Urera tenax* and *S. latifolia* were preferred (Table 1.2). Almost 80% of roost cavities at both sites were situated in trees with no dead material. However, trees which comprised more than 60% dead material were used more frequently at the inland site than on the coast (Table 1.3). Quadrats of 100 m^2 sampled in *Acacia* thornveld showed that no suitable roost cavities were present in such habitat at

Table 1.1. Possible predator species (of Redbilled Woodhoopoes) recorded at the coastal and inland study areas.

	Coast	Inland
Nocturnal predators:		
Felis lybica	X	X
F. domesticus	X	-
Genetta tigrina	X	X
G. genetta	-	X
Diurnal predators:		
Buteo rufofuscus	X	X
Accipiter minullus	X	X
A. melanoleucus	X	X
A. tachiro	X	X
Polyboroides typus	X	X
Falco biarmicus	X	X

X present
\- absent

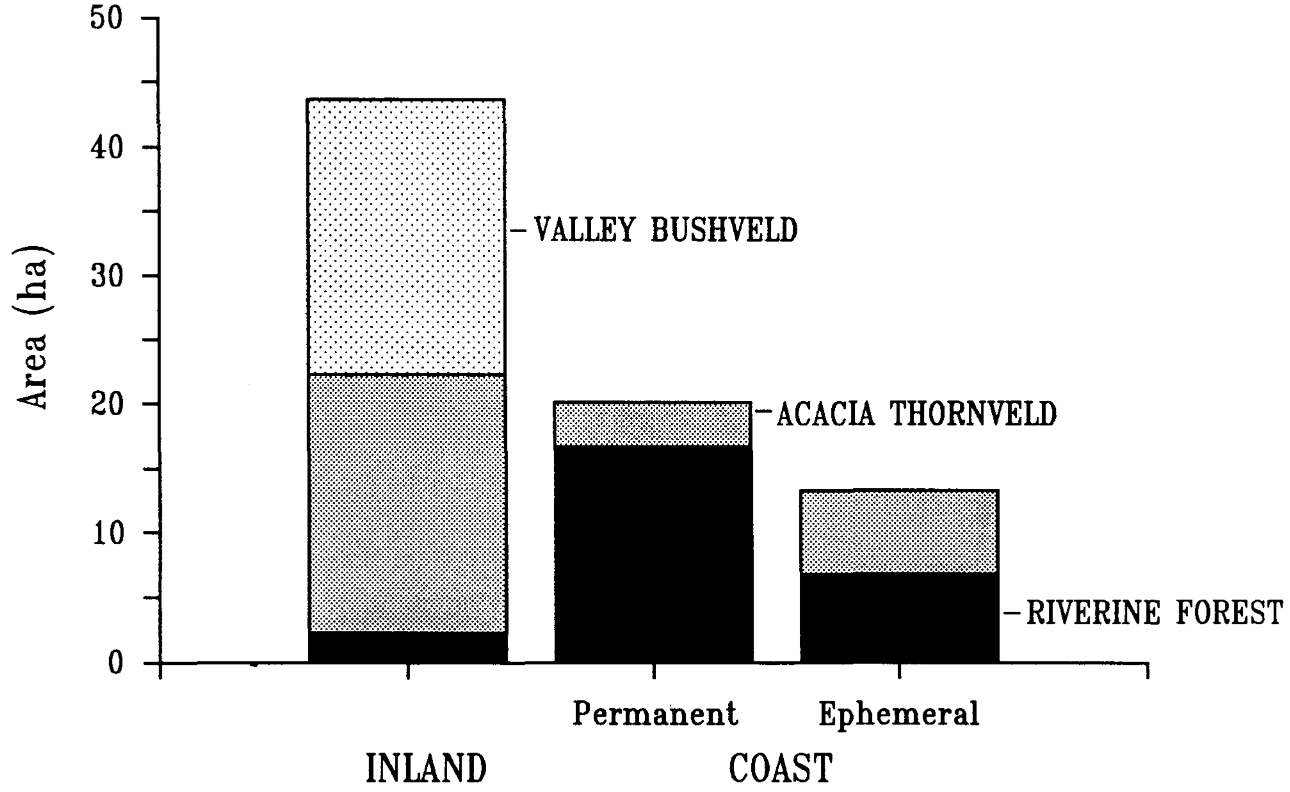

Figure 1.3. Mean territory size (ha) and mean relative abundance of vegetation types in inland, permanent coastal, and ephemeral coastal Redbilled Woodhoopoe territories.

Table 1.2. Relative frequency (%) of Redbilled Woodhoopoe roost cavities in different tree species (n_{coast} = 84; n_{inland} = 26).

Tree species	Frequency (%)	
	Coast	Inland
Harpephyllum caffrum	9.5	-
Schotia latifolia	9.5	23.1
S. afra	-	7.7
Protorhus longifolia	2.4	-
Mimusops caffra	4.8	-
Calodendrum capense	4.8	-
Sideroxylon inerme	7.0	7.7
Ekebergia capensis	2.4	-
Commiphora harveyi	4.8	-
C. woodii	4.8	-
Euphorbia spp.	3.6	15.3
Vitellariopsis marginata	11.9	-
Strelitzia nicolai	2.4	-
Ficus spp.	9.5	7.7
Strychnos decussata	1.2	-
Cussonia spicata	2.4	7.7
Urera tenax	-	23.1
Dead trunk	19.0	7.7

Table 1.3. Indices of permanence of cavity-bearing trees at the coastal and inland study sites (**1** : > 60% dead material; **2** : 0 < dead material < 60%; **3** : no dead material).

Index of permanence	Frequency (%)	
	Coast	Inland
1	9.5	19.0
2	12.0	4.0
3	79.5	77.0

either site; the same applied to valley bushveld without *Euphorbia* spp. at the inland site.

Trees which were between 5 and 12 m in height contained 95% of Redbilled Woodhoopoe cavities, the majority of such trees being between 6 and 10 m tall. Mensural characteristics of cavities and cavity-bearing trees are summarized in Table 1.4. At the coastal site, natural cavities were used for roosting in 63.2% of cases and woodpecker/barbet holes in 36.8% of cases, whereas the trend at the inland site was reversed (42.1% natural *vs* 57.9% woodpecker/barbet holes).

Most cavities were vertical or almost vertical and over 80% were at angles of between 45 and 90° to the horizontal (range 0 - 90; n= 110) (Figure 1.4). Cavity entrance orientation showed no clear trends of directionality, although almost 40% of entrances faced either south or southeast (Figure 1.5).

At both sites, Redbilled Woodhoopoe territories were more or less evenly dispersed throughout the riverine forest, which constituted on average 83.1% of coastal and 5.3% of inland territories (Figure 1.3). Furthermore, quadrats sampled independently of woodhoopoes were similar at both study sites with respect to mean number of apparently suitable roost cavities per unit area of riverine forest (coast: 4.25 ha^{-1}; inland: 4.00 ha^{-1}), as well as mean number of trees per unit area of riverine forest (coast: 18.7 ha^{-1}; inland: 17.1 ha^{-1}).

There was considerable overlap between entrance dimensions of cavities that were used by several species at both study sites. Dimensions of cavities utilized by Cardinal Woodpecker *Dendropicos fuscescens*, Olive Woodpecker *Mesopicos griseocephalus*, Knysna Woodpecker *Campethera notata*, Bearded Woodpecker *Thripias namaquus* and Blackcollared Barbet *Lybius torquatus* showed greatest overlap with Redbilled Woodhoopoes in the range of smaller roost-cavity entrances. Woodland Dormouse *Graphiurus murinus* overlapped extensively with Redbilled Woodhoopoes in the range of larger roost-cavity entrances (Figure 1.6).

Table 1.4. Characteristics of roost cavities used by Redbilled Woodhoopoes (n= 110).

Cavity characteristics	Mean (m)	SD	Range (m)
Total tree height	8.20	2.16	2.00 - 13.00
DBH	0.61	0.45	0.11 - 2.20
DEH	0.28	0.16	0.09 - 1.02
Entrance height (above ground level)	3.89	2.10	0.45 - 9.00
Cavity depth	0.64	0.38	0.24 - 2.20
Cavity inner diameter	0.12	0.04	0.07 - 0.27
Entrance height	0.06	0.04	0.03 - 0.16
Entrance width	0.05	0.03	0.03 - 0.18

DBH diameter at breast height
DEH diameter at cavity entrance height

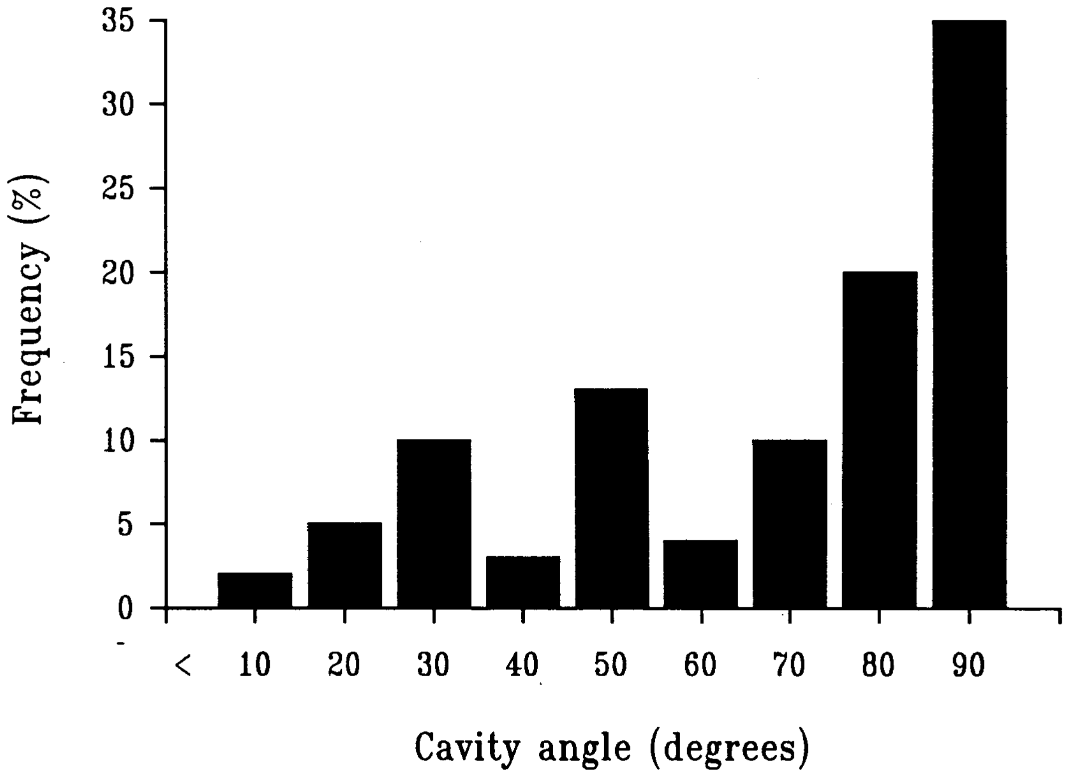

Figure 1.4. Inclination of Redbilled Woodhoopoe roost cavities.

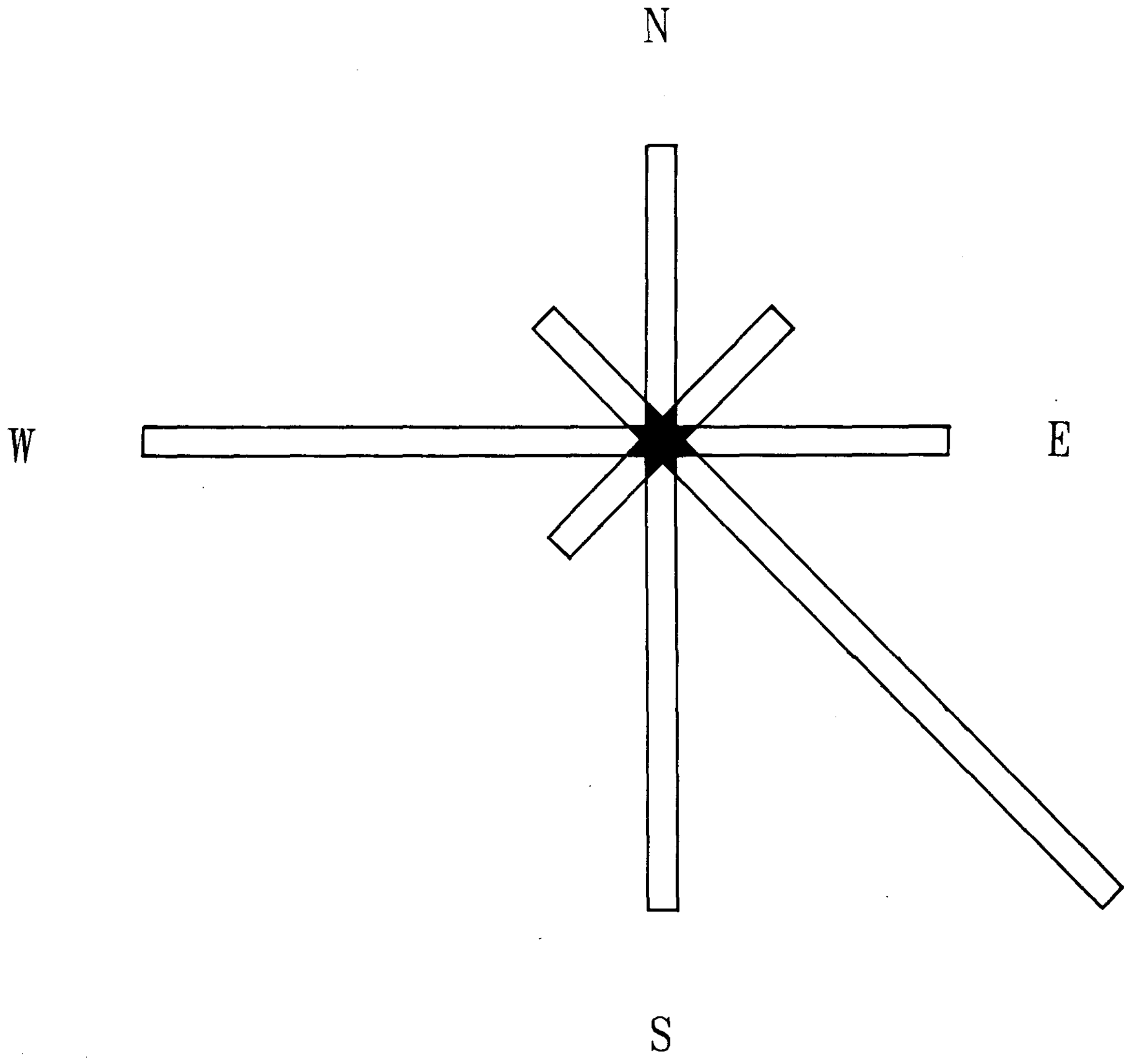

Figure 1.5. Orientation of Redbilled Woodhoopoe roost cavities.

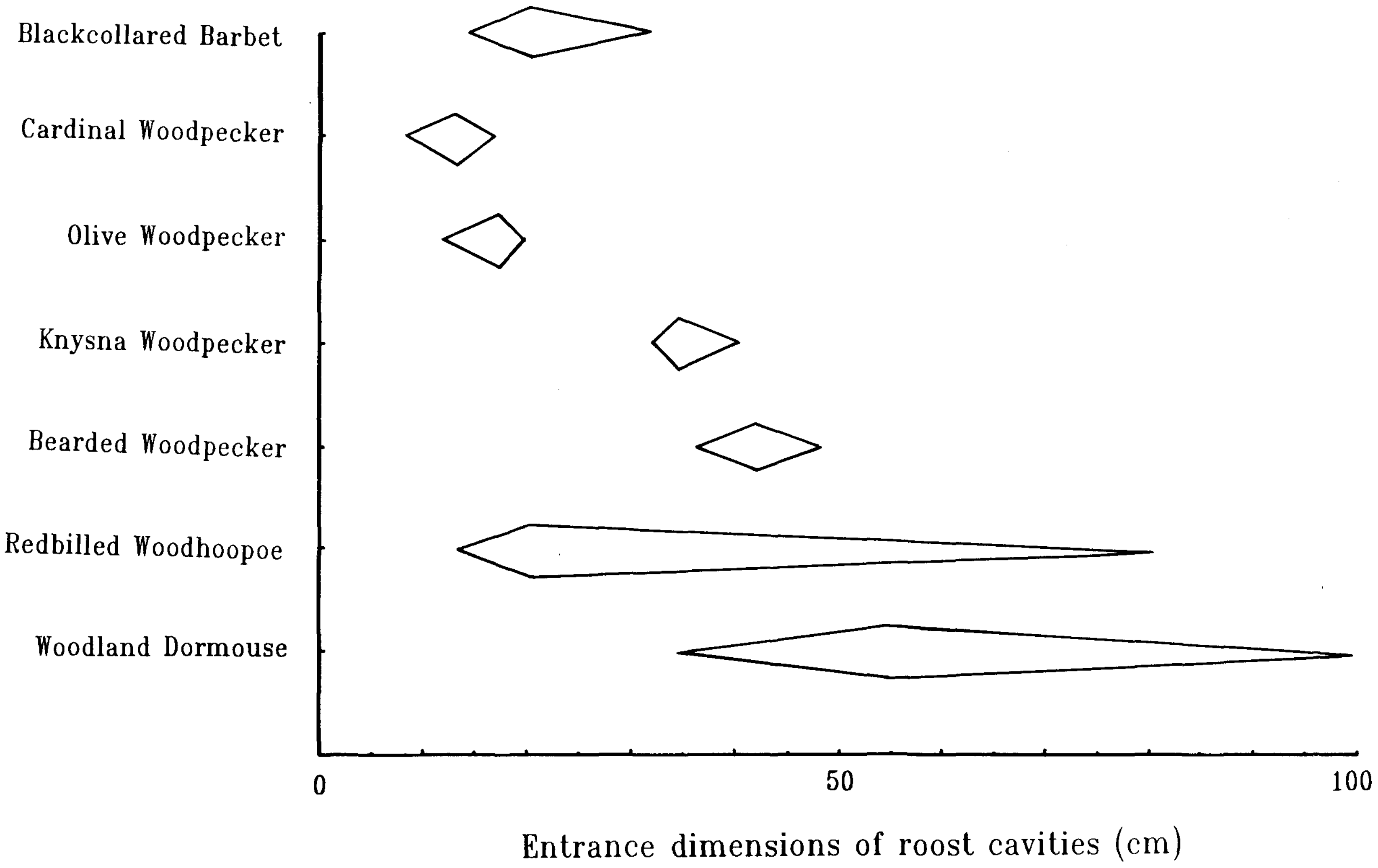

Figure 1.6. Entrance dimensions (height x width) of cavities used by Redbilled Woodhoopoes and six sympatric cavity-using species.

As roost cavities were blocked experimentally, there was a tendency for the birds to use holes with progressively larger entrances (Figure 1.7): these cavities generally were natural in origin rather than the abandoned holes of other bird species. All roost cavities used were in riverine forest habitat. The mean number of cavities available to Redbilled Woodhoopoes was significantly higher in permanent coastal territories (mean= 10.9 ± 5.2; n= 7) than in inland territories (mean= 2.9 ± 0.7; n= 7) (Kruskal-Wallis ANOVA: H= 10.07; $P< 0.01$). Analysis of two ephemeral coastal territories showed significantly lower cavity availability than permanent coastal territories (mean= 3.0 cavities/territory) (Kruskal-Wallis ANOVA: H= 4.27; $P< 0.05$). The mean number of cavities available per hectare of riverine forest was significantly lower at permanent coastal (mean= 0.75 ± 0.17; n= 7) than at inland sites (mean= 1.29 ± 0.33; n= 7) (Kruskal-Wallis ANOVA: H= 5.60; $P< 0.05$).

DISCUSSION

Even though cavity density was 72 % greater at the inland site, cavity availability per territory was much less than on the coast, because of the limited amount of riverine forest at the former. Woodhoopoes apparently selected cavities with small entrance sizes. Factors which may have determined such preference include body size, predatory pressure (Ligon 1981) and energetic considerations (Ligon & Ligon 1988; Ligon *et al.* 1988). Body size should only influence the lower limits of entrance dimensions and, although energetic benefits could be gained from communal cavity roosting, many roost cavities were found to have cracks or more than one entrance. Rather, predatory pressure is hypothesized to have been a selective force behind the cavity-roosting behaviour of woodhoopoes. The predation hypothesis is supported by the fact that woodhoopoe remains were occasionally found near roost cavities, coinciding with the disappearance of one or more flock members (Ligon & Ligon 1978; Ligon 1981; pers. obs). The choice of the smallest

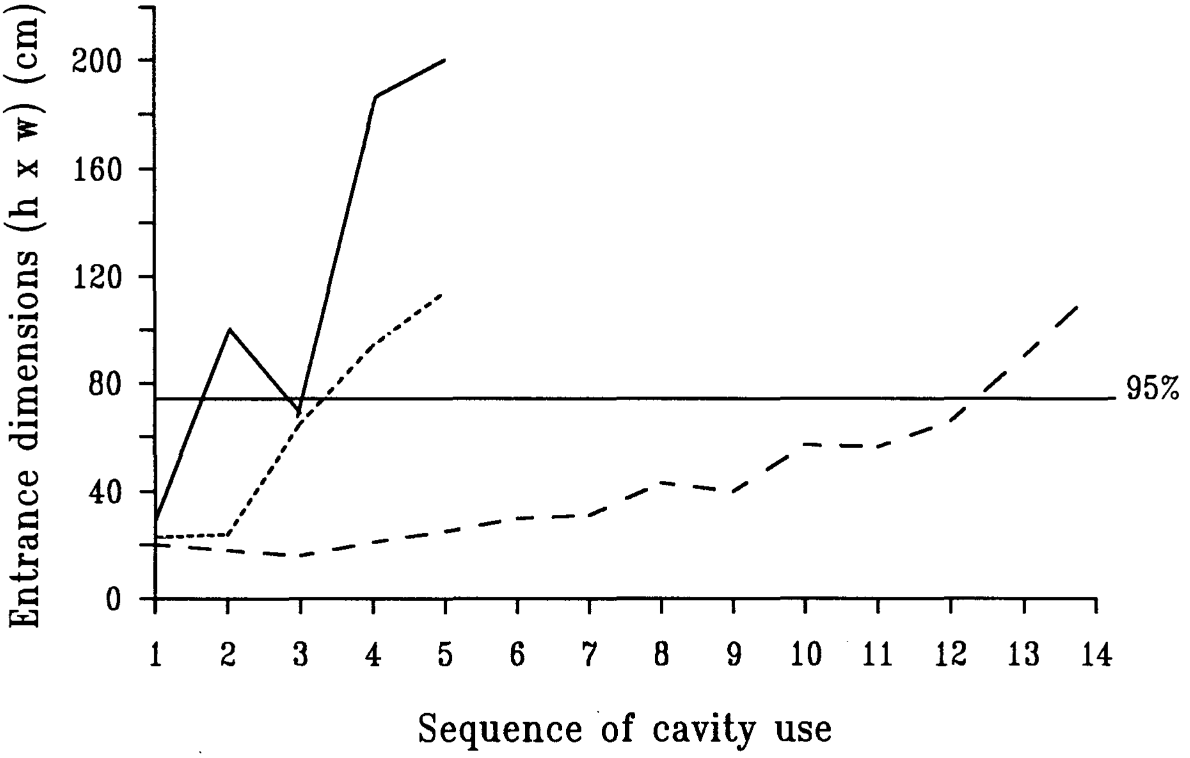

Figure 1.7. Entrance dimensions of cavities used sequentially during experimental plugging of Redbilled Woodhoopoe roost cavities (solid horizontal line: 95% confidence limits; refer to cavity dimensions used under natural conditions) at inland (dotted line), permanent coastal (dashed line), and ephemeral coastal (solid line) territories.

entrance possible is parallelled by *Tockus* hornbills (Kemp 1970, 1976), where this behaviour, as well as sealing of the cavity entrance, has origins in predator avoidance.

Fewer dead trunks were available for excavation by woodpeckers and barbets at the coast than inland, as dead woody material was intensively collected for firewood by local inhabitants at this site. This may explain the less frequent use of woodpecker/barbet holes on the coast, together with a lower frequency of utilization of trees with low indices of permanence. Early roosting might also have the positive effect, by usurping excavators, of forcing them to make additional roost holes.

Overlap in entrance dimensions of roost cavities used by different species was high. Nilsson (1984, 1986) found that larger cavity-using species dominate smaller ones for possession of cavities, and that the smaller species can, in this way, be relegated to inferior cavities. However, I suggest that early occupation of the cavity provides the holder with an advantage over other species, regardless of its size. The early roosting habits of Redbilled Woodhoopoes (Appendix 2), which enter the roost cavity about 45 minutes before dark, may have developed in response to interspecific competition. Early roosting may also have the added effect, by usurping cavity excavators, of 'forcing' them to make additional roost cavities.

At the inland site, woodhoopoes spent most of the daylight period foraging on the slopes in valley bushveld or on the plateaus in *Acacia* thornveld. Each territory included a small patch of riverine forest of sufficient size to satisfy the roosting requirements of the birds. Woodhoopoes never occurred in areas far from suitable forest patches although extensive suitable foraging areas were available away from the forests. The distribution of suitable roost cavities therefore appeared to curtail the distribution of woodhoopoe feeding activity in this area. All forest habitat at the inland site was included within woodhoopoe territories and the habitat was therefore saturated in this respect.

At the coastal site, where the valleys support narrow bands of riverine forest, roost cavities were relatively evenly distributed throughout the permanent territories; allowing woodhoopoes even utilization of the entire territory with no apparent shortage of suitable roost cavities. However, in the ephemeral coastal territories, where suitable roost cavities were limited, woodhoopoe feeding distribution often was curtailed by roost-cavity distribution. This may have had an influence on woodhoopoe survival during 'bad' years and may have caused the instability of ephemeral territory occupation in these marginal habitats.

The absence of marginal forest habitat at the inland site, coupled with the lack of other habitats with available cavities, severely restricts the options for local dispersal by surplus individuals. At the coastal site, marginal forest areas allow dispersal and, in some years, woodhoopoes breed successfully in these habitats. Marginal territories may serve as halfway stations pending dispersal to better areas as these become available (Koenig & Pitelka 1981). The presence of marginal habitat at the coastal site therefore ensures an outlet for young birds from their natal territories, resulting in smaller flock sizes. Lack of such habitat at the inland site results in forced retention of young in their natal territories and hence larger flock sizes.

The 'marginality' of habitats is determined principally by cavity availability, and the presence and abundance of marginal habitats directly influences local flock sizes. The variation in social organization exhibited by Redbilled Woodhoopoes, ranging from single pairs to group territorality, suggests that the species' reproductive and social behaviour are plastic, and change in response to selective pressures, particularly variations in roost-cavity availability. However, no single factor is likely to account for all variation in flock sizes: differences in competitor density, predation pressure, food availability and other critical localized resources could all influence group size through their effects on population dynamics, in particular on productivity. Experimental manipulations of cavity availability are now underway in order to examine further the influence of this factor on group size variation. It is predicted that increased cavity availability will lead to reduced group size at the inland site, whereas it will have little effect on group size at the coast.

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CHAPTER 2

RESOURCE PATCHINESS AS A DISPERSAL CONSTRAINT: CONSEQUENCES FOR PHILOPATRY AND INBREEDING

SUMMARY

Life histories and dispersal patterns of two populations of Redbilled (Green) Woodhoopoes *Phoeniculus purpureus*, occupying different habitats, were studied and compared over a period of eight years in the eastern Cape Province, South Africa. The two study sites differed significantly with regard to woodhoopoe flock size, dispersal frequency and dispersal distance. The birds are dependent on the presence of suitable roost cavities and it is suggested that where cavities are in short supply, long-distance scouting forays are undertaken at a risk of not finding a safe roost site to sleep in, with a concomitant risk of being preyed upon. Differential dispersal with regard to age and sex strongly suggested that a form of behavioural dominance was operative; males dispersed significantly earlier in life than did females. The extent to which Redbilled Woodhoopoes mated incestuously equalled the most extreme cases of inbreeding reported among group-territorial birds. Ecological constraints, in the form of roost-cavity availability and hence dispersal opportunities, profoundly affected the degree of genetic interchange between unrelated individuals. Comparison of fledging success and survivorship of offspring of incestuously-mated and unrelated pairs indicated no obvious deleterious effects of inbreeding. It is proposed that the group-territorial social system and high level of inbreeding of Redbilled Woodhoopoes have evolved primarily in response to environmental constraints on dispersal, namely availability and dispersion of roost cavities, rather than by particular benefits that arise from group living.

INTRODUCTION

The idea that habitat saturation limits dispersal opportunities, which in turn promotes group living and cooperative breeding, was first proposed over 20 years ago (Selander 1964). Since that time this notion has been refined and verified in a number of reviews of cooperatively-breeding bird species (Brown 1974, 1987; Emlen 1978,1982; Koenig & Pitelka 1981; Emlen & Vehrencamp 1983). Many species of cooperatively-breeding birds live in sedentary territorial social units. Typically, such units comprise one breeding pair and one or more nonbreeding helpers which participate in territorial defence, feeding of nestlings and other flock activities, except breeding.

Redbilled Woodhoopoes are cooperatively-breeding, group-territorial birds, which live in flocks of between two and 12 individuals. Cavities suitable for roosting apparently are a critical resource throughout their range (Ligon & Ligon 1978a, 1988, Ligon *et al.* 1988; Chapter 1). Each territory may contain several cavities that are used on a rotational basis, and usually all flock members roost together each night in a single cavity. Individuals often remain nonbreeders for several years, and helpers accumulate in some territories. Most nonbreeders in a flock are therefore related to at least one of the breeders. Birds are physiologically capable of reproducing by the end of their first year, but usually are prevented from doing so by limited breeding opportunities. Nonbreeders sometimes leave the natal flock to join another flock in which no breeding vacancy exists, and assist in the raising of unrelated juveniles. In such instances, the individual involved always improves its dominance ranking above that which it held in the natal flock. It has been stressed that the development of dominance relationships within social groups should be considered in discussions of dispersal and philopatry, but that no field data exist on comparative dispersal patterns of individuals with different social ranks (Bekoff *et al.* 1984).

Because young may eventually become breeders in the natal flock, the potential exists for close inbreeding. However, the relatively few studies of inbreeding in cooperatively-breeding birds have produced contradicting results. Inbreeding occurs at low levels in the Mexican Jay *Aphelocoma ultramarina* (Johnson & Brown 1980) and Florida Scrub Jay *A. coerulescens* (Woolfenden & Fitzpatrick 1984), at intermediate levels in the Acorn Woodpecker *Melanerpes formicivorus* (Koenig & Mumme 1987), and at high levels in the Splendid Fairy-wren *Malurus splendens* (Rowley *et al.* 1986) and Pukeko *Porphyrio porphyrio* (Craig & Jamieson 1988).

This paper describes and compares Redbilled Woodhoopoe *Phoeniculus purpureus* dispersal patterns at two South African study sites with different topography, climate and vegetation. The main objectives of this study were (1) to describe spatial and temporal patterns of dispersal in relation to age, sex and social status of dispersers, (2) to establish whether dispersal is opportunistic in relation to the availability of breeding vacancies, (3) to record the degree of inbreeding, and (4) to test the hypothesis that inbreeding is deleterious to individual fitness.

METHODS

Redbilled Woodhoopoes were studied at two sites in the eastern Cape Province, South Africa, between 1981 and 1988. At Morgan's Bay (32°43'S, 28°19'E), 29 flocks were monitored in an area of 33 km^2 where riverine forest forms belts along river valleys. Territories are linearly arranged along these river courses. In the Kubusi River Valley (32°32'S, 27°47'E), 24 flocks were monitored in an area of 45 km^2 of valley bushveld vegetation (Acocks 1975). Here, riverine forest occurs in small patches in tributary valleys and the remainder of the area is dominated by valley bushveld. Roost cavities are almost entirely restricted to trees in the riverine forest patches.

Males and females were easily separable in the field on both bill length and vocal dimorphism (Ligon & Ligon 1978a). Birds could also be separated into three age classes on the basis of bill wear and coloration: (1) first years (< 12 months); (2) 2 - 3 year olds (12 - 36 months); (3) adults (> 36 months). The reliability of this method was verified by experience with birds of known age.

Two types of movement away from the natal territory were recognized. Dispersal occurred if an individual acquired membership of another flock and did not return to the natal territory for at least one breeding season. Scouting forays lasted between a few hours and two weeks, after which the bird returned to its natal flock.

A band approximately 5 km wide around each study area was searched at least twice a year for birds which had dispersed from the study areas. Most individuals which left natal flocks were relocated in territories within or adjacent to the study areas, suggesting that most short-distance dispersal was detected. The frequency of successful long-distance dispersal is more difficult to estimate, but was assumed to be nil as observed emigration rates were slightly higher than immigration rates at both study sites (unpubl. data). Although Stacey & Ligon (1987) point out that for certain analogous species (e.g. Florida Scrub Jay, Woolfenden & Fitzpatrick 1984) it may be unjustified to use immigration rates to estimate undetected dispersal, Redbilled Woodhoopoes are not strong fliers and this presumably acts as a constraint on long-distance dispersal. The simplifying assumption has therefore been made that disappearances from the study population represent death.

Details of both scouting forays and successful dispersal were recorded in terms of sex, and, where possible, age of participants, together with the time of year at which dispersal occurred.

Dispersal distance was estimated by counting the minimum number of territories between the pre- and post-dispersal territories occupied. The number of territories through which an individual passes to become a breeder is a useful biological measure of dispersal distance, particularly in cases where territories are stable. Actual dispersal distances (km) were calculated assuming straight-line dispersal.

Information was gathered on cavity availability, independent of woodhoopoes. All trees with DBH (diameter at breast height) > 0.08 m, were counted in 12 randomly chosen 100 m^2 quadrats at each site, and were searched for potentially suitable roost cavities. In addition, the woodhoopoes themselves were used as indicators of effective cavity availability. In seven territories at both inland and coastal sites, known roost cavities were closed up. The birds were thus forced to use alternative roost sites available to them. New cavities used were closed up until two cavities, with entrance dimensions (height x width) outside the 95% confidence limits of cavities used under undisturbed conditions, were used on consecutive nights. The number of cavities falling within the normal size range was then regarded as the effective number of cavities available to woodhoopoes in a given territory (Chapter 1).

The parameter $\mathbf{D_0}$ is an index of potential competition for breeding vacancies (i.e. availability of vacancies *vs* availability of nonbreeders), and was calculated using the formula (Woolfenden & Fitzpatrick 1984):

$$\mathbf{D_0} = \frac{(1-l_{br})\,(1-l_h)}{ml_1 - (1-l_{br})\,l_h}$$

where **m** = mean number of fledglings produced per flock divided by the mean number of breeders per flock (i.e. fecundity), and $\mathbf{l_{br}}$, $\mathbf{l_h}$ and $\mathbf{l_1}$ are, respectively, the annual survivorship of breeders, nonbreeding adults and first year birds.

To validate calculations made using this formula, the severity of potential competition for breeding vacancies was tested empirically by comparing the number of nonbreeders with the number of breeding vacancies arising per year.

A 'home' dominance ranking was assigned to each dispersing individual by considering its sex, age and/or behavioural interactions with other flock members (Chapter 4). An index of dominance was then calculated, taking into account the number of fellow flock members, of the same sex, with which an individual had to compete for social status:

$$\text{Dominance index} = \frac{\text{No. individuals of own sex}}{\text{Intrasexual dominance rank}}$$

To test the hypothesis that secure roost/nest cavities limit woodhoopoe distribution, a manipulative experiment was conducted at another study area, Zuluberg (32°28'S, 27°52'E), 12 km from the Kubusi River Valley study site. The vegetation of this 4 km^2 area comprises a homogenous stand of *Acacia karoo* savanna (height: 2 - 4 m). A thorough survey of the area in February 1988, immediately prior to manipulations, confirmed the absence of any permanent woodhoopoe territories, although it appeared suitable as a feeding area. Twenty artificial nest boxes were then placed at random throughout the area at a height of 2 - 4 m, and these were checked every day for two months following manipulation.

Only incestuous matings (i.e. father/daughter, mother/son, brother/sister) were classified as inbreeding. All other matings (almost invariably between totally unrelated birds) were regarded as cases of outbreeding. Incidents of incestuous matings (degree of relatedness ≥ 0.5) between individuals were only counted once during their lifetimes, even though such matings, involving the same individuals, were likely to occur in more than one season.

To test for possible deleterious effects of inbreeding, five measures of productivity were used as indices of 'fitness' and were compared between inbred and outbred pairings. These were : (1) the percentage of pairings that produced no chicks; (2) the mean number of young fledged per mated pair; (3) the mean number of young fledged by successful pairs; (4) the survivorship of young to 12 months of age; and (5) the survivorship of young to 24 months of age.

One breeding bird was removed from each of six flocks of Redbilled Woodhoopoes in the Kei River Valley (32°31'S, 27°58'E), 15 km from the Kubusi River Valley study area, to monitor restructuring of flocks and to determine relatedness between new breeders (Chapter 4).

RESULTS

Scouting forays

Redbilled Woodhoopoe males scout for breeding vacancies at an earlier age than females. During more than 2500 hours of observation over eight years, I observed a total of 256 scouting forays. At the coastal site 91% of scouting males were younger than 36 months (n= 67), compared to 16% of scouting females (n= 68). At the inland site 84% of scouting males were younger than 36 months (n= 32), compared to 13% of females (n= 30). There were no differences in scouting frequency by males and females at the two sites. Scouting forays peaked during the months prior to the onset of the breeding season at both study sites (Figure 2.1). Seasonal patterns of forays were broadly similar between males and females at both inland and coastal sites.

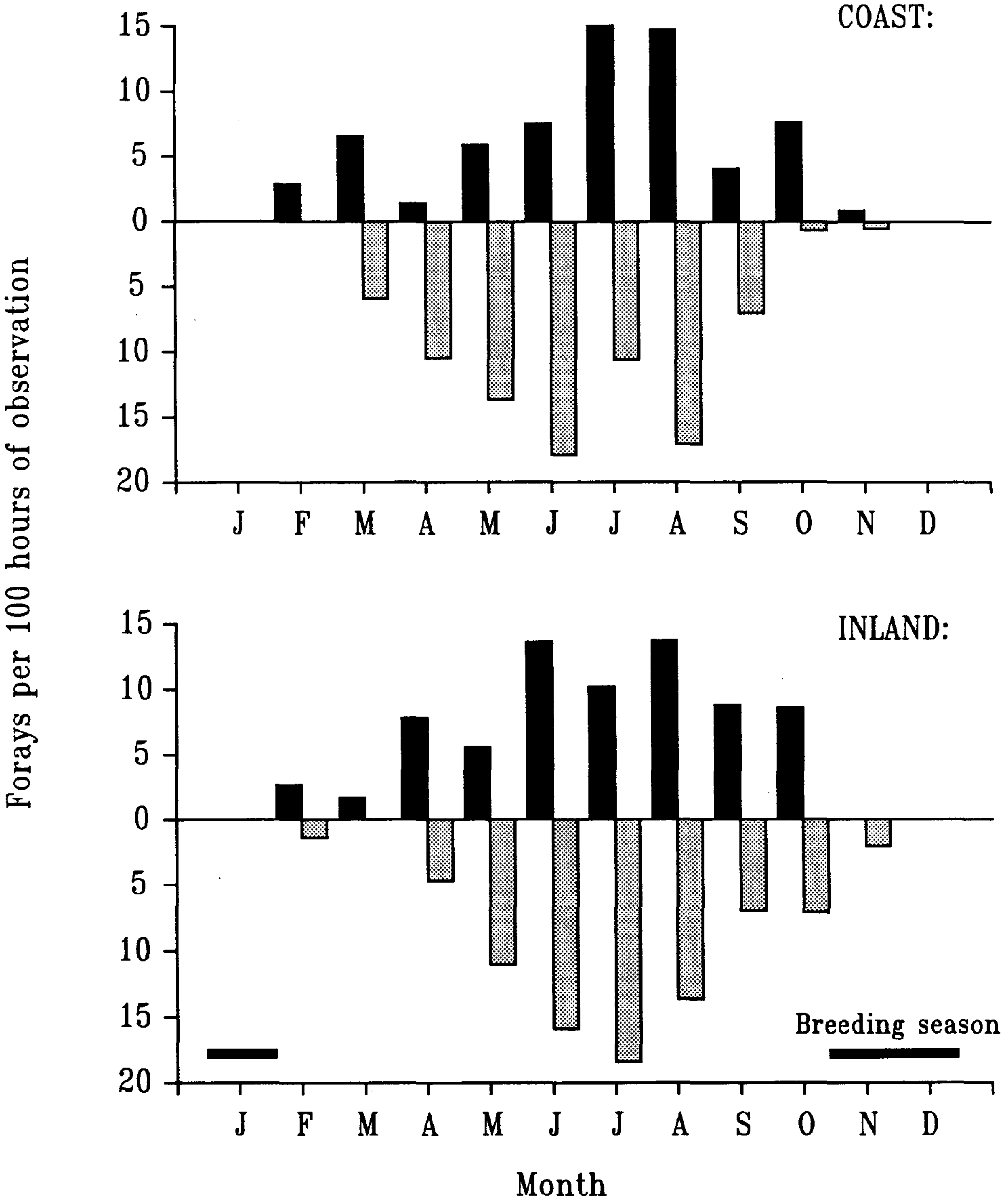

Figure 2.1. Seasonality of scouting forays undertaken by males (black bars) and female (stippled bars) Redbilled Woodhoopoes at the coastal ($n_{males} = 81$; $n_{females} = 91$) and inland ($n_{males} = 40$; $n_{females} = 44$) sites respectively.

Dispersal

I observed 43 cases of colour-banded birds leaving the natal flock and successfully establishing themselves elsewhere. With data combined for both study sites (there was no significant difference between sites), 80% of dispersing males were between 12 and 24 months old, whereas 80% of dispersing females were more than 48 months old; these differences were significant ((Mann-Whitney U: $z = 5.691$; $P < 0.001$). The mean age at successful dispersal for males was 18.5 ± 6.7 (S.D.) months ($n = 22$), and 45.7 ± 5.8 (S.D.) months for females.

Dispersing females had a mean dominance index value of 1.85 ± 0.88 ($n = 10$; both sites combined), whereas males had a significantly lower mean dominance index value of 1.06 ± 0.16 ($n = 13$) (Mann-Whitney U: $z = 3.274$; $P < 0.001$). Six of the 13 dispersing males were ranked second to the breeding male; all females that dispersed were ranked second only to the breeding female in female dominance hierarchies. Dispersal occurred most often during Autumn and Spring (Figure 2.2).

Birds of both sexes traversed the same number of territories during dispersal at both study sites. Sixteen successful dispersal events by coastal males and 14 by coastal females were recorded in which the flock of origin was known; comparable data were available for nine inland males and six females. In the longest recorded dispersal events on the coast, birds traversed six territories, whereas inland birds traversed a maximum of four territories (Figure 2.3). These differences only showed a weak trend (Mann-Whitney U: $z = 1.771$; $P = 0.08$), but this may have been due to the relatively small inland sample size. All incidental searches up to 20 km away from the study areas produced negative results. The median dispersal distance of coastal Redbilled Woodhoopoes was 1.8 km and was significantly farther than that of inland birds (0.8 km) (Mann-Whitney U: $z = 2.112$; $P < 0.05$). Twenty per cent of coastal dispersal events were over a distance of 4 km or more (maximum 7 km), whereas the maximum recorded dispersal distance at the inland site was 3 km.

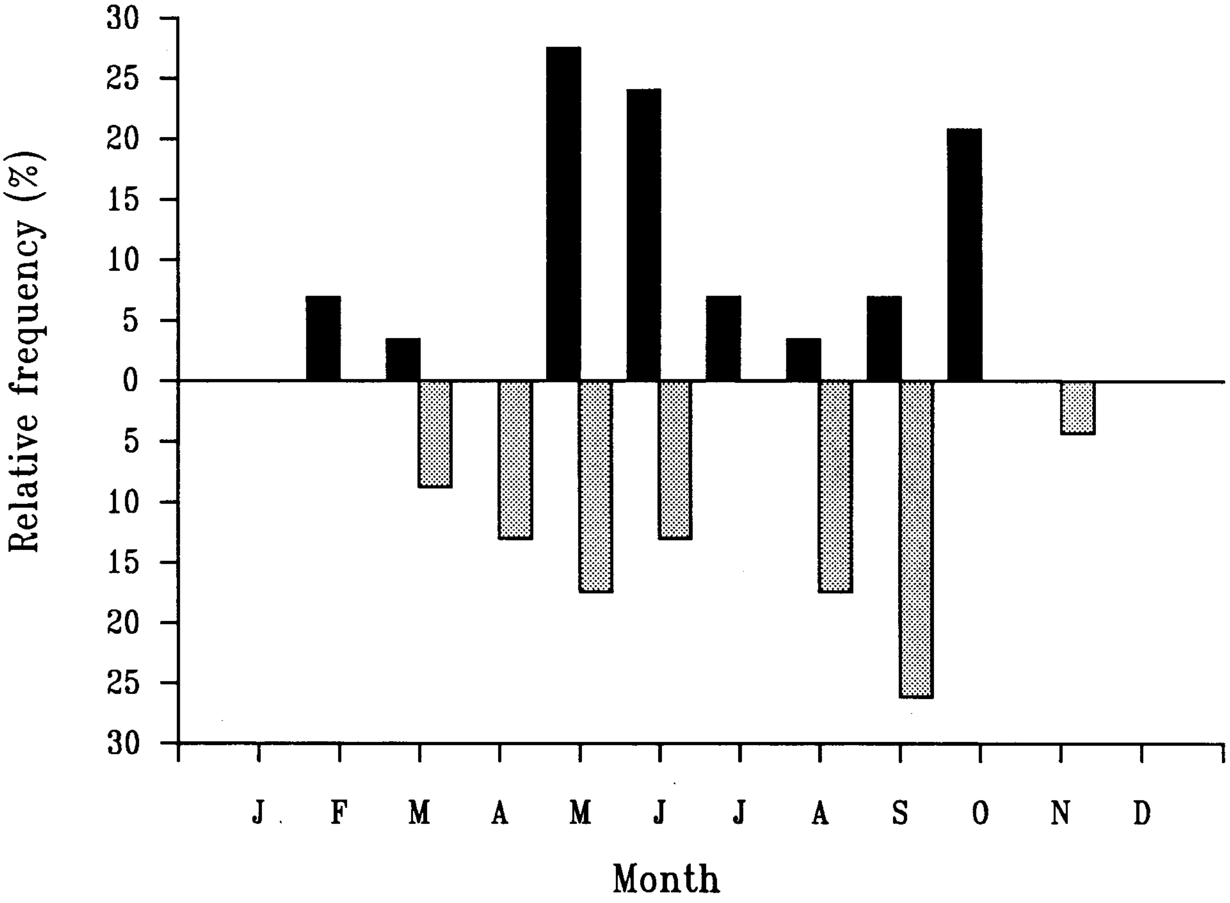

Figure 2.2. Seasonality of successful dispersal of male (black bars) and female (stippled bars) Redbilled Woodhoopoes; data from the two study sites are combined.

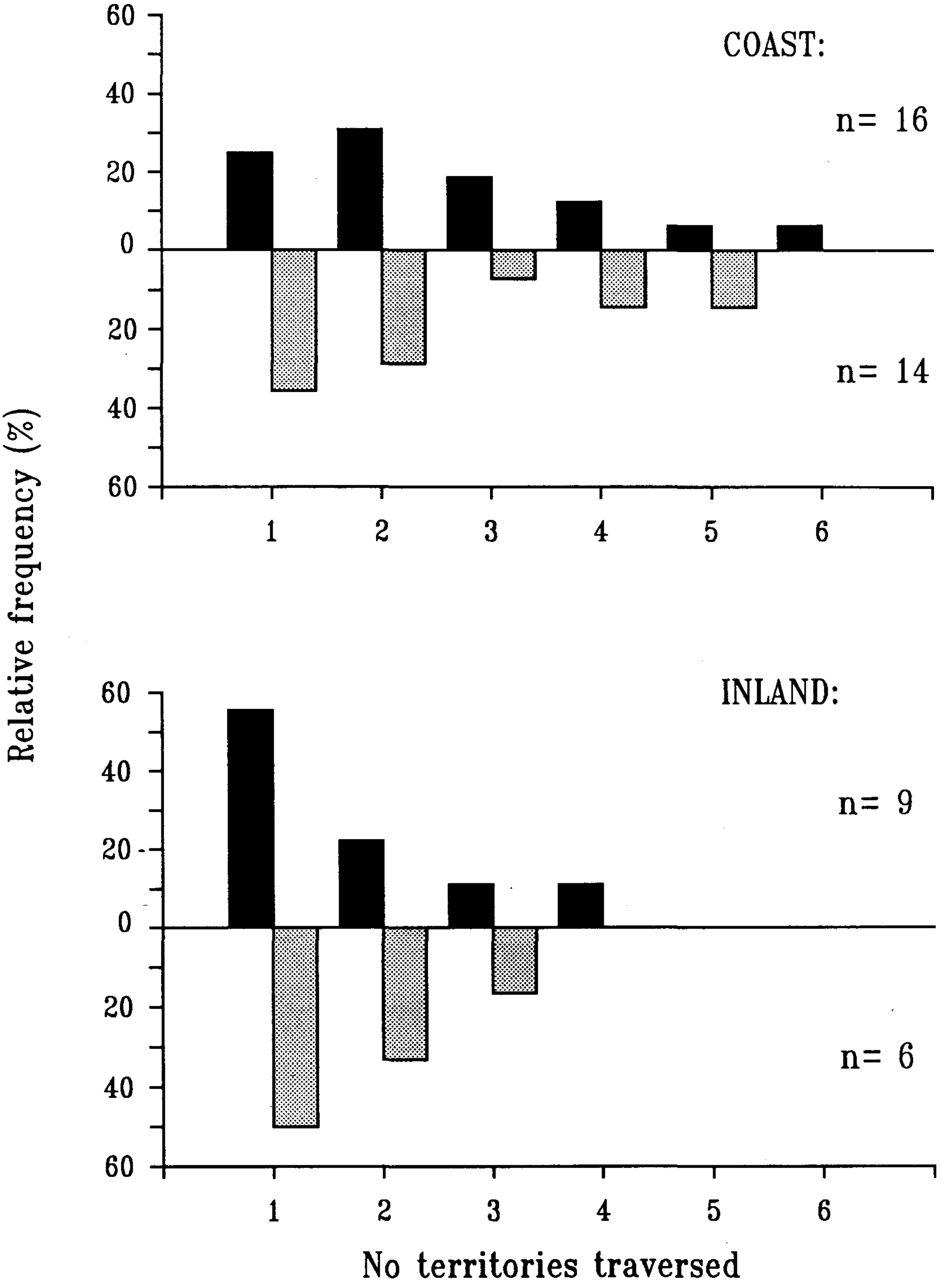

Figure 2.3. Dispersal distances between pre- and post-dispersal territories of male (black bars) and female (stippled bars) Redbilled Woodhoopoes at the coastal and inland study sites respectively; distance is measured in number of territories crossed.

From life-history parameters in Table 2.1, the theoretical index of competition for breeding vacancies $\mathbf{D_0}$ was 0.16 for males and 0.13 for females on the coast. This is equivalent to six male and eight female nonbreeders potentially competing for each breeding vacancy. At the inland site $\mathbf{D_0}$ was 0.14 for males and 0.11 for females, representing seven male and nine female nonbreeders available to fill each vacancy.

These values agree well with direct observations of breeding vacancies *vs* numbers of nonbreeders in the population (Table 2.2). At the coast, on average, five males and eight females were available to fill each vacancy. The surplus at the inland site was greater: seven males and 11 females.

Fate of offspring

An equally large proportion of males and females were present as nonbreeders in their natal flock at the end of their first year at both study sites (Table 2.3 & 2.4). Breeding status was attained most frequently by both sexes at both study sites by waiting until a breeding vacancy arose in the natal flock. The frequency with which young inherited their natal territory was similar at both sites; however, males generally inherited breeding status at a younger age than females. At both study sites, a larger proportion of males than females became breeders in non-natal territories to which they emigrated, and males achieved breeding status in such territories at a younger age than females. At both study sites a small proportion of males and females emigrated from the natal flock to become nonbreeders elsewhere. This option was short-lived and was adopted by younger males than females at the coast, but by birds of approximately equal ages at the inland site. Younger males than females emigrated from the natal flock and established new territories elsewhere. However, such territories were seldom occupied for more than

Table 2.1. Life-table parameters used (1981-1987) in estimating an index of competition (D_o) for Redbilled Woodhoopoe breeding vacancies. Ranges are given in brackets.

	Males	Females
COAST:		
Annual survivorship of:		
breeders (l_{br})	0.87 (0.79-0.96)	0.90 (0.80-0.97)
mature nonbreeders (l_h)	0.82 (0.76-0.91)	0.83 (0.74-0.89)
first-year birds (l_1)	0.75 (0.63-0.79)	0.64 (0.49-0.69)
Fecundity (**m**)	0.34 (0.33-1.42)	0.34 (0.33-1.42)
Index of breeding competition ($\mathbf{D_0}$)	0.16	0.13
INLAND:		
Annual survivorship of:		
breeders (l_{br})	0.82 (0.71-0.92)	0.88 (0.73-0.90)
mature nonbreeders (l_h)	0.82 (0.73-0.87)	0.79 (0.71-0.84)
first-year birds (l_1)	0.67 (0.51-0.74)	0.56 (0.43-0.64)
Fecundity (**m**)	0.57 (0.54-1.67)	0.57 (0.54-1.67)
Index of breeding competition ($\mathbf{D_0}$)	0.14	0.11

$$\mathbf{D_0} = \frac{(1 - l_{br})\,(1 - l_h)}{\mathbf{m}l_1 - (1 - l_{br})\,l_h}$$

Table 2.2. Estimation of an index of breeding competition for Redbilled Woodhoopoes at the coastal and inland sites.

			A	B	
Year	First-year birds	Older nonbreeders	Total nonbreeders	Breeding vacancies opening	B/A
MALES:					
Coast	35	46	81	15	**0.185**
Inland	37	76	113	16	**0.142**
FEMALES:					
Coast	25	61	86	10	**0.116**
Inland	32	85	117	10	**0.085**

Table 2.3. Fate of Redbilled Woodhoopoe offspring by sex and age at the coastal (Morgan's Bay) study site, 1981-1987 ($n_{male} = 58$; $n_{female} = 57$).

	Frequency of occurrence (%)							
	Age (years)							
	1	2	3	4	5	6	7	8
NONBREEDER IN NATAL FLOCK:								
Males	75.9	28.3	8.1	3.6	0	0	0	0
Females	75.4	52.8	37.5	25.6	0	0	0	0
BREEDER IN NATAL FLOCK:								
Males	3.4	23.9	35.1	32.1	25.0	6.3	6.3	6.3
Females	1.8	9.4	12.5	7.0	2.8	3.2	3.4	3.6
BREEDER IN N0N-NATAL TERRITORY:								
Males	3.4	13.0	16.2	21.4	5.0	6.3	6.3	0
Females	0	1.9	2.1	4.7	13.9	6.5	3.4	0
NONBREEDER IN NON-NATAL FLOCK:								
Males	3.4	2.2	0	0	0	0	0	0
Females	0	0	0	2.3	5.6	0	0	0
BREEDER IN NEW EPHEMERAL TERRITORY:								
Males	0	6.5	5.4	0	0	0	0	0
Females	0	0	0	0	5.6	3.2	0	0
DEAD/DISAPPEARED:								
Males	13.8	26.1	35.1	46.4	70.0	87.5	87.5	93.7
Females	22.8	35.8	47.9	60.5	72.2	87.1	93.1	96.4

Table 2.4. Fate of Redbilled Woodhoopoe offspring by sex and age at the inland (Kubusi) study site, 1981-1987 ($n_{male} = 64$; $n_{female} = 70$).

	Frequency of occurrence (%)							
	Age (years)							
	1	2	3	4	5	6	7	8
NONBREEDER IN NATAL FLOCK:								
Males	71.8	39.3	22.6	13.3	0	0	0	0
Females	61.4	38.7	25.5	12.0	2.2	2.2	0	0
BREEDER IN NATAL FLOCK:								
Males	1.6	14.8	22.6	17.8	17.9	8.9	5.4	2.8
Females	1.4	1.6	1.8	4.0	8.7	8.9	9.1	4.8
BREEDER IN N0N-NATAL TERRITORY:								
Males	1.6	4.9	1.9	2.2	0	0	0	0
Females	0	0	2.0	2.2	0	0	0	0
NONBREEDER IN NON-NATAL FLOCK:								
Males	0	0	1.6	0	0	0	0	0
Females	0	0	2.0	0	0	0	0	0
BREEDER IN NEW EPHEMERAL TERRITORY:								
Males	0	0	0	0	0	0	0	0
Females	0	0	0	0	0	0	0	0
DEAD/DISAPPEARED:								
Males	25.0	39.3	52.8	66.7	82.1	91.9	94.6	100.0
Females	37.1	59.7	72.7	80.0	86.9	88.9	90.9	95.2

one year, after which flock members usually disappeared. At the inland site, no birds established ephemeral territories.

Although mortality was apparently higher among females than males during the first four years of life at both study sites, it evened out later on, and overall, there was no difference between mortality of the sexes at each site (Figure 2.4).

Age at first breeding

Of 56 Redbilled Woodhoopoe males and 32 females of known age that achieved breeding status, the combined mean age at first reproduction was 26.5 and 30.5 months for males at the coastal and inland sites respectively. Corresponding values for females were 46.4 and 51.6 months.

Males which inherited breeding status in the natal flock were generally younger than females which did so, although the difference was only significant at the inland site (Table 2.5). Females at the inland site were older at first reproduction than were females on the coast. There was no difference between the sites in the age at which males first bred. Intersexual differences in age at first reproduction in established non-natal territories were significant at the coast, but not at the inland site (probably due to small sample size). Intrasexual differences between the sites were not significant for both sexes. Males became breeders in ephemeral non-natal territories at the coastal site significantly earlier than did females (Table 2.5).

Experimental manipulation of cavity-availability

No woodhoopoes permanently inhabited the Zuluberg study area prior to the introduction of artificial nest/roost cavities. However, individuals from flocks which

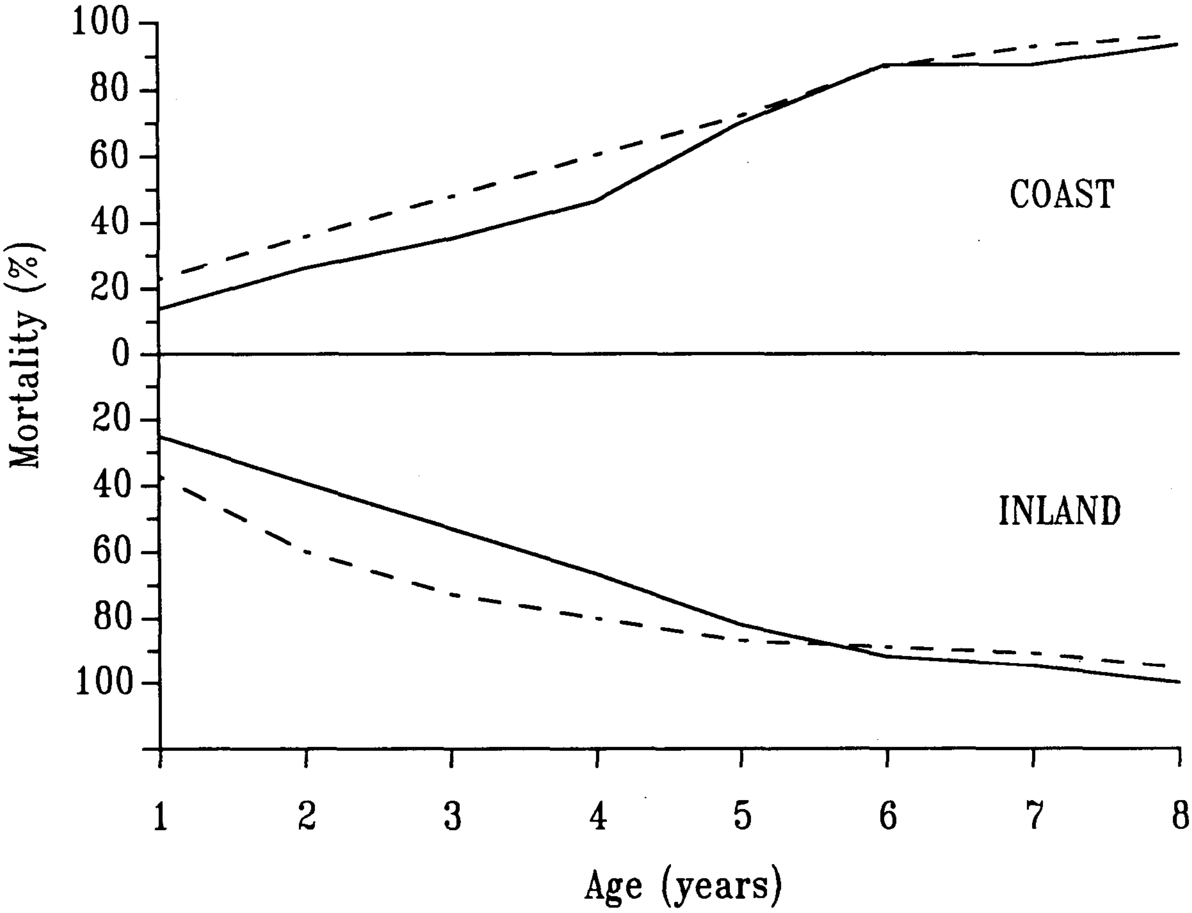

Figure 2.4. Relationship between male (solid line) and female (broken line) Redbilled Woodhoopoe cumulative mortality (%) at the coastal and inland study sites respectively.

Table 2.5. Summary of age at first reproduction of Redbilled Woodhoopoes, and the way in which it was achieved at the coastal and inland study sites respectively.

Study site	Mean age of reproduction (months) (± SD)		
	Male	Female	
BREEDER IN NATAL TERRITORY:			
Coast	27.0 ± 11.2 n= 16	29.3 ± 13.6 n= 9	**n.s.**
Inland	32.5 ± 13.3 n= 17	51.0 ± 21.0 n= 8	*
	n.s.	*	
BREEDER IN ESTABLISHED NON-NATAL TERRITORY:			
Coast	24.9 ± 7.7 n= 13	56.4 ± 9.9 n= 10	**
Inland	24.0 ± 8.5 n= 5	54.0 ± 8.5 n= 2	**n.s.**
	n.s.	**n.s.**	
BREEDER IN EPHEMERAL NON-NATAL TERRITORY:			
Coast	28.8 ± 6.6 n= 5	64.0 ± 6.9 n= 3	*

Mann-Whitney U:

*	P< 0.05
**	P< 0.001
n.s.	not significant

were based in the adjoining river valleys occasionally visited the area. No other cavity-roosting species were found in this homogenous stand of *Acacia* savanna. More than 90% of all trees had a DBH smaller than 0.15 m, and none contained cavities suitable for nesting or roosting in.

Within two weeks of introducing the nest boxes, a flock of three woodhoopoes moved into a corner of the experimental area, using a nest box to roost in. After two months, five flocks (2 - 3 individuals in each) had established territories in this area, and four of these flocks bred in the boxes at the end of 1989. All roosting and breeding in this area was restricted to these boxes.

Inbreeding

The frequency of incestuous matings (degree of relatedness ≥ 0.5) at the inland site was greater than at the coast (62.5% *vs* 33.3%; $X^2 = 4.325$; 1 df; $P < 0.05$) (Table 2.6).

The proportion of outbred pairs that produced no fledglings exceeded that of inbred pairs at both sites; the difference being significant at the inland site. At the inland site, average fecundity of inbred and outbred pairs was identical (Table 2.7). Considering only successful pairs, mean fecundity of inbred and outbred pairs on the coast was identical, whereas at the inland site, outbred pairs produced significantly more young than inbred pairs. There was no significant difference in the survivorship of inbred and outbred young up to the age of 12 months at both study sites. Survivorship to the age of 24 months was almost identical for inbred and outbred individuals at both study sites.

Table 2.6. Summary of the frequency of inbreeding and likely outbreeding by Redbilled Woodhoopoes at two study sites (given as percentage of total number of observations in brackets).

Mating pattern	Study site	
	Coast	Inland
Inbreeding:		
Father & daughter	1	6
Mother & son	7	5
Brother & sister	1	4
TOTAL	9 (15.3)	15 (29.4)
Outbreeding:		
Immigration *	13	7
Emigration *	5	2
TOTAL	18 (30.6)	9 (17.6)
Unknown:		
Relatedness unknown	32 (54.1)	27 (53.0)
TOTAL	59	51

* includes only instances in which relatedness between both disperser and its new mate are known.

Table 2.7. Summary of inbreeding data for Redbilled Woodhoopoes at the coastal study area; Mann-Whitney U-tests were used to test significance between the 'number of young fledged' categories, and chi-square for the 'survivorship' categories.

Category	Relatedness of mated pair		
	Incestuous	Unrelated	
COASTAL SITE:			
% pairings producing 0 chicks:	41.7 (n= 12)	65.2 (n= 23)	n.s.
Mean # chicks of successful pairs:	x= 2.000 ± 1.155 (n= 7)	x= 2.000 ± 1.069 (n= 8)	n.s.
Mean # chicks per mated pair:	x= 1.167 ± 1.337 (n= 12)	x= 0.696 ± 1.146 (n= 23)	n.s.
Survivorship (%):			
12 months	85.7	75.0	n.s.
24 months	71.4	75.0	n.s.
INLAND SITE:			
% pairings producing 0 chicks:	32.1 (n= 28)	62.5 (n= 8)	*
Mean # chicks of successful pairs:	x= 1.842 ± 0.834 (n= 19)	x= 3.333 ± 0.577 (n= 3)	*
Mean # chicks per mated pair:	x= 1.250 ± 1.110 (n= 28)	x= 1.250 ± 1.753 (n= 8)	n.s.
Survivorship (%):			
12 months	50.0	33.3	n.s.
24 months	34.6	33.3	n.s.

DISCUSSION

The presence of one or more nonbreeding subordinates in a group leaves an individual one of two options to attain breeding status: (1) to remain in the group and wait for the breeder of its own sex to die; i.e. to stay on as a 'hopeful reproductive' (West-Eberhard 1975), or (2) to disperse and attempt to attain breeding status elsewhere. Species with high survival tend to have 'patient strategies', which are characterized by delayed maturity and prolonged association of young with parents and other relatives. Young New World jays remain with their parents on the natal territory for one year in some species, two or more years in others (Brown 1974). Offspring of Mexican Jays may breed on the natal territory in the company of their parents (Brown & Brown 1981).

A breeder should be able to manipulate or control threats to its reproductive interests if other nonbreeding, but sexually mature adults are tolerated in the same flock. In cooperative breeders with monogamous mating systems, this protection is maintained in one or both of the following ways: (1)'psychological castration,' where nonbreeders show low levels of sexual activity as a result of being dominated by the breeder (Rood 1980; Macdonald & Moehlmann 1982; Vehrencamp 1982); (2) 'mate guarding,' where nonbreeders are physically prevented from copulating with the breeding female (Mumme *et al.* 1983; Emlen & Wrege 1986; Reyer *et al.* 1986).

Redbilled Woodhoopoe breeding vacancies arise only when breeders die. Copulation usually takes between 90 and 180 seconds (Ligon & Ligon 1978a, 1988; pers. obs.), and it is unlikely that successful extra-pair matings can take place as male breeders guard their females closely during the two to three weeks before egg-laying. In over 2500 hours of observations of woodhoopoes, no extra-pair copulations were observed.

Woodhoopoes joined non-natal flocks, as either breeders or nonbreeders, less often at the inland site than on the coast. Furthermore, the added option of establishing ephemeral territories during good years, in marginally suitable habitat, was available to birds at the coast, but not inland (Chapter 1). At both sites, most birds remained in the natal flock, either as breeders or nonbreeders, although inland birds usually acquired breeding status in the natal flock later than coastal birds. Mortality rates of coastal birds, which were followed from birth, generally were lower than those of inland birds. Although it was not possible to confirm that mortality occurred during dispersal, I suggest that the difference in mortality rates was at least partly associated with dispersal.

In a group-living situation, a trade-off exists between individual interests. Because individual bird qualities may vary, variation in the degree to which breeders dominate their subordinates (the dominance gradient) may exist in different flocks. The dominance gradient determines the probability of a subordinate's genetic contribution to the brood. A steep dominance gradient between a breeder and its subordinates should reduce the likelihood of cuckoldry. An individual nonbreeder is affected by competitive relations with all other nonbreeders, and hence the intensity of competition must increase with group size (Gaston 1978). Breeding vacancies among Redbilled Woodhoopoes occur rarely, and, when they do, an individual nonbreeder must be sufficiently dominant to ensure its own reproductive status. Subordinate birds are unlikely to succeed in competing for breeding vacancies, and some may never contribute genetically to the population more than by helping. The importance of such dominance behaviour in determining future reproductive advantages has been shown for Blackcapped Chickadees *Parus atricapillus* and Florida Scrub Jays (Smith 1979; Woolfenden & Fitzpatrick 1977).

Differential dispersal with regard to age and sex implies that there are sex-related differences in behavioural dominance among Redbilled Woodhoopoes. Dominance hierarchies are strongly contested from an earlier age in males (< 1Y) than females (> 3Y) (Chapter 4). A male, subordinate only to the male breeder, spends much time establishing himself as dominant over all other nonbreeding males within the flock. He could surrender this position should he leave the flock for periods to scout for breeding vacancies elsewhere. On the other hand, a young subordinate male may only be second or lower in line for filling a breeding vacancy in the natal flock, but by scouting at irregular intervals for vacancies elsewhere, he stands to lose little status in his home flock, but to gain substantially if he finds a breeding vacancy elsewhere.

Competition for breeding status among females is greatest among individuals older than 36 months. Nonbreeding adult females interact frequently with nestlings and young birds by way of feeding, preening and other social displays such as 'auntie behaviour' (Ligon & Ligon 1978a; Chapter 4). The frequency and apparent strength with which maternal behaviour is manifested in high-ranking nonbreeding females may drive them to look for breeding vacancies elsewhere. Short absences from the natal flock by adult females, in contrast to males, have little influence on their dominance status on their return.

Both theoretical and empirical calculations show that there are slightly more woodhoopoes, of both sexes, available for filling breeding vacancies on the coast than at the inland site. However, at the coastal site, birds sometimes (during favourable seasons) have the additional option of establishing ephemeral territories in marginal habitats, thereby increasing breeding opportunities. There are no marginal areas at the inland site (Chapter 1). There may therefore be about the same number, or slightly fewer competitors, per breeding vacancy in established territories on the coast.

Other cooperative breeders for which data on mean age at first reproduction exist are the Kenyan Redbilled (Green) Woodhoopoe (Ligon & Ligon 1988), the Florida Scrub Jay (Woolfenden & Fitzpatrick 1984), and the Acorn Woodpecker (Koenig & Mumme 1987) (Table 2.8). Kenyan woodhoopoe males breed later in life than do males at both South African sites, but the reasons for this are unclear: no such difference exists for females. The age at which Redbilled Woodhoopoe males

Table 2.8. Comparison of the ages at first reproduction for the two sexes in three group-territorial species.

Species	Age at first reproduction (months)		Source
	Male	Female	
Florida Scrub Jay	35.5	29.5	Woolfenden & Fitzpatrick (1984)
Acorn Woodpecker	25.0	22.9	Koenig & Mumme (1987)
Redbilled Woodhoopoe			
Kenyan site	39.1	47.2	Ligon & Ligon (1988)
Coastal site	26.5	46.4	this study
Inland site	30.5	51.6	this study

first breed, at both South African study sites, is intermediate between that of Acorn Woodpeckers and Florida Scrub Jays. However, females of the latter two species usually breed earlier in life than males. This pattern is reversed (significantly) in Redbilled Woodhoopoes (Tables 2.5 & 2.8).

Ligon (1981, 1983) and Ligon & Ligon (1978b, 1983, 1988) have made a strong case for alloparental behaviour of nonbreeding Redbilled Woodhoopoes as providing reciprocal benefit to donor and recipient nestling. They argued that young individuals return the help that older nonbreeders provide them during their nestling and fledgling stages, by later assisting such individuals to acquire and retain breeding status in a non-natal flock. Such dispersal was never witnessed in either the present study, or during Woolfenden & Fitzpatrick's (1984) extensive observations of Florida Scrub Jays.

The low mortality rate of breeding Redbilled Woodhoopoes in the present study, which contrasts strongly with that found in Kenyan Redbilled Woodhoopoes (14 - 17% *vs* 30 - 38%) (Ligon & Ligon 1988), may explain the rarity of group dispersal. Little cooperation is evident among Redbilled Woodhoopoes at this phase of their lives and dispersal should be regarded as an event in which selfish individual interests are promoted.

Proximate determinants of dispersal patterns

The homogenous *Acacia* savanna vegetation in the experimental site was probably a result of man-induced bush encroachment. Although the trees provided suitable foraging habitat, they lacked suitable roost cavities. Establishment of five woodhoopoe territories in the area subsequent to the experimental introduction of artificial cavities, supports the hypothesis that roost cavities are a critical resource.

Resource dispersion (particularly food resources) is considered important in determining the degree of philopatry/dispersal, group size, and social organization of carnivores which forage socially (European Badger *Meles meles*, Kruuk 1978; Red Fox *Vulpes vulpes*, von Schantz 1981). Habitat-related factors appear to be primarily responsible for the lower dispersal frequency and shorter dispersal distances of Redbilled Woodhoopoes at the inland site compared to the coast, even though flock sizes are larger (Chapter 1), and competition for breeding vacancies is perhaps slightly greater. The availability and distribution of safe roost cavities are the ecological factors constraining dispersal in South African woodhoopoes; this is in agreement with Ligon & Ligon (1988) who suggested that the philopatric nature of Kenyan Redbilled Woodhoopoes has evolved in response to the the critical dependence of these birds on safe roost cavities. This dependence has been explained in terms of both predator avoidance (Ligon 1981; Chapter 1) and physiological constraints (Ligon *et al.* 1988). Whatever the proximate reason for this dependence on roost cavities, it has influenced woodhoopoe dispersal patterns profoundly.

Where cavities are in short supply and unevenly distributed, such as at the inland site, long-distance scouting forays are undertaken at a risk of not finding a safe roost site at night, with a concomitant risk of being preyed upon. Scouting individuals are forced either to return to a safe known roost cavity in the natal territory every night, thus limiting potential dispersal distance, or to run the risk of sleeping in unsuitable places in unknown territories, and thus being vulnerable to predation.

Effects of inbreeding

A further indirect effect of environmentally-induced, differential dispersal between the two study sites, is a difference in the frequency of inbreeding. In comparing the frequency of incestuous matings between the two study areas, it becomes evident that the severity of ecological constraints, in the form of roost-cavity dispersion, and hence availability, influences the degree of genetic interchange between unrelated individuals. Although the availability of suitable roost cavities may be important, it is primarily roost-cavity dispersion which affects dispersal patterns in this species. At the inland site this resource is not only less abundant than on the coast, but it is clumped in small patches of riverine forest (Chapter 1).

The extent to which Redbilled Woodhoopoes mate incestuously at the inland study site (58%) almost equals that of the Pukeko (62%) (Craig & Jamieson 1988), the most extreme case of inbreeding reported among group-territorial birds. Ligon & Ligon (1988) suggested that high levels of inbreeding among Kenyan Redbilled Woodhoopoes led to reduced hatchability of eggs, without being a particularly important cost to reproductive fitness. The risks of avoiding inbreeding are high, and there is little evidence from both South African study populations that inbreeding has a deleterious effect on either fecundity (measured in terms of fledging success), or on survivorship of offspring.

A growing number of researchers are questioning the assumption that inbreeding is invariably deleterious and that natural selection has resulted in mechanisms reducing the likelihood of incestuous mating (e.g. Shields 1983; Bulger & Hamilton 1988; Craig & Jamieson 1988). Extreme outbreeding can be equally or more disadvantageous than inbreeding, and some organisms typically achieve a balance between the two (e.g. Bateson 1978; Price & Waser 1979; Shields 1982). Some species avoid inbreeding through behavioural mechanisms; specifically by dispersal of one of the sexes before first breeding (Greenwood *et al.* 1978; Pusey 1980; Packer 1985), or by the absence of breeding behaviour if such dispersal does not occur (Dobson 1982; Hoogland 1982; Garrett & Franklin 1988). If a population with a long history of inbreeding suffers few disadvantages, then males should breed with any available females regardless of their genetic relatedness (Craig & Jamieson 1988).

There is no evidence for a selective disadvantage to inbreeding or advantage to outbreeding in Redbilled Woodhoopoes. The influence of ecological factors on the shaping of social systems in which reduced dispersal is shown (e.g. Koenig & Pitelka 1981), can be regarded as the primary cause of the high levels of (apparently non-deleterious) inbreeding in some communal species. Outbreeding incurs the cost associated with dispersal, but the benefit countering this appears to be an increased probability of early breeding due to enhanced social status following dispersal. However, data do not suggest that woodhoopoes disperse solely in order to increase social status. Game theory (Maynard Smith 1982) would predict that all individuals should disperse if they can improve their social status, and thus their closeness to breeding status. Such a dispersal strategy would tend towards an equalization of group sizes within a population towards some optimal number. However, the wide variation in flock sizes within a particular habitat implies that such equalization does not occur.

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SECTION 2

SOCIAL BEHAVIOUR

CHAPTER 3

RECIPROCITY AND REINFORCEMENT OF SOCIAL STATUS: MULTIPLE FUNCTIONS OF ALLOPREENING

SUMMARY

The function of allopreening or allogrooming has been interpreted in a number of different ways. To evaluate these hypotheses, the allopreening behaviour of six Redbilled Woodhoopoe *Phoeniculus purpureus* flocks was studied. Redbilled Woodhoopoes are group-territorial birds in which reproduction is limited to a single pair within the group. Reciprocal allopreening was directed mainly at body parts that birds were unable to reach themselves and occurred at a constant rate throughout the year. The rate at which the breeding pair was involved remained constant with increasing flock size. Non-reciprocal allopreening was directed at all parts of the body and was seasonal in intensity. The rate at which the breeding pair was involved increased with increasing flock size. The functional origin of allopreening probably lies in ectoparasite removal achieved by way of reciprocal allopreening. Thereafter allopreening may have gained increasing social significance as the birds' social system became more complex, as evidenced by patterns of non-reciprocal allopreening. Previously, no distinction has been made between the importance of reciprocal and non-reciprocal allopreening. Failure to recognize differences between the two types of interactions may have obscured or distorted interpretations of the functions of allopreening in some previous studies.

INTRODUCTION

The function of allopreening, whereby one bird preens another, has been interpreted in several different ways. Three hypotheses have been proposed to explain the function of allopreening in terms of its immediate and long-term consequences: (1) it serves entirely or in part, to control ectoparasites (e.g. Freeland 1976; Goodwin 1983; Brooke 1985); (2) it is a 'tension reduction mechanism' (e.g. Terry 1970; Gaston 1977); and (3) it helps establish and maintain close social bonds between individuals (e.g. Carpenter 1942; Harrison 1965; Simmons 1967; Gaston 1977; Barbour & De Gange 1982; Welty 1982; Katzir 1983; Mills 1983). These hypotheses are not mutually exclusive, and many authors have emphasized the presumed multiple consequences of allopreening and allogrooming (e.g. Selander & La Rue 1961; Sade 1965; Sparks 1967; Mason 1967; Kummer 1968; Jolly 1972; Charles-Dominique & Bearder 1979; Seyfarth 1977, 1980; Broom 1981).

There have been several attempts to categorize species in which allopreening is performed. Mitchell (1979) reported that in primates, allogrooming is performed mostly by species which display strong sexual dimorphism. In contrast, Barbour & De Gange (1982) found that in Nuthatches *Sitta* spp., allopreening occurs only in species which are not sexually dimorphic. Brown (1978) stated that allopreening is conspicuous in many communal birds among all members throughout the year, but is restricted in non-communal species to mated individuals at certain times of the breeding season.

Redbilled Woodhoopoes *Phoeniculus purpureus* (Order Coraciiformes) are long-billed, insectivorous, group-territorial birds that inhabit a wide range of woodland types across a broad Afrotropical range (Fry 1978; Ligon & Ligon 1978). They live throughout the year in flocks of two to 12 birds which contain a single breeding pair. Other flock members, usually relatives of one or both breeders, are full participants in all other flock activities, and dispersal, although infrequent, involves both sexes (Chapter 2).

Ligon & Ligon (1978) pointed out that allopreening is an important intra-group behaviour in the Redbilled Woodhoopoe in Kenya, and suggested, but did not demonstrate, that a functional basis for allopreening could exist apart from its social significance. This study analyses patterns of allopreening in Redbilled Woodhoopoes in South Africa, and considers possible functions of this behaviour. It also addresses the question of the origin of allopreening behaviour in woodhoopoes.

METHODS

Observations of allopreening were made during a study of the behavioural ecology of woodhoopoes, spanning eight years, in the eastern Cape Province of South Africa. All allopreening records relate to observations of six colour-banded flocks, of different size and composition, resident in riverine forest at Morgan's Bay in the Komga district (32°43'S 28°19'E) (Chapter 1). These flocks were studied continuously from February 1986 to February 1987.

Allopreening was defined as the behaviour whereby one woodhoopoe brought its bill into firm contact with the feathers of another in a preening motion. Whenever a bird presented its head or outstretched neck, while sidling up to another, it was classified as soliciting allopreening.

Birds preening other birds were described as the active participants and those being preened were the passive participants. Values given for the frequency of involvement include all interactions in which an individual took part, whether as the active or passive participant. It always was possible to sex the participants on bill length, but it was sometimes impossible to determine social status and age. Observations in which the latter were unknown were only used for general analyses. An allopreening interaction or 'bout' was considered complete when the birds separated or when no allopreening took place for 30 seconds. The body parts that were allopreened were divided into two categories: areas which were inaccessible to the recipient, i.e. the head and neck, and areas which the passive participant could preen itself.

Six measures of allopreening were used to identify differences between birds of different age, sex and breeding status. These were (1) the frequency with which a bird took part in non-reciprocal allopreening, whether as the active or passive participant, (2) the frequency with which a bird took part in reciprocal allopreening, (3) the relative frequency of active and passive involvement in non-reciprocal allopreening, termed the 'preen ratio' (Gaston 1977), (4) the relative frequency of non-reciprocal allopreening in relation to status class, (5) the relative frequency of reciprocal allopreening in relation to social class, and (6) the relative frequency with which allopreening was directed at accessible and inaccessible parts of the plumage.

One hundred and fourteen Redbilled Woodhoopoes were colour-banded between February 1986 and February 1987. All birds were examined for the presence of ectoparasites and awarded an index of 'ectoparasite load', ranging from 0 (no ectoparasites visible) to 3 (severe infestation). Birds were always handled as they came out of their communal roost cavity, where the transfer of ectoparasites between birds was presumed to be maximal.

RESULTS

Allopreening behaviour

Three types of allopreening were recorded: (a) 'reciprocal allopreening', where two birds preened each other simultaneously or in succession; (b) 'non-reciprocal allopreening, where one bird remained a passive participant; (c) and, 'allopreening orgies', in which most or all flock members clumped on a branch and actively allopreened birds on either side and occasionally changed positions within the group (Figure 3.1a).

Allopreening was actively solicited in some instances, and the actions involved were similar to those described for estrildid finches (Morris 1956) and Jungle Babblers *Turdoides striatus* (Gaston 1977) (Figure 3.1b). An individual usually solicited allopreening from another after having preened itself for a while, and almost invariably presented one of the body parts that it was unable to attend to itself.

Reciprocal allopreening was directed at the head and neck region significantly more than at body parts that were accessible to the recipient (656 of 702 occasions) ($X^2 = 265.03$; 1 df; $P < 0.001$), whereas the reverse was true for non-reciprocal interactions (447 of 680 occasions) ($X^2 = 33.67$; 1 df; $P < 0.001$).

Breeding males were the most active solicitors of allopreening and did so significantly more frequently than expected in all flocks of three or more birds (all $P < 0.05$) (Table 3.1). There was a tendency for the rate at which the breeding male solicited allopreening to increase with flock size. In general, males solicited allopreening more often than did females, and older birds solicited more often than did younger birds.

During allopreening the passive bird usually remained completely still, other than occasionally offering a different part of its body. The feathers of the different regions were erected as they were preened. Active birds searched and stroked feathers with soft jabs of the bill. Running the feathers through the bill, as described by Sparks (1964) for the estrildid *Amandava amandava*, was often observed, especially when retrices were allopreened. Allopreening between woodhoopoes usually took place in the higher strata of the forest and always in a position with a wide view.

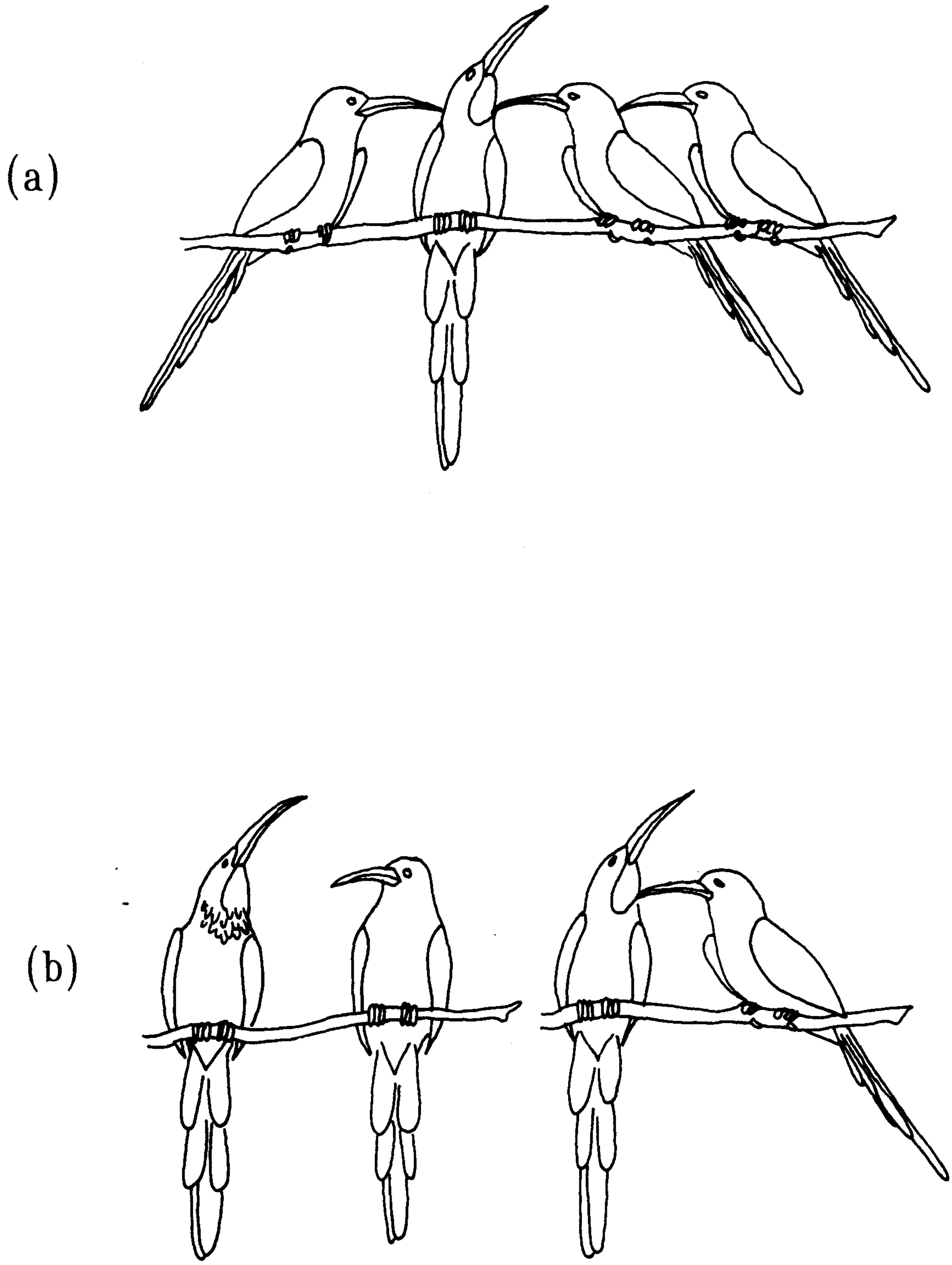

Figure 3.1. Schematic representation of poses adopted by Redbilled Woodhoopoes during (a) allopreening 'orgies', and (b) the solicitation of allopreening (sketched by D.J. Verwoerd).

Table 3.1. Observed and expected frequencies with which breeding Redbilled Woodhoopoe males solicited allopreening from other flock members. The null hypothesis, for calculation of expected frequencies, is that no difference in the frequency of this behaviour exists between flock members.

Flock size	Observed	Expected	Total	X^2	
2	2	1.0	2	2.00	
3	5	2.0	6	6.75	**
4	8	4.0	16	5.33	*
5	13	5.8	29	11.17	**
7	16	5.1	36	27.14	**
8	7	1.9	15	15.68	**
Total		51	104	55.43	

* $P < 0.05$
** $P < 0.01$

Seasonal variations in allopreening frequency and ectoparasite load

Allopreening was more frequent during winter than during summer, reflecting the seasonality of non-reciprocal allopreening (Figure 3.2). Reciprocal allopreening was maintained at a constant rate throughout the year. There was no significant difference in the duration of reciprocal allopreening bouts through the year (Kruskal-Wallis ANOVA: $H= 8.67$; 349 df; $P> 0.8$). Although data are few for allopreening orgies, these were most frequent in the months following breeding; i.e. January-April (Figure 3.3). Allopreening was observed at all times of the day and no clear daily pattern was apparent. However many allopreening bouts occurred immediately after the flock had been disturbed by a predator, another woodhoopoe flock or the observer.

There was little seasonal variation in ectoparasite load, although indices were greater in the months shortly after the breeding months than in winter months ($X^2= 8.70$; 3 df; $P< 0.05$) (Figure 3.4). No birds were handled during the pre-breeding and breeding period (Sept. - Dec.). The breeding pair had significantly lower ectoparasite loads than other classes only during the winter months (May-Aug.) (Kruskal-Wallis ANOVA: $H= 8.06$; 78 df; $P< 0.05$) (Table 3.2). There was no significant difference in ectoparasite loads between the sexes for all age classes (Kruskal-Wallis ANOVA $H= 2.70$; 1 df; $P= 0.26$). The maximum parasite index value (3) was awarded in only six instances; twice to solitary ‘scouting’ adult females and four times to recently-fledged juvenile birds that were members of flocks comprising only a breeding pair and three or more siblings.

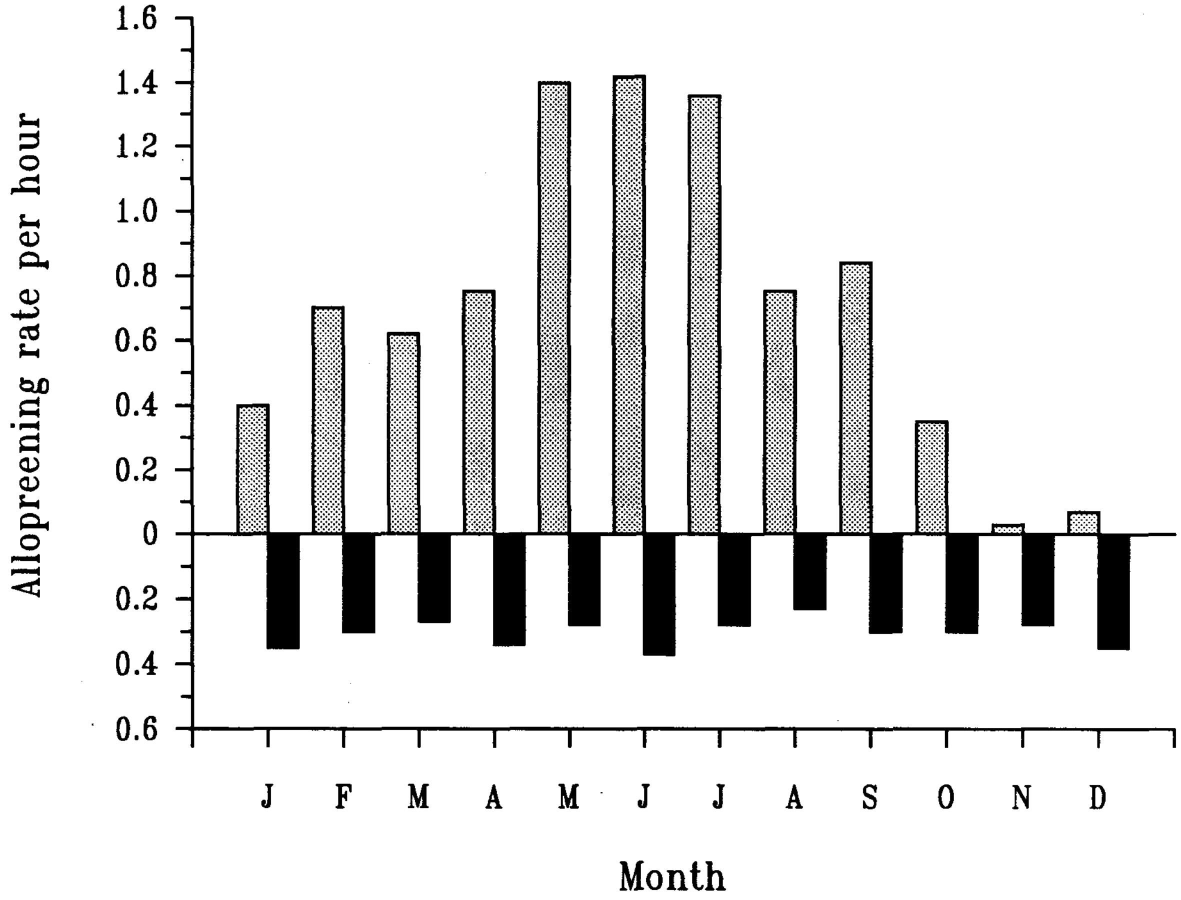

Figure 3.2. Seasonal changes in the mean frequency of reciprocal (black) and non-reciprocal (stippled) allopreening interactions of Redbilled Woodhoopoes (all flocks combined).

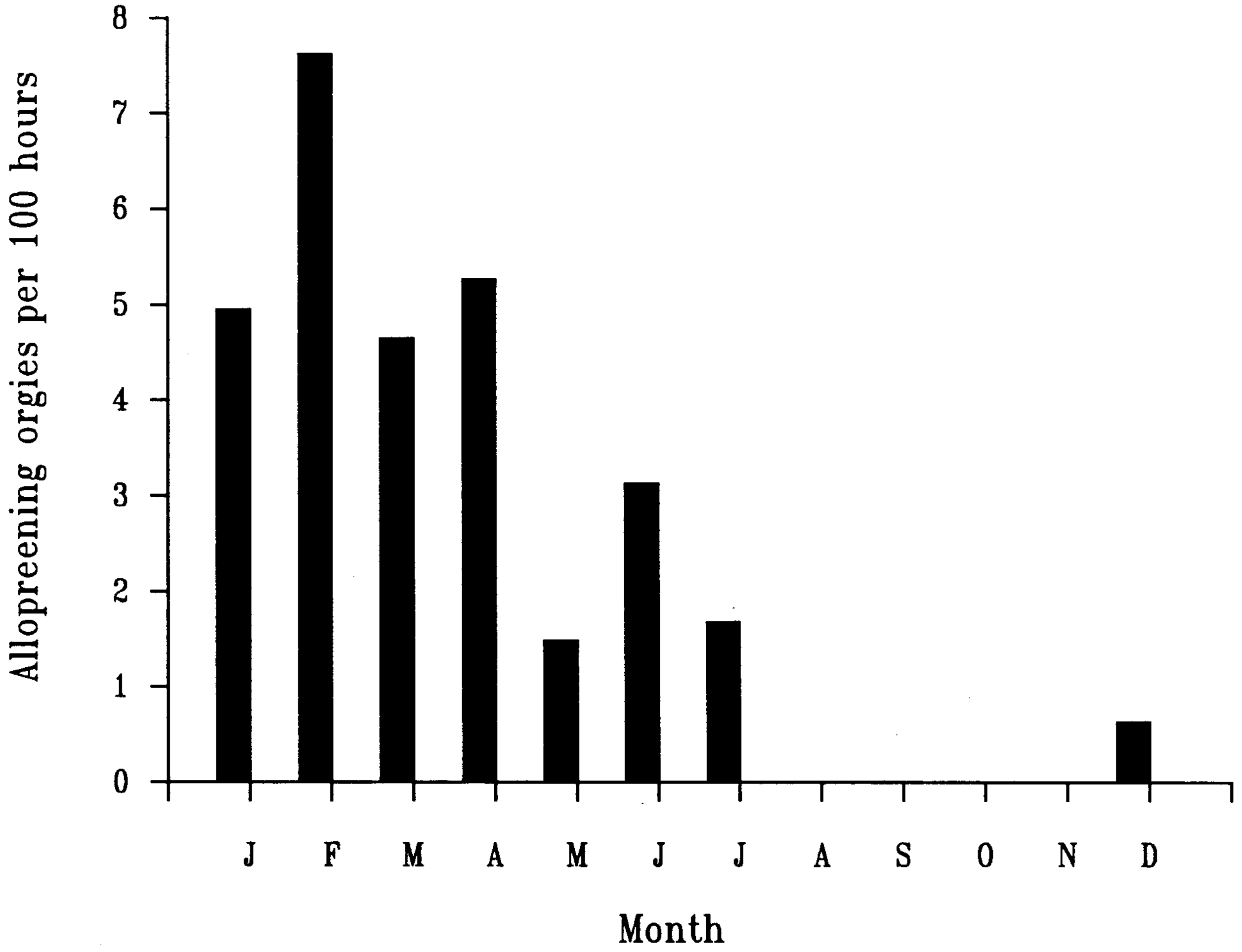

Figure 3.3. Seasonal changes in the mean frequency of Redbilled Woodhoopoe allopreening orgies per hundred hours of observation (all flocks combined).

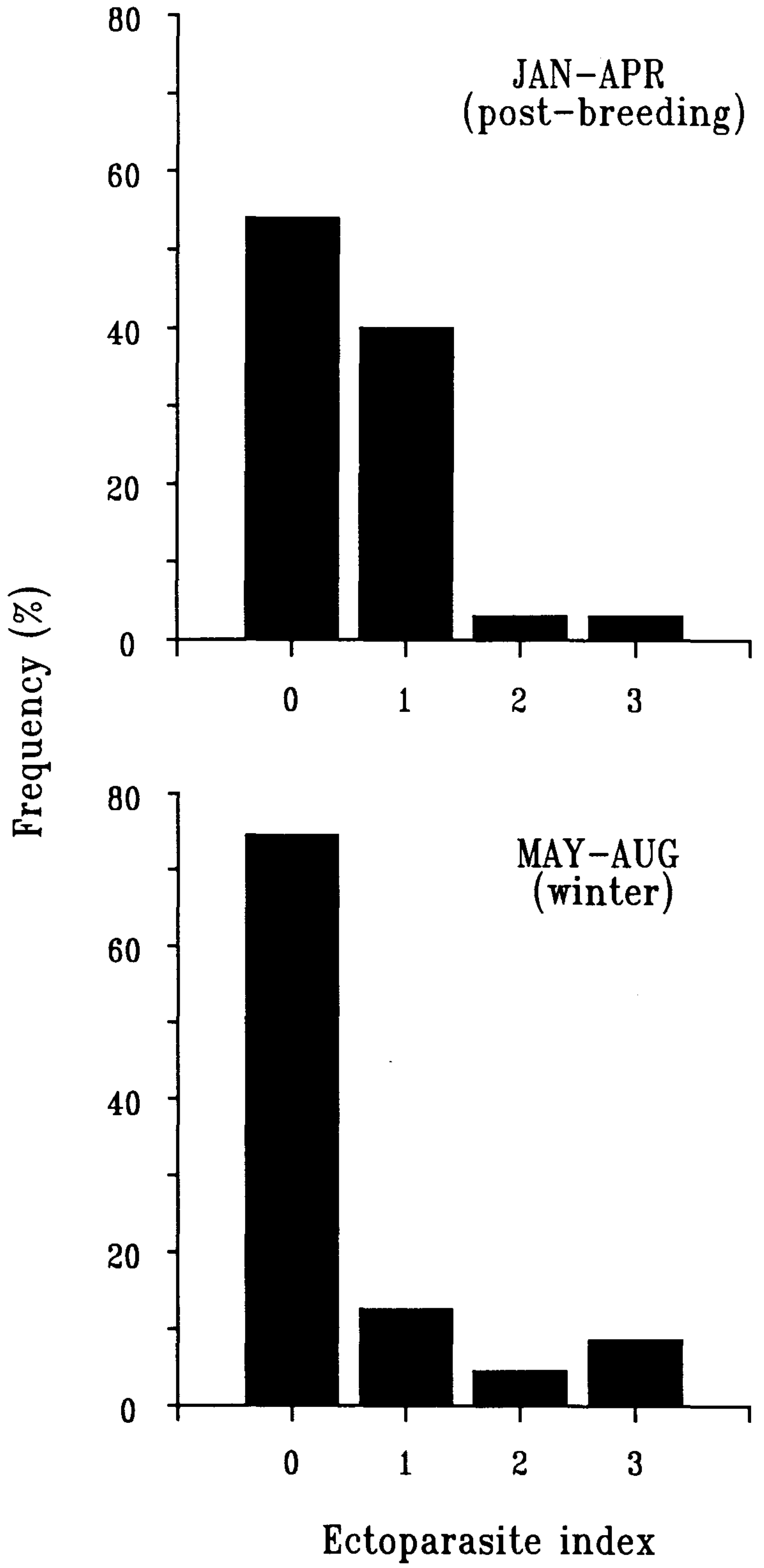

Figure 3.4. Comparison of Redbilled Woodhoopoe ectoparasite load in the post-breeding season (Jan-Apr; n= 35) and winter (May-Aug; n= 79).

Table 3.2. Frequency of occurrence of ectoparasite indices of 0 and > 0 for Redbilled Woodhoopoe breeders and nonbreeders respectively for the time periods between January - April and May - August (BR - breeders; NBR - nonbreeders).

Class	Ectoparasite index		H	
	0	>0		
JANUARY-APRIL:				
BR	10	5	3.620	**ns**
NBR	9	11		
MAY-AUGUST:				
BR	34	6	8.062	*
NBR	25	14		

ns not significant
* $P<0.05$

Allopreening in relation to age, sex and breeding status

The frequency with which the breeding pair actively participated in non-reciprocal allopreening increased with increasing flock size more rapidly than did their participation in reciprocal allopreening (Figure 3.5).

Among birds of two years and older, a hierarchical pattern of non-reciprocal allopreening was evident: females took the active role more often than males, and younger birds more often than older ones. Breeding females and non-breeding adult males had 'preen ratios' close to unity when they interacted with each other, and second year males were allopreened by non-breeding adult females more often than they preened such females. No non-reciprocal allopreening interactions were observed between birds belonging to the same age, sex and social class (Table 3.3). However, a different picture arises when first year bird involvement is included in the analysis of non-reciprocal allopreening. Adult males were never involved in non-reciprocal allopreening with first year birds, but in all other interactions involving a first year bird and an older bird, the older bird exhibited greater active involvement (i.e. a preen ratio greater than one) (Table 3.3).

In contrast, reciprocal allopreening was evenly distributed amongst age and social classes: there were no significant differences in the involvement of different classes for five flocks (all $P > 0.50$); the sixth flock could not be compared since it contained only one pairing combination (Table 3.4).

DISCUSSION

In Jungle Babblers, allopreening is solicited mostly by the low-ranking individuals of the group (Gaston 1977), whereas in Redbilled Woodhoopoes the situation is reversed. The positive relationship between frequency of solicitation and social status in woodhoopoes suggests that this behaviour has developed beyond the

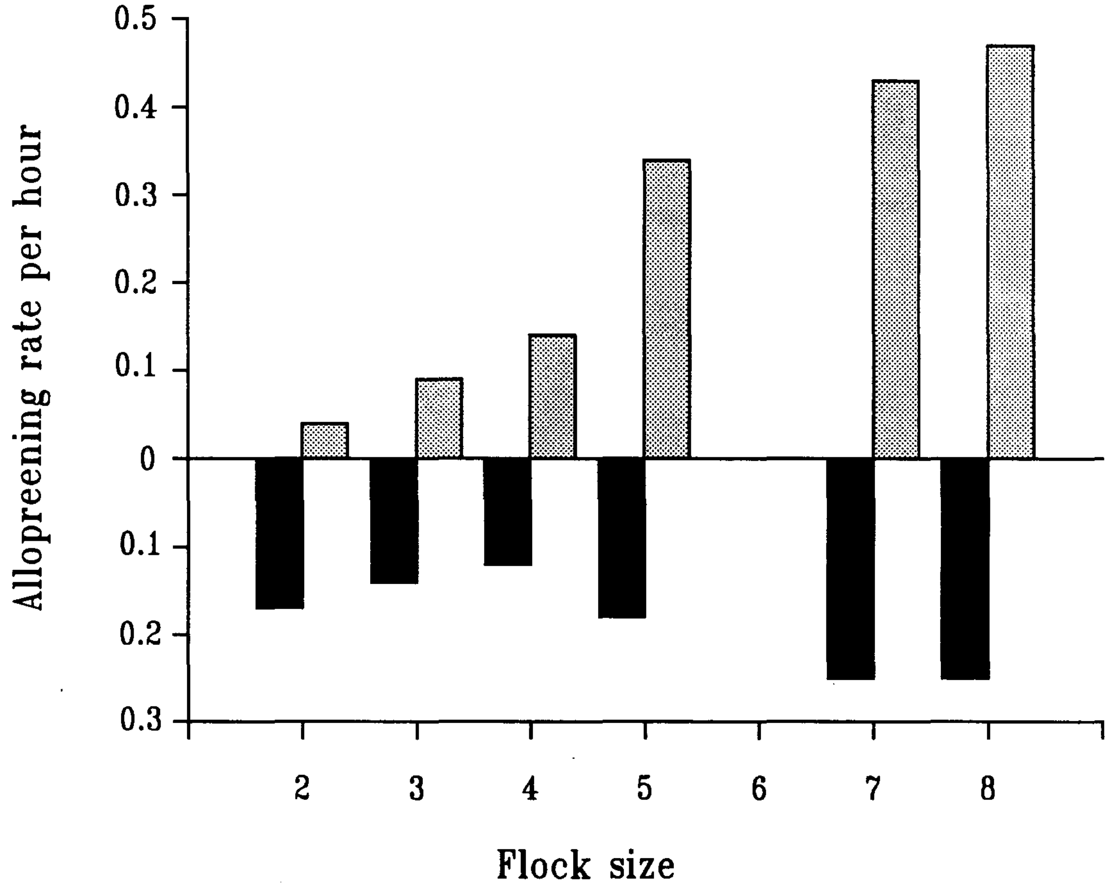

Figure 3.5. Mean frequencies of reciprocal (black) and non-reciprocal (stippled) allopreening by Redbilled Woodhoopoe breeding pairs in relation to flock size.

Table 3.3. Non-reciprocal 'preen ratios' of different Redbilled Woodhoopoe age and sex classes presented as a matrix; values > 1 represent more active than passive allopreening interactions (columns represent active and rows passive involvement).

	BR♂	BR♀	AD♂	AD♀	2Y♂	2Y♀	1Y♂	1Y♀
BR♂	-							
BR♀	0.5	-						
AD♂	0.4	1.0	*					
AD♀	0.4	0.3	0.6	-				
2Y♂	0.5	0.5	0.2	1.2	-			
2Y♀	0.5	0.3	0.6	0.5	0.3	*		
1Y♂	4.2	15.2	*	9.0	1.4	6.3	*	
1Y♀	3.4	14.5	*	8.4	1.4	6.0	0.8	-

* instances in which interactions were possible, but not observed

Table 3.4. The number of reciprocal allopreening interactions between Redbilled Woodhoopoes of different age and social classes and their frequency relative to the number of birds of each class within each flock (BR = breeders, AD = nonbreeding adults, 2Y = two year olds, 1Y = first years).

Flock	Interaction	C	N	N/C	X^2	
SP	BR : BR	1	8	8.00	-	
FT	BR : BR	1	6	6.00		
	BR : 1Y	2	10	5.00	0.126	*
EP	BR : BR	1	4	4.00		
	BR : 2Y	4	17	4.25		
	2Y : 2Y	1	3	3.00	0.313	*
KA	BR : BR	1	8	8.00		
	BR : 1Y	6	51	8.50		
	1Y : 1Y	3	19	6.33	1.359	*
NR	BR : BR	1	8	8.00		
	BR : AD	6	42	7.00		
	BR : 2Y	4	27	6.75		
	AD : AD	3	18	6.00		
	AD : 2Y	6	49	8.17		
	2Y : 2Y	1	4	4.00	3.041	*
TM	BR : BR	1	3	3.00		
	BR : AD	2	7	3.50		
	BR : 2Y	6	17	2.83		
	BR : 1Y	4	10	2.50		
	AD : 2Y	3	8	2.67		
	AD : 1Y	2	6	3.00		
	2Y : 2Y	3	8	2.67		
	2Y : 1Y	6	15	2.50		
	1Y : 1Y	1	2	2.00	2.052	*

C - number of possible pairing combinations
N - number of interactions observed
* $P > 0.50$

point where it merely suppresses (Gaston 1977) or induces (Katzir 1983) aggression, to the level where it serves as a mechanism for an individual to confirm and demonstrate its social status in the flock.

Allopreening is particularly prevalent in bird species where individuals are forced into close proximity, a situation which facilitates the transfer of ectoparasites from one individual to another (Cullen & Ashmole 1963; Harrison 1965). Redbilled Woodhoopoes roost communally at night in confined cavities throughout the year, sometimes using the same cavity for many months. This behaviour clearly promotes ectoparasite transfer. Higher levels of ectoparasite infestation following the breeding season may result from transfer of high parasite loads from birds which have spent the breeding season in the nest cavity. The higher incidence of non-reciprocal allopreening in winter could also have had some effect on ectoparasite loads, since the breeders, which were the major recipients during such interactions at that time of the year, showed lower ectoparasite loads than other classes. Both solitary scouting individuals that were caught had maximum indices of ectoparasite infestation, suggesting that one function of allopreening in woodhoopoes is the removal of ectoparasites. The high levels of infestation of four immature birds, in flocks without helpers, suggests additionally that breeding adults without helpers are unable to control the ectoparasite loads of their offspring as effectively as are larger groups, again pointing to the importance of allopreening in reducing ectoparasite loads.

Reciprocal allopreening was directed almost exclusively at the head and neck, the parts of the body which birds were unable to attend to themselves, and occurred at a relatively constant rate throughout the year. This suggests that a baseline allopreening frequency exists for effective ectoparasite removal and this function is satisfied by self-preening of accessible body parts and reciprocal allopreening of inaccessible parts; this is further supported by the even distribution of reciprocal allopreening between different age and social classes.

Among birds older than one year, females preened males, and younger birds older ones, more often than they themselves were preened. Subordinates may therefore communicate their social position to the rest of the flock by preening birds of higher social status. This may be important if one views the group as 'an intensely competitive arena' (Zahavi 1974), and if coalitions are considered an important factor in determining individual status (Sparks 1967; Seyfarth 1977). Non-reciprocal allopreening is beneficial to both preener and recipient: to the former in that it associates itself with a high-ranking bird, and to the latter for confirmation of its social status within the flock. Dominant individuals initiate such interactions by soliciting allopreening, whilst unsolicited non-reciprocal allopreening is initiated by subordinates. The high incidence of birds older than one year preening first year birds is best explained as a period in which young birds learn such behaviour (Appendix 1). Adult females show particularly high preen ratios in interactions with one year olds, displaying 'auntie behaviour' (*sensu* Ligon & Ligon 1978), in which they appear to be most interested in contact with the young, rather than in accruing any obvious functional benefit to themselves.

Non-reciprocal allopreening often was directed at body parts which the recipient was able to attend to itself and the frequency of occurrence of this behaviour changed seasonally. A peak of non-reciprocal allopreening occurred during the nonbreeding season. It is at this time that the rate of food provisioning to juveniles decreases rapidly (pers. obs), suggesting that, unless compensated for, flock unity of cooperative group-territorial species may be at its lowest during this 'weaning' period. Among Redbilled Woodhoopoes compensation for potential decreased group cohesion apparently is achieved, at least in part, through an increased frequency of non-reciprocal allopreening between flock members. A secondary consequence of the increased frequency of non-reciprocal allopreening during winter is a slight (but significant) reduction in ectoparasite loads.

Previously no differentiation was made between reciprocal and non-reciprocal allopreening. Failure to recognize differences between these two types of interactions may have obscured or distorted interpretations of allogrooming or -preening in many studies.

The inability of Redbilled Woodhoopoes to reach a large portion of the body as a result of having a long bill, together with regular opportunities for ectoparasite transfer through close physical contact between members in communal roost cavities, are conditions that might promote the evolution of allopreening. Selection for individuals which allowed their individual distance to be violated may have occurred. It is suggested that allopreening initially was selected for because of the functional benefits of ectoparasite removal, and in the Redbilled Woodhoopoe this was achieved by means of reciprocal allopreening. Thereafter allopreening may have gained increasing social significance as the birds' social system became more complex, as evidenced by seasonal patterns of non-reciprocal allopreening, and the increasing relative frequency of non-reciprocal allopreening by the breeding pair with increasing flock size.

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CHAPTER 4

DOMINANCE AND SOCIALITY: BALANCING CONFLICT AND COOPERATION

SUMMARY

Detailed behavioural observations were made of six free-ranging Redbilled (Green) Woodhoopoe *Phoeniculus purpureus* flocks in the eastern Cape Province of South Africa. Redbilled Woodhoopoes are group-territorial birds that live in flocks throughout the year. Flocks contain two to 12 birds, but only one breeding pair. Nonbreeding flock members, usually relatives of one or both breeders, participate fully in all flock activities except breeding. Dominance hierarchies were constructed on the basis of individual involvement in displays and other behavioural interactions, such as allopreening, allofeeding, inititation of movements, and perch site displacement. The breeding pair dominate all other individuals: among other flock members, males dominate females and old birds dominate younger ones. The breeding male dominates the breeding female, but also ensures by his presence that nonbreeding males act submissively to the breeding female. High social rank is correlated with the probability of achieving breeding status. It is suggested that apparently altruistic acts, such as allopreening and allofeeding, function primarily to promote selfish reproductive interests in terms of achieving high social status. The achievement or retention of reproductive status is the primary function of dominance hierarchies in group-territorial societies.

INTRODUCTION

Group-territorial social organizations are widespread among birds (for review see Brown 1987). However, few detailed studies of social relationships within free-living groups exist (Gaston 1977; Zack 1986), and the apparent paradox of cooperation and conflict within the same social unit is poorly understood (Barkan *et al.* 1986, Carlisle & Zahavi 1986, Jamieson & Craig 1987).

Dominance has been demonstrated to result from agonistic behaviour expressed in the competition for resources. Some workers relate dominance to differential success in exploiting limited food supplies (Wrangham 1980; Frank 1986). Among communal species, dominance has been related to reproductive interests of the various group members (Woolfenden & Fitzpatrick 1977; Emlen 1978, 1982; Stallcup & Woolfenden 1978).

Redbilled Woodhoopoes *Phoeniculus purpureus* are group-territorial birds which inhabit a wide range of woodland types across a broad Afrotropical range (Ligon & Ligon 1978). They live throughout the year in flocks of two to 12 birds which contain only a single breeding pair. Other flock members, usually relatives of one or both breeders, are full participants in all other flock activities. Dispersal, although infrequent, involves both sexes (Chapter 2).

In this paper I describe the social relationships of Redbilled Woodhoopoes with respect to: (1) the relative importance of displays and behavioural interactions in determining dominance hierarchies; and, (2) the function of the dominance hierarchy in terms of how members of different social classes balance cooperation with conflicting selfish interests.

METHODS

Observations of Redbilled Woodhoopoes were made in two areas of the eastern Cape Province of South Africa; one comprising 33 km^2 of coastal and riverine forest at Morgan's Bay (32°43'S 28°19'E), and the other comprising 45 km^2 of valley bushveld in the Kubusi River valley (32°32'S 27°47'E) (Chapter 1).

Between January 1976 and December 1985 more than 2500 hours of observation were made on 60 different flocks, of which all individuals in 40 flocks were uniquely colour-ringed. Each group was followed for at least 10 hours in each month of the year. Between 1986 and 1988, six flocks, of differing composition, were studied intensively. Only data obtained from observations on these flocks are used in analyses of displays which are discussed in terms of social status and age; otherwise data from all flocks are used.

The linearity (where A dominates B and C, and B dominates C) of the ranking order in each social unit's hierarchy, determined by relative frequency of intraspecific perch site displacement (PSD), was calculated using both Landau's index (h) (Landau 1951) and Kendall's coefficient (K) (Appleby 1983).

The relative frequency of interactions between different age and sex classes was compared. Because different numbers of individuals from the various classes occurred in different social units, observed interaction frequencies were compared with expected frequencies for each class using the formula derived by Barkan *et al.* (1986) from Altmann & Altmann (1977). Heterogeneity was tested using the chi-squared statistic.

Behaviour patterns: description and analysis

During allofeeding, adult and immature birds which are old enough to forage for themselves feed each other: this behaviour is unrelated to breeding. The social status, age and sex of both active and passive participants in allofeeding were recorded. Breeder/breeder and adult/juvenile interactions were excluded from analysis of the display, as it was difficult in these instances to distinguish between allofeeding, courtship feeding and provisioning of juveniles.

An attempt was made to determine whether initiation of flock movements by individuals was related to their age, sex or social status. An initiation of movement was only considered as such when it was preceded by mobilization vocalizations. A movement was defined as being over a distance greater than 30 m, and when the entire flock followed.

Aggressive displacement behaviour occurred when one bird flew at another and forcibly displaced the latter from its perch. During such active PSD the sex, age and social status of each displacing and displaced individual were recorded. A 'perch site displacement ratio' was calculated as the number of times that individuals of one social class displaced other birds or were displaced. Birds less than three months old were excluded from these analyses, because their clumsy actions soon after fledging regularly forced older birds off their perches, but were unrelated to social behaviour *per se*.

Experimental removal of individuals

Individuals were removed from six flocks at a site 15 km from the Kubusi River Valley study area, (in the Kei River Valley 32°31'S 27°58'E). One breeder was removed from each of four flocks (two of each sex in total) in which at least one subordinate of the same sex was present. In a further two flocks, where no subordinates of the same sex were present, one breeder was removed. The composition of manipulated flocks was determined three months later, immediately prior to the breeding season.

RESULTS

Allofeeding behaviour

Most allofeeding behaviour involved breeders passing food to nonbreeding adult and second-year birds of the same sex. Nonbreeding adult males passed food to other nonbreeding adult and second-year males, and nonbreeding adult females passed food to second-year females (Table 4.1). The only exceptions to this order were five cases (5.6%) in which nonbreeding adult males fed the breeding female. This latter behaviour occurred only in the absence of the breeding male. Allofeeding behaviour was almost entirely restricted to the nonbreeding season (Figure 4.1).

Woodhoopoes usually ensured that most or all other flock members watched the transfer of food to subordinates, as in Arabian Babblers *Turdoides squamiceps* (Carlisle & Zahavi 1986). During instances where a food item was offered to a subordinate and there was no audience, the item would be withdrawn from the subordinate's reach and re-offered several times. If this still failed to attract an audience, the dominant bird would eat the food item itself.

Leadership behaviour

The contribution of the breeding pair to the initiation of movements was significantly greater than expected (male: $X^2 = 288.5$; 1 df; $P < 0.001$. female: $X^2 = 12.7$; 1 df; $P < 0.001$) (Table 4.2). In all classes males initiated movements more often than females and older birds more often than younger ones (Table 4.3).

Table 4.1. Frequency of food-passing between different social classes of Redbilled Woodhoopoes; the active participant is always mentioned first.

Social classes			*Comb. (A)	**Frequency (B)	B/A
BR♂	:	AD♂	2	19	9.50
	:	AD♀	2	2	1.00
	:	2Y♂	3	16	5.33
	:	2Y♀	4	1	0.25
BR♀	:	AD♂	2	0	0
	:	AD♀	2	8	4.00
	:	2Y♂	3	1	0.33
	:	2Y♀	4	10	2.50
AD♂	:	AD♂	1	10	10.00
	:	AD♀	2	1	0.50
	:	2Y♂	2	9	4.50
	:	2Y♀	2	0	0
AD♀	:	2Y♂	2	0	0
	:	2Y♀	3	12	4.00
2Y♂	:	2Y♀	4	1	0.25
2Y♀	:	2Y♀	1	0	0

* the number of possible pairing combinations between the classes concerned

** number of interactions observed

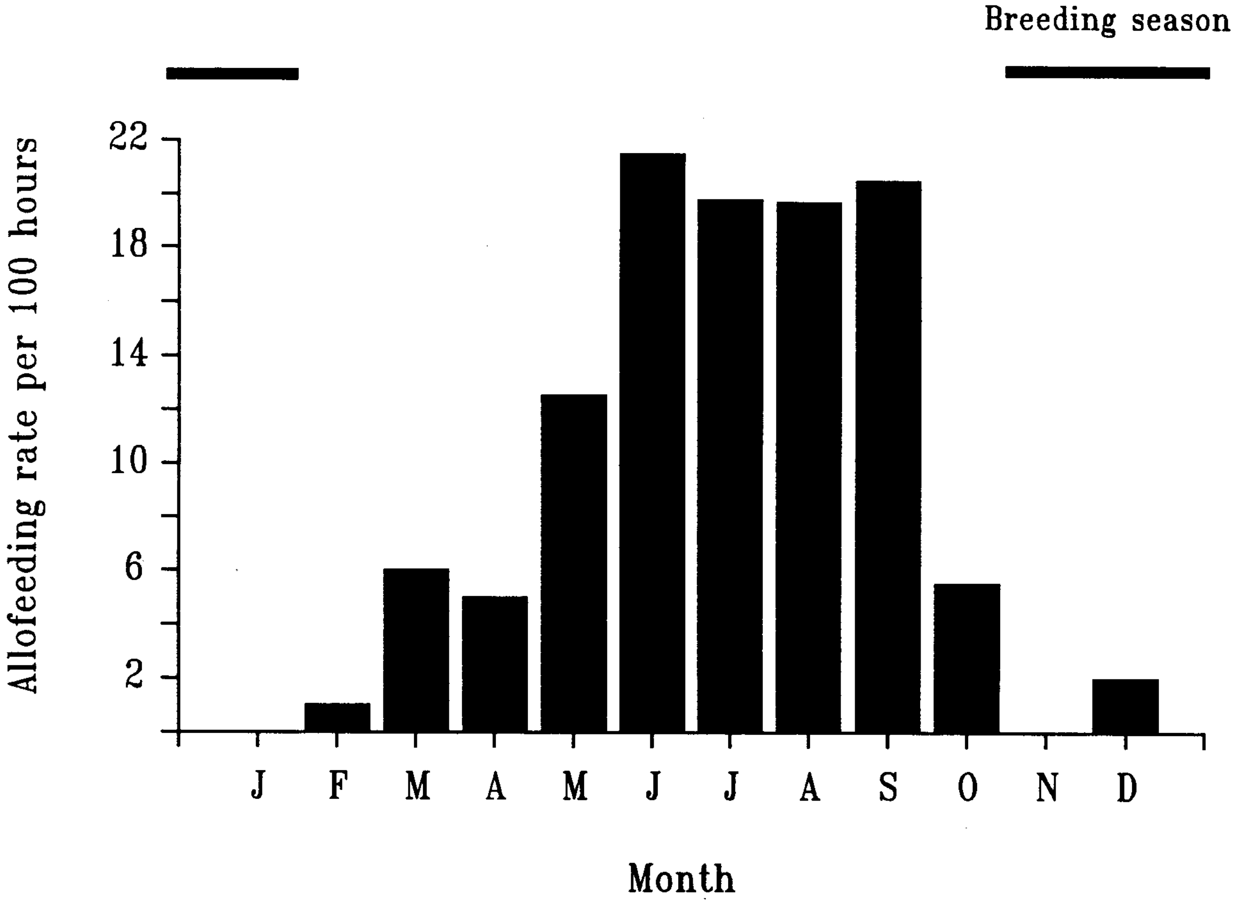

Figure 4.1. Seasonality of allofeeding frequency in six Redbilled Woodhoopoe flocks (first year birds are excluded).

Table 4.2. Contribution of the breeding pair to the initiation of movement in Redbilled Woodhoopoe flocks of varying size.

Flock	Breeding pair contribution	
size	Observed	Expected
3	78	54.0
4	58	49.5
5	124	55.2
7	47	26.6
8	32	13.8

* $X^2 = 137.5$; 5 df; $P < 0.001$

Table 4.3. Summary of the contribution of different age, sex and social classes to the initiation of flock movement by Redbilled Woodhoopoes.

Class	Hours of observation (A)	Frequency (B)	B/A (X 100)
Br♂	1160	264	22.8
Br♀	1160	140	12.1
Ad♂	444	33	7.4
Ad♀	396	14	3.5
2Y♂	581	39	6.7
2Y♀	755	23	3.0
<1Y♂	835	16	1.9
<1Y♀	427	2	0.5

Perch site displacement behaviour

Perch site displacement behaviour usually was performed at or near favoured feeding sites or when birds were perched close to the nest/roost cavity entrance. In many instances of PSD behaviour, the displacer immediately searched for food and offered the item to the displaced bird in an elaborate display of offering and withholding.

Male breeders showed by far the highest intraspecific 'PSD ratio' (Table 4.4). Males displaced other males as frequently as they displaced females ($X^2 = 0.09$; 1 df; $P > 0.7$; $n = 88$), but females displaced other females significantly more frequently than they displaced males ($X^2 = 4.5$; 1 df; $P < 0.05$; $n = 16$). Of all PSD behaviour, males were the active participants significantly more frequently than females ($X^2 = 24.92$; 1 df; $P < 0.001$; $n = 104$). Frequency per individual of PSD did not vary with flock size: consequently, absolute frequency of PSD increased with increasing flock size (Figure 4.2).

Allopreening behaviour

Reciprocal allopreening, when two birds preened each other simultaneously or in succession, was directed mainly at body parts that birds were unable to reach themselves and occurred at a constant rate throughout the year. The frequency of involvement by the breeding pair remained constant independent of flock size. Non-reciprocal allopreening, when one bird remained a passive participant, was directed at all parts of the body and was seasonal in intensity. The rate at which the breeding pair was involved increased with increasing flock size (Chapter 3).

Table 4.4. Summary of the intraspecific perch site displacement (PSD) ratios (displacer: displaced) by different Redbilled Woodhoopoe social classes.

Social class	Displacer	Displaced	Ratio
BR♂	62	3	20.67
BR♀	10	15	0.67
AD♂	17	15	1.13
AD♀	6	12	0.50
2Y♂	8	13	0.62
2Y♀	1	24	0.04
<1Y♂	1	21	0.05
<1Y♀	0	2	0

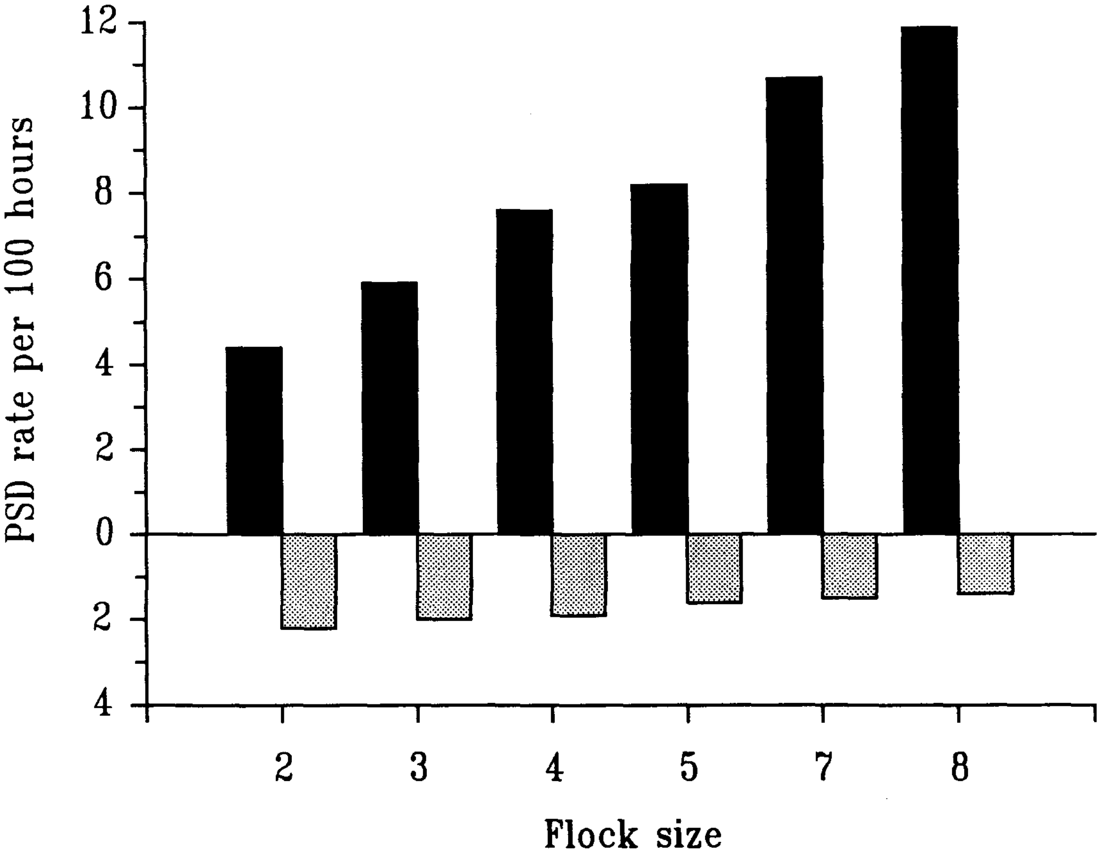

Figure 4.2. Rate of perch site displacement (PSD) by individuals (stippled bars) and within flocks (black bars) as a function of flock size.

Dominance related to age and sex

Little sign of overt intraspecific aggression was apparent amongst Redbilled Woodhoopoes and intraspecific PSD behaviour was the highest level of aggression observed. Social hierarchies were constructed, using PSD behaviour as a measure of dominance, for six flocks. Using the wins greater than losses criterion, all but one of the hierarchies had indices of linearity greater than 0.7 (Table 4.5). However, no hierarchy in a group of less than six individuals can have a statistically significant level of linearity (Appleby 1983). The two flocks with more than six individuals both had values which were significant at the 0.05 level or better. Hierarchies constructed on the basis of individual involvement in behaviour such as allopreening (Chapter 3), allofeeding, initiation of movements, and perch site displacement indicate that individuals have different rankings for different behavioural acts and displays (Table 4.6). However, when the mean ranks are calculated on the basis of the four types of behavioural interactions, all five flocks containing three or more members showed a clear pattern in which the breeding pair dominated all other classes : for the rest, males dominated females and older birds dominated younger ones. The breeding male dominated the breeding female, but also ensured by his presence that nonbreeding males did not engage in acts which dominated the female breeder.

Experimental removal of individuals

Both male and female breeding vacancies, created by the experimental removal of individuals, were filled by the highest ranking subordinate of the required sex from within the flock (Table 4.7). In cases where no successor was present to fill such a vacancy from within the flock, a single immigrant from a neighbouring flock assumed breeder status within seven days of the manipulation.

Table 4.5. Landau's index (h) and Kendall's coefficient (K) of linearity in six Redbilled Woodhoopoe social units according to PSD observations.

Social Unit	N	Wins	>	Losses
		h		K
SP	2	1.000		1.000
FT	3	1.000		1.000
EP	4	1.000		1.000
KA	5	0.700		0.657
NR	7	0.964		0.733
TM	8	0.798		0.881
$\bar{x}$	4.8	0.910		0.879

Table 4.6. Comparisons of status ranking within six Redbilled Woodhoopoe flocks based on allopreening, allofeeding, leadership and perch site displacement (PSD).

Flock	Allopreening	Allofeeding	Leadership	PSD	Mean
SP:					
BR♂	2	1	1	1	1.25
BR♀	1	2	2	2	1.75
FT:					
BR♂	1	1	1	1	1.00
BR♀	2	2	2	2.5	2.13
<1Y♂	3	3	3	2.5	2.87
EP:					
BR♂	2	1	1	1	1.25
BR♀	1	2	2	3	2.00
2Y♂	3	3	3	2	2.75
2Y♀	4	4	4	4	4.00
KA:					
BR♂	2	1	1	1	1.25
BR♀	1	2	2	2	1.75
<1Y♂	3	3	3.3	3.5	3.20
<1Y♂	4	4	3.3	3.5	3.70
<1Y♀	5	5	3.3	5	4.58
NR:					
BR♂	1	1	1	1	1.00
BR♀	3	2	2	3	2.50
AD♂	2	3	3	2	2.50
AD♂	4	4	4	4.5	3.12
AD♀	7	6	6	6	6.25
2Y♂	5	5	5	4.5	4.88
2Y♀	6	7	7	7	6.75
TM:					
BR♂	1	1	1	1	1.00
BR♀	2.5	2	2	3	2.37
AD♀	2.5	3	3	2	2.63
2Y♂	5	4	4	4	4.25
2Y♀	4	5.5	6	5.5	5.25
2Y♀	7	5.5	5	7	6.12
<1Y♂	6	7	7.5	5.5	6.50
<1Y♀	8	8	7.5	8	7.88

Kendall coefficients of concordance (W) for the four rankings:

SP:	$W = 0.50$,	$X^2 = 1.000$,	1 df,	$P < 0.50$
FT:	$W = 0.89$,	$X^2 = 7.125$,	2 df,	$P < 0.05$
EP:	$W = 0.83$,	$X^2 = 9.900$,	3 df,	$P < 0.02$
KA:	$W = 0.73$,	$X^2 = 12.194$,	4 df,	$P < 0.02$
NR:	$W = 0.94$,	$X^2 = 23.063$,	6 df,	$P < 0.001$
TM:	$W = 0.91$,	$X^2 = 25.958$,	7 df,	$P < 0.001$

Table 4.7. Pre- and post-manipulation composition of six Redbilled Woodhoopoe flocks in which breeding adults were removed (BR= breeding adult; AD= nonbreeding adult; 2Y= second year; 1Y= first year).

FLOCK 1			**FLOCK 2**		
JUL '87		OCT '87	JUL '87		OCT '87
BR♂	**remove**		**BR♂**	**remove**	
AD♂	------	BR♂	2Y♂	------	BR♂
BR♀	------	BR♀	2Y♂	**emigr.**	
2Y♀	------	2Y♀	BR♀	------	BR♀
			AD♀	------	AD♀
			1Y♀	**dead**	

FLOCK 3			**FLOCK 4**		
BR♂	------	BR♂	BR♂	------	BR♂
2Y♂	------	2Y♂	2Y♂	------	2Y♂
BR♀	**remove**		1Y♂	------	1Y♂
2Y♀	------	BR♀	**BR♀**	**remove**	
1Y♀	------	1Y♀	AD♀	------	BR♀
			1Y♀	------	1Y♀

FLOCK 5			**FLOCK 6**		
BR♂	**remove**		BR♂	------	BR♂
	------	**BR♂immigr.**	AD♂	------	AD♂
BR♀	------	BR♀	AD♂	------	AD♂
AD♀	------	AD♀	**BR♀**	**remove**	
1Y♀	------	1Y♀		------	**BR♀ immigr.**

remove - experimental removal of breeders
immigr. - immigration to fill breeding vacancy
emigr. - emigration (dispersal) from flock
dead - death by natural causes

DISCUSSION

The significance of social interactions

Ligon & Ligon (1978) described some of the behavioural interactions and displays performed by Redbilled Woodhoopoes and proposed some interpretations; however, they provided no quantitative analysis of individual displays.

It has been suggested that allofeeding behaviour serves a communicative function whereby individuals demonstrate their dominance over others by passing food to them (Arabian Babbler, Zahavi 1977; Carlisle & Zahavi 1986; Southern Ground Hornbills *Bucorvus leadbeateri*, Kemp & Kemp 1980). Ligon & Ligon (1983) propose that dominant Redbilled Woodhoopoes develop ties with younger ones whose cooperation could be critical to their own future reproductive success.

Allofeeding amongst woodhoopoes occurred mainly between birds of the same sex and older birds fed younger ones almost exclusively, indicating that the direction of food passing was from dominant birds to subordinates. Under the tenets of kin selection theory, the primary function of allofeeding a related subordinate would not be display, but direct investment. Kin selection does not adequately explain instances in which unrelated Redbilled Woodhoopoes partake in allofeeding, nor those in which food is offered and then withheld. Since dispersal involves only single birds (Chapter 2) and the direction of food passing within the social hierarchy remains constant, there is little support for the hypothesis that allofeeding represents reciprocal altruism (see Ligon & Ligon 1983). These observations support Carlisle & Zahavi's (1986) explanation that the main purpose of allofeeding in group-territorial societies is to communicate the social status of an individual to the rest of the flock.

Displays of offering and withholding food, similar to those performed by Redbilled Woodhoopoes, are performed by Southern Ground Hornbills. In this species, withholding food was interpreted as assertion of dominance (Kemp & Kemp 1980). I suggest that the principal motivation of allofeeding behaviour is to display dominance and, that of withholding food, to attract an audience. This provides further support to the idea that allofeeding serves to communicate social status.

From the large contribution that breeders made to initiation of flock movements, it is evident that they play a major role in influencing flock activities. A small difference in leadership contribution between nonbreeding adult and second-year males provides further evidence for the male dominance hierarchy being more strongly contested than the female hierarchy: in females competition apparently only develops later in life (*sensu* Chapter 2).

Displacement from perch sites has been used as a measure of dominance in other studies (Woolfenden & Fitzpatrick 1977; Birkhead 1981; Barkan *et al.* 1986). Displacement from perch sites around roosts, when most or all flock members were watching, probably served to confirm and communicate intraflock relationships. This was particularly evident during displacement from feeding sites, where allofeeding often followed and confirmed the dominance demonstrated by displacement. It is proposed that displacements from perch sites were usually performed with the purpose of confirming or establishing relationships within flocks, and not as acts of immediate personal gain.

Allopreening by Redbilled Woodhoopoes serves multiple functions (Chapter 3). Reciprocal allopreening reduces parasite burdens, while non-reciprocal allopreening and allopreening 'orgies' serve to confirm social status.

Communication of social status to other group members is an important function of social interactions. Among Redbilled Woodhoopoes, at least four types of behaviour function in this way. High social rank is correlated with the probability of achieving breeding status. The establishment of dominance hierarchies is a complex social phenomenon related to the individual interests of group members. Retention of young in the natal flock is inevitable because dispersal opportunities are limited by the availability of roost cavities (Ligon & Ligon 1978, 1988; Chapters 1 & 2). The significance of social interactions therefore revolves around both the individual and the flock. Although flocks appear to be well integrated, harmonious social units, considerable effort is expended in achieving personal gains which attend a high social ranking. The high degree of behavioural dominance that breeding males exert over all other males prevents the latter from breeding, without expelling them from the flock.

Dominance in group-territorial societies

Birds in which there is retention of young, group foraging and territorial defence, and cooperative breeding, have been classed as 'advanced subsocial' (Wilson 1975). The greater the cohesiveness and permanence of the social group, the more complex the dominance order becomes. Most recent studies have reported breeders to dominate nonbreeders, which are usually the younger individuals (e.g. Greycrowned Babbler *Pomatostomus temporalis*, King 1980; Pukeko *Porphyrio p. melanotus*, Craig 1979, Jamieson & Craig 1987; Arabian Babbler, Carlisle & Zahavi 1986). Adult dominance over young has also been widely reported for species which do not breed cooperatively (Wilson 1975; Gauthreaux 1978).

Several authors have reported high levels of aggression among the juveniles of group-territorial species in which there is little aggression among adults (Acorn Woodpeckers *Melanerpes formicivorus*, MacRoberts & MacRoberts 1976; Jungle Babblers, Gaston 1977; Florida Scrub Jays *Apelocoma coerulescens*, Woolfenden & Fitzpatrick 1977). Overt aggression in group-living societies should be suppressed on the grounds of being counterproductive. However, during inter-territorial encounters, aggression may be beneficial, if only rarely and for short duration. I suggest that intra-flock aggression is suppressed, to a large extent by adults, to reduce predation risks which may arise from overt within-group conflict. The aggressive behaviour of juveniles may be moulded into subtle displays, by which dominance relationships are established through cultural transmission. Cultural transmission has been considered a possible way in which Redbilled Woodhoopoes pass 'new' behaviour patterns on to other flock members (Appendix 1). Formation of dominance relationships between individuals may take long in some species and could be related either to a species' ability to pass such behaviour on to offspring, or to the complexity of its mating system. However, the rare use of overt within-group aggression is primarily to confirm status between residents and establish the status of unfamiliar individuals. This should serve the purpose of maintaining the integrity of the hierarchy.

Dominance hierarchies in group-living species have typically been interpreted to be the result of intraspecific competition for limited food resources (Wrangham 1980; Frank 1986). However, for Redbilled Woodhoopoes, any resultant enhanced access to food may be of secondary, short-term benefit. This is evidenced in observations of allofeeding, where dominant individuals offer food to subordinates. It is suggested that such apparently altruistic acts are performed primarily to promote individual interests in terms of higher social rank. There was no correlation between body mass and dominance status within either of the sexes (males: n= 43; females: n= 56); nor was there a correlation between dominance and survivorship for 35 individuals followed for two to three years after fledging (unpubl. data). I therefore propose that the function of woodhoopoe dominance hierarchies is not related to differential access to food resources.

Some evidence exists that achievement or retention of reproductive status is a basic, long-term motivation for the existence of dominance hierarchies in group-territorial societies (Woolfenden & Fitzpatrick 1977; this study). It is important for a woodhoopoe to establish itself as high in the dominance hierarchy as possible, because the highest-ranking individual invariably fills any breeding vacancy within the flock. Hierarchies ensure that dominance relationships are well-defined among potential competitors (for breeding status), and thereby minimize disruption to flock cohesion upon the death of a breeder. At this time, within-group conflict could lead to either disintegration of the flock, or attract potential competitors from neighbouring flocks (unpubl. data). If competition for the breeding vacancy arose at the time of the breeder's death, the resultant delay in occupancy of the breeding vacancy would increase the likelihood of competition from unrelated birds. The existence of a dominance hierarchy therefore allows immediate occupation of a breeding vacancy, hence abating competition from outsiders. I suggest that the frequent inheritance of breeding status by an individual related to the dead breeder can be viewed as one consequence of a clearly defined dominance hierarchy. The establishment of such hierarchies is therefore adaptive in the context of the direct fitness component of kin selection.

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CHAPTER 5

BEHAVIOURAL MAINTENANCE OF GROUP TERRITORIALITY

SUMMARY

Behavioural observations were made of six free-ranging Redbilled (Green) Woodhoopoe *Phoeniculus purpureus* flocks in the eastern Cape Province of South Africa. Redbilled Woodhoopoes are group-territorial birds that live in flocks containing two to 12 birds, but only one breeding pair. Nonbreeding flock members participate fully in all flock activities except breeding. Rally displays serve the purposes of both advertising breeding vacancies to neighbouring flocks, and of promoting group cohesion by inciting concerted aggression among flock members. The function of flag-waving displays revolves around both individual and group interests: it communicates social rank to conspecifics and promotes group cohesion among flock members. Group cohesion is particularly important in cases where breeding opportunities are limited. I suggest that the rally and flag-waving displays serve as the mechanism whereby within-group conflict is reduced, and successful maintenance of the group territory is achieved.

INTRODUCTION

Group-territorial social organizations are widespread among birds (reviewed by Brown 1987). It is likely that group-territorial behaviour evolved in some species through prolonging the period during which offspring remained in the natal territory (Brown 1974). Group living is believed to be the result of either habitat saturation, in the sense that no suitable habitat is available for a nonbreeder to survive and breed on its own (Emlen 1982; Brown 1987), or that the benefits attributable to philopatry exceed those of dispersal and independent breeding (Stacey & Ligon 1987).

It is assumed that parents could drive their offspring out of the territory, since dominance within groups is usually related to age (Woolfenden & Fitzpatrick 1977; Barkan *et al.* 1986; Chapter 4). However, parents cannot prevent their offspring from leaving the natal territory.

In this chapter I describe the social relationships of Redbilled Woodhoopoes with respect to group-territorial displays. I then consider how these behavioural mechanisms contribute to the maintenance of both group cohesion and group territory.

METHODS

Observations of Redbilled Woodhoopoes were made in two areas of the eastern Cape Province of South Africa; one comprising 33 km^2 of coastal and riverine forest at Morgan's Bay (32°43'S 28°19'E), and the other comprising 45 km^2 of valley bushveld in the Kubusi River valley (32°32'S 27°47'E) (Chapter 1). Observations were made at irregular intervals between January 1976 and December 1985; between January 1986 and March 1988, six flocks, of differing composition, were studied intensively. More than 2500 hours of observation were made on 60 different flocks of which all individuals in 40 flocks were uniquely colour-ringed. The methods of observation are described in Chapter 4.

The relative frequencies of interactions between different age and sex classes were compared. Because different numbers of individuals from the various classes occurred in different social units, observed interaction frequencies were compared with expected frequencies for each class using the formula derived by Barkan *et al.* (1986) from Altmann & Altmann (1977). Heterogeneity was tested using the chi-squared statistic.

Behaviour patterns: description and analysis

The rally display is a territorial display and involves most or all flock members cackling vigorously whilst raising and lowering their tails and swaying their bodies back and forth in a serpentine manner (Ligon & Ligon 1978a). For each rally observed, duration, and, where possible, cause were recorded. Duration was defined as extending from the first to the last flock rally, with no more than 150 seconds of silence between individual rallies.

The flag-waving display occurs occasionally during territorial encounters, and involves one or more flock members carrying an object in the bill tip and waving it vigorously back and forth whilst rallying (Ligon & Ligon 1978a). The social status and sex of flag wavers were recorded, in addition to the nature of the flag, and the position that the flagwaver took in relation to (1) its own flock and (2) the cause of the display. Occasionally flags were passed between flock members: the social status and sex of each individual involved in the sequence were recorded.

Intraspecific perch site displacement (PSD) was considered to be important in the establishment and maintenance of woodhoopoe dominance hierarchies (Chapter 4). Thus, for the purposes of this chapter, only aggressive interspecific PSD was recognized, when one bird flew at, and forcibly displaced a heterospecific from its position. During such active PSD, displacing individuals were categorized either as first year or adult birds. The species of the displaced individual was recorded. A 'perch site displacement rate' was calculated as the number of times that individuals of each age class actively displaced birds of other species per observation hour.

Experimental removal of individuals

Individuals were removed from six flocks at a site 15 km from the Kubusi River Valley study area, (in the Kei River Valley 32°31'S 27°58'E), to monitor restructuring of flocks and/or formation of new dominance hierarchies within flocks (Chapter 4).

One breeder was removed from each of four flocks (two of each sex in total) in which at least one subordinate of the same sex was present. In a further two flocks, where no subordinates of the same sex were present, one breeder was removed (Chapter 4). After experimental removal of flock members from these flocks, the frequency of rallies was recorded and compared to that of undisturbed flocks.

RESULTS

Rally displays

The duration of rally displays increased significantly with flock size (Kruskal-Wallis ANOVA: $H = 59.6$; 5 df; $P < 0.05$) (Figure 5.1). Intraspecific rallies were directed at neighbouring flocks on territory boundaries, and at intruding woodhoopoe scouts (Chapter 2). Older birds often bowed and cackled to younger

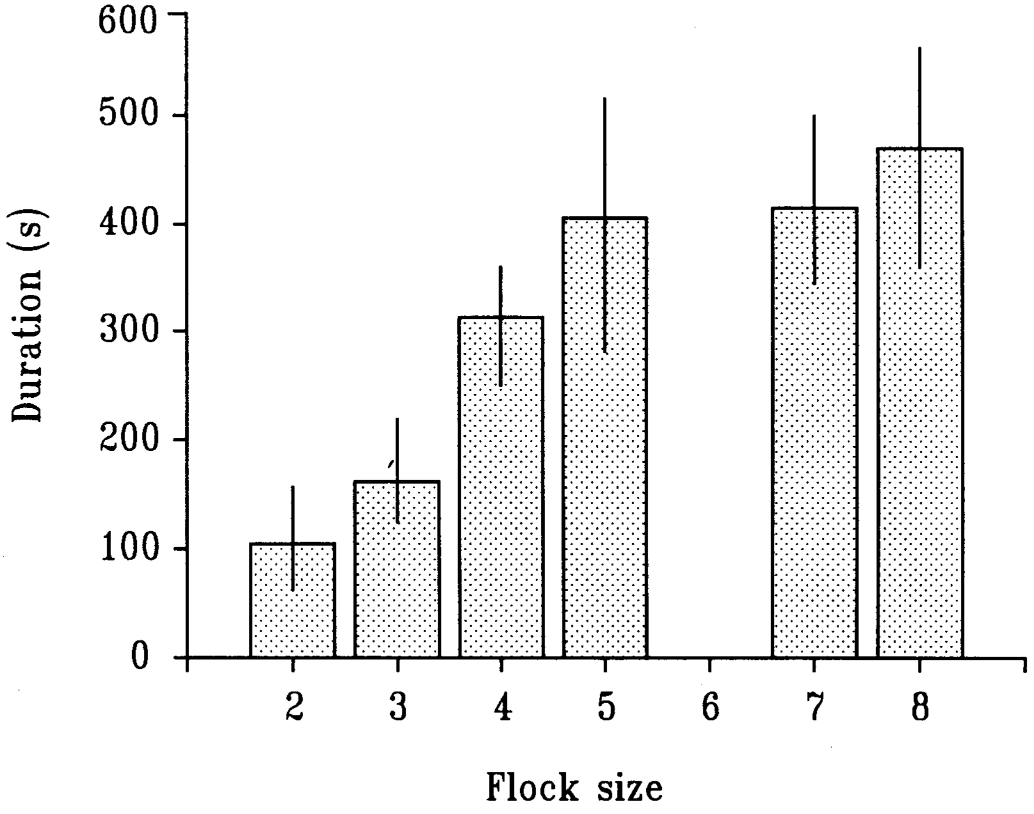

Figure 5.1. Mean (+ 1 S.D.) durations of rally displays of Redbilled Woodhoopoe flocks of different sizes.

birds until the latter participated in the display. Intraspecific territorial disputes were dominated significantly more by larger flocks than by smaller ones ($X^2 = 32.9$; 1 df; $P < 0.001$; $n = 722$). Interspecific rallies were most frequent immediately before and after breeding, whereas intraspecific rallies occurred at greatest frequency during the non-breeding season (Figure 5.2a).

There were obvious differences in the causes of interspecific rallies before and after the breeding season (Figure 5.2b). At the onset of breeding, interspecific rallies were directed mainly at other hole-nesting species in attempts to obtain or retain possession of breeding sites, but were directed mainly at aerial predators shortly after the breeding season, when juveniles were still poor fliers.

Flocks in which breeders of either sex had been removed, and which contained subordinate birds of the same sex, rallied significantly more frequently than undisturbed flocks ($X^2 = 9.67$; 1 df; $P < 0.01$). However, the rally rate decreased rapidly with time. Manipulated flocks which contained no replacements rallied significantly more frequently than did manipulated flocks containing replacements ($X^2 = 25.16$; 1 df; $P < 0.001$), and the rally rate was maintained at a high (almost constant) level for at least six hours after manipulation (Figure 5.3).

Flag-waving displays

Flag waving was directed not only at other woodhoopoe flocks, but also at snakes, other birds and mammals. Bark and lichens were used as flags most often (62%; n= 154), while leaves, twigs, berries and insects were used on other occasions.

Three types of flag-waving displays were recognized, dependent on the position of the flag waver relative to other flock members. The back-to-back display, in which flock members faced outwards (Figure 5.4a), was performed only during

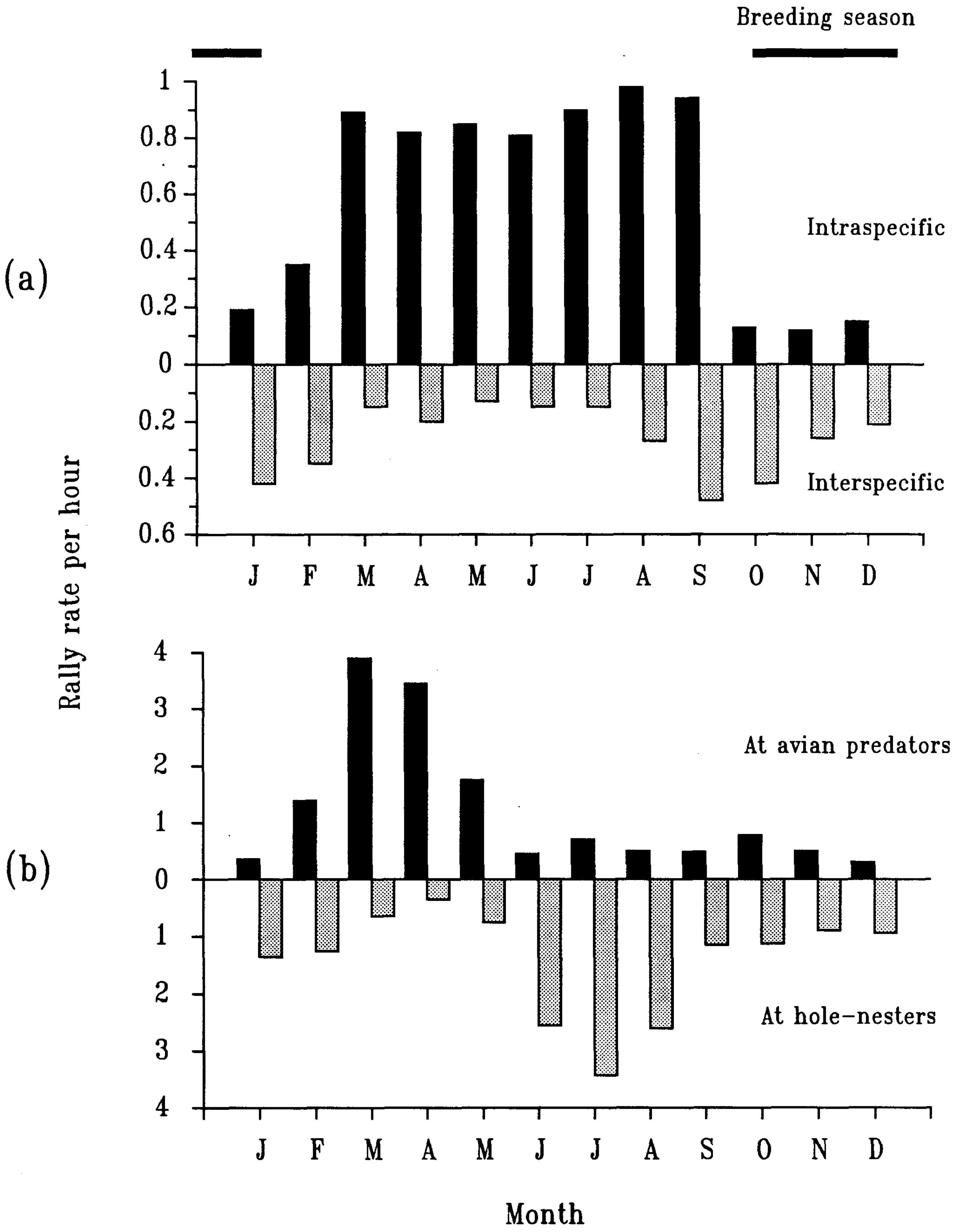

Figure 5.2. Seasonality of (a) intraspecific and interspecific rally rates (per hour) and, (b) interspecific rally rates directed at hole-nesters and avian predators respectively, of six Redbilled Woodhoopoe flocks.

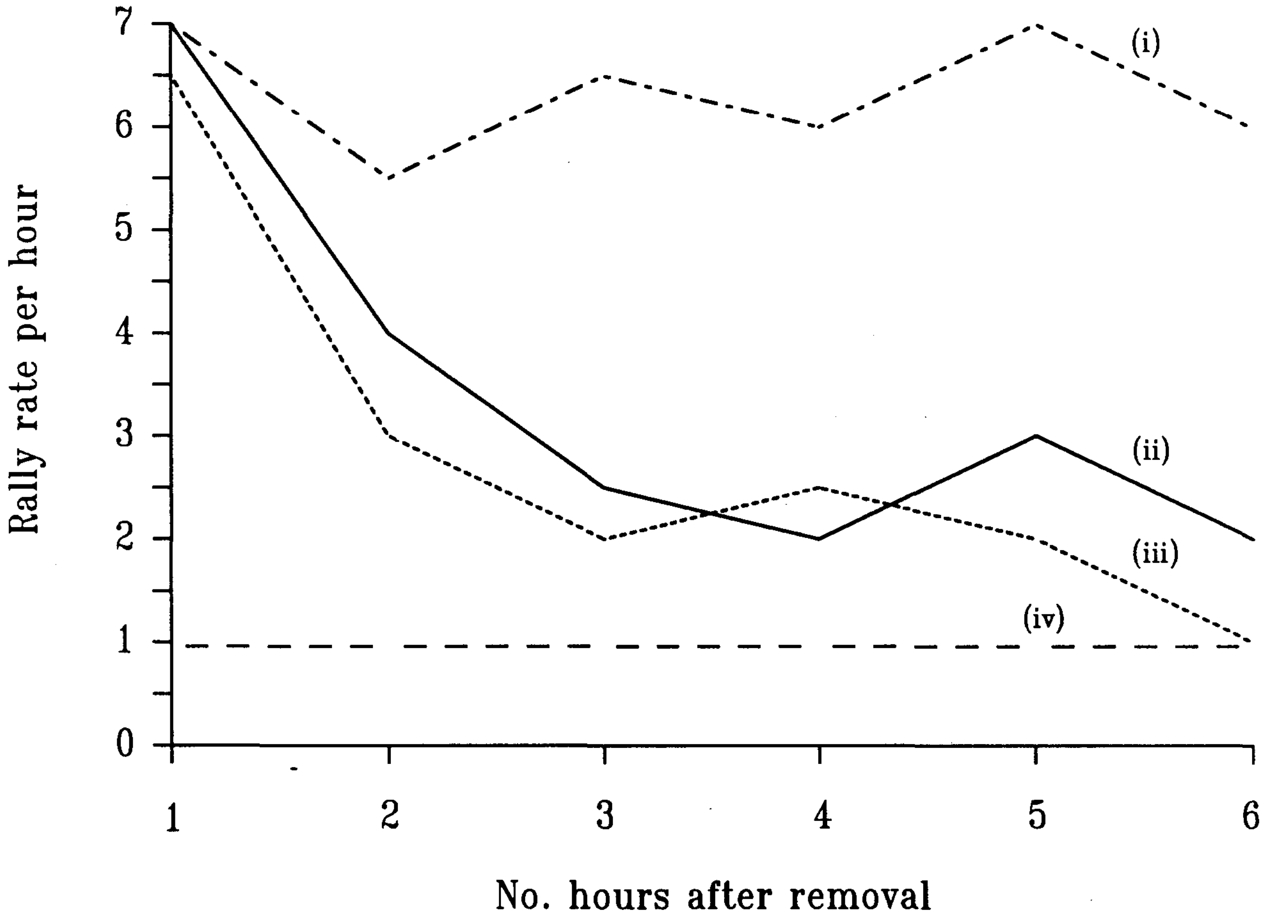

Figure 5.3. Rally rates of Redbilled Woodhoopoe flocks in which breeders were experimentally removed from flocks without helpers of (i) the removed birds' sex, and those in which (ii) a breeding male, and (iii) a breeding female, were removed from flocks with one or more helpers of both sexes present; (iv) represents the control (i.e. rally rate under undisturbed conditions).

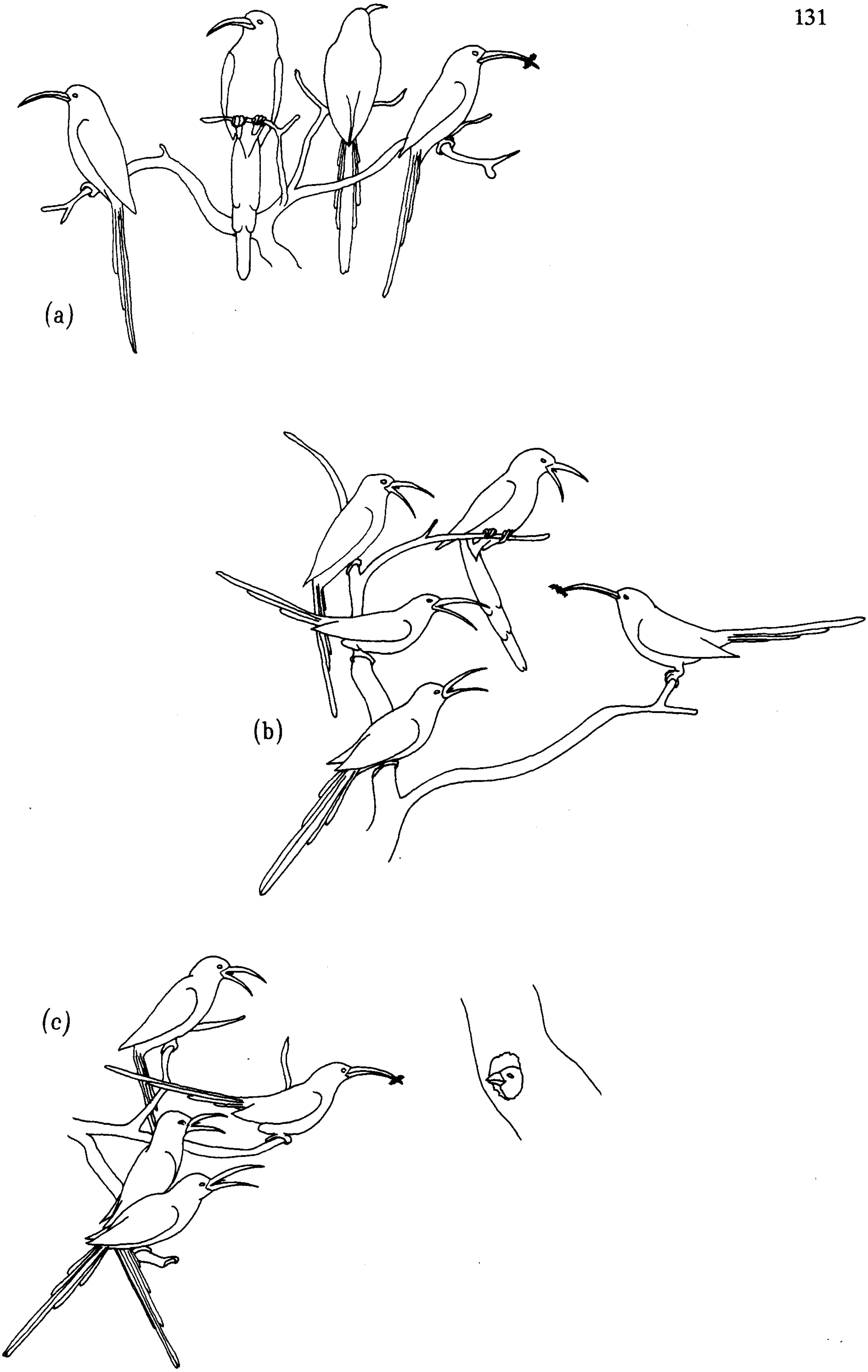

Figure 5.4. Illustration of (a) back-to-back, (b) directed, and (c) head-on flag-waving displays of Redbilled Woodhoopoes (sketched by D.J.Verwoerd).

intraspecific encounters and constituted 30% of the total. In the majority of these displays (69%), the intruding flock had been heard, but not seen. In the directed flag-waving display, the flag waver faced members of its own flock (Figure 5.4b). This display was only performed during territorial disputes, and made up 30% of the total. In the head-on flag-waving display, the flag waver faced the intruders and thrust a flag directly at them, while its own flock members rallied vigorously behind and on its flanks (Figure 5.4c). This display accounted for 40% of all flag-waving displays and was distributed approximately equally between inter- and intraspecific encounters.

Females carried flags more frequently than males (64.2% vs 35.8%). First year birds of either sex rarely carried flags, but among other classes, young birds carried flags more frequently than older birds. The involvement of nonbreeding adult males was similar to that of breeding females (Table 5.1). The frequency of flag waving increased with flock size (Figure 5.5), and peaked during the non-breeding season (Figure 5.6).

Flags were never passed to older birds of the same sex as the flag passer. Males passed flags significantly more often to other males than to females. Among females, only the breeding female passed significantly more flags to other females than to males (Table 5.2). Whenever insects were used as flags they were never passed on to other individuals, but were eaten by the waver.

Interspecific perch site displacement behaviour

No clear pattern was evident in interspecific PSD ratios. However, one year old birds displaced other species almost twice as frequently as did older individuals. Compared to older birds, first year birds directed perch site displacements disproportionately frequently at birds smaller in body size than themselves ($x^2 = 21.75$; 1 df; $P < 0.001$) (Table 5.3). Most displacements were of insectivorous

Table 5.1. Flag waving rates of different social classes of Redbilled Woodhoopoes; data for six flocks combined.

Social class (A)	Hours of observation (B)	Frequency (x 100)	B/A
BR♂	1160	28	2.41
BR♀	1160	67	5.78
AD♂	444	19	4.28
AD♀	396	36	9.09
2Y♂	581	37	6.37
2Y♀	755	78	10.33
<1Y♂	835	8	O.96
<1Y♀	427	4	0.94

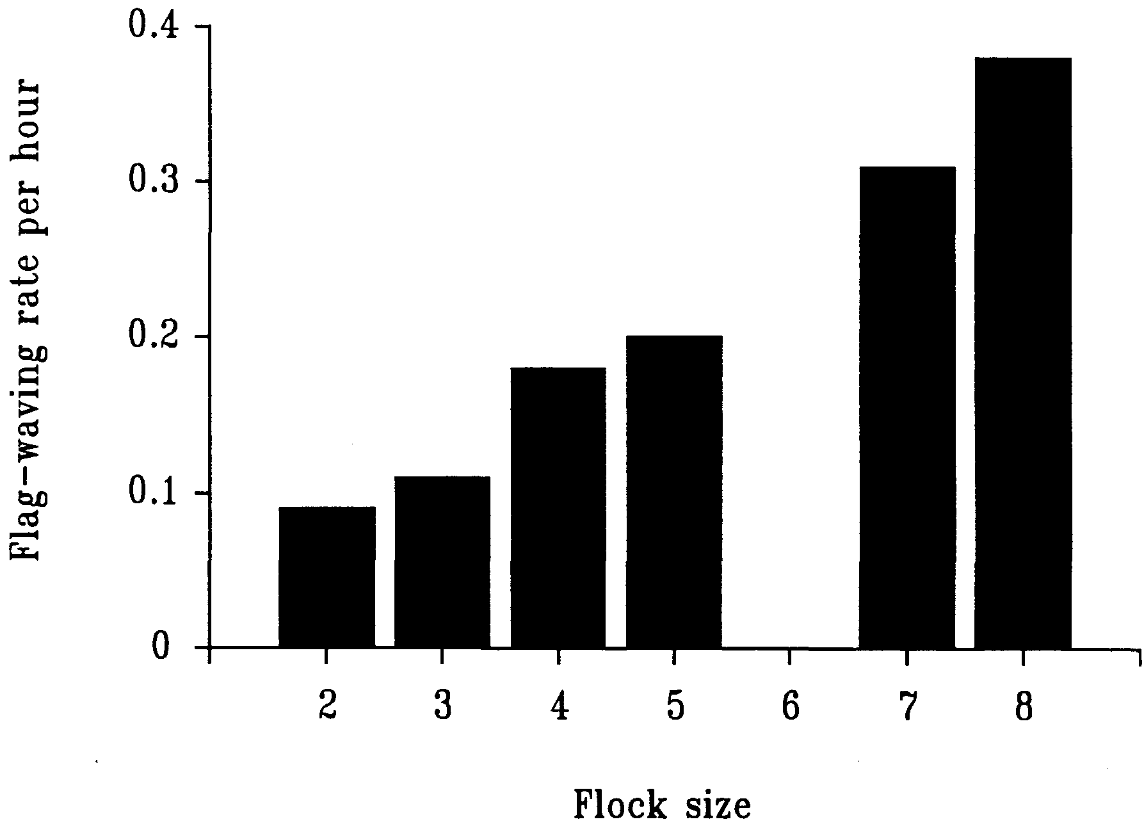

Figure 5.5. **Rates of Redbilled Woodhoopoe flag-waving displays in relation to flock size.**

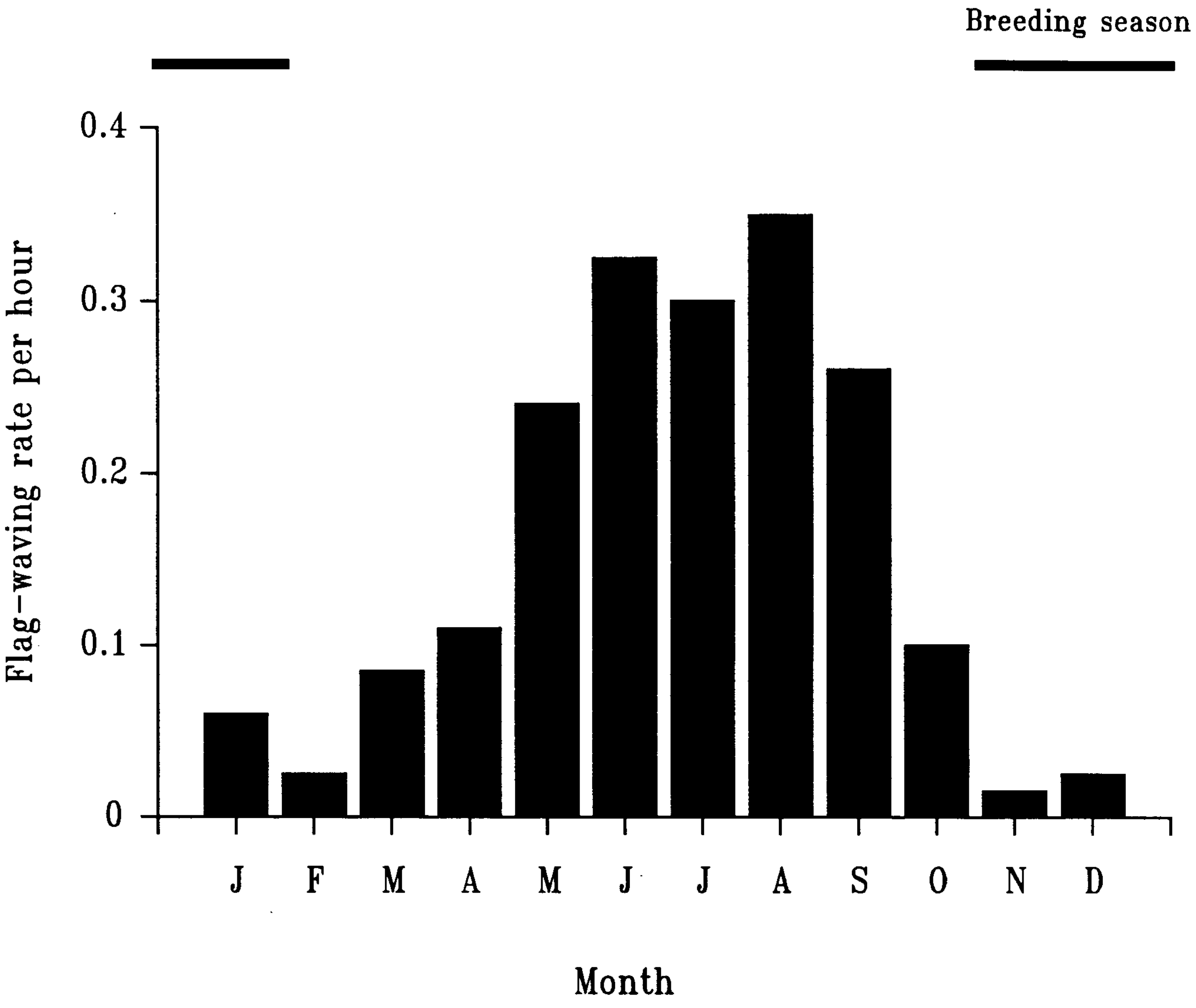

Figure 5.6. Seasonality of flag-waving displays for six Redbilled Woodhoopoe flocks.

Table 5.2. Summary of frequency of flag-passing orders by different sex and social classes (active category mentioned first).

Social class	#Comb.	##Observed	Expected	
BR♂ :♂♂	9	28	12.9	
			29.01	*
BR♂ :♀♀	14	5	20.1	
BR♀ :♂♂	9	3	7.4	
			5.55	**
BR♀ :♀♀	8	11	6.6	
AD♂ :♂♂	3	13	6.9	
			9.48	*
AD♂ :♀♀	4	3	9.1	
AD♀ :♂♂	3	4	6.4	
			1.57	ns
AD♀ :♀♀	4	11	8.6	
2Y♂ :♂♂	1	4	1.00	
			10.80	*
2Y♂ :♀♀	5	2	5.00	
2Y♀ :♂♂	2	5	4.40	
			0.14	ns
2Y♀ :♀♀	3	6	6.60	
<1Y♂ :♂♂	1	5	1.80	
			7.66	*
<1Y♂ :♀♀	3	2	5.20	

#	Comb. = the number of possible pairing combinations between the classes concerned
##	number of interactions observed
*	$P < 0.05$
**	$P < 0.001$
ns	not significant

Table 5.3. Comparison of interspecific perch site displacement rates by Redbilled Woodhoopoes older and younger than one year of age in relation to the body mass of the displaced species.

Relative body mass of displaced species	Displacement rate (per hour) Age Class		X^2	
	>1Y	<1Y		
> own body size	0.013	0.016	0.31	
< own body size	0.032	0.082	21.75	*

* P< 0.001; df= 1

species and only three species lacking dietary overlap with woodhoopoes were displaced; first year woodhoopoes were involved in all such instances.

DISCUSSION

Rally displays are performed by several group-territorial species (MacRoberts & MacRoberts 1976; Zack 1986; Grimes 1980; Tarboton 1981; Councilman 1977; Gaston 1977). There are two hypotheses concerning the function of rally displays in cooperatively-breeding species: (1) they advertise the presence or absence of breeders in the flock (Hannon *et al.* 1985; Zack 1986); and (2) they promote flock cohesion by inciting concerted aggression among flock members (MacRoberts & MacRoberts 1976; Ligon & Ligon 1978a, 1978b).

Flock size determined the duration of rally displays by Redbilled Woodhoopoes. Larger flocks usually 'won' territorial confrontations as a result of their longer displays. Intraspecific rally displays therefore contribute to inciting concerted aggression and to facilitating group cohesion and territorial maintenance. The occurrence of unprovoked rally displays points to their performing a functional role in maintaining or promoting group cohesion. Bouts of non-reciprocal allopreening or allopreening 'orgies', which serve social purposes (Chapters 3 & 4), usually followed unprovoked rally displays.

As sexes have distinctive voices, it is possible to determine flock composition from vocalisations during rallies. Significantly higher rally rates of flocks in which all members of a particular sex had been removed support the theory that the display functions, at least in part, to advertise the presence or absence of breeding vacancies. Higher rally rates in experimentally disturbed flocks were not only in response to the physical disturbance of removal, but also to the presence or absence of replacements for the lost breeder from within the flock.

Rood (1986) reported that large packs of Banded Mongooses *Mungos mungo* typically form a tight bunch and frequently stand up while approaching a predator, giving the appearance of a single large animal. This usually causes the predator to run, and a chase then ensues. Redbilled Woodhoopoe rally displays may intimidate predators or nest site competitors in a similar way. However, it is improbable that this display has the same effect intra-specifically.

Flag-waving displays were most frequent in the nonbreeding season, when the tendency for nonbreeders to scout for breeding vacancies was greatest (Chapter 2), and rally rate was highest. Head-on flag-waving displays probably serve to incite concerted aggression in the flock. Back-to-back flag-waving displays apparently occur when the flock is uncertain about the whereabouts of the intruder(s), and are possibly best interpreted in terms of group vigilance. Contributions to flag bearing were inversely related to dominance ranking within flocks, resulting in significantly more flag bearing by females. Flag bearing may be used by subordinate individuals to improve their social rank in the flock, especially during directed flag-waving displays, since flags were conspicuously waved in full view of all flock members. Higher flag-waving frequencies in larger flocks are presumably the result of longer rally displays by larger flocks. However, they could also reflect the presence of more subordinate individuals in the flock which try to better their rank, at the same time resulting in greater concerted aggression towards other woodhoopoe flocks, predators and competitors.

Passing orders of flags followed a similar pattern to that of allofeeding by Jungle Babblers (Zahavi 1977; Carlisle & Zahavi 1986) and Redbilled Woodhoopoes. Dominant birds pass flags (and food) to subordinate individuals. Because flag passing occurred most frequently within sexes, it may also serve to confirm dominance hierarchies within sexes. Nonbreeding adult males occasionally passed flags to female breeders, but only when the male breeder was absent, indicating the extent to which the presence of the male breeder suppresses other males.

Interspecific perch site displacement was directed mainly at insectivorous species, suggesting that there may be some competition for access to food resources. Smaller species usually were dominated by woodhoopoes, but sometimes one or more birds would displace larger species by joint effort. Only first year birds displaced non-insectivorous species: this may be a consequence of clumsiness or inexperience.

Behavioural mechanisms have evolved in group-living species by which both individual and group interests are served. Individual interests, expressed in dominance hierarchies, are maintained and communicated by displays and interactions such as allopreening and allofeeding, intra-specific perch site displacement, and leadership behaviour (Chapter 4). When several individuals compete for a single breeding position within each flock, within-group behavioural conflict must be minimized in the face of competition from neighbouring flocks. Woodhoopoes achieve this by way of at least two displays, rallying and flag waving. Besides promoting group unity, these displays serve the purpose of maintaining the group territory through concerted aggression.

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SECTION 3

EVOLUTIONARY IMPLICATIONS OF SOCIALITY

CHAPTER 6

THE ROLE OF HELPERS IN FEEDING CHICKS

SUMMARY

Observations were made of ten Redbilled Woodhoopoe *Phoeniculus purpureus* flocks during the breeding season in order to quantify the relationship between flock size and the amount of food delivered to chicks. Neither woodhoopoe feeding visit rates, nor the total amount of food brought to chicks, increased with flock size. Although nonbreeders did not increase the net rate of food provisioning to chicks, they reduced parental input in chick rearing, and hence energy expenditure by the breeding pair. However, over an eight year study period, this resulted in neither increased breeding frequency, nor enhanced survival of breeders. There is thus no evidence that helping *per se* improves (or reduces) inclusive fitness of helpers.

INTRODUCTION

The costs and benefits of helping behaviour (Skutch 1961) to donors and recipients are of special interest to evolutionary biologists because of the importance of this behaviour in determining the applicability of the concept of inclusive fitness in vertebrate species (Hamilton 1964; Brown *et al.* 1978; Brown 1987). One of the most conspicuous and quantifiable types of assistance is the feeding of chicks, behaviour which is found in most cooperatively-breeding bird species. Several studies of cooperatively-breeding birds have considered the role which nonbreeders play in the feeding of young (see Brown 1987). However, there is disagreement as to whether flocks containing many helpers deliver more food to young birds than do smaller flocks.

Redbilled Woodhoopoes *Phoeniculus purpureus* (Order Coraciiformes) are insectivorous, group-territorial birds that inhabit a wide range of woodland types across a broad Afrotropical range (Fry 1978). They live throughout the year in flocks of two to 12 birds which contain only a single breeding pair. Other flock members, usually (but not always) relatives of one or both breeders, are full participants in all other flock activities.

Breeding females are fed mainly by breeding males during incubation, although nonbreeding helpers may also contribute. However, when nestlings are present, both breeders and most (usually all) nonbreeders assist in providing food for the nestlings. During the first half of the 30-day nestling period, all food brought to the nest is passed to the breeding female who transfers it to the nestlings. Towards the end of the nestling phase some nonbreeding individuals attempt, and occasionally succeed, in bypassing the breeding female and feeding the nestlings themselves (Ligon & Ligon 1978, pers. obs.).

The aim of this study was to test the two hypotheses that, (1) there is a positive correlation between the total amount of food delivered to chicks and the number of nonbreeding helpers present, and (2) food provisioning to young by nonbreeding helpers translates into indirect fitness benefits to nonbreeding Redbilled Woodhoopoes.

METHODS

Observations were made of a population of colour-marked Redbilled Woodhoopoe flocks in riverine forest around Morgan's Bay (32°43'S, 28°19'E) in the eastern Cape Province, South Africa. Demographic data for between 10 and 29 flocks (144 flock years) were gathered at this site between 1981 and 1989 (Chapter 7).

Ten flocks - two each comprising two, three, four, five, and eight members - were observed during the breeding season between 27 December 1986 and 6 January 1987 for a total of 82 hours. The short study period was chosen to minimize seasonal effects on feeding rate, such as prey availability. Further standardization of conditions included: simultaneous watches (2 - 4 observers) and standardized observation periods (06h00 - 12h00), weather conditions (clear skies, no wind on eight of 10 days), number of nestlings (two in each case), and age of nestlings (7 - 14 days).

All flock members were individually identifiable and watched with binoculars from distances ranging between 20 and 35 m. Flocks usually resumed their normal activities around the nest within 10 - 15 minutes of the observer's arrival. However, flocks were allowed 30 minutes to become used to the observer's presence before feeding observations commenced, even if they showed no signs of disturbance.

A distinction was made between feeding visit frequency and feeding rate. 'Feeding visit frequency' was the number of feeding visits individuals paid to the nestlings per observation hour. To calculate feeding rate per hour, a prey size index, expressed as the ratio of prey length to bill length of a female woodhoopoe, was awarded to each prey item brought to the nest, and summed for each observation hour. When males fed nestlings directly, prey size relative to bill length was adjusted by a factor of 1.3 to correct for the difference in mean bill lengths between the sexes (male = 62.5 mm ± 2.1, n = 56; female = 47.1 mm ± 3.0, n = 51).

RESULTS

Food types

Of 746 items fed to nestlings, 93% were insects, 6% were spiders and 1% was fruit. Taking prey size as well as frequency into account, caterpillars, centipedes and cockroaches constituted more than 50% of food brought to nestlings.

The type and size of food items brought to chicks differed with sex and social status (Table 6.1). Breeding males brought the largest prey items offered to nestlings (ANOVA: $F = 23.908$; $P < 0.001$), and breeding females were at the other end of the range.

Feeding visit frequency and feeding rates

There was no significant relationship between the total number of feeding visits and flock size (Kruskal-Wallis ANOVA: $H = 2.980$; $P = 0.561$)(Figure 6.1a). However, the feeding contributions by different sex and social classes varied with flock size and composition: feeding frequency by both male and female breeders decreased with increasing flock size (Figure 6.2).

Taking prey size into account, there was still no significant difference between chick provisioning rates by flocks of different sizes (ANOVA: $F = 1.005$; $P = 0.410$) (Figure 6.1b). However, the amount of food delivered by the breeding

Table 6.1. Summary of the frequency with which different food items were offered to nestlings by different Redbilled Woodhoopoe sex and social classes.

Social Class	Frequency of occurrence of different food types									Prey size index (± SD)	N
	1	2	3	4	5	6	7	8	9		
Breeding male	22.0	14.7	12.9	5.2	3.0	6.5	6.5	25.4	3.9	0.47 (0.03)	232
Breeding female	9.0	3.0	1.2	10.2	5.4	16.3	11.4	43.4	0	0.29 (0.03)	166
Nonbreeding male	19.7	11.4	8.3	4.5	5.3	5.3	8.3	36.4	0.8	0.40 (0.04)	132
Nonbreeding female	15.7	10.2	3.7	5.1	6.0	4.2	7.9	45.8	1.4	0.36 (0.03)	216
[a]Total frequency	16.9	10.2	6.8	6.2	4.8	7.8	8.3	37.3	1.7		
[b]Total contribution	22.6	17.9	12.0	3.5	5.2	3.8	7.7	25.0	2.3		

Codes:

1 -	caterpillar	(Order Lepidoptera)
2 -	centipede	(Class Chilopoda)
3 -	cockroach	(Order Blattodae)
4 -	spider	(Order Opiliones)
5 -	mantid	(Order Mantodae)
6 -	termite	(Order Isoptera)
7 -	bug	(Order Hemiptera)
8 -	unidentified insects	(Order Embioptera) (Order Psocoptera) (Order Zoraptera) (and others)
9 -	fruits and berries	

[a]Total frequency - taking feeding visit rate into account
[b]Total contribution - taking prey size into account

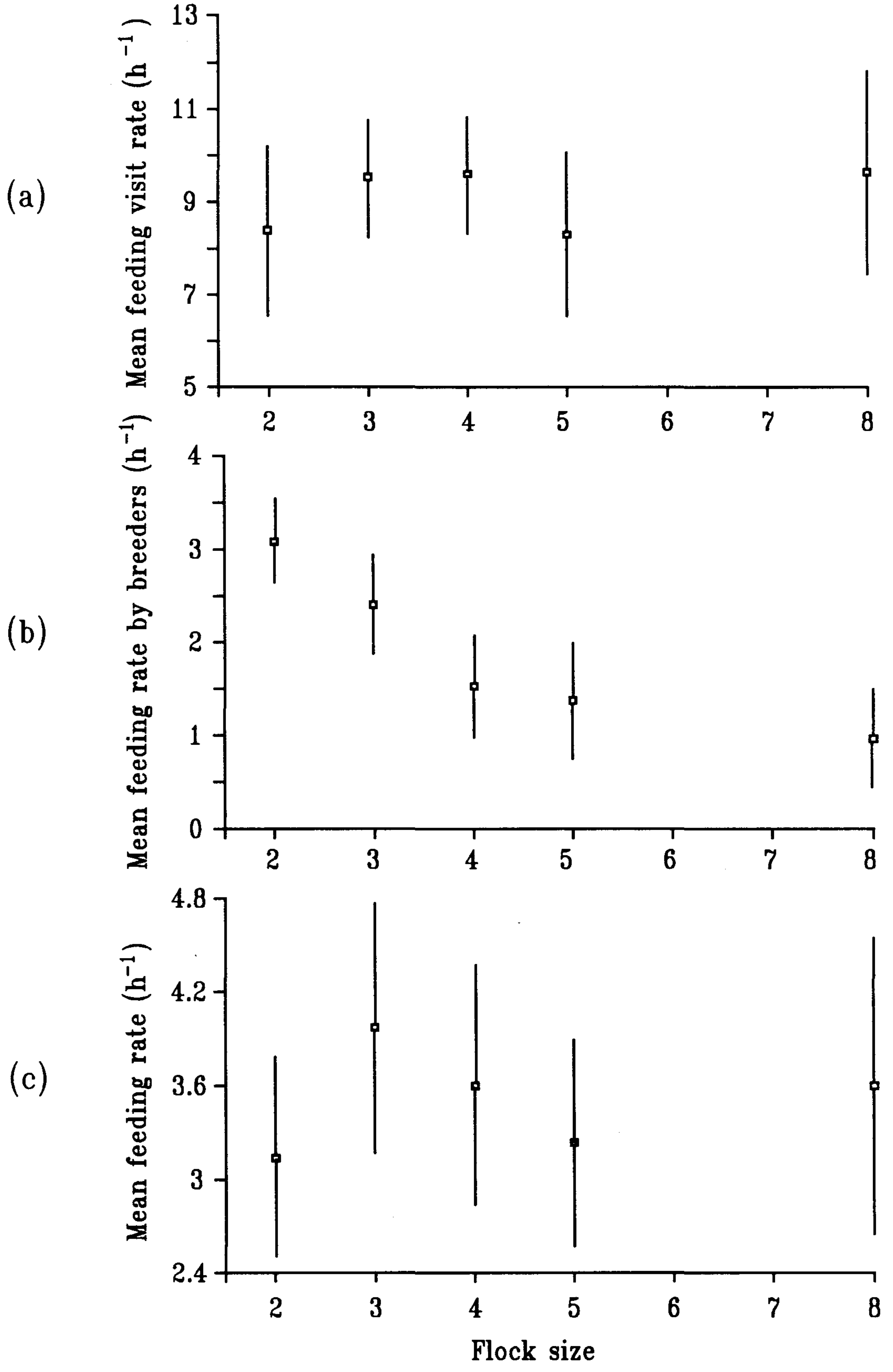

Figure 6.1. Relationship between Redbilled Woodhoopoe flock size and (a) mean feeding visit rate to nestlings; (b) feeding rate (taking food size into account); and, (c) breeder feeding rate (taking food size into account).

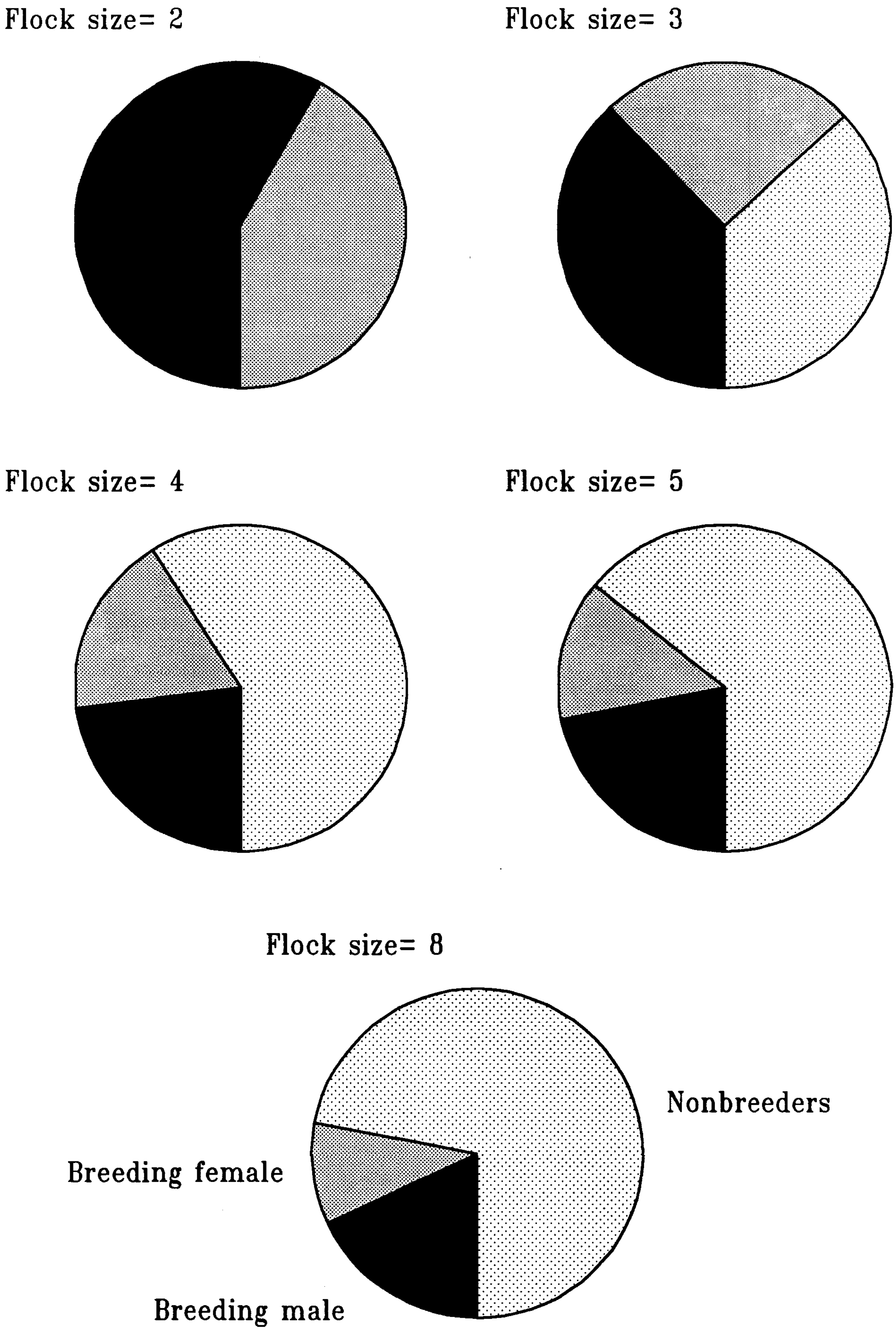

Figure 6.2. Frequency of participation in feeding visits to Redbilled Woodhoopoe nestlings by individuals from different social classes in relation to flock size.

birds decreased rapidly as the number of nonbreeding helpers in the flock increased (Figure 6.1c).

Independent of flock size, the contribution by the breeding male was greater than that by any individual helper in terms of the absolute amount of food brought (ANOVA: $F= 18.226$; $P< 0.05$). Nonbreeding females made the second largest contribution, and breeding females obtained least food for nestlings.

DISCUSSION

The intersexual difference in food types brought to chicks can be ascribed to sexual dimorphism in bill length. Males, having longer bills, retrieve more insects from deep under the bark of trees than females, which take more prey from near and above the bark surface. Female breeders guard the nest closely and seldom move more than 30-50m from it during the nestling stage, and consume some of the food brought by other flock members themselves. Nonbreeding females, on the other hand, bring food for the nestlings from all over the flock's territory, and, if foraging by the breeding female causes local prey depletion in the vicinity of the nest, this may account for their contribution of larger prey. Nonbreeding females make a small contribution to nest guarding relative to the breeding female. However, nonbreeding females attempt to interact personally with nestlings as much as possible ('auntie behaviour'), often leading to conflict when the breeding female prevents them from doing so (*sensu* Ligon & Ligon 1978; unpubl. data).

Results from studies which have looked at the relationship between feeding frequency and the number of nonbreeding helpers involved are summarized in Table 6.2. In 49% of cases, the presence of helpers increased feeding frequency. However, an important variable omitted from these studies was the size of the food items. Hunter's study (1987) is an exception, and showed that the amount of food brought to chicks of Purple Gallinules *Porphyrula martinica*, increased with more

Table 6.2. Summary of results from studies which have looked at the relationship between feeding visit rates and the number of nonbreeding helpers involved.

Species		Reference
Helpers increase the number of feeding visits to nestlings in:		
House Sparrow	*Passer domesticus*	1
Australian Bell Miner	*Manorina melanophrys*	2
Chestnutbellied Starling	*Spreo pulcher*	3
Redbilled Woodhoopoe (Kenya)	*Phoeniculus purpureus*	4
Whitefronted Bee-eater	*Merops bullockoides*	5
Pied Kingfisher	*Ceryle rudis*	6
Whitebrowed Sparrow-weaver	*Plocepasser mahali*	7
Acorn Woodpecker	*Melanerpes formicivorus*	8
Helpers do not increase the number of feeding visits to nestlings in:		
Kookaburra	*Dacelo novaequineae*	9
Greycrowned Babbler	*Pomatostomus temporalis*	10
Florida Scrub Jay	*Aphelocoma coerulescens*	11
Stripebacked Wren	*Campylorhynchus nuchalis*	12
Bicoloured Wren	*C. griseus*	13
Whitewinged Chough	*Corcorax melanorhamphus*	14
Arrowmarked Babbler	*Turdoides jardinei*	15
Longtailed Tit	*Aegithalos caudatus*	16
Black Tit	*Parus niger*	17
Purple Gallinule	*Porphyrula martinica*	18

References:

1 Sappington (1977)
2 Clarke (1984)
3 Wilkinson & Brown (1984)
4 Ligon & Ligon (1978)
5 Emlen (1984)
6 Reyer (1980,1984)
7 Earle (1983)
8 Koenig & Mumme (1987)
9 Parry (1973)
10 Brown et al. (1978)
11 Stallcup & Woolfenden (1978)
12 Rabenold (1984)
13 Austad & Rabenold (1985)
14 Rowley (1977)
15 Vernon (1976)
16 Gaston (1973)
17 Tarboton (1981)
18 Hunter (1987)

helpers, although the feeding visit rate was not related to group size. This was achieved by breeders bringing fewer, but larger food items. Any contribution made by additional group members therefore added to the absolute quantity of food received by young.

Ligon & Ligon's (1978) long-term study of Kenyan Redbilled Woodhoopoes showed that although feeding visit frequencies increased slightly with flock size, reproductive success was not related to flock size. In the present study, neither woodhoopoe feeding visit rates, nor the total amount of food brought to chicks, increased with flock size. Therefore, if food provisioning rates are an important determinant of breeding success, breeding success should be independent of flock size. Under natural conditions, flocks without helpers raised more than two young in one breeding season as frequently as flocks with helpers (coast: 8.5% *vs* 4.1%). This suggests that the presence of helpers does not necessarily enable large flocks to provide more successfully for larger broods than do small flocks.

Although nonbreeding helpers do not increase the net rate of food provisioning to chicks, their contribution does reduce parental input in chick rearing, and hence energy expenditure by the breeding pair. On this basis it could be predicted that breeding frequency will be increased by the presence of helpers. However, unlike some other cooperatively-breeding species (e.g. Greycrowned Babbler *Pomatostomus temporalis*, Brown *et al.* 1978), Redbilled Woodhoopoes never breed more than once in the same season at the South African coastal study site.

Even if breeding frequency is not affected by flock size, reduced energy expenditure by breeders during chick rearing may enhance breeder survival. Koenig & Mumme (1987) suggested for Acorn Woodpeckers *Melanerpes formicivorus* that a major portion of the indirect fitness accruing to nonbreeders comes not from direct aid to younger siblings, but from increased survivorship of male breeders. However, they suggested that such indirect fitness benefits may be the result of nonbreeders' contribution to antipredatory behaviour, rather than alloparental behaviour. Helping by nonbreeders lighten the workload of Redbilled Woodhoopoe breeders (Ligon & Ligon 1978), but such savings apparently do not correspond to effects on direct fitness as measured by survivorship (Chapter 7). Therefore, contrary to expectation, bringing of food to the young and other forms of alloparental care appear not to cause any measurable benefits to parent or young Redbilled Woodhoopoes.

The intuitive assumption that helpers help is true in as much as they reduce pressure on breeding birds to provision their chicks. However, this study was unable to demonstrate any fitness benefit beyond this in terms of either enhanced productivity or enhanced survival of breeding birds. There is thus no evidence that helping *per se* improves the inclusive fitness of helpers. Equally, there is no evidence that it reduces such fitness.

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CHAPTER 7

CONSEQUENCES OF SOCIALITY FOR INDIVIDUAL FITNESS

SUMMARY

The hypothesis that helpers increase the lifetime reproductive success of breeder-recipients has been 'surprisingly controversial' (*sensu* Brown 1987). This hypothesis is tested with data of cooperatively-breeding Redbilled Woodhoopoes *Phoeniculus purpureus*. Life-history data were gathered for a total of 258 woodhoopoe flock-years in two South African populations. Most woodhoopoes obtained breeding status in the natal flock rather than elsewhere: however, breeding success and survivorship were equal for 'dispersers' and 'non-dispersers', indicating that the advantage of residency is not fecundity *per se*. Woodhoopoes breeding for the first time were as successful as more experienced ones, confounding the hypothesis that experience gained as a helper has been important in the evolution of cooperative breeding. Over an eight year period, there were no significant differences between the performance of flocks with and those without helpers in terms of the following criteria: number of young fledged per year, survival of young in their first year, breeder and nonbreeder survivorship and the number of breeder-offspring produced. Both South African woodhoopoe study populations showed higher adult survivorship than a population in Kenya (Ligon & Ligon 1988). Survival rates of woodhoopoe females at both sites increased with age and was not consistent with the view that older individuals should exhibit greater reproductive effort than yearlings because of their lower survival. Reciprocity was ruled out as an explanation for the evolution of alloparental feeding behaviour, as a fundamental prerequisite of such behaviour, group dispersal, was not met in the present study. If reciprocity is excluded as an explanation of helping behaviour in woodhoopoes, the non-selective hypothesis, in which helping behaviour is regarded as misdirected parental care, best explains it.

INTRODUCTION

In most vertebrate species, independent young disperse or are expelled from their natal territory before subsequent breeding attempts by the parents (Brown 1987). There are two basic mechanisms by which a change in this general pattern can occur. Offspring may gain an indirect benefit by postponing dispersal and independent reproductive effort, although space for breeding exists elsewhere. Alternatively, offspring may be ecologically constrained from dispersing and breeding on their own by the limitation of some critical resource (Emlen 1982; Brown 1987; Koenig & Mumme 1987). By examining which components of fitness increase and decrease as a function of group size, and identifying the ecological and social variables that affect these components, one can evaluate the cost and benefit trade-offs that favour the evolution of sociality and cooperation (Vehrencamp *et al.* 1986).

In the context of cooperatively-breeding birds, the hypothesis that helpers increase the lifetime reproductive success of breeder-recipients has been 'surprisingly controversial' (*sensu* Brown 1987). Studies of cooperative breeders have yielded important demographic information (e.g. Vehrencamp 1978; Gaston 1978; Ligon 1981; Ligon & Ligon 1988), but the only species for which comprehensive life-table analyses have been attempted are the Florida Scrub Jay *Aphelocoma coerulescens* and the Acorn Woodpecker *Melanerpes formicivorus* (Woolfenden & Fitzpatrick 1984; Koenig & Mumme 1987).

No measurable fitness benefit has been identified to recipient breeders, their offspring, or nonbreeding helpers among Redbilled (Green) Woodhoopoes *Phoeniculus purpureus* in Kenya (Ligon & Ligon 1978a, 1978b, MS; Ligon 1981, 1983). In his review of communal breeding, Brown (1987: 248) conceded that this finding remains enigmatic, as the evidence for indirect selection is weak.

Redbilled Woodhoopoes are useful for comparative intraspecific studies of life history, demography and sociality since, in South Africa, they display varying degrees of sociality; i.e. from unaided pairs, to flocks containing up to 12 birds. Flocks of more than two birds contain only a single breeding pair and other flock members, usually (but not always) relatives of one or both breeders, are full participants in all other flock activities, including care of young. Redbilled Woodhoopoes are physiologically capable of reproducing at the end of their first year, but usually do not do so due to limited breeding opportunities. In the eastern Cape Province of South Africa, woodhoopoes breed synchronously once a year and very rarely attempt renesting. Such attempts are made only when the contents of a nest are lost early during the incubation period (0.4% of observed cases; n= 256; unpubl. data). Suitable cavities, for roosting, apparently are a critical resource to woodhoopoes throughout their range (Ligon & Ligon 1978a, 1988; Ligon *et al.* 1988; Chapters 1 & 2). Flocks defend permanent territories, the traditional boundaries of which change little; breeders never change territories.

Several measures have been used to quantify fitness of cooperatively-breeding species: (1) number of young fledged; (2) number of young fledged *per capita*; (3) number of young surviving to reproductive maturity; (4) survivorship of breeders; and, (5) survivorship of nonbreeders (see Brown 1987 for a thorough review). Perhaps the most meaningful criteria for assessing fitness are the number of breeder-offspring (F_1) and grand-offspring (F_2) produced. However, such data are not easily collected, particularly when long-lived species are involved.

In this paper I test the hypothesis that nonbreeding helpers increase the inclusive fitness of breeding Redbilled Woodhoopoes. This hypothesis is examined using a comparative analysis of the pattern of differential reproductive success and survivorship of Redbilled Woodhoopoes in two different study sites.

METHODS

Comparative life history data were gathered for two Redbilled Woodhoopoe populations between 1981 and 1989 in the eastern Cape Province, South Africa. At Morgan's Bay (32°43'S, 28°19'E), between nine and 29 flocks were monitored annually where riverine forest forms belts along river valleys; Redbilled Woodhoopoe territories were restricted to these valleys. In the Kubusi River Valley (32°32'S, 27°47'E), between six and 24 flocks were monitored. Here, riverine forest occurs in small patches in tributary valleys and the remainder of the area is dominated by either valley bushveld or *Acacia* thornveld (Acocks 1975). Roost cavities are almost entirely restricted to trees in the riverine forest patches.

Between 1981 and 1985, and again in 1988 and 1989, pre- and postbreeding population censuses were made at each site; monthly censuses were made in 1986 and 1987. A band approximately 5 km wide around each study area was searched at least twice a year for birds which had dispersed from the study areas. Data for a total of 144 coastal and 114 inland 'flock years' (*sensu* Koenig & Mumme 1987) were gathered during the study period.

Before the present study commenced in 1981, I spent over 400 hours observing Redbilled Woodhoopoes in another area nearby (Appendix 1: 252), and found that disturbance at the nest during incubation often led to nest desertion. For this reason, no data on clutch size or hatching success were collected.

For the purpose of this study, flock size was taken as that at the onset of the breeding season (early November). Annual reproductive success was defined as the number of young fledged. As flock size may vary considerably over the lifetime of individuals, it is impossible to measure accurately the effects of a particular group size on the life span of an individual. Therefore, for calculating individual annual survivorship I used the average flock size during the year in question for individuals which survived, and actual flock size at the time of death for those which died.

Because of variability in age at first breeding, a distinction was made between the effects of age and breeding experience on reproductive success. Age was thus weakly related to helping experience, but not to breeding experience because of the variability in the age at first reproduction. Nonbreeders invariably assisted breeders during their reproductive efforts. However, on average, more than 50% of all breeding attempts, at both sites, failed for some reason and therefore complicated the accurate quantification of 'helper experience'.

Life tables were constructed for both study populations using age at reproductive maturity, age-specific fecundity, and age-specific survivorship. Year classes were selected because of the strict annual reproductive cycle of this species at both sites. I used f_x as the average fecundity (chicks fledged) of individuals of age x and d_x as the proportion of birds surviving to age x that were breeders. Hence, $f_x d_x = m_x$, the average fecundity of females at age x, as is convention. Formulae used for life-table calculations were the following: net reproductive rate (R_0) (Ricklefs 1973), annual rate of increase (r) (Lotka 1907, using the FORTRAN program in Caughley 1976), mean generation time (T) (Ricklefs 1973), and reproductive value (V_x) (Fisher 1930).

RESULTS

Exogenous influences on fitness

The most significant correlation between precipitation for a specific time of year and reproductive success over the eight year period, was a weak negative trend between April/May rainfall and the number of young fledged (the following December/January) (coast: r= -0.57; P= 0.13; inland: r= -0.85; P= 0.01). A similar, but weak relationship existed between April/May precipitation and the proportion of flocks that successfully fledged one or more young (coast: r= -0.68; P= 0.06; inland: r= -0.62; P= 0.10).

The correlation of overall reproductive success with population density, taken at the start of the breeding season in November, was not significant (coast: r= -0.30; n= 8; P= 0.47; inland: r= 0.19; n= 8; P= 0.65) (Figure 7.1). The woodhoopoe population density was consistently higher at the coastal site than at the inland site.

There were several other environmental and flock-related differences between the coastal and inland woodhoopoe study populations (Table 7.1).

Endogenous influences on fitness

Males which inherited breeding status in their natal territories at the coast fledged significantly more young per year than did males which bred in non-natal territories (Mann-Whitney U: z= 2.492; $P < 0.05$) (Table 7.2). However, there were no significant differences in annual reproductive success or survivorship between heirs and non-heirs for inland males, or for females at either site.

Effects of group size

There was no clear relationship between fecundity, breeding experience and flock size for either sex at either site (Table 7.3). The productivity of breeders was slightly enhanced by the presence of helpers during the first breeding attempt by both sexes at both sites, but never significantly so (vertical comparisons).

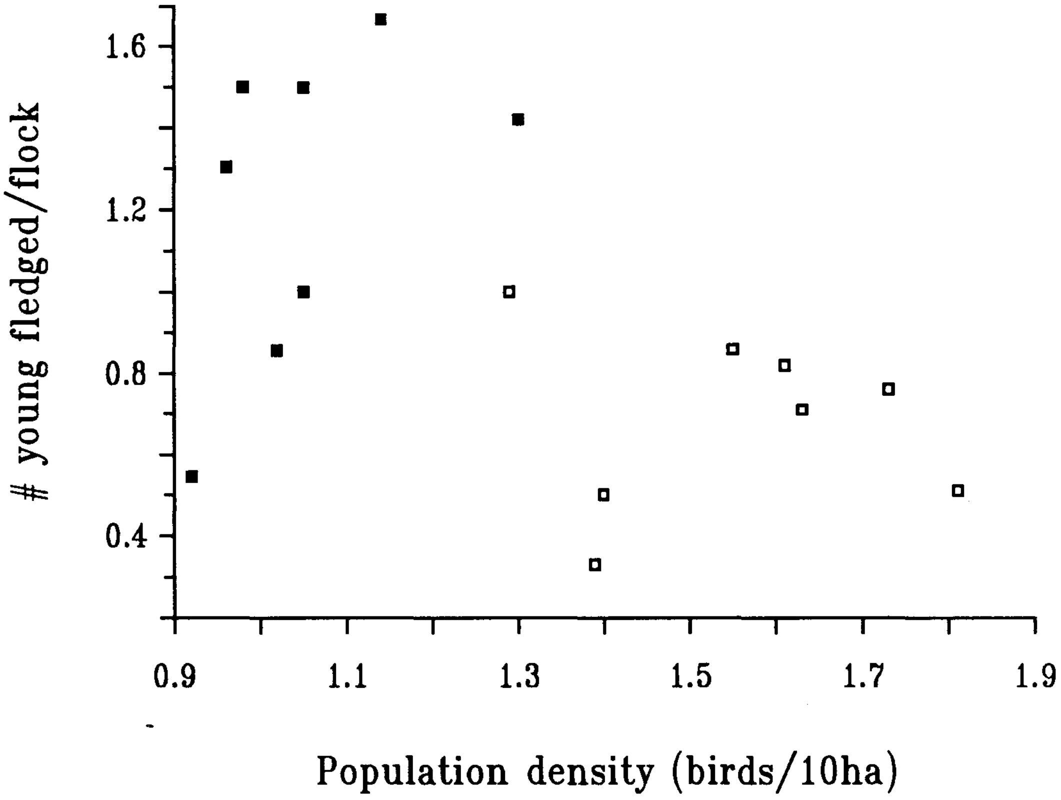

Figure 7.1. Relationship between Redbilled Woodhoopoe population density and the mean number of young fledged annually per flock between 1981 and 1988. Open squares: coastal site; solid squares: inland site.

Table 7.1. Comparative summary of various climatic, habitat, flock and reproductive success parameters at the coastal and inland sites respectively.

Parameter	Coast	Inland
Average annual rainfall (mm)	1007 (14 years)	433 (22 years)
Habitat[1]	RIVERINE FOREST ACACIA SAVANNA	RIVERINE FOREST ACACIA SAVANNA VALLEY BUSH
Territory size (ha)	11 - 25 16.8 ± 3.3 (n= 29)	25 - 64 35.5 ± 10.1 (n= 24)
Flock size[1]	3.41 ± 1.38 (n= 123)	4.74 ± 1.87 (n= 93)
% of all flocks without helpers	50.7 (n= 144)	21.1 (n=114)
Breeding success[2]:		
Mean # young fledged per year	0.33 - 1.42 (n= 8)	0.54 - 1.67 (n= 8)
% successful flocks	22.1 - 58.3 (n= 8)	31.8 - 83.3 (n= 8)
Frequency of no nesting attempts (%)	13.8 (n= 144)	8.8 (n= 114)
Main cause of breeding failure[3]	NEST FLOODING	DEPREDATION OF NESTLINGS

[1] Chapter 1
[2] Appendix 7.1
[3] Appendix 7.2

Table 7.2. Comparison of annual reproductive success and survivorship of birds inheriting their natal territory and those moving elsewhere to breed.

	Inherited	Moved	
COAST:			
Males:			
# young fledged (per year)	1.28 ± 1.23 (n= 18)	0.48 ± 0.83 (n= 29)	*
% annual survivorship	83.3	96.6	ns
Females:			
# young fledged (per year)	0.36 ± 0.92 (n= 11)	0.74 ± 1.24 (n= 19)	ns
% annual survivorship	90.9	89.5	ns
INLAND:			
Males:			
# young fledged (per year)	1.11 ± 1.05 (n= 35)	1.13 ± 1.51 (n= 15)	ns
% annual survivorship	85.7	93.3	ns
Females:			
# young fledged (per year)	0.60 ± 1.18 (n= 15)	1.00 ± 1.18 (n= 24)	ns
% annual survivorship	93.3	91.7	ns

ns not significant
* $P < 0.05$ (Mann-Whitney U)

Table 7.3. Fecundity in relation to duration as a breeder among male and female Redbilled Woodhoopoes at the coastal and inland sites respectively.

	Number of young fledged					
	Males Breeding Year			Females Breeding Year		
	1	≥2		1	≥2	
COASTAL SITE:						
Flocks without helpers:						
Mean	0.75	1.00		0.38	1.67	
S.D.	(1.16)	(1.11)	**n.s.**	(0.74)	(1.88)	*
N	20	22		8	9	
Flocks with helpers:						
Mean	0.91	0.65		0.50	0.22	
S.D.	(0.83)	(0.62)	**n.s.**	(1.22)	(0.79)	**n.s.**
N	11	31		6	9	
	n.s.	**n.s.**		**n.s.**	*	
INLAND SITE:						
Flocks without helpers:						
Mean	1.00	0.00		0.00	0.44	
S.D.	(1.41)	(0.00)	*	(0.00)	(0.56)	**n.s.**
N	11	8		2	9	
Flocks with helpers:						
Mean	1.13	1.06		1.18	0.92	
S.D.	(1.30)	(0.76)	**n.s.**	(1.08)	(0.81)	**n.s.**
N	15	32		11	13	
	n.s.	**		**n.s.**	**n.s.**	

n.s. not significant
* $P < 0.05$ (Mann-Whitney U)
** $P < 0.01$

Reproductive success

With data combined and averaged for all eight years, 50.7% of coastal flocks and 78.9% of inland flocks contained nonbreeding helpers.

When considering all flocks, fledging success was not related to flock size for either of the study populations (Kruskal-Wallis ANOVA: coast: H= 2.931; P= 0.711; inland: H= 10.303; P= 0.112) (Figure 7.2a). Inland flocks fledged more young on average than coastal flocks (Mann-Whitney U: z= 2.685; P= 0.007). This difference was due to higher productivity of inland flocks with helpers (Mann-Whitney U: z= 3.209; P= 0.001). Fledgling production by flocks without helpers was the same at both sites (Mann-Whitney U: z= 0.579; P= 0.562). Considering successful flocks only, there were no significant relationships between productivity and group size (Kruskal-Wallis ANOVA: coast: H= 2.471; P= 0.481; inland: H= 8.569; P= 0.199) (Figure 7.2b), and fledgling production did not differ between sites (Multifactor ANOVA: F= 1.446; P= 0.231).

The proportion of successful flocks (i.e. fledging one or more young per year) was not related to flock size at either site (coast: X^2= 4.641; 3 df; P= 0.201; inland: X^2= 5.896; 3 df; P= 0.117) (Figure 7.2c).

There was no significant correlation between flock size and the number of young fledged in any one year at either site. During the year in which reproductive success (in terms of the total number of young fledged) was at its lowest (1986), coastal flocks with helpers fledged an average of 0.53 ± 0.80 (SD) (n= 19) compared with 0.80 ± 0.92 (SD) young fledged in flocks without helpers (n= 10) (Mann-Whitney U: z= 0.770; P= 0.44). Comparative figures at the inland site were 1.11 ± 0.96 (SD) (n= 18) and 0.67 ± 1.21 (SD) (n= 6) respectively (Mann-Whitney U: z= 1.091; P= 0.275).

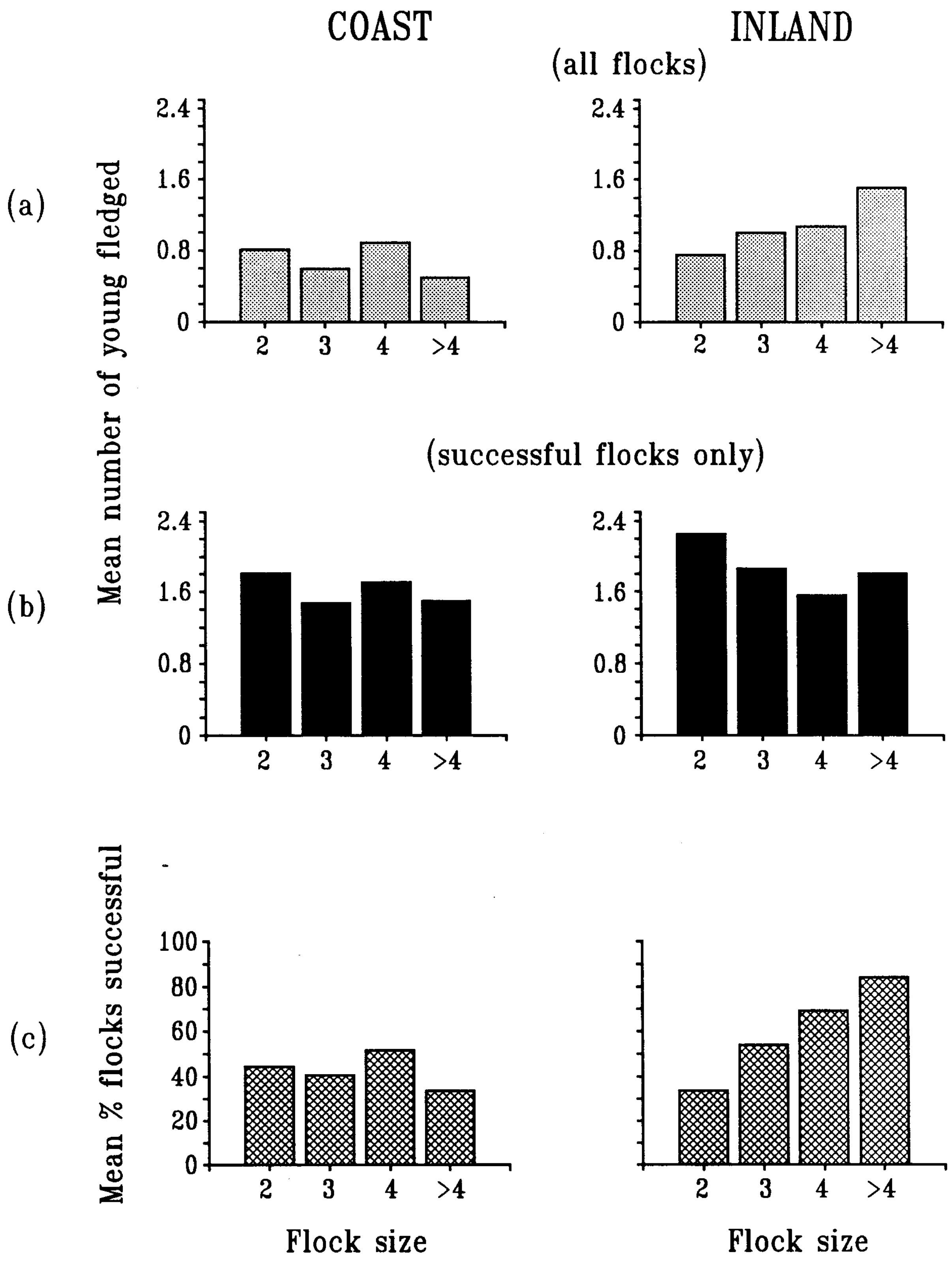

Figure 7.2. The relationship between the mean number of young fledged when considering (a) all flocks; and (b) only flocks that fledged one or more young; (c) relates flock size to the proportion of flocks that were successful in fledging at least one young.

Survivorship

At the coastal site, an average of 0.55 ± 0.85 (SD) (n= 57) young produced by flocks without helpers survived to the age of 12 months, compared to 0.40 ± 0.75 (SD) (n= 66) from flocks with helpers (i.e. when considering all flocks). Corresponding figures for the inland site were 0.50 ± 0.73 (SD) (n= 17), and 0.60 ± 0.84 (SD) (n= 76). These differences were not significant when considering all flocks or successful flocks only.

Flock size (successful flocks only) and survivorship to six months were unrelated at the coastal site ($r= -0.09$; $n= 51$; $P= 0.53$), and negatively correlated at the inland site ($r= -0.28$; $n= 62$; $P= 0.03$). Net production per flock (by all flocks) of young surviving to 12 months was 0.63 ± 0.81 (n= 93) and 0.47 ± 0.80 (n= 123) at the inland and coastal sites respectively. These differences were not significant, and this remained the case when analyses were restricted to successful flocks only

Survivorship of breeders and nonbreeders of both sexes was not influenced by flock size at either site (Appendices 7.3 & 7.4). During the eight year study period there was little variation in adult survivorship at either site. During years in which survivorship was relatively low for both males and females, flock size still had no significant influence on survivorship.

At the coastal site, the size of flocks from which individuals originated had no effect on the probability of their becoming breeders later in life (without helpers: 40.5%; with helpers: 40.9%) (Table 7.4). This remained the case when data were separated for males and females. With data combined for the sexes, there was no difference in the frequency with which individuals originating in flocks with and without helpers became breeders in natal, as opposed to non-natal territories.

At the inland site, individuals originating in flocks without helpers had a higher probability of becoming breeders than those raised by flocks with helpers (54.5% *vs* 20.0%) ($X^2= 10.182$; 1 df; $P< 0.005$). Again, this remained the case when

Table 7.4. Analysis of the frequency with which breeding positions were attained by individuals originating from flocks with, versus those without helpers at the coastal and inland sites respectively. Data for males and females combined; sample sizes of fledglings followed until death or acquisition of breeding status in brackets.

Breeding status in:	% Breeder-offspring originating from flocks:			
	Without helpers		*With helpers*	
COASTAL SITE:				
Natal flock	58.8		11.1	
Elsewhere	41.2		88.9	
% of total		**40.5**		**40.9**
N	(42)		(22)	
INLAND SITE:				
Natal flock	100.0		57.2	
Elsewhere	0		42.8	
% of total		**54.5**		**20.0**
N	(22)		(84)	

data were separated for males and females. With data combined for the sexes, there was a weak trend for individuals originating in flocks with helpers to attain breeder status more often in non-natal territories than individuals from flocks without helpers ($X^2 = 6.661$; 3 df; $P < 0.10$).

Comparative life-tables

Survivorship:

Fledgling survival over the first 12 months of life was higher at the coast than at the inland site (Figure 7.3). At the coastal site most fledgling deaths were evenly distributed over the first six months of life, whereafter mortality remained relatively constant. At the inland site the first three months of life were critical for fledgling survival.

At both sites survival of breeding males was high early in life and gradually decreased with age (Figure 7.4); nonbreeding adult male survivorship improved slightly with age. Breeding female survivorship did not decrease with age. Nonbreeding adult female survivorship increased with age in an almost linear fashion at both sites.

When data for all banded individuals were included (including those of unknown age), breeding males at both sites had fractionally lower survivorship than females (coast: 0.86 *vs* 0.88; inland: 0.83 *vs* 0.85), whilst nonbreeding male and female survivorship were almost identical (coast: 0.79 *vs* 0.80; inland: 0.80 *vs* 0.78).

Lifetable parameters

As indicated by the $l_x m_x$ schedule, the majority of young among each year's recruits were the product of old females paired with young males. (Figure 7.5).

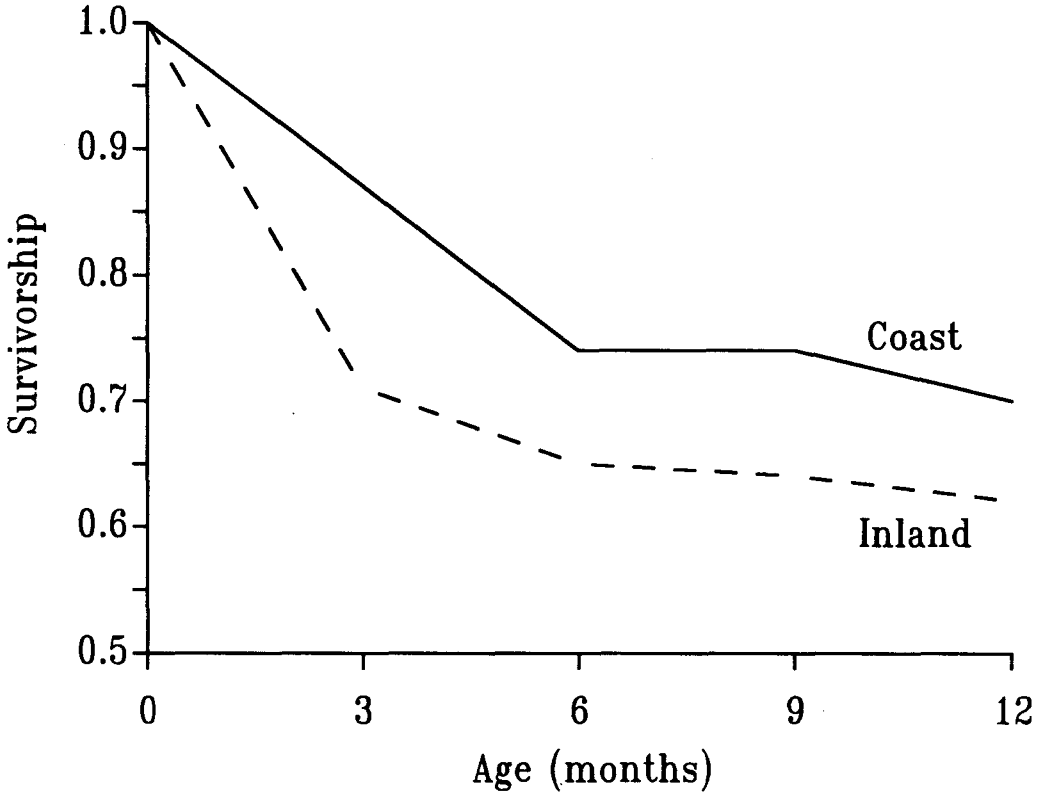

Figure 7.3. Relationship between age and survivorship of Redbilled Woodhoopoes during their first year of life, between 1985 and 1988, at the coastal (n= 77) and inland (n= 107) sites.

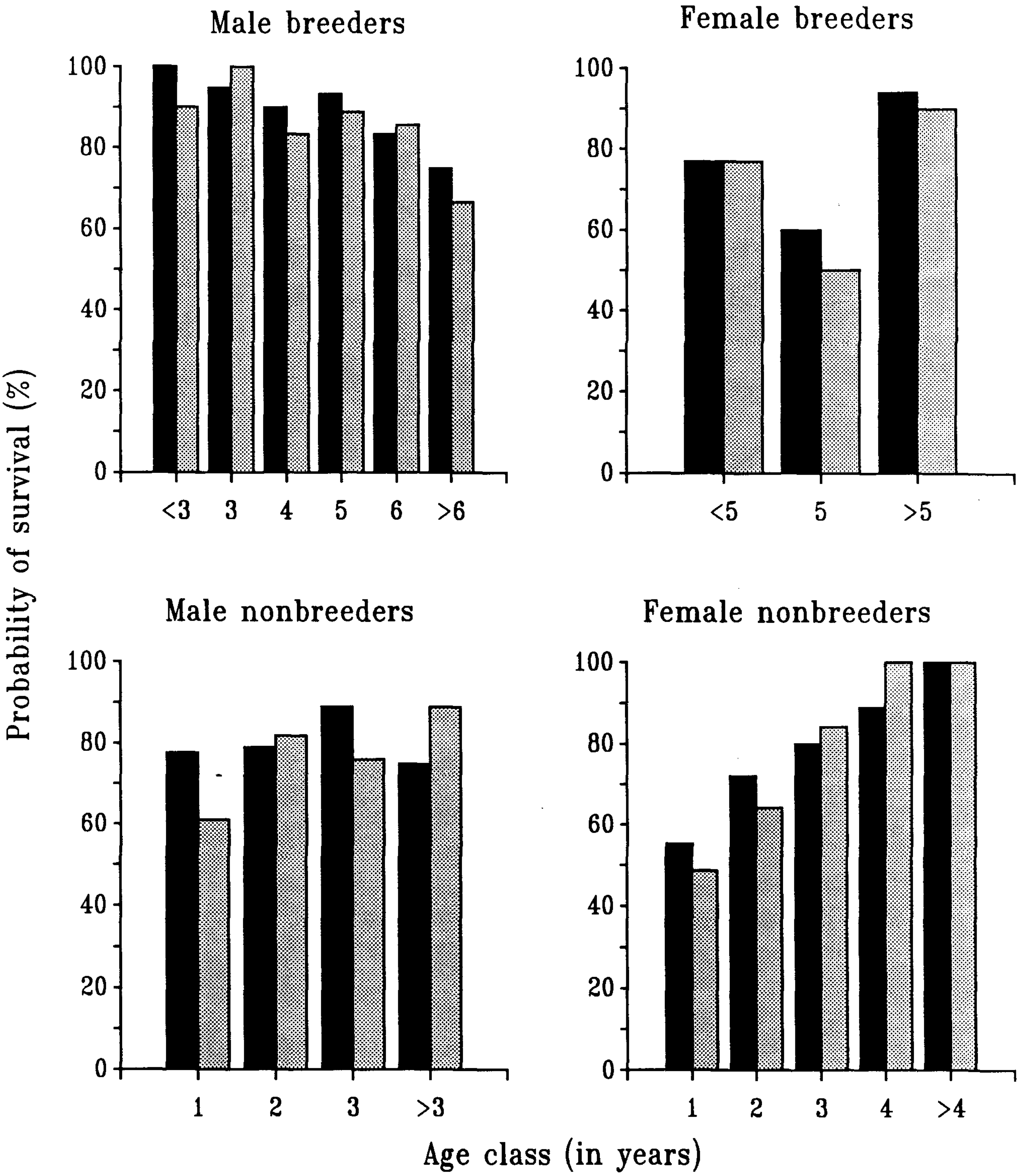

Figure 7.4. Relationship between age (in years) and survivorship of Redbilled Woodhoopoe breeders and nonbreeders of both sexes, at both coastal (black bars) and inland (stippled bars) study sites.

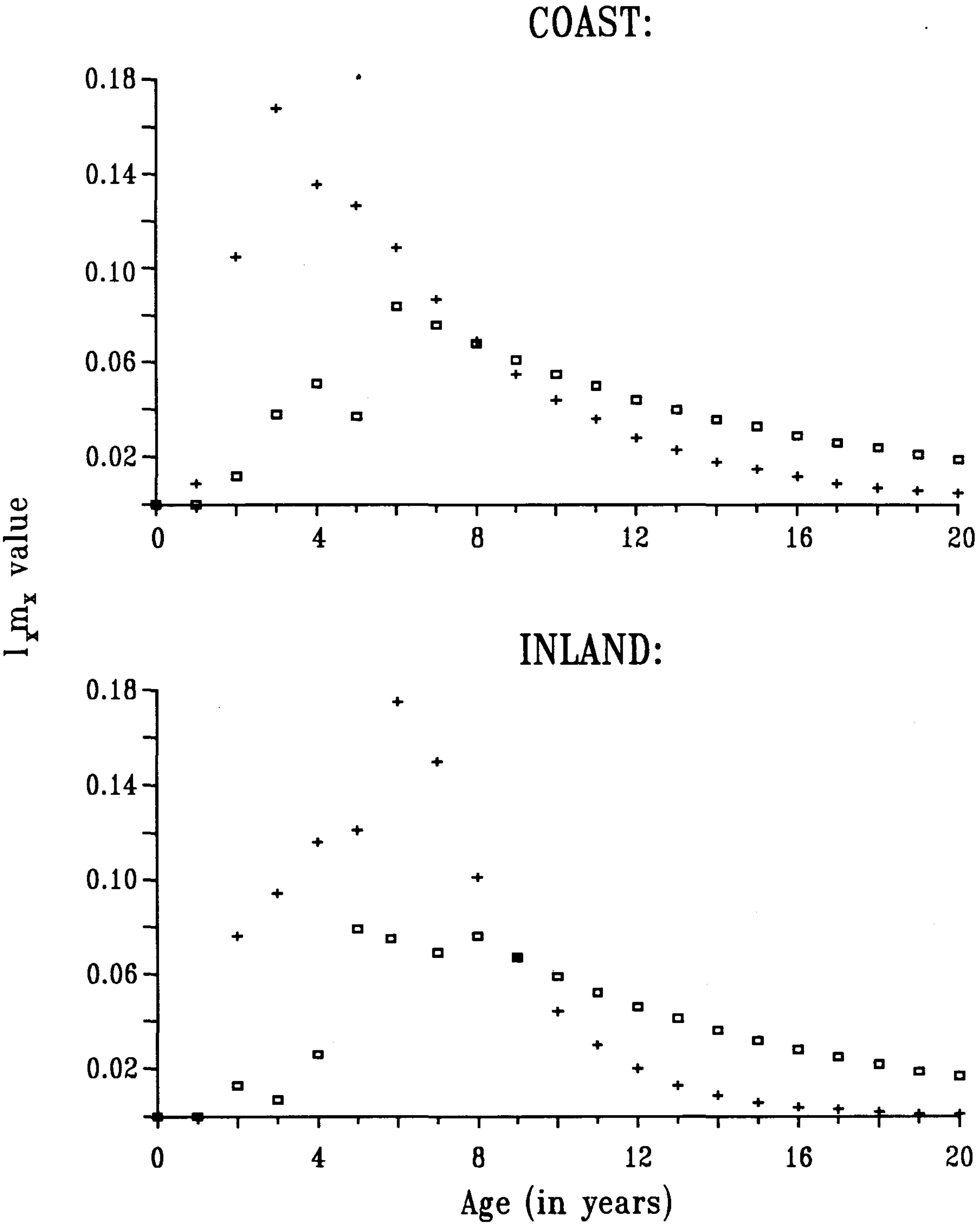

Figure 7.5. The observed $l_x m_x$ curves for males (crosses) and females (squares) at coastal and inland study sites. The areas under the curves indicate the contribution of that age class to the total reproductive output of the population.

At the coastal site the overall estimated net reproductive rate (R_0) for males and females was 1.085 and 0.952 respectively, compared to 1.033 and 0.820 at the inland site (Tables 7.5, 7.6, 7.7 & 7.8).

Mean generation times (T) for males were almost identical at both sites (5.439 *vs* 5.411 years), whereas coastal females had a shorter generation time than their inland counterparts (6.149 *vs* 9.923 years).

Reproductive values (V_x) for males and females followed similar patterns in both study populations (Figure 7.6). Females had higher reproductive values than males, and these generally peaked later in life (males: 4 years; females: 6 - 8 years).

DISCUSSION

Exogenous influences on fitness

Ligon (MS; pers. comm.) found that the amount of rainfall in the dry season preceding breeding negatively influenced reproductive success of woodhoopoes in Kenya. He suggested that high rainfall reduced the abundance of moth larvae, the main food brought to nestling woodhoopoes, by causing high mortality of moth pupae. Although lepidopteran larvae constituted only about 25% of food brought to nestlings at my study sites, a similar negative relationship between dry season rainfall and reproductive success existed at both coastal and inland sites (Chapter 6). However, the reproductive cycles of insects, other than lepidopterans, which are fed to nestling woodhoopoes need not be similarly affected by high rainfall during the dry season. Starvation was an uncommon cause of nestling mortality in my study sites, as in Kenya (Ligon & Ligon MS). The relationship may stem from other environmental factors which remain speculative, such as high parasite infestation levels following heavy dry season rains.

Table 7.5. Synthetic life table for coastal Redbilled Woodhoopoe females (starting with fledglings). The symbols used are: l_x = age-specific annual survivorship; l_x = cumulative survivorship to age x; d_x = proportion of birds surviving to age class x that are breeders; m_x = age-specific fecundity (female fledglings per female, or male fledglings per male); sum of $l_x m_x$ = net reproductive rate (R_0) (Ricklefs 1973); V_x = reproductive value (Fisher 1930).

Age	l_x	l_x	d_x	m_x	$\mathrm{l}_x m_x$	V_x
0-1	0.552	1.000	0.000	0.000	0.000	0.914
1-2	0.741	0.552	0.074	0.027	0.012	1.656
2-3	0.850	0.409	0.250	0.092	0.038	2.205
3-4	0.733	0.348	0.400	0.147	0.051	2.483
4-5	0.800	0.255	0.400	0.147	0.037	3.188
5-6	0.900	0.229	1.000	0.367	0.084	3.389
6-7	0.900	0.206	1.000	0.367	0.076	3.359
7-8	0.900	0.186	1.000	0.367	0.068	3.312
8-9	0.900	0.167	1.000	0.367	0.061	3.281
9-10	0.900	0.150	1.000	0.367	0.055	3.247
10-11	0.900	0.135	1.000	0.367	0.050	-
11-12	0.900	0.121	1.000	0.367	0.044	-
12-13	0.900	0.109	1.000	0.367	0.040	-
13-14	0.900	0.098	1.000	0.367	0.036	-
14-15	0.900	0.089	1.000	0.367	0.033	-
15-16	0.900	0.080	1.000	0.367	0.029	-
16-17	0.900	0.072	1.000	0.367	0.026	-
17-18	0.900	0.065	1.000	0.367	0.024	-
18-19	0.900	0.058	1.000	0.367	0.021	-
19-20	0.900	0.052	1.000	0.367	0.019	-
20-21	0.900	0.047	1.000	0.367	0.017	-
21-22	0.900	0.042	1.000	0.367	0.015	-
22-23	0.900	0.038	1.000	0.367	0.014	-
23-24	0.900	0.034	1.000	0.367	0.012	-
24-25	0.900	0.031	1.000	0.367	0.011	-
25-26	0.900	0.028	1.000	0.367	0.010	-
26-27	0.900	0.025	1.000	0.367	0.009	-
27-28	0.900	0.023	1.000	0.367	0.008	-
28-29	0.900	0.020	1.000	0.367	0.007	-
29-30	0.900	0.018	1.000	0.367	0.007	-
	...	...	...	...	...	
Total		4.691			0.952	

r_x = -0.008; f_x = 0.367; T= 6.149

Table 7.6. Synthetic life table for coastal Redbilled Woodhoopoe males (starting with fledglings). Symbols used are as for Table 7.5.

Age	l_x	l_x	d_x	m_x	$\mathrm{l}_x m_x$	V_x
0-1	0.780	1.000	0.025	0.009	0.009	0.985
1-2	0.867	0.780	0.367	0.135	0.105	1.379
2-3	0.929	0.676	0.679	0.249	0.168	1.438
3-4	0.870	0.425	0.870	0.319	0.136	1.875
4-5	0.938	0.369	0.937	0.344	0.127	1.807
5-6	0.800	0.296	1.000	0.367	0.109	1.819
6-7	0.800	0.236	1.000	0.367	0.087	1.815
7-8	0.800	0.189	1.000	0.367	0.069	1.825
8-9	0.800	0.151	1.000	0.367	0.055	1.828
9-10	0.800	0.121	1.000	0.367	0.044	1.818
10-11	0.800	0.097	1.000	0.367	0.036	-
11-12	0.800	0.077	1.000	0.367	0.028	-
12-13	0.800	0.062	1.000	0.367	0.023	-
13-14	0.800	0.050	1.000	0.367	0.018	-
14-15	0.800	0.040	1.000	0.367	0.015	-
15-16	0.800	0.032	1.000	0.367	0.012	-
16-17	0.800	0.025	1.000	0.367	0.009	-
17-18	0.800	0.020	1.000	0.367	0.007	-
18-19	0.800	0.016	1.000	0.367	0.006	-
19-20	0.800	0.013	1.000	0.367	0.005	-
20-21	0.800	0.010	1.000	0.367	0.004	-
21-22	0.800	0.008	1.000	0.367	0.003	-
22-23	0.800	0.007	1.000	0.367	0.003	-
23-24	0.800	0.005	1.000	0.367	0.002	-
24-25	0.800	0.004	1.000	0.367	0.001	-
25-26	0.800	0.003	1.000	0.367	0.001	-
26-27	0.800	0.003	1.000	0.367	0.001	-
27-28	0.800	0.002	1.000	0.367	0.001	-
28-29	0.800	0.002	1.000	0.367	0.001	-
29-30	0.800	0.001	1.000	0.367	-	-
Total		4.720			1.085	

r_x= 0.015; f_x= 0.367; T= 5.439

Table 7.7. Synthetic life table for inland Redbilled Woodhoopoe females (starting with fledglings). Symbols used are as for Table 7.5.

Age	l_x	l_x	d_x	m_x	$\mathrm{l}_x m_x$	V_x
0-1	0.486	1.000	0.000	0.000	0.000	0.794
1-2	0.650	0.486	0.025	0.013	0.006	1.634
2-3	0.842	0.316	0.000	0.000	0.000	2.494
3-4	1.000	0.266	0.083	0.044	0.012	2.962
4-5	0.778	0.266	0.556	0.297	0.079	2.917
5-6	0.882	0.183	0.857	0.098	0.018	3.809
6-7	0.882	0.161	0.800	0.428	0.069	4.217
7-8	0.882	0.142	1.000	0.535	0.076	4.296
8-9	0.882	0.125	1.000	0.535	0.067	4.272
9-10	0.882	0.111	1.000	0.535	0.059	4.207
10-11	0.882	0.098	1.000	0.535	0.052	-
11-12	0.882	0.086	1.000	0.535	0.046	-
12-13	0.882	0.076	1.000	0.535	0.041	-
13-14	0.882	0.067	1.000	0.535	0.036	-
14-15	0.882	0.059	1.000	0.535	0.032	-
15-16	0.882	0.052	1.000	0.535	0.028	-
16-17	0.882	0.046	1.000	0.535	0.025	-
17-18	0.882	0.041	1.000	0.535	0.022	-
18-19	0.882	0.036	1.000	0.535	0.019	-
19-20	0.882	0.032	1.000	0.535	0.017	-
20-21	0.882	0.028	1.000	0.535	0.015	-
21-22	0.882	0.025	1.000	0.535	0.013	-
22-23	0.882	0.022	1.000	0.535	0.012	-
23-24	0.882	0.019	1.000	0.535	0.010	-
24-25	0.882	0.017	1.000	0.535	0.009	-
25-26	0.882	0.015	1.000	0.535	0.008	-
26-27	0.882	0.013	1.000	0.535	0.007	-
27-28	0.882	0.012	1.000	0.535	0.006	-
28-29	0.882	0.010	1.000	0.535	0.005	-
29-30	0.882	0.009	1.000	0.535	0.005	-
	...	...	...	...	...	
Total		3.846			0.820	

r_x = -0.020; f_x = 0.535; T= 9.923

Table 7.8. Synthetic life table for inland Redbilled Woodhoopoe males (starting with fledglings). Symbols used are as for Table 7.5.

Age	l_x	l_x	d_x	m_x	$\mathrm{l}_x\mathrm{m}_x$	V_x
0-1	0.610	1.000	0.000	0.000	0.000	0.942
1-2	0.837	0.610	0.233	0.125	0.076	1.569
2-3	0.842	0.514	0.342	0.183	0.094	1.862
3-4	0.875	0.432	0.500	0.268	0.116	1.998
4-5	0.867	0.378	0.600	0.321	0.121	1.976
5-6	0.857	0.328	1.000	0.535	0.175	1.909
6-7	0.667	0.281	1.000	0.535	0.150	1.602
7-8	0.667	0.188	1.000	0.535	0.101	1.601
8-9	0.667	0.125	1.000	0.535	0.067	1.600
9-10	0.667	0.083	1.000	0.535	0.044	1.602
10-11	0.667	0.056	1.000	0.535	0.030	-
11-12	0.667	0.037	1.000	0.535	0.020	-
12-13	0.667	0.025	1.000	0.535	0.013	-
13-14	0.667	0.017	1.000	0.535	0.009	-
14-15	0.667	0.011	1.000	0.535	0.006	-
15-16	0.667	0.007	1.000	0.535	0.004	-
16-17	0.667	0.005	1.000	0.535	0.003	-
17-18	0.667	0.003	1.000	0.535	0.002	-
18-19	0.667	0.002	1.000	0.535	0.001	-
19-20	0.667	0.001	1.000	0.535	0.001	-
Total		4.103			1.033	

r_x= 0.006; f_x= 0.535; T= 5.411

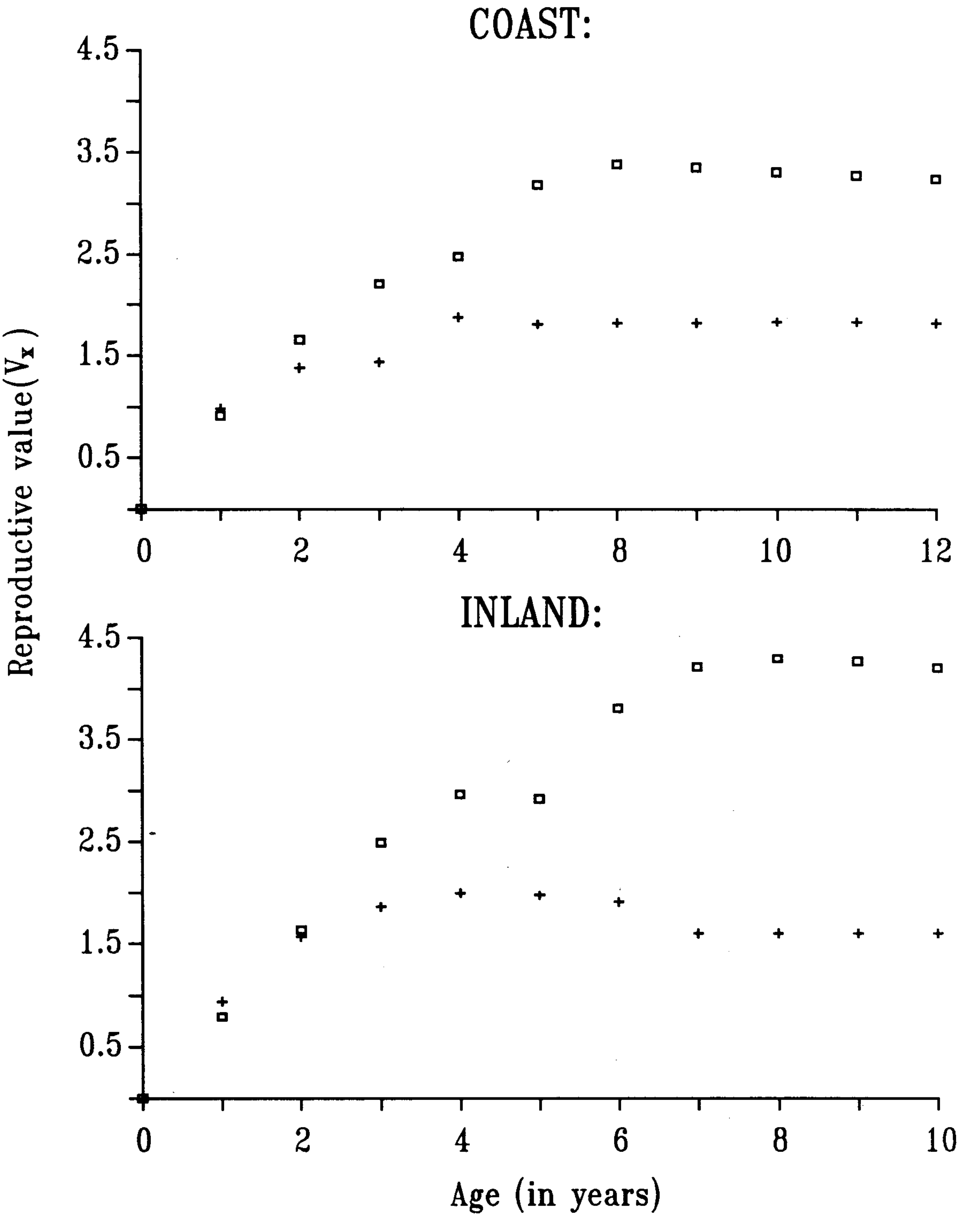

Figure 7.6. Age-specific reproductive value (V_x) for males (crosses) and females (squares) at both the coastal and inland sites

In addition to the rarity of chick mortality through starvation, two lines of evidence suggest that food was not a limiting factor at the coastal study site. Firstly, territory boundaries are traditional, and change only when an entire flock disappears from a territory (presumably through predation), which happens rarely. Secondly, territory boundaries do not change with flock size. At no time during the study period was there a correlation between flock and territory size.

At the inland site, vegetation composition of territories differed widely (Chapter 1), thereby complicating the relationship between flock and territory size. However, the feeding rates of woodhoopoes at the two study sites were almost identical during the nonbreeding season (Feb. - Oct.) (unpubl. data). The only detectable difference in the feeding behaviour of birds between the sites was that flocks at the inland site moved over greater distances than coastal flocks during a day's foraging. This difference reflects lower tree densities (and hence foraging surface area) at the inland site (Chapter 1). Average territory size inland was therefore larger than at the coast. However, at both sites territory size remained relatively constant with time, and changes in flock size.

Endogenous influences on fitness

Most woodhoopoes obtain breeding status in the natal flock rather than elsewhere. However, breeding success and survivorship were equal for 'dispersers' and 'non-dispersers', indicating that the advantage of residency is not fecundity *per se*. It is difficult to explain the exception to this pattern (i.e. coastal males), but it may have been influenced by the inclusion of data concerning emigrants which attempted to breed in 'ephemeral territories' (*sensu* Chapter 1).

The reproductive success of Florida Scrub Jays with helping experience is higher than that of inexperienced ones, although not significantly so (Woolfenden & Fitzpatrick 1984). Koenig & Mumme (1987) showed, for Acorn Woodpeckers, that prior helping experience was not critical to successful reproduction, but suggested that the experience gained as a result of helping could still contribute to subsequent breeding success.

Woodhoopoes breeding for the first time were as successful as more experienced ones (Chapter 8). Therefore, delayed breeding in this species should not maximise lifetime reproduction, but curtail it (Nol & Smith 1987; but see Williams 1966; Curio 1983). This result also confounds the helper-experience hypothesis because, even if age affects reproductive success independently of helper experience, it fails to explain why an individual does not attempt to gain such experience by breeding itself, thereby increasing its own direct fitness. Thus, I reject the postulated benefit of experience gained by a nonbreeder through aid-giving as having been an important factor in the evolution of cooperative breeding in woodhoopoes.

Fitness consequences of group size

Rather than being responsible for raising larger broods, large flocks had a greater probability of fledging at least one young than did small flocks. I suggest that this difference is best explained by greater vigilance and more efficient anti-predatory behaviour of larger flocks around the nest. Most predation attempts at the nest were made by snakes and Harrier Hawks (Gymnogenes) *Polyboroides typus*, birds with highly flexible tarsal joints that enable them to reach deep into holes. Mobbing is probably a more effective deterrent to snakes than to Harrier Hawks. Such benefits of large group size were not detectable at the coast. At the coast, nest flooding rather than predation was the main cause of nest failure and acted independently of group size.

The use of averages in assessing reproductive performance can obscure subtle effects provided by environmental conditions in different years (Brown &

Brown 1984). However, at neither site was there a significant correlation between reproductive success and flock size in any one year.

The probability of a fledgling reaching reproductive maturity was unaffected by the presence or absence of helpers at either site. In order to establish whether the above survival values were artifacts of early, undetected dispersal, survivorship to the age of six months was considered. Observation of a total of 256 dispersal forays and 72 successful dispersal events over a period of eight years, indicated that no dispersal occurred in the first eight months after fledging (Chapter 2). Fledgling survival to six months was negatively correlated with group size at the inland site.

If food was a limiting factor during the nonbreeding season in some years, large flocks should attempt to increase their territory size accordingly as they are able to dominate smaller groups in (ritualized) boundary contests (Chapter 5). This was not the case. However, the relatively large distances that inland flocks cover while foraging, could make them more vulnerable to predation. Large flocks would be forced to move more frequently from tree to tree and over greater distances, as a result of localized prey depletion and widely dispersed prey. The mortality of juveniles, which cannot fly as strongly as adults until they are at least six months old, could be a result of predation during these foraging movements.

A universal and widespread cost of group living is increased transmission of ectoparasites and disease (Alexander 1974; Brown & Brown 1988). However, it was shown that woodhoopoes in large flocks do not have higher ectoparasite loads than those in small flocks, because of the presumed functional benefits of non-reciprocal allopreening (Chapter 3). However, although the disadvantages of postulated higher ectoparasite loads associated with large flocks should hold true for the coastal population, it does not.

The consequence of the pattern of high fledgling production and low juvenile survivorship at the inland site is a net productivity equal to that at the coastal site.

Large flocks have the potential for producing more surviving offspring than small flocks, but this apparently is nullified by environmental factors. Release from such constraints on juvenile survivorship may result in a selective advantage for flocks with helpers. However, such benefit was never realized during the present study.

Brown (1987) cautioned that even production of mature offspring is not a reliable index of breeder fitness in communal birds. Many mature birds in communal species do not achieve breeding status at all. In a heavily age-structured population, the ideal currency of fitness would be the number of 'breeder-equivalents' or the number of 'grandchild-equivalents' (Woolfenden & Fitzpatrick 1984), in preference to any of the previous estimates. These measures would more closely correlate with the actual replication of genetic material through successive generations, but no such data have been published for any cooperatively-breeding vertebrate species.

One would predict that individuals originating from small flocks stand a proportionately better chance of inheriting breeding status in the natal flock than those originating from large flocks, due to a 'queue-effect'. Additionally, large flocks should provide proportionally more breeder-offspring that acquire breeding status elsewhere than do small flocks, since some small flocks do not have potential 'candidates'.

These theoretical predictions are well supported by empirical data from both study sites (Table 7.4). However, at the inland site, offspring originating from flocks without helpers invariably acquired breeding status in the natal flock, suggesting that it is profitable for an individual to remain in the natal flock and to disperse only when a breeding vacancy occurs elsewhere. The tolerance by breeders of offspring in the natal flock therefore facilitates the chances of such individuals eventually obtaining breeding status. The above differences between the two sites provides further support for the hypothesis that the inland population is more severely constrained by roost-cavity availability and dispersion than their coastal counterparts (Chapter 2).

Game theory (Maynard Smith 1982) would predict that all individuals should disperse if they could improve their social status (and thus decrease their 'distance' from breeding status), provided that dispersal does not hold a significant mortality risk. Such a dispersal strategy would tend towards equalization of flock sizes. However, flock size equalization did not occur at either site, suggesting that benefits of such dispersal were counterbalanced by substantial risks. Dispersal takes place less frequently and over smaller distances inland than at the coast (Chapter 2). This was ascribed largely to differences in roost-cavity dispersion and availability. Individuals from large flocks generally were more successful at establishing themselves as breeders in non-natal flocks than were birds from small flocks. Upon the death of a breeder, small flocks were sometimes in the position where no members of the deceased bird's sex were present to replace it from within the flock.

It appears as if birds originating in large flocks take the dispersal option more frequently than their small-flock counterparts. It may be a more advantageous strategy for individuals from small flocks to opt for queueing for a breeding vacancy in the natal flock, than to disperse. To test this hypothesis data are required on the frequency with which birds, originating from flocks of different sizes, undertook scouting forays in search of breeding vacancies. After eight years, I still do not have enough such data, as it was often not possible to determine the flock of origin of scouts.

It has long been suspected that survivorship of cooperative breeders may be enhanced by living in groups. However, few studies have addressed this question empirically, and some found no evidence of higher survival among birds in larger groups (e.g. Redbilled (Green) Woodhoopoes, Ligon & Ligon 1978a, this study; Groovebilled Anis *Crotophaga sulcirostris*, Vehrencamp 1978; Stripebacked Wrens *Campylorhynchus nuchalis*, Rabenold & Christensen 1979; and, Galapagos

Mockingbirds *Nesomimus parvulus*, Kinniard & Grant 1982). Three recent studies, however, have demonstrated a significant positive relationship between group size and breeder survivorship (Florida Scrub Jays *Aphelocoma coerulescens*, Woolfenden & Fitzpatrick 1984; Pied Kingfishers females *Ceryle rudis*, Reyer 1984; and, Acorn Woodpeckers males *Melanerpes formicivorus*, Koenig & Mumme 1987).

Several advantages have been attributed to living in groups: (1) location of concentrated food sources (Brown 1987); (2) increased vigilance (Ferguson 1987, and references therein); (3) more successful harassment of predators (Brown 1978, 1987); and (4) physiological benefits of communal roosting (Ligon *et al.* 1988; Ligon & Ligon 1988). Proposed benefits of group living should translate into some measurable fitness improvement as manifested in life-history characteristics of a population. Survivorship of breeders and nonbreeders could be regarded as one such parameter.

In woodhoopoes there was no correlation between breeder and nonbreeder survivorship and flock size at either study site. This may have been the result of several factors:

1) Woodhoopoe food resources were not clumped; i.e. all individuals did not necessarily benefit when one found a prey item.

2) Increased group vigilance in larger groups (Rasa 1986) may have been counterbalanced by increased conspicuousness (in particular loud vocal displays), and hence attraction of predators.

3) Predator harassment is effective against snakes near the nest cavity during the breeding season, but apparently not against diurnal avian or nocturnal mammalian predators. Harassment of snakes may increase nestling survival (see above), but is unlikely to affect adult survival.

4) A strong case has been put forward to explain cavity-roosting behaviour of Redbilled Woodhoopoes in terms of energetic benefits obtained by roosting with conspecifics (Ligon *et al.* 1988). Although this may be true in some areas, such benefits are not realized in terms of survivorship, as this is unrelated to flock size in both the Kenyan and two South African study populations (Ligon 1978a; this study).

The significance of relatedness between breeders and nonbreeding helpers has been disputed. Ligon & Ligon (1983) reported that in 8% of cases, Redbilled Woodhoopoe helpers were unrelated to the young they fed and used this as an argument against the role of indirect selection in the evolution of helping in this species. However, Brown (1987) argued that the low incidence (i.e. 8%) of nonbreeding birds feeding unrelated young makes it unnecessary for individuals to assess fine gradations of relatedness. Data from both my woodhoopoe study populations suggested that the incidence of unrelatedness was slightly higher than that in the Kenyan population (coast: 10.8%; inland: 10.9%). Brood parasitism contributed even further to this component of unrelatedness (coast: 11.0%; inland: 6.8% of flocks successfully raising at least one heterospecific fledgling). However, the average relatedness between individuals within a flock remained high as a result of frequent inbreeding (e.g. father x daughter) (Chapter 8), largely due to obligate group living because of patchily distributed roost cavities (Chapter 2).

Survivorship

Other studies of breeder survivorship have reported either identical values for males and females (0.82, Florida Scrub Jay, Woolfenden & Fitzpatrick 1984), higher survivorship values for males (0.84 *vs* 0.72, Acorn Woodpecker, Koenig & Pitelka 1987), or lower survivorship values for males (0.62 *vs* 0.70; 0.86 *vs* 0.88; 0.83 *vs* 0.85, Redbilled Woodhoopoes, Ligon & Ligon 1988; this study: coast, inland).

Among Kenyan woodhoopoes nonbreeding adult survivorship of males was higher than females (0.60 *vs* 0.67) (Ligon & Ligon 1988). Comparative values for the South African populations were higher (coast: 0.80 *vs* 0.79; inland: 0.78 *vs* 0.81), and of the same magnitude as the difference between male and female breeders (although reversed for inland males and females). Survival differences within and between the South African study populations were, however, very small.

In Kenya, survivorship of first year males was lower than that of females (0.61 *vs* 0.73) (Ligon & Ligon 1988). The reverse was true at South African study sites (coast: 0.75 *vs* 0.57; inland: 0.61 *vs* 0.52).

Ligon (1981) suggested that the differences in survivorship between sexes was 'probably related to the larger size of males and the consequent usage by them of roost cavities that are less predator proof than those most often used by females' (see also Appendix 2: 257). He therefore related the almost identical intrasexual mortality rates of individuals of different age and social classes to the effects of nocturnal roost-site predation.

Woodhoopoes almost never split into single-sex groups to roost at the two South African sites (Appendix 2), which may partly explain the small intersexual differences in adult survivorship compared to that reported from Kenya, where single-sex roosts are the norm (Ligon & Ligon 1978a, 1988). Juvenile males are bigger than their female counterparts and outreach them for food in the nest. Fledgling males were stronger fliers in the first few weeks after fledging (pers. obs.), and I propose that this difference confers a survival advantage on young males.

Life-table analysis

Cooperative breeders offer a number of complications to traditional life-table analysis. The proportion of individuals breeding cannot be assumed to be a simple step-function, as in species in which all surviving individuals reach reproductive maturity and breed at the same age. Also, survivorship of a cohort varies depending on the proportion of individuals that are breeders and nonbreeders. However, with appropriate modifications, such problems can and have been overcome (Florida Scrub Jay: Woolfenden & Fitzpatrick 1984; Acorn Woodpecker: Koenig & Mumme 1987).

The $l_x m_x$ schedule for woodhoopoes was skewed towards older age classes and compares with those of Florida Scrub Jays and Acorn Woodpeckers (*opp. cit.*). Reproductive output peaked earlier in males than females, but the latter maintained a relatively high productivity for longer. This could be related to the earlier age at first reproduction of males (26 - 30 months *vs* 46 - 51 months) (Chapter 2), and the high survivorship experienced by old (> 5 years) breeding females (see Tables 7.5, 7.6, 7.7 & 7.8).

Mean generation time of females (T) was longer than that of males at both sites as a result of their higher sustained survivorship. Results for female Redbilled Woodhoopoes and Florida Scrub Jays, the only other singular, cooperatively-breeding species (*sensu* Brown 1987) for which comparative data are available, were similar (Redbilled Woodhoopoes: T= 6.15 - 9.92, this study; Florida Scrub Jays: T= 7.26, Woolfenden & Fitzpatrick 1984).

The reproductive value (V_x) of an individual is derived from its expectation of future offspring production weighted by the fact that the value of young born at subsequent ages decreases in growing populations and increases in declining populations (Ricklefs 1973). The difference in the value of V_x between sexes, at both woodhoopoe study sites, was a result of such weighting. Over the eight years covered by the study, male populations showed signs of growth, whereas females showed the opposite. This could be attributed to differences in juvenile mortality rates during the study period (males: 61 - 78%; females: 49 - 55%).

Life-history evolution

A major problem in interpreting field observations of interpopulation variation in life history is the difficulty in distinguishing whether causative agents are genetic or environmental. Baird *et al.* (1986) showed that it is quite possible that the range of life-history characteristics reported for a species between different sites could fall within the range of environmentally induced variability at a single site.

Life-history traits of natural populations have been examined in the context of life-history theory in several interspecific mammalian studies (see Zammuto 1987). However, few studies have examined life history traits in more than one population of a single species. Any realistic assessment of the reproductive or life history patterns of animals depends not only on breeding performance in individual years, but on total lifetime reproductive output (Stearns 1976; Kemp 1984). Few such data are available for birds.

Survival rates of woodhoopoe females at both sites increased slightly with age, presumably due to the acquisition of breeding status. This is not entirely consistent with the view that older individuals should exhibit greater reproductive effort than yearlings because of their lower probability of survival and hence, future breeding opportunities (Williams 1966; Pianka & Parker 1975). The case for males remained equivocal, as differences in survival patterns existed with age.

In a study of a Redbilled Woodhoopoe population in Kenya, Ligon & Ligon (MS) found that unassisted pairs rarely bred successfully, and then only under a combination of 'unusual conditions'. They also suggested that, under favourable conditions, helpers allowed breeders to renest more frequently. These observations contrast markedly with the South African situation, where unassisted pairs frequently bred successfully, and none breed more than once per year. If food is the factor constraining breeding success in Kenya, and food availability determines whether large flocks renest in good seasons (Ligon & Ligon MS), it poses a paradox.

Why don't large flocks in the two South African populations breed more than once a year during most or all years, since food apparently is not limiting? At present productivity levels (i.e. one breeding attempt per year) and relatively high survivorship of adults (78 - 88%), between 40 and 60% of individuals that reach sexual maturity never get the opportunity to breed. This suggests that breeding effort may be regulated by density-dependent factors (see Figure 7.1).

General discussion

The effect of aid provided by helpers on the reproductive success of breeders determines not only the advantage to the breeder, but also influences the trade-off for the helper between remaining in the natal territory or dispersing. Criticisms of studies in which helpers were found to contribute little or no benefit to the lifetime reproductive success of recipients (*sensu* Zahavi 1974; Gaston 1978; Ligon & Ligon 1978a; Craig 1979), include chance, small sample size, high variance, aberrant study periods, effects of heavy and erratic predation, or that researchers measured the wrong component of recipient fitness (Brown 1987).

This study provides no support to the hypothesis that the presence of nonbreeding helpers enhances reproductive (hence genetic) output of Redbilled Woodhoopoe flocks. Bearing Brown's criticisms of other studies in mind, I speculatively offer a number of plausible explanations of the apparent lack of indirect fitness benefits of group living and alloparental feeding behaviour by Redbilled Woodhoopoes.

(1) The South African populations were studied at the southern limit of the species' range. Group living and alloparental feeding behaviour must have evolved under conditions where inclusive fitness of individuals was increased in the ancestral population. Even though Ligon & Ligon (MS) report that in Kenya (at the centre of this species' present range) unassisted Redbilled Woodhoopoe pairs without helpers

have a low probability of breeding at all (owing to the difficulty of holding a territory), and that under favourable conditions helpers may allow breeders to nest more frequently. However, they found no relationship between number of helpers and number of young produced per year (Ligon & Ligon 1978a, MS; Ligon 1981;). More data on the effects of group size on survivorship and the production of breeder-offspring in Kenya, could cast more light on this apparent paradox.

2) If it is selectively neutral during typical years (no cost, no benefit), but beneficial in atypical years, then group living has a selective advantage. However, my data over a study period of eight years, involving 258 'flock-years' at two study sites, did not include such an exceptional season, and only studies over a time period more closely approaching that of an individual's maximum longevity (20 - 30 years), could test this hypothesis. The situation at the inland site would favour the 'atypical year' hypothesis, since the production of more fledglings by larger groups at the inland study site could provide, at best, the potential for more young (in absolute terms) to be raised to independence. An 'atypical year' in this case would be one in which larger flocks were released from the factor(s) suppressing survivorship of young to reproductive maturity, particularly during the first six months of life.

3) A model of 'parental facilitation' was proposed in which it is not necessary for helpers to increase the reproductive success or the survival of the parents for the parents to benefit from retaining their offspring in the natal territory (Brown & Brown 1984). If retention of offspring in the natal flock improves survivorship of these offspring by reducing pressure for early dispersal, then a direct fitness benefit to the breeder is obtained. Here, the assumption is made that dispersal risks are minimized by nonbreeders leaving the natal flock only when vacancies occur elsewhere. Under this hypothesis the parents can even experience a small non-altruistic reduction in lifetime reproductive success and still profit in direct fitness. The parent may profit by substituting a smaller quantity of high quality offspring for a large quantity of low quality offspring (*sensu* Brown 1987). My data for lifetime

reproductive success of the second generation are too few to test this hypothesis conclusively, but it is not entirely supported by comparative data of the production of breeder-offspring by flocks with, and those without helpers at both study sites.

I propose that as suitable habitat became saturated with woodhoopoe-territories in the evolutionary past, initial selection was for tolerance of nonbreeding flock members in the natal territory. This is best explained by the parental facilitation model, and the selective benefits gained as a result of such tolerance. However, the parental facilitation hypothesis does not explain alloparental behaviour, as it does not require nonbreeding helpers to increase the reproductive success of recipient breeders.

4) Ligon (1981,1983) and Ligon & Ligon (1978b, 1983, 1988) have made a strong case for alloparental behaviour of nonbreeding Redbilled Woodhoopoes providing reciprocal benefit to donor and recipient nestling. They argued that young individuals return the help that older nonbreeders provide them during their nestling and fledgling stages by later assisting such individuals to acquire and retain breeding status in a non-natal flock. This explanation is based on the occurrence of social dispersal (i.e. when an individual disperses together with subordinate flock mates). Such dispersal was not witnessed in either of my study sites (Chapter 2). It seems improbable that score-keeping reciprocity would be maintained in a population with survivorship as low as that of Kenyan woodhoopoes (60 - 70%). Additionally, unrelated birds, with no known previous interaction between them, occasionally joined forces to secure a breeding vacancy (Ligon & Ligon 1978a, MS; Ligon 1981; Chapter 9), suggesting that subordinates willingly aid dominants, whether they had been fed by the dominant or not.

5) Helping behaviour can be regarded as misdirected parental care (Williams 1966; Price *et al.* 1983) 'that is maintained by the same stimulus-response mechanism that results in parents feeding their own young or a host species feeding parasitic young'. There is no reasonable adaptive explanation for such behaviour

(Jamieson & Craig 1987; Jamieson 1988, 1989). For both Florida Scrub Jays and Acorn Woodpeckers, the two most extensively studied cooperatively-breeding species, it has been suggested that helping *per se* may not necessarily be of selective advantage, and may be selectively neutral (Woolfenden & Fitzpatrick 1984; Koenig & Mumme 1987). If reciprocity is excluded as an explanation of helping behaviour of Kenyan Redbilled Woodhoopoes (*contra* Ligon 1981, 1983; Ligon & Ligon 1978b, 1983, 1988), then the non-selective hypothesis would best explain helping behaviour. This hypothesis cannot be rejected out of hand (at least for Redbilled Woodhoopoes), since there was little evidence for nonbreeding woodhoopoe helpers gaining indirect fitness benefits as a result of helping behaviour.

I suggest that woodhoopoe breeders tolerate the presence of nonbreeding helpers (usually offspring) in their territories because there is no within-group conflict over a particular resource, such as food. The availability of suitable roost cavities appears to be a limiting resource for Redbilled Woodhoopoes (Ligon & Ligon 1988; Chapter 1). This should not present the potential for within-group conflict in itself as up to ten birds roost together in a single cavity (Appendix 2). If some resource is limiting and individuals compete for it within a territory, the tolerance of nonbreeding birds by breeders should be selected against, unless the additional nonbreeding flock members contribute to the breeders' inclusive fitness in some way. When some resource, such as food, that holds the potential for within-group conflict is limited, a positive contribution to the breeders' inclusive fitness is a prerequisite for nonbreeder flock-membership. Such benefit need not be related to alloparental care *per se*.

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Appendix 7.1. Inter-annual variations in fledgling production of Redbilled Woodhoopoes at the coastal and inland study sites.

Year	Fledglings per flock (x ± SD)	% flocks successful	N
Coast:			
1981	0.333 ±0.707	22.2	9
1982	0.500 ±0.707	40.0	10
1983	1.417 ±1.564	58.3	12
1984	0.714 ±0.825	50.0	14
1985	0.818 ±1.006	50.0	22
1986	0.586 ±0.825	37.9	29
1987	0.760 ±1.128	44.0	25
1988	0.857 ±1.014	47.6	21
Total		44.4	142
Inland:			
1981	1.000 ±0.894	66.7	6
1982	1.667 ±1.366	83.3	6
1983	1.500 ±1.225	83.3	6
1984	0.857 ±0.900	57.1	7
1985	1.500 ±1.147	80.0	20
1986	1.000 ±1.022	58.3	24
1987	1.304 ±1.185	56.5	23
1988	0.545 ±0.912	31.8	22
Total		59.6	114

Appendix 7.2. Summary of the causes of Redbilled Woodhoopoe nest mortality at the coastal and inland study sites respectively (coast: n= 79; inland: n=46).

Losses due to:	% of nests		
	Coast	Inland	
Nest-site competition	12.7	15.2	**n.s.**
Predation	17.7	37.0	*
Cavity failure:			
disintegration	5.1	2.2	**n.s.**
flooding	11,4	0	*
Hatching failure	6.3	4.3	**n.s.**
Desertion	2.5	2.2	**n.s.**
Adult death	1.3	0	**n.s.**
Starvation	0	2.2	**n.s.**
Brood parasitism	10.1	10.9	**n.s.**
Unknown	19.0	17.4	**n.s.**
No known nesting attempt	13.9	8.6	**n.s.**

Statistic (Chi-square):

*	P< 0.001
n.s.	not significant

Appendix 7.3. Mean annual survivorship of Redbilled Woodhoopoes at the coastal study site.

	Flock size				
	2	3	4	>4	Total
Breeding males:					
Survived	52	33	24	14	123
Died	7	5	4	4	20
% survival	88.1	86.8	85.7	77.8	86.0
Breeding females:					
Survived	56	31	24	15	126
Died	3	6	6	2	17
% survival	94.9	83.8	80.0	88.2	88.1
Nonbreeding males:					
Survived	-	10	10	7	27
Died	-	4	1	2	7
% survival	-	71.4	90.9	77.8	79.4
Nonbreeding females:					
Survived	-	13	16	16	45
Died	-	1	3	7	11
% survival	-	92.9	84.2	69.6	80.4
First year males:					
Survived	-	9	17	10	36
Died	-	3	2	7	12
% survival	-	75.0	89.5	58.8	75.0
First year females:					
Survived	-	2	10	12	24
Died	-	4	4	10	18
% survival	-	33.3	71.4	54.5	57.1

Appendix 7.4. Mean annual survivorship of Redbilled Woodhoopoes at the inland study site.

	Flock size					
	2	3	4	5	>5	Total
Breeding males:						
Survived	17	21	29	16	15	98
Died	2	9	1	6	2	20
% survival	89.5	70.0	96.7	72.7	88.2	83.0
Breeding females:						
Survived	16	23	25	20	15	99
Died	3	4	4	2	2	15
% survival	84.2	85.2	86.2	90.9	88.2	85.3
Nonbreeding males:						
Survived	-	9	21	14	19	63
Died	-	0	4	5	6	15
% survival	-	100.0	84.0	73.7	76.0	80.8
Nonbreeding females:						
Survived	-	10	18	19	22	69
Died	-	2	5	4	8	19
% survival	-	83.3	78.3	82.6	73.3	78.4
First year males:						
Survived	-	3	9	12	11	34
Died	-	1	2	4	15	22
% survival	-	75.0	81.8	75.0	42.3	60.7
First year females:						
Survived	-	3	11	10	13	37
Died	-	0	6	10	18	34
% survival	-	100.0	64.7	50.0	41.9	52.1

CHAPTER 8

HELPING AT THE NEST: A TEST OF HYPOTHESES

SUMMARY

Several hypotheses have been erected to explain the origins of helping behaviour in cooperatively-breeding birds. The following hypotheses were tested for Redbilled Woodhoopoes *Phoeniculus purpureus*: (1) experience in feeding young improves a helper's later reproductive success; (2) social ties are formed between donor and recipient, which later provide reciprocal benefit to helpers; (3) a helper's indirect fitness may benefit from helping close relatives; (4) helping may decrease the predation risks created by begging young by silencing them; (5) helping increases the probability of acquiring a mate; (6) helping advertises dominance status; (7) helping is an unselected consequence of parental care ('misdirected parental care').

Prior helping experience did not improve the reproductive success of individuals during their first, compared to subsequent, breeding attempts. Twenty percent of donors were unrelated to recipients - the highest published value to date. Social dispersal did not occur and thus there were no opportunities for subsequent reciprocity between donors and recipients. There were no apparent fitness benefits reflected in breeding success, survivorship, or the number of breeder-offspring produced by flocks with and without helpers. Helpers did not avoid begging chicks by moving away from the 'zone of predator attraction'. Immigrants were accepted as breeding partners even though their helping capabilities were unknown. These results were not in accordance with most of the predictions of the experience, social bonding, indirect fitness, predation-avoidance, or mate-acquisition hypotheses. Old nonbreeding females made a large contribution to helping, consistent with the advertising hypothesis. However, there was no positive relationship between male dominance and helping behaviour. The occurrence of interspecific feeding (including brood parasitism), the relatively high incidence of unrelatedness between donor and recipient, and stimulus/response experiments support the hypothesis that helping represents misdirected parental care.

INTRODUCTION

Three attributes associated with most communal breeding systems are delayed dispersal, delayed breeding and helping. Delayed dispersal and breeding reflects ecological constraints (Selander 1964; Brown 1974, 1987; Stacey 1979; Koenig & Pitelka 1981; Emlen 1982; Koenig & Mumme 1987). Although the benefits of helping behaviour (given constraints on dispersal) seem intuitively obvious, several detailed studies have failed to demonstrate that these positive benefits exist (Zahavi 1974; Gaston 1978; Ligon & Ligon 1978a; Ligon 1981).

Several hypotheses have been proposed to account for the evolution of helping behaviour. (1) A helper may gain experience in feeding young and hence improve its later reproductive success (Rowley 1977; Brown 1987). (2) Social ties may be formed between donor and recipient and the latter may later assist the former in acquiring a breeding vacancy ('reciprocal altruism', *sensu* Ligon & Ligon 1978b, 1983, 1988; Ligon 1981, 1983). (3) A helper's indirect fitness (*sensu* Brown 1980) may benefit through increasing the reproductive success of a close relative (Hamilton 1964; Reyer 1980, 1984; Curry 1988; Emlen & Wrege 1988; Clarke 1989). (4) By feeding begging chicks a helper reduces noise at the nest and hence reduces audible cues to potential predators (Caraco & Brown 1986). (5) A helper may be more likely to acquire a mate (Woolfenden & Fitzpatrick 1984; Emlen *et al.* 1986), in that they sometimes mate with a breeder they have helped (e.g. Reyer 1980). (6) Helping may serve to advertise or improve dominance status of an individual within the group by attracting collaborators and deterring rivals (Zahavi 1976; Emlen 1978; Carlisle & Zahavi 1986). (7) Helping has no adaptive value *per se*, but is a response to begging stimuli from the chicks and represents 'misdirected parental care' (Williams 1966; Price *et al.* 1983; Woolfenden & Fitzpatrick 1984; Ligon 1985; Jamieson 1986, 1989a; Jamieson & Craig 1987; Koenig & Mumme 1987).

Redbilled (Green) Woodhoopoes *Phoeniculus purpureus* live throughout the year in flocks of two to 12 birds, containing only a single breeding pair. Nonbreeding flock members, usually (but not always) relatives of one or both breeders, are full participants in all flock activities, including food provisioning and care of young (Ligon & Ligon 1978a; Chapter 4).

The aim of this study was to test the applicability of the above hypotheses in explaining the origins of helping behaviour in Redbilled Woodhoopoes.

METHODS

Demographic data were gathered between 1981 and 1989 for Redbilled Woodhoopoe populations at Morgan's Bay (32°43'S, 28°19'E) and in the Kubusi River Valley (32°32'S, 27°47'E), in the eastern Cape Province of South Africa (Chapter 1).

Because of variability in age at first breeding, a distinction was made between the effects of age and breeding experience on reproductive success. Nonbreeders invariably assisted breeders during their reproductive efforts, but more than 50% of all breeding attempts failed. Since it is impossible to quantify the experience gained by helpers at failed nests, experience was considered to be related to age. The experience gained by a helper was restricted not only to food provisioning behaviour during breeding, but to general foraging skills and anti-predatory behaviour in the non-breeding season. The age at first breeding was therefore regarded as an index of experience. Relatedness was assigned only to individuals of known parentage.

Experiments, involving food provisioning stimuli, were undertaken with birds breeding in nest-boxes in 1987 and 1988. These experiments were done in territories outside the main study areas and these birds were not included in demographic analyses.

A clay model of a begging woodhoopoe was attached to the inside of a nest-cavity entrance. Two models were shaped and painted to represent a begging chick and a begging adult. A third model was of a begging adult female, but the gape was painted green, not flesh-coloured. A model was placed in position between 0600 and 0800 h and the flock was given 30 minutes to settle down before observations began. Observations were made from 20-30 metres away (Chapter 6) and lasted for 30 minutes per nest per day. Four observation periods were made for each experimental treatment at each of two nests (A and B). No nest was manipulated on two sucessive days. Nestlings produced sounds that were audible outside the nest at 2-3 days after hatching. Begging calls of nestlings were recorded and a 30 minute sequence of continuous begging calls was used during playback experiments.

Manipulations were done in the following ways: (1) using only visual stimuli - by removing the fledgling(s) from the nest and placing a clay model at the nest-cavity entrance; (2) using only vocal stimuli - by removing all supports inside the nest box so that nestlings were unable to reach the entrance, and using the clay model with the green gape to provide a foreign visual stimulus; (3) by using a combination of visual and vocal stimuli - by using a combination of (1) and (2).

To test the relationship between begging stimuli elicited by chicks and subsequent provisioning responses of adult birds, models were set up in the nest box used for breeding by woodhoopoes and, on separate occasions, in an identical nest box between 15 and 20 m away. The order in which models were presented (i.e. on different days) was reversed for the two flocks (A and B) to control for the effects of familiarity with the nest site. However, during manipulations at adjacent nests, the combination of visual and vocal stimuli were always done before the pure visual ones.

A feeding attempt was recorded when an adult, carrying food in its bill, approached to within five metres of the nest. A positive feeding response (i.e. deception) was considered successful if an adult woodhoopoe approached the nest and actively offered a food item to the clay model by touching the model's inner gape with it. Feeding attempts by the same individual, with the same food item, were considered as separate events only if the bird moved further than five metres from the nest for more than two minutes.

RESULTS

Effects of experience on future reproductive success

There was no relationship between breeder age and breeding success for either sex at either site, when all flocks and all breeding attempts were included in the analyses (Figures 8.1 & 8.2). However, when considering successful breeding attempts only, chick production by inland females increased with age (exponential regression: $r = 0.71$; $P = 0.003$). Data for females at the two sites were combined due to small sample size of successful breeding attempts.

Within breeding individuals retaining the same mate, there was no difference in fledgling production between the first and second breeding attempt (Table 8.1).

Fitness criteria

There was no significant difference at either site in the mean number of young fledged annually by flocks with and without helpers (Table 8.2). For the same comparison, there also was no significant difference (all $P > 0.05$) in the survivorship of offspring to sexual maturity, or survival of breeding birds, as well as the number of breeder-offspring produced (see Chapter 7).

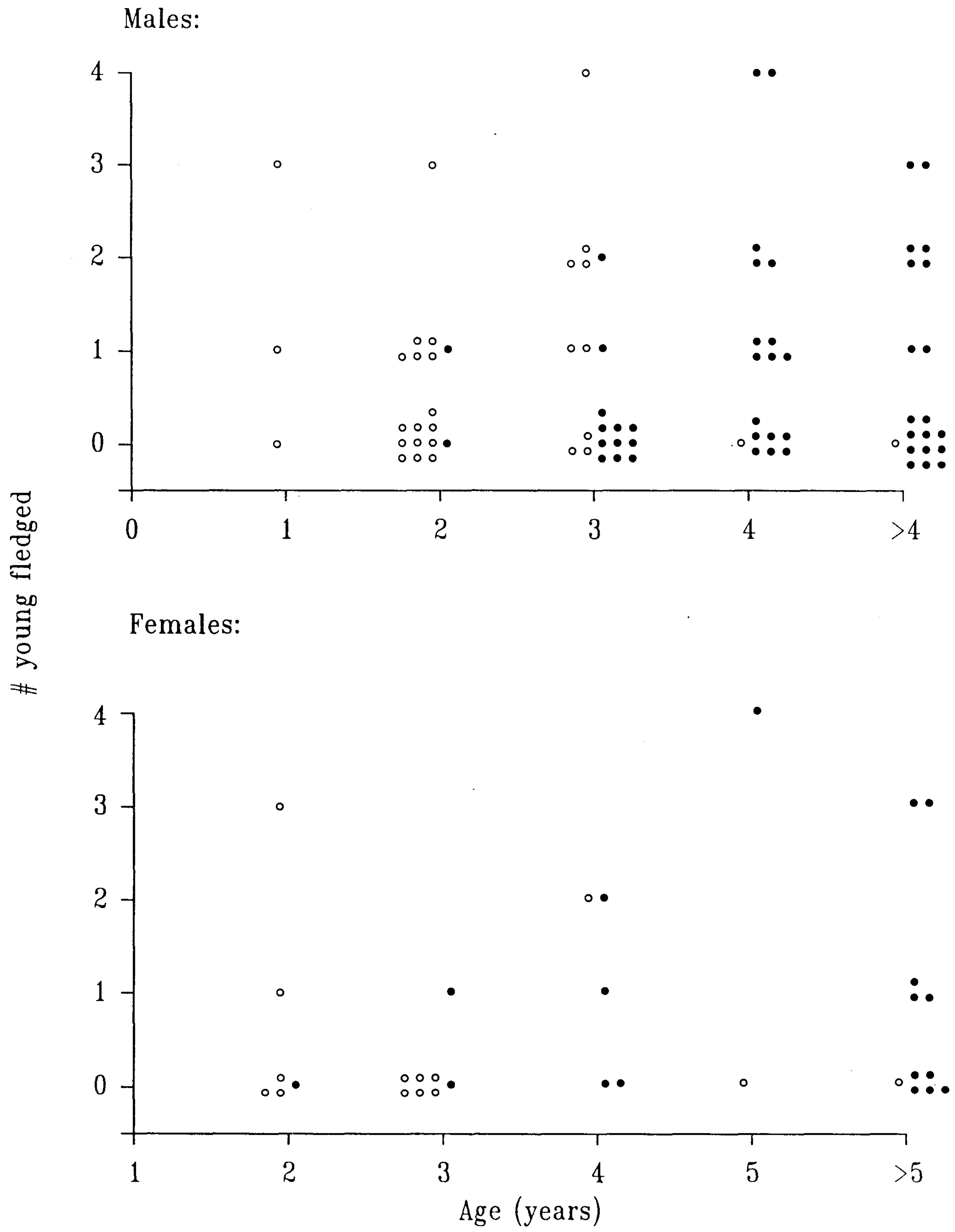

Figure 8.1. Relationship between the number of young fledged per flock per year, and age of breeders during their first (open circles) and subsequent (closed circles) breeding attempts at the coastal site.

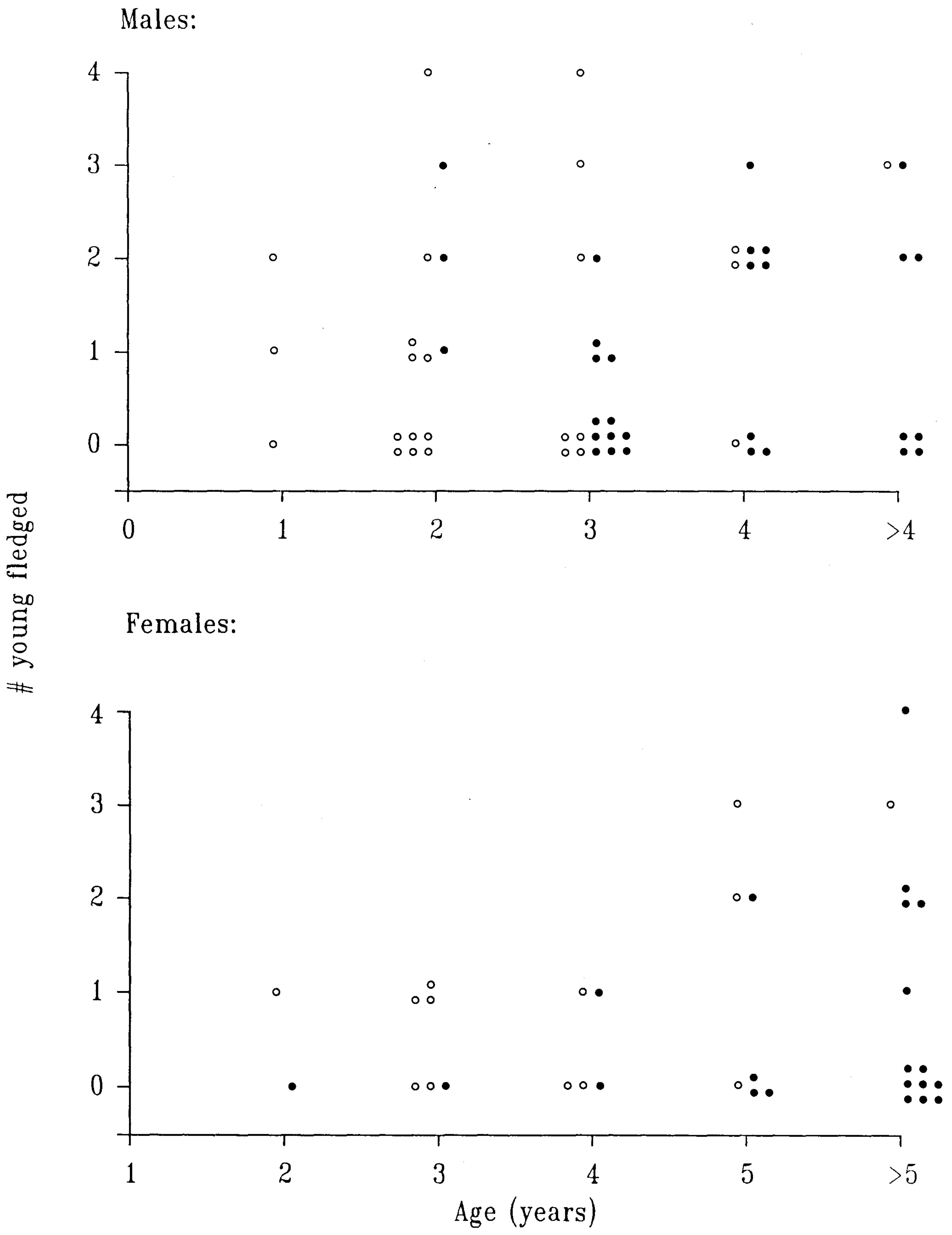

Figure 8.2. Relationship between the number of young fledged per flock per year, and age of breeders during their first (open circles) and subsequent (closed circles) breeding attempts at the inland site.

Table 8.1. Comparative fledgling production by Redbilled Woodhoopoe males and females during their first versus second breeding attempts.

Breeding	Individual										
attempt	1	2	3	4	5	6	7	8	9	10	11
MALE:											
Coastal:											
1st	2	2	2	1	4	1	3	1	0	1	1
2nd	0	3	0	0	3	0	0	2	1	1	0
Statistic: Wilcoxon sign-rank test: Z= 0.949; P= 0.343											
Inland:											
1st	1	1	0	2	2	3	1	1	4	2	
2nd	0	1	3	1	2	1	2	0	1	2	
Statistic: Wilcoxon sign-rank test: Z= 0.756; P= 0.450											
FEMALE:											
Coastal & Inland:											
1st	0	0	3	1	3	1	2	1			
2nd	2	1	1	0	2	1	2	0			
Statistic: Wilcoxon sign-rank test: Z= 0.408; P= 0.683											

Table 8.2. Comparison of fitness effects of group size at the coastal and inland study sites in terms of a number of different criteria (values are means; see Chapter 7).

	Flocks:	
	without helpers	with helpers
Coast:		
# young fledged	1.10	0.93
Survival to 12 months	0.55	0.40
Breeder-offspring produced (%)	40.5	40.9
Breeding male survivorship (%)	88.1	84.5
Breeding female survivorship (%)	94.9	83.3
Inland:		
# young fledged	0.75	1.17
Survival to 12 months	0.50	0.60
Breeder-offspring produced (%)	54.5	16.7
Breeding male survivorship (%)	89.5	81.8
Breeding female survivorship (%)	84.2	87.3

Relatedness

The average relatedness between male helpers and recipient breeders was 0.46 ± 0.17 at the coastal and 0.47 ± 0.21 at the inland site, and between female helpers and recipient breeders was 0.43 ± 0.19 and 0.45 ± 0.20 respectively (Table 8.3). Modal values equalled 0.50 in all instances. In 11% of cases at both sites, helpers were unrelated to either breeder ($n_{coast} = 111$; $n_{inland} = 156$).

Interspecific feeding

During nest observations of a woodhoopoe flock consisting of the breeding pair, a three year old male, and a two year old female, three Crowned Hornbill *Tockus alboterminatus* chicks hatched in a nest box about 15 metres away from the woodhoopoe nest. The hornbill eggs hatched about six days before the woodhoopoe eggs were due to hatch. As soon as the hornbill eggs had hatched, woodhoopoes, with the exception of the incubating female, re-directed most of their food provisioning efforts to the begging hornbill female and chicks. Eventually the incubating female woodhoopoe was forced to leave the nest and beg food from her flock mates from the lid of the hornbill nest box.

In another instance, a woodhoopoe flock, consisting of a breeding pair, two nonbreeding males and a nonbreeding female, re-directed their food provisioning efforts to a Crowned Hornbill nest with chicks, in a way similar to the above. In the second case the hornbill nest was 30 metres from the woodhoopoe nest. After woodhoopoes had fed the hornbill for four days, the breeding woodhoopoe female learnt to intercept food from her flock mates at the entrance to the hornbill nest.

Table 8.3. Relationship of Redbilled Woodhoopoe helpers to recipient breeders at the coastal and inland sites respectively.

Relationship of helpers to breeders			Helpers		Total	(%)
			Males	Females		
***COASTAL SITE:**						
Brother	x Mother	0.75	4	3	7	6.3
Father	x Mother	0.50	42	40	82	73.9
Father	x Halfsister	0.375	0	3	3	2.7
Father	x Unrelated	0.25	2	1	3	2.7
Unrelated	x Mother	0.25	2	2	4	3.6
Unrelated	x Unrelated	0	5	7	12	10.8
Total			55	56	111	
****INLAND SITE:**						
Brother	x Mother	0.75	5	6	11	7.1
Father	x Sister	0.75	8	4	12	7.7
Father	x Mother	0.50	43	53	96	61.5
Father	x Halfsister	0.375	1	4	5	3.2
Halfbrother	x Mother	0.375	2	1	3	1.9
Brother	x Halfsister	0.375	3	0	3	1.9
Father	x Unrelated	0.25	1	0	1	0.6
Unrelated	x Mother	0.25	2	5	7	4.5
Unrelated	x Halfsister	0.125	0	1	1	0.6
Unrelated	x Unrelated	0	8	9	17	10.9
Total			73	83	156	

* Based on 71 Redbilled Woodhoopoe individuals of known age and parentage during 111 helper seasons (40 male *vs* 31 female)

** Based on 81 Redbilled Woodhoopoe individuals of known age and parentage during 156 helper seasons (37 male *vs* 44 female)

Brood parasitism

Greater Honeyguides *Indicator indicator* and Lesser Honeyguides *I. minor* occasionally parasitized Redbilled Woodhoopoes (3.5% and 2.2% of 228 nesting attempts respectively). Of all flocks that successfully raised at least one young (i.e. both con- and heterospecific young), chicks of brood parasites were raised in 11.0% of cases by coastal flocks (n= 73), compared to 6.8% by inland flocks (n= 73).

Clay model experiments

At birds' own nest

There was little difference in the effects of visual stimuli alone, and a combination of visual and vocal stimuli, on allofeeding responses at the birds' own nest using either adult or juvenile models (Table 8.4). However, in the absence of a vocal stimulus, the green model elicited no response. When the vocal stimulus was added, there was a weak positive response by one of the two experimental flocks.

At adjacent nest

Combined visual and vocal stimuli, at adjacent nests elicited a significantly higher frequency of positive feeding responses than did visual stimuli alone. The green model stimulated only a small response when presented together with a vocal stimulus. In both sets of experiments, only one flock responded at all to the green model, and this flock responded only when the green model was the last experimental treatment.

Table 8.4. Summary of results of clay model experiments. Models were presented to flocks in the following sequence: (A) 1,2,3; (B) 3,2,1.

Model and Stimulus	% Positive feeding responses			
	At own nest		At adjacent nest	
	A	B	A	B
(1) Juvenile:				
Visual	90.9 (11)	92.3 (13)	28.6 (14)	45.5 (22)
Visual & vocal	91.7 (12)	100.0 (8)	87.5 (16)	100.0 (16)
	n.s.	n.s.	*	*
(2) Adult:				
Visual	90.0 (11)	85.7 (14)	20.0 (10)	23.1 (13)
Visual & vocal	100.0 (9)	90.0 (10)	85.7 (14)	92.9 (14)
	n.s.	n.s.	*	**
(3) Green:				
Visual	0 (7)	0 (8)	0 (6)	0 (6)
Visual & vocal	14.3 (7)	0 (7)	10.0 (10)	0 (9)
	n.s.	n.s.	n.s.	n.s.

Chi-square statistic:

n.s.	not significant
*	$P < 0.05$
**	$P < 0.02$

DISCUSSION

Experience

This hypothesis fails to explain why individuals should try to gain experience by helping other individuals raise their offspring, rather than breed themselves, and hence increase their own direct fitness while gaining such experience. Even though woodhoopoes are forced to remain as nonbreeders in the natal flock by ecological constraints (Ligon & Ligon 1988; Chapter 2), the experience hypothesis does not adequately explain helping behaviour, because first-time breeders were as successful as more experienced breeders (Table 8.1). Both extensively-studied cooperative breeders, the Florida Scrub Jay *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1984) and the Acorn Woodpecker *Melanerpes formicivorus* (Koenig & Mumme 1987), showed no significant increase in reproductive success with greater experience.

Reciprocal altruism

This hypothesis rests on conditions whereby a recipient can 'repay' a donor for help it received during the nestling and fledgling stages (*sensu* Ligon & Ligon 1978b). This condition is satisfied by social dispersal in Kenyan Redbilled Woodhoopoes, where it is argued that the initial recipient 'repays' the donor by assisting the latter in achieving breeding status in non-natal flocks (Ligon & Ligon 1978b; Ligon 1981). At the South African study sites, social dispersal never occurred and I therefore reject the hypothesis that allofeeding behaviour has evolved as a mechanism whereby social bonds are formed on the basis of reciprocity.

Indirect fitness

Indirect selection is unimportant in the decision of a nonbreeder to become a helper if donor and recipient are typically unrelated, or no more than randomly related, or if recipients do not benefit from related helpers (Brown 1987).

Redbilled Woodhoopoe helpers usually were closely related to recipient young in both South African study populations. Ligon & Ligon (1983) found that nonbreeding Redbilled Woodhoopoe helpers in Kenya were unrelated to recipients in 8% of cases (168 helper years). However, Brown (1987) rejected this relatively low level of unrelatedness as a strong enough selection pressure for such behaviour to be avoided. Estimates of the proportion of unrelated helpers present, for a variety of species, ranged from 0 to 10.1% (for references, see Brown 1987). In this study spanning 267 woodhoopoe helper years, the degree of unrelatedness (11%) equated with the highest recorded for any other species. When cases of brood parasitism were included, between 17 and 22% of helpers fed unrelated nestlings. These values are much higher than those recorded for any cooperatively-breeding species studied thus far. I would therefore argue that the case for indirect selection, based on relatedness between donor and recipient, is not convincing for either of the South African study populations. Aid provided by nonbreeding woodhoopoe helpers provided no obvious benefits to recipient young in either the Kenyan or two South African populations (Ligon & Ligon 1978a, 1983; Ligon 1981; this study).

Indirect fitness benefits accruing to nonbreeders do not necessarily come via direct aid to younger siblings, but from the increased survivorship of related breeders (Florida Scrub Jay, Woolfenden & Fitzpatrick 1984; Acorn Woodpeckers, Koenig & Mumme 1987). Helping may increase survivorship of breeders by reducing the pressures associated with provisioning of chicks. Although alloparental behaviour apparently lightened the load of woodhoopoe breeders (Chapter 6), such putative benefits were not reflected in increased survivorship of breeders in either of the South African study populations during the eight year study period (Table 8.3; Chapter 7). Koenig & Mumme (1987) convincingly showed that survivorship of breeding Acorn Woodpeckers was enhanced mainly through the contribution of nonbreeders to anti-predatory behaviour, and not by allofeeding *per se*.

Categorical acceptance or rejection of the indirect fitness hypothesis is confounded by problems in defining a cut-off limit to 'benefit' derived by nonbreeding helpers (see Sherman 1988; 1989; Jamieson 1989b). The indirect fitness hypothesis is rejected as an explanation for woodhoopoe helping behaviour because of the lack of increased breeder survivorship or enhanced production of offspring (F_1).

Predation-avoidance

Feeding of hornbill chicks and 'begging clay models' close to the woodhoopoes' own nest, supports the predation-avoidance theory to some degree. However, it does not give a satisfactory explanation of why helpers should feed nestlings in order to enhance their own survivorship, because territories are large enough for nonbreeders to ignore the begging chicks and remain outside the 'zone of predator attraction'.

Mate-acquisition

This hypothesis pre-supposes that nonbreeding individuals are selected to fill breeding vacancies on the basis of their 'aid-giving performance', as assessed by the breeder of the opposite sex. However, it does not adequately explain instances in which immigrants (coast: 58%; inland: 23%) are accepted as breeding mates.

never had the opportunity to assist at a nest, acquired breeding status upon the death of a breeder in its natal flock.

Advertising social status

Old nonbreeding females made the largest nonbreeder contribution to food provisioning ('auntie behaviour', *sensu* Ligon & Ligon 1978a), and the converse was true for males (Chapter 6). However, following the death of a breeder of either sex, the breeding vacancy was invariably filled from within the same flock by the most dominant (oldest) nonbreeder of the required sex.

Misdirected parental care

It has been shown that exposure to an appropriate stimulus is a prerequisite for eliciting food provisioning behaviour, whereas prior breeding experience or hormonal conditioning is not (Eisner 1960). Woodhoopoes were 'deceived' into feeding inanimate objects when crude visual and/or vocal stimuli were presented. It may be argued that such responses reflect familiarity with the nest, rather than strong evolutionary pressure to select for discrimination between their own and other nestlings at their own nest (*cf.* Brown 1987: 205). However, results from experiments at adjacent nests suggest that the begging stimulus may be more important than familiarity with the nest. Interspecific feeding of begging Crowned Hornbills (birds about three times the size of woodhoopoes) supports this contention.

The relatively high frequency with which nonbreeders assisted in raising unrelated young, together with instances of brood parasitism, provide further support for a non-adaptive explanation of helping behaviour. In most species of birds, only breeding adults provision offspring. If it is assumed that resource limitation led to obligate group living, as in the widely accepted habitat-saturation hypothesis (Koenig & Pitelka 1981; Emlen 1982; Brown 1987), nonbreeding individuals are likely to encounter and interact with begging offspring of the breeding pair. The high probability of interacting with kin can then be regarded as an effect, not a cause, of group living.

It has been suggested that there may be no selective advantage to provisioning behaviour *per se*, and that this phenomenon could be selectively neutral (Florida Scrub Jay, Woolfenden & FitzPatrick 1984, 1986; Acorn Woodpecker, Koenig & Mumme 1987). Food provisioning might then be explained as a case of misdirected parental care (Price *et al*. 1983; Jamieson 1986, 1988, 1989a; Jamieson & Craig 1987). The evidence from studies of Redbilled Woodhoopoes in South Africa, both observational and experimental, support the selective neutrality of helping behaviour. This behaviour is best viewed as misdirected parental care arising as a consequence of obligate group living.

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SECTION 4

SYNTHESIS

SUMMARY OF FINDINGS

A study was made of two Redbilled (Green) Woodhoopoe *Phoeniculus purpureus* populations spanning an eight year period (1981-1988) and 258 'flock-years', in the eastern Cape Province of South Africa. The main objectives of the study were to investigate (a) why woodhoopoes live in groups; (b) why nonbreeders do not also breed; and, (c) why nonbreeders provision young that are not their own?

1) Environmental selection pressures are reflected by the variability in woodhoopoe social and reproductive behaviour. Roost cavities are a critical resource to woodhoopoes, and a reduction in cavity availability, as witnessed at the inland site, lead to increasing group size.

2) Where suitable roost cavities are in short supply, long-distance scouting forays are undertaken at the risk of not finding a safe roost site to sleep in, with a concomitant risk of being preyed upon. Results from this study indicate that the level of inbreeding among Redbilled Woodhoopoes equals that of the most extreme cases of inbreeding among group-territorial birds. Roost-cavity availability and dispersion profoundly affect the degree of genetic interchange between unrelated individuals.

3) Behavioural interactions such as allofeeding, allopreening, initiation of movements and intraspecific perch site displacement serve in the establishment and maintenance of woodhoopoe dominance hierarchies. Behavioural dominance hierarchies ensure that dominance relationships are well-defined among potential competitors (for breeding status), and thereby minimize disruption to flock cohesion upon the death of a breeder. The breeding pair dominate all other individuals: among other flock members, males dominate females and old birds dominate younger ones.

4) Group-territorial displays such as rallying and flag-waving serve to promote group cohesion and incite aggression, and thereby maintain the group territory.

5) Although nonbreeding helpers do not increase the net rate of food provisioning to chicks, they reduce the parental input in chick rearing, and hence energy expenditure by the breeding pair. However, this results in neither increased breeding frequency, nor enhanced survival of breeders. There is thus no evidence that helping *per se* improves (or reduces) inclusive fitness of helpers.

6) There is no significant difference in the reproductive success or the survivorship of birds inheriting breeding status in their natal territory and those moving elsewhere to breed.

7) The effect of aid provided by helpers on the reproductive success of breeders determines not only the advantage to the breeder, but also the trade-off for the helper between remaining on the natal territory to help raise young (usually siblings), as opposed to the more risky and uncertain option of dispersal. At neither study site is there a significant correlation between flock size and any of the following fitness parameters: fledging success, first year survivorship, nonbreeder survivorship, breeder survivorship, or the number of breeder-offspring produced.

8) Prior helping experience does not improve the reproductive success of individuals during their first, compared to subsequent, breeding attempts. Social dispersal does not occur and thus there are no opportunities for subsequent reciprocity between donors and recipients. Immigrants are occasionally accepted as breeding partners even though their helping capabilities are unknown.

CHAPTER 9

TOWARDS AN UNDERSTANDING OF SOCIALITY

INTRODUCTION

Since cooperative breeding was first described by Skutch (1935), it has attracted much theoretical treatment, because of the apparent paradox such behaviour presents for conventional interpretation of natural selection. There are numerous instances in which individuals of vertebrate species do not breed for a large portion of their adult lives, and spend much time caring for young that are not their own. Assistance provided by nonbreeders include food provisioning of young, protection against predators, nest building and incubation (see Brown 1987).

Unfortunately, confusion of issues has, in some instances, clouded interpretations of cooperative breeding behaviour. There are essentially three major questions, not entirely distinct, concerning the evolution of cooperative breeding: (1) why do nonbreeders delay dispersal; (2) why do birds that do not disperse not breed on their own; and (3) why do nonbreeders help raise young that are not their own?

In this section the main findings of this study are summarized, and placed in the context of a general theory to explain sociality and helping behaviour. Drawing on the analyses presented in preceding chapters, I create a scenario of the critical steps and features leading to group living and cooperative breeding in Redbilled Woodhoopoes.

Redbilled Woodhoopoes are group-territorial, singular breeding cooperative breeders, and woodhoopoes are totally dependent on the presence of safe roost cavities. This dependence has been explained in terms of either predator avoidance (Ligon 1981; Chapters 1 & 2), physiological constraints (Ligon *et al.* 1988), or both (Ligon & Ligon 1988). Suitable roost cavities are a critical resource and have influenced woodhoopoe social behaviour profoundly (Ligon & Ligon 1978a, 1988; Ligon 1981; Ligon *et al.* 1988; Chapters 1 & 2). Where cavities are in short supply, long-distance dispersal forays are undertaken at a risk of not finding a safe roost site to sleep in. Although single-sex groups frequently disperse together in Kenya (Ligon & Ligon 1978a), such social dispersal never occurs in two South African populations (Chapter 2). Individuals never disperse more than once in a lifetime (n= 46).

Flock size does not influence the number of young fledged, survivorship of any age, sex or social class, or the number of breeder-offspring produced. There apparently are no fitness benefits attached to remaining in the natal flock and helping, compared to dispersing and breeding elsewhere. Once breeding status is achieved, both productivity and survivorship of dispersers and non-dispersers are virtually identical (Chapter 7).

WHY LIVE IN GROUPS?

Ecological constraints or benefits of philopatry ?

There are two basic mechanisms through which group living can evolve: (1) offspring are ecologically constrained from dispersing and breeding independently because some resource is limiting, or (2) offspring gain an intrinsic advantage by deferring independent breeding, although opportunities to breed exist elsewhere. The first hypothesis has received wide acceptance as the most important explanation of group living (Selander 1964; Brown 1974; 1987; Koenig & Pitelka 1981; Emlen 1982; Koenig & Mumme 1987). The validity of the habitat-saturation hypothesis has gone largely unchallenged and has long been regarded as 'the sole *modus operandi* for ecological thinking concerning the evolution of cooperative breeding' (*sensu* Emlen 1982). However, the benefits of philopatry, rather than the costs of dispersal, have been proposed as an alternative explanation for the evolution of group living (Rabenold 1984, 1985; Austad & Rabenold 1985; Stacey & Ligon 1987). Under this premise, habitat saturation may be regarded as the result, rather than the cause, of group living.

Empirical evidence demonstrates that Redbilled Woodhoopoe nonbreeders increase their inclusive fitness by acquiring breeding status. Only when all suitable woodhoopoe habitat is saturated does it become necessary to consider the cost of dispersing to become a nonbreeder elsewhere as an alternative to remaining as a nonbreeder in the natal flock.

For societies in which social facilitation selects for group living, ecological constraints may make successful independent reproduction prohibitive, even if the opportunity exists for nonbreeders to attempt breeding on their own. On the other hand, the habitat-saturation hypothesis proposes that individuals are capable of breeding independently, but that ecological constraints prevent them from doing so. At least in this sense (i.e. when reproduction by pairs is prohibitive), the habitat-saturation and benefits-of-philopatry hypotheses are not always mutually exclusive (see Emlen 1982; Koenig & Mumme 1987).

Redbilled Woodhoopoe life-history data support the habitat-saturation hypothesis in explaining the evolution of group living. When all suitable habitat is saturated with woodhoopoe territories, parental tolerance of young remaining in the natal flock is necessary. Only after all suitable habitat is saturated are philopatric benefits realized.

The trend to greater parent-offspring involvement can be seen as an increasing tolerance by breeders of their maturing offspring. Under circumstances in which it becomes increasingly difficult to become established as a breeder, efforts by the parents to facilitate this process may increase accordingly. Tolerance of young is first expressed merely as an increased period of association between parents and their young, which may lead to plural breeding (Brown 1987).

Since dispersal is a unique event during a woodhoopoe's lifetime, it is reasonable to assume that the survival of offspring is enhanced as a consequence of staying at home. The reason why individuals do not, as a rule, disperse to non-natal territories other than to assume breeding status, can be viewed as a strategy in which cumulative lifetime dispersal risks are minimized. The natal territory is used as a springboard from which to gather information about possible breeding vacancies in nearby territories, which can be weighed against the probability of achieving breeding status in the natal flock. Such a strategy reduces exposure to risks during either dispersal to, or establishment (familiarization) in another territory.

Parental facilitation and tolerance

A model of parental facilitation has been proposed which can account for the apparent lack of fitness benefits derived by nonbreeders (Brown & Brown 1984; Brown 1987). If the parent reduces the risk of dispersal for its offspring by retaining them as helpers, then the parent can profit without increasing its own lifetime reproductive success. It has been shown that a parent can experience a small reduction in lifetime reproductive success and still profit in direct fitness (Brown & Brown 1984).

My woodhoopoe study shows that fitness benefits derived through breeders' tolerance of offspring in the natal territory for extended periods are few. However, having mature nonbreeding offspring can be regarded as an investment which may pay dividends under particularly good or harsh conditions. The availability of safe roost cavities has been identified as the resource defining habitat saturation. However, a roost cavity is a resource for which potentially little intra-flock competition exists, since up to 12 individuals (i.e. from the same flock) may roost together in the same cavity.

I therefore propose, as an additional refinement to the parental facilitation model, that the nature of critical resources needs to be considered in terms of the evolution of tolerance (by breeders) of nonbreeders in a single territory. If dispersal is risky and the habitat is saturated with territories, parents should tolerate young in the natal flock to improve the survivorship of their own offspring. In situations where the nature of the critical resource(s) is such that it leads to competition between breeders and nonbreeders, the fitness benefits arising due to nonbreeders' helping contribution (e.g. food provisioning, detection and harassment of predators, etc.), should be significant. On the other hand, if the critical resource is such that there is little or no intra-flock competition for it (e.g. woodhoopoe roost cavities), there may not have been strong selection for fitness benefits arising from helping behaviour. According to this hypothesis, when the critical resource(s) holds the potential for intense intra-flock competition, the nonbreeder(s) should provide sufficient assistance to the breeders to raise the latter's fitness to a level greater than that attainable by driving the nonbreeder(s) away. This hypothesis differs from Gaston's (1978) 'payment principle' in that it predicts that under certain conditions, i.e. when there is little conflict over access to a critical resource, no 'repayment' is involved.

WHY DELAY BREEDING?

Groups of cooperatively-breeding vertebrates are often characterized by social hierarchies, which lead to either rank-related reproduction (Mumme *et al.* 1983), or exclusive reproduction of a dominant pair assisted by nonbreeding helpers (reviewed by Brown 1987). When individuals live together socially, the expression of behavioural dominance is predictable. However, to realize the benefits of group living, aggressive behaviour that might disrupt group unity or cohesiveness should be repressed. Compared to non-cooperative group-living birds, levels of aggression in cooperatively-breeding species are low (Brown 1987).

Overt aggression within Redbilled Woodhoopoe flocks is uncommon (Ligon & Ligon 1978a; Chapter 4). Woodhoopoe dominance hierarchies, constructed on the basis of displays and other behavioural interactions such as allopreening, allofeeding, initiation of movements, and perch site displacement, indicate that males dominate females, and older birds dominate younger ones. High social rank is correlated with the probability of achieving breeding status in the natal flock. Although flocks appear to be well integrated, harmonious units in which little overt aggression occurs, considerable efforts are made by individuals to achieve personal gain (Chapter 4).

Males have been observed to be the dominant individuals in many group-territorial societies (Florida Scrub Jay *Aphelocoma coerulescens*, Woolfenden & Fitzpatrick 1977; Mexican Jay *A. ultramarina*, Barkan *et al.* 1986; Greycrowned Babbler *Pomatostomus temporalis*, King 1980; Stripebacked Wren *Campylorhynchus nuchalis*, Rabenold 1985; Green Woodhoopoe, Ligon & Ligon 1978a; Chapter 4; Brown Hyaena *Hyaena brunnea*, Mills 1983). It has been assumed that domination by breeders prevents subordinates from breeding, without driving the latter from the territory. This is reflected by high testosterone levels in male Pied Kingfisher *Ceryle rudis* breeders, as opposed to lower levels in primary helpers (Reyer *et al.* 1986). Low levels of sexual activity in subordinate individuals have been reported for several cooperatively-breeding vertebrate species (Naked Mole-rat *Heterocephalus glaber*, Jarvis 1981; Dwarf Mongoose *Helogale undulata*, Rood 1980; Groovebilled Ani *Crotophaga sulcirostris*, Vehrencamp 1982).

WHY HELP?

Alloparental behaviour in Redbilled Woodhoopoes: a case for reciprocity?

A strong case has been made for reciprocal altruism as the driving force in the evolution of allofeeding behaviour of Redbilled Woodhoopoes in Kenya (Ligon & Ligon 1978a, 1978b, 1983; Ligon 1981, 1983). These authors have argued that the forming of close social ties with nestlings results in helpers using younger birds of their own sex to gain entry to and establishment in a new territory. Young woodhoopoes in the nest are thus viewed as an essential resource that can be utilized by the current helpers for their own personal gain at a later stage.

The following objections can be directed against the social bonding hypothesis: (1) it is difficult to explain why an alloparental bond would take precedence over a parental bond; (2) social bonds are occasionally formed between unrelated adults from different flocks, with no known previous interaction between them; and, (3) because adult mortality is high in the Kenyan population (30-40% per year), the probability of a helper surviving to benefit from reciprocity is low. However, in defense of the last point, Ligon (1983) has suggested that the high turnover of birds means that an individual does not have the time to follow a passive long-term waiting strategy and is forced to run the risk of being cheated by non-reciprocation. If the probability of death is significantly greater for older, dominant individuals than for their subordinate allies, then a beta bird may be repaid fairly quickly by acquiring breeding status.

Social dispersal, although prominent in the Kenyan study population (Ligon 1981), was never recorded in eight years at two South African study sites. Immigrating individuals almost invariably acquired breeding status on their own; the few exceptions (n= 4) were all cases in which two unrelated individuals, with no known previous interaction between them, simultaneously joined another flock.

Although the formation of social bonds may hold significant benefits for Redbilled Woodhoopoes in some areas, it may not be a sufficient explanation for the evolution of helping behaviour, particularly allofeeding, *per se*. Both Kenyan and South African populations probably have a common origin of helping behaviour, and a general explanation is required which satisfies conditions throughout the species' range.

The role of allofeeding behaviour: an evaluation

Even though many studies have failed to demonstrate benefits to recipients from helping behaviour, the 'benefit hypothesis' (*sensu* Brown 1987) is still largely unchallenged. Theories invoking indirect selection as the evolutionary driving force behind allofeeding behaviour predict that such behaviour results in an increase in the donor's inclusive fitness. Food provisioning behaviour can affect the inclusive fitness of nonbreeders in a number of ways: (1) increased reproductive success of the flock; (2) enhanced breeder survivorship due to a lightened workload; and, (3) multiple breeding attempts as a result of breeders being released from extended care of offspring.

The effects of allofeeding behaviour on reproductive success need to be put in perspective, since an increase in reproductive success can result from factors other than allofeeding of dependent young and/or breeding females. Helpers can engage in a variety of activities which can be potentially beneficial: allopreening, detection and harrassment of predators and/or brood parasites, food location, territory defense (intra- and interspecific), nest building, incubation and brooding.

Of 23 cooperative, singularly-breeding (i.e. only one pair breeds) species, 14 show a positive relationship between group size and reproductive success (Table 9.1). Increased fledgling production has been attributed to factors other than alloparental behaviour in half of cases. Thus, in a maximum of only seven studies (30%) can alloparental feeding potentially explain increased reproductive success of groups (cases in which the factor(s) enhancing reproductive success are unstated or unknown are included in this figure). When plural and colonial breeding species are included in the analysis, this figure rises to 36% of all cases (n= 33). In only one study has enhanced breeder survival, with increasing flock size, been directly attributed to the allofeeding contribution of nonbreeders (Reyer 1980). In three other studies in which breeder survivorship is enhanced, fitness benefits are

Table 9.1. Summary of results obtained for the effects of group size on various fitness parameters for different species.

Species	# offspring produced per year	First year survivorship (%)	Breeder survivorship (%)	Reference
SINGULAR BREEDERS:				
Harris' Hawk *Parabuteo unicinctus*	0			Mader 1975
Redcockaded Woodpecker *Dendrocopos borealis*	++	0		Lennartz *et al.* 1987
Superb Blue Wren *Malurus cyaneus*	0			Rowley 1965
Buffrumped Thornbill *Acanthiza reguloides*	0			Bell *in* Brown 1987
Pygmy Nuthatch *Sitta pygmaea*	+	0		Sydeman 1989
Tasmania Native Hen *Tribonyx mortieri*	0			Ridpath *in* Emlen 1978
Dunnock *Prunella modularis*	-			Birkhead 1981
Hoatzin *Opisthocomus hoazin*	++			Strahl *in* Brown 1987
Purple Gallinule *Gallinula martinica*		+		Hunter 1985
Kookaburra *Dacelo novaeguineae*	+			Parry 1973
Redbilled Woodhoopoe *Phoeniculus purpureus*				
Kenya	+			Ligon & Ligon 1978a
Coastal (S.A.)	-	0	0	Chapter 7
Inland (S.A.)	+	-	0	Chapter 7
Bicolored Wren *Campylorhynchus griseus*	++		++	Austad & Rabenold 1985
Stripebacked Wren *C. nuchalis*	++		0	Rabenold 1984, 1985
Blackcapped Donacobius *Donacobius atricapillus*	0			Kiltie & Fitzpatrick 1984
Greycrowned Babbler *Pomatostomus temporalis*	+			Brown & Brown 1981
Common Babbler *Turdoides caudatus*	0			Gaston *in* Emlen 1978
Arabian Babbler *T. squamiceps*	+			Zahavi 1974; Brown 1975
Jungle Babbler *T. striatus*	-			Gaston 1978
Longtailed Tit *Aegithalos caudatus*		++		Glen & Perrins 1988
Bell Miner *Manorina melanophrys*	+			Clarke 1989
Florida Scrub Jay *Aphelocoma coerulescens*	++	0	+	Woolfenden & Fitzpatrick 1984
Beechey Jay *Cyanocorax beecheii*	+	0		Raitt *et al.* 1984
Greybacked Fiscal Shrike *Lanius excubitorius*	++			Zack 1986

Table 9.1. *(continued)*

Species	# offspring produced per year	First year survivorship (%)	Breeder survivorship (%)	Reference
PLURAL BREEDING:				
Pukeko *Porphyrio porphyrio*	-			Craig 1980
Acorn Woodpecker *Melanerpes formicivorus*	+ +		+ +	Koenig & Mumme 1987
Chestnutbellied Starling *Spreo pulcher*	+ +			Wilkinson 1982; Wilkinson & Brown 1984
Mexican Jay *Aphelocoma ultramarina*	0			Brown 1972
Galapagos Mockingbird *Nesomimus parvulus*	**+**	0		Kinniard & Grant 1982
COLONIAL BREEDERS:				
Pied Kingfisher *Ceryle rudis*			**++**	Reyer 1980
Lake Naivasha	0			Reyer 1980
Lake Victoria	**++**			Reyer 1980
Redthroated Bee-eater *Merops bullocki*	**++**			Dyer & Fry 1980
Whitefronted Bee-eater *M. bullockoides*	**+**			Emlen 1978
Brown-and-yellow Marshbird *Pseudoleistes virescens*	0			Orians *et al. in* Emlen 1978

+ +	positive effects (P< 0.05)
+	positive effects (P> 0.05; n> 30)
0	slight positive or negative effects (n< 30)
-	negative effects (P> 0.05; n> 30)

++/+: possibly resulting from nonbreeder allofeeding contribution
++/+: specifically not due to effects of allofeeding

achieved mainly by anti-predatory behaviour (Woolfenden & Fitzpatrick 1984; Austad & Rabenold 1985; Koenig & Mumme 1987).

Sober (1984) has argued that the concept of 'overall fitness' is limited in that it describes the net force of selection, not its components. A certain trait (e.g. delayed dispersal) may have great selective importance, whereas other traits (e.g. allofeeding of dependent young) may be neutral (Woolfenden & Fitzpatrick 1984; Koenig & Mumme 1987; Jamieson 1989). The same distinctions could be made between the respective fitness contributions of several different types of helping behaviour, such as allofeeding, allopreening and predator avoidance.

Until more studies have conclusively shown that allofeeding behaviour *per se* results in fitness benefits, there is no reason to believe that it has an adaptive advantage. Considering its relatively small contribution to inclusive fitness of nonbreeding helpers in several species, it is plausible that allofeeding behaviour has no underlying genetic basis other than that of misdirected parental behaviour.

Misdirected parental care: the alternative

Brown (1987) acknowledged that 'it is a small step from accidental or deceptive interspecific helping to accidental or incidental intraspecific helping'. Yet, he considers that 'it seems likely that many cases of intraspecific helping, particularly those of a sporadic or accidental nature, are not adaptive for the alloparent, while cases of regular helping may indeed be adaptive'. However, for helping behaviour to have adaptive value, the assumption is made that it is a discrete behavioural trait with an underlying genetic component upon which selection could act. As the comparative analysis of several cooperatively-breeding species shows, this is not a valid assumption. I suggest that regular helping is, like all the other cases of inter- and intraspecific helping, maintained by the same stimulus-response mechanism that results in parents feeding their own young (Jamieson 1986, 1988, 1989; Jamieson & Craig 1987).

To suppress the feeding response of a nonbreeding bird to a begging stimulus would require the evolution of a special mechanism. The ability of a bird to discriminate between stimuli evoking the provisioning response is presumably difficult to evolve, since any associated reduction in direct parental care would be maladaptive (Rohwer 1986).

The strongest cases in support of selection for indirect fitness benefits have come from studies of colonial species in which nonbreeders have a choice between helping kin or non-kin, or not helping at all (see Brown 1987). A strong preference for helping kin has been shown for Pied Kingfishers (Reyer & Westerterp 1985), European Bee-eaters *Merops apiaster* (Avery in Brown 1987), and Whitefronted Bee-eaters *M. bullockoides* (Emlen & Wrege 1988).

A strategy of indiscriminate feeding of young in colonial species would be susceptible to cheating, hence parent-offspring recognition abilities have presumably evolved as a result of direct selection. The trait of recognition therefore has a genetic basis, and explains why nonbreeding helpers, in some colonial species, discriminate between kin and non-kin. However, the term 'kin recognition' may be misleading, since Curry (1988) found that for plural breeding Galapagos Mockingbirds *Nesomimus parvulus*, prior association with breeders, rather than relatedness, is a better predictor of allofeeding behaviour.

Helping behaviour exists in a wide variety of species and social contexts, and Brown (1987) suggests that such behaviour may have multiple origins involving different selection pressures and requiring different explanations. No unambiguous indirect fitness benefits, as a result of helping behaviour, can be shown for at least three of the most extensively studied cooperatively-breeding species (Florida Scrub Jays, Woolfenden & Fitzpatrick 1984; Acorn Woodpeckers, Koenig & Mumme

1987; Redbilled Woodhoopoes, Ligon & Ligon 1981; this study). I therefore propose that the unselected (misdirected parental care) hypothesis is a viable alternative to the 'functional hypotheses'.

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APPENDIX 1

THE DEVELOPMENT OF KLEPTOPARASITIC BEHAVIOUR

In review of kleptoparasitism, Brockmann & Barnard (1979) state that birds from some orders are disproportionately likely to exhibit this behaviour. Kleptoparasitism frequently has been recorded among passerines and predatory non-passerines but seldom among insectivorous non-passerines. In particular, only three instances have been documented in which members of the order Coraciiformes exhibited interspecific kleptoparasitic behaviour, namely Common Kingfisher *Alcedo atthis*, Carmine Bee-eater *Merops nubicus* and Abyssinian Roller *Coracias abyssinica* (Grist 1934; Moncur 1946; Tye & Tye 1983). I report here on three observations of interspecific kleptoparasitism involving another member of this order, the Redbilled Woodhoopoe *Phoeniculus purpureus*. Redbilled Woodhoopoes are long-billed, insectivorous, group-territorial birds, weighing about 75 g. They inhabit a wide variety of woodland types across a broad Afrotropical range (Ligon 1981). They live throughout the year in flocks of 2-12 birds, have a cooperative breeding system (Ligon & Ligon 1978), and a dispersal system involving both males and females.

The present observations were made during a study of woodhoopoe behaviour in the eastern Cape Province, South Africa, involving more than 50 flocks observed for 500 days during a ten-year period. All records of kleptoparasitism relate to a single, resident, colour-banded flock (BD) in the Queenstown district (31°47'S 26°47'E), which was monitored from January 1976 until 1984 when the flock disappeared. During this period, more than 200 h of observations were made of the BD flock.

In December 1980, two Redbilled Woodhoopoes from flock BD interacted aggressively with a pair of Cardinal Woodpeckers *Dendropicos fuscescens* at the latter's nest cavity in a Willow Tree (*Salix* sp.). The woodpeckers were trying to feed their nestlings, but the woodhoopoes obstructed them and attempted to steal food intended for the young woodpeckers. On one occasion a woodpecker successfully evaded the woodhoopoes and fed a nestling, whereupon the woodhoopoe male

(WW) hopped to the entrance of the nest hole, inserted his bill into the nestling's mouth, retrieved a small insect, and swallowed it. This successful retrieval of food from a nestling resulted in a change in the woodhoopoes' behaviour, whereby the adult woodpeckers were now allowed to feed their young unharassed, and the woodhoopoes would then take the food from the nestlings with little difficulty. A young woodhoopoe female (WB) took over WW's role whenever he carried food back to the breeding female (WY) 80 m away. In one hour, WW took four food items and WB three, in the course of as many provisions of food by the woodpeckers.

In April 1981 the same two woodhoopoes, WW and WB, were observed molesting and kleptoparasitizing Acacia Pied Barbets *Lybius leucomelas* in a similar fashion. The woodhoopoes again waited for the barbets to feed their nestlings, whereupon one of them hopped to the nest entrance and retrieved whatever was fed. In this instance, five food items were robbed in 22 min (four by WW and one by WB) before the woodhoopoe flock moved on.

In February 1983, when WW and WB were no longer present in the BD flock (presumably having died), members of the same flock were seen molesting a pair of Paradise Flycatchers *Terpsiphone viridis*, feeding three downy chicks, in an identical manner. The nest was partially obscured and I did not see actual retrieval of food from the chicks, but the woodhoopoes exhibited exactly the same behaviour as previously observed.

Redbilled Woodhoopoes occasionally probe unoccupied nests of Masked Weavers *Ploceus velatus* (Spence 1974), occupied open-nest structures of Cape Sparrows *Passer melanurus* (Newman 1975), House Sparrows *P. domesticus* (Newman 1981), and Paradise Flycatchers (pers. obs.), and vacant nest cavities of Blackcollared Barbets *Lybius torquatus*, Knysna Woodpeckers *Campethera notata*, Cardinal Woodpeckers, Bearded Woodpeckers *Thripias namaquus*, and Olive Woodpeckers *Mesopicos griseocephalus* (pers. obs.). In these instances, they presumably are feeding on insect larvae which hatched in the nest cavities or structures. Although I have recorded such nest probing on 41 occasions in 13 different woodhoopoe flocks, only the BD flock indulged in kleptoparasitic behaviour. Similarly, J.D. Ligon (pers. comm.) recorded woodhoopoes tearing dried cattle droppings apart and eating the small beetles inside, but in only one of his Kenyan study flocks. Here also, unusual foraging behaviour persisted in the flock even when the original members had all disappeared and been replaced.

Where members of one species feed on the products, scraps, or parasites of another, the development of kleptoparasitic behaviour is enhanced (Rand 1954). I suggest that the observed woodhoopoe kleptoparasitism had its origins in this type of interspecific interaction. During the woodhoopoe-woodpecker interaction, the woodhoopoes were under considerable feeding pressure because they were providing food for the breeding female and three nestlings. This may have provided the stimulus for a change from simple nest probing to active attempts at food interception. The observed adjustment of the initial interception suggests that it was a new behaviour for the woodhoopoes and that a process of tactical refinement or learning was involved. The woodhoopoe-barbet interaction observed a few months later, when the flock was under little feeding pressure, and the woodhoopoe-flycatcher interaction, when the initial kleptoparasites (WW and WB) were no longer present, point to the adoption of new, opportunistic, feeding behaviour by the BD flock. This, together with J.D. Ligon's observations of manure shredding, suggests that certain behaviours may develop by chance and then be culturally transmitted to younger flock members. The fact that dispersal in woodhoopoes takes place only very infrequently implies that any such new behaviour pattern may either take many generations to spread through the population or never extend beyond the flock in which it was initiated, as was probably the case with the kleptoparasitic habits of the BD flock.

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APPENDIX 2

BEHAVIOURAL AND PHYSIOLOGICAL INFLUENCES ON ROOSTING BEHAVIOUR

INTRODUCTION

The phenomenon of group territoriality and cooperative breeding has attracted much attention recently, and many aspects of this behaviour have been intensively studied (reviewed by Brown 1987). However, the roosting behaviour of group-territorial birds has largely been neglected. Apart from a study of Jungle Babbler *Turdoides striatus* roosting behaviour, nothing more than general accounts have been published (Gaston 1977).

I report here on the roosting behaviour of Redbilled Woodhoopoes *Phoeniculus purpureus*. Redbilled Woodhoopoes are group-territorial birds that live in flocks of 2-12 individuals, and have a cooperative breeding system. They inhabit a wide variety of woodland types across a broad Afrotropical range (Ligon 1981), and are obligate cavity-roosters. The evolution of woodhoopoes' cavity-roosting behaviour has been explained in terms of both predator avoidance (Ligon & Ligon 1978; Ligon 1981; Chapter 1), and physiological constraints (Ligon *et al.* 1988).

Redbilled Woodhoopoes usually roost in disused barbet/woodpecker holes or natural cavities in trees (Ligon & Ligon 1978; Chapter 1). All flock members usually enter the same cavity, but occasionally flocks divide shortly before entering their roosts. 'Dormitory' behaviour, in which the sexes roost separately, has been observed frequently in Kenyan woodhoopoes (Ligon & Ligon 1978, 1982).

METHODS

Observations of Redbilled Woodhoopoes were made in two areas of the eastern Cape Province of South Africa; one comprising 33 km^2 of coastal and riverine forest at Morgan's Bay (32°43'S 28°19'E), and the other comprising 45 km^2 of valley bushveld in the Kubusi River valley (32°32'S 27°47'E) (Chapter 1). Observations were made between January 1976 and March 1988. More than 2500 hours of observation were made of 60 different flocks, of which all individuals in 40 flocks were uniquely colour-ringed. Observations of roosting behaviour, commencing at least one hour before birds first entered the roost cavity, were made on 430 occasions.

Redbilled Woodhoopoe behaviour prior to and during entry into roost cavities was recorded for several flocks in terms of sex, age and social status (n= 30 observations each month of the year). Pre-roost sentinel behaviour (PRSB) was defined as sentinel behaviour performed during the hour or so before woodhoopoes entered the roost cavity. The relative frequency of PRSB by males and females was calculated as follows:

$$\textbf{Frequency PRSB involvement} = N_{PRSB}/\, N_d \times N_b,$$

where N_{PRSB} = observed frequency of PRSB, N_d = no. days of observations, and N_b = no. birds present of the same sex.

The times at which birds entered and left their roosts were recorded to calculate a mean activity period outside the roost cavity for each month. Field metabolic rate (FMR, in kJ) - the total daily energy cost to an animal - was calculated for woodhoopoes using the equation:

$$\mathbf{FMR = aW^b},$$

where **W** = body mass (g), **a** = 10.9 kJ/day and **b** = 0.64 kJ/day respectively (Nagy 1987). Body mass values used were 84.9 g for males and 70.1 g for females (unpubl. data).

RESULTS

During the hour or two before entering the roost, woodhoopoe flocks were alert and often moved several hundred metres without obvious reason. This was usually followed by a noisy 'false roost' entrance by the whole flock before silently retreating to the final roost site. False roosting behaviour is also performed by

Southern Ground Hornbills *Bucorvus leadbeateri* (A. Kemp pers. comm.). 'Dormitory' behaviour, in which sexes roost separately (*sensu* Ligon & Ligon 1978, 1982), was observed on only 15 of 430 occasions, and involved only five of 54 flocks observed. In 48 instances flocks split into mixed-sex groups immediately prior to roosting.

A form of sentinel behaviour (*sensu* Andrews & Naik 1970; Gaston 1977; Zahavi 1977) was observed an hour or so before woodhoopoes entered the roost. Pre-roosting sentinel behaviour (PRSB), in which one or more birds sat motionless on a high vantage point, was observed in more than 50% of roost entry sequences.

Females undertook 78.3% of all PRSB. Although the breeding pair's contribution to PRSB decreased with increasing flock size, they still participated disproportionately frequently ($X^2 = 87.0$; 1 df; $P < 0.001$), due largely to the female breeder's contribution. The contribution of flock members to PRSB decreased with decreasing social status (Table 1). Male involvement in PRSB was at its lowest during the nonbreeding season, and this was compensated for by increased female involvement (Figure 1). The time of entering and leaving the roost was related to the time of sunset and sunrise: 13.5 hours were spent outside the roost each day in mid-summer compared with 9.5 hours in mid-winter (Figure 1). The longer activity period of males reflects their greater field metabolic rate (187.2 kJ/day *vs* 165.3 kJ/day for females).

The rate at which individuals entered the roost cavity varied, but usually was rapid after the first bird had entered. On some occasions a single bird remained outside, or individuals took turns to look out of the hole, until it was dark. From 43 observations in which the order of roost entrance was determined for flocks comprising four or more individuals, it was evident that the middle positions were favoured by the breeders (n= 37). Younger birds usually entered first, while nonbreeding adults were often the last ones to enter.

Table 1. Analysis of the frequency of involvement in pre-roost sentinel behaviour (PRSB) by different Redbilled Woodhoopoe social classes.

Flock size	Frequency of involvement								
	BR♂	BR♀	AD♂	AD♀	2Y♂	2Y♀	<1Y♂	<1Y♀	Total
2	13	48	-	-	-	-	-	-	61
3	10	41	-	-	-	-	3	-	54
4	8	41	-	-	4	16	-	-	69
5	6	34	-	-	-	-	6*	10	57
7	5	29	8*	28	5	17	-	-	91
8	3	21	6	14	3	16*	2	6	71
Total	45	214	14	42	12	49	11	16	403

* 2 birds present from the same class

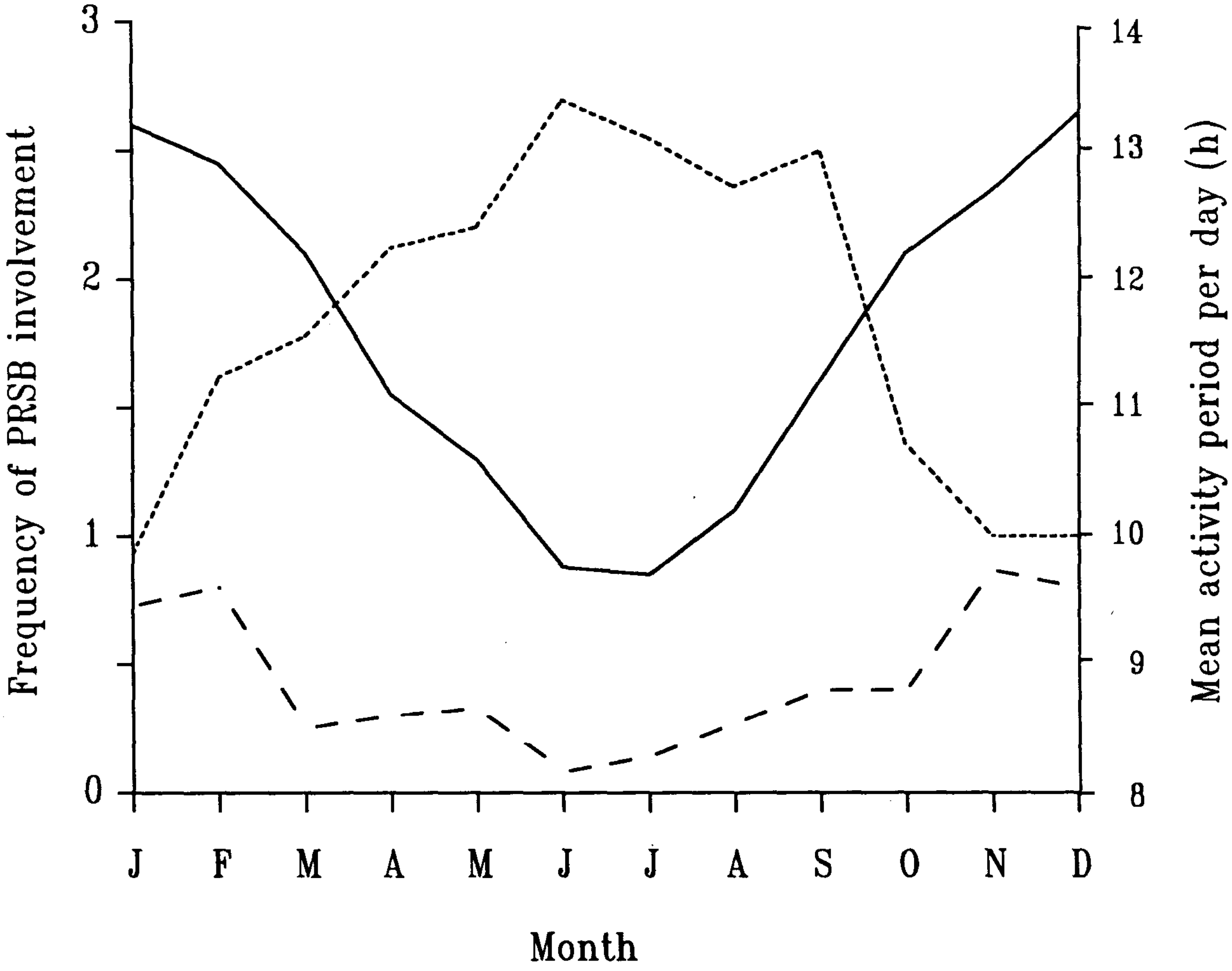

Figure 1. Frequency* of pre-roost sentinel behaviour (PRSB) by males (solid line) and females (dotted line), and the mean number of daylight hours (dashed line) in which Redbilled Woodhoopoes were active - defined as the period between the first bird leaving the roost and the last bird entering the roost - for each month of the year. *(see text)

DISCUSSION

It has been reasoned that woodhoopoe 'dormitory' behaviour, in which sexes roost separately, is a consequence of sexual dimorphism, whereby the smaller females are able to enter roost sites whose openings are too small for males to enter (Ligon & Ligon 1982). However, data from this study indicate that flocks divide randomly either when cavities are too small to accommodate the entire flock, or when roost-cavity availability is high (Chapter 1). This difference may be due largely to the abundance of Grey Woodpeckers *Dendropicos goertae* in Kenya that excavate cavities which male woodhoopoes are unable to enter (J.D. Ligon pers.comm.).

The occurrence of false roosting behaviour, PRSB, as well as seemingly preferred orders of entering roost cavities, indicate that roosting behaviour is strongly linked to predator avoidance. Entering a cavity first presents the risk of encountering a snake or rodent, and young birds normally are the first to enter roost cavities. Once safe entrance has been achieved, the breeders often make use of displacing tactics in order to enter next. The birds that enter last are the ones that remain closest to the entrance, presumably throughout the period inside the cavity, predisposing these birds to risk of predation by genets *Genetta genetta* and *G. tigrina*, or other nocturnal predators. Breeders may thus use other flock members to buffer them from potential hazards. In Jungle Babblers the male and female breeders always take the proximal positions in their open, branch roost sites (Gaston 1977), again showing signs of using other flock members as a predation buffer.

Small birds expend more energy per unit body mass than large birds, but the sexual dimorphism of Redbilled Woodhoopoes is such that the males, which are 15g heavier than females, have an absolutely greater FMR. The smaller contribution of males to pre-roost sentinel behaviour (PRSB) is best explained by this difference in FMR and the need for males to forage longer to satisfy their energy demand. This is supported by (1) the negligible participation of males in PRSB during mid-winter, when the available time spent outside roost cavities is 65% of that during mid-summer; and (2) the active foraging behaviour of males while females undertake sentinel duties during winter.

Individual contribution to sentinel behaviour has been interpreted as a means by which high quality birds advertise their food-finding abilities, and hence social status, in terms of the 'handicap principle' (Gaston 1977; Zahavi 1977). According to this hypothesis, males should contribute more to sentinel behaviour than females when males dominate females, as in Redbilled Woodhoopoes (Chapter 4). However, for woodhoopoes, in which female contribution to PRSB exceeds that of males, the social function of this behaviour appears to be overridden by energetic constraints on males, particularly during winter.

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