

Limits to cooperative polyandry in birds

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SUMMARY

In communally breeding birds the number of helpers at the nest is less when helping depends on shared paternity (cooperative polyandry) rather than on collateral kinship with the brood (helpers are siblings, aunts or uncles). We suggest that this is because a helper's relatedness to the brood decreases with an increasing number of helpers in the first case but not in the second. By using the dunnock, *Prunella modularis*, as a model system, we investigated why cooperative polyandry in this species rarely involves more than two males by removing females to increase male availability in the population. Females defended by just one male actively solicited matings from a second male who settled on their territory. By contrast, although widowed males also attempted to settle on territories already defended by two males, females usually refused to mate with them even though they had ample opportunity to do so. We show that a female would be unlikely to increase the total parental help she gained by sharing matings between more than two males because of the way males reduce their parental effort in relation to paternity loss, and suggest that mating with more males would also increase sexual harassment. We conclude that female choice may set a limit to cooperative polyandry in birds.

1. THE NUMBER OF HELPERS IN COMMUNAL BREEDERS

Many species of birds (*ca.* 2.5%) are communal breeders, in which three or more individuals cooperate to raise a brood (Brown 1987). In some cases this arises through cooperative polyandry, where several males share matings with a female and so are potential fathers of the young (table 1; case A). For example, in the dunnock, *Prunella modularis*, two males will help a female raise a brood provided both have gained a share of the matings with her, which often results in mixed paternity (Davies 1992). More commonly, communal breeding occurs when a monogamous breeding pair is assisted by helpers who are collateral kin of the brood (table 1; case B). The helpers may be previous offspring of one or both breeders, and so half or full-sibs of the brood (e.g. Florida scrub jay, *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1990)), or they may be sibs of one of the breeders, and so uncles or aunts of the brood (e.g. long-tailed tit, *Aegithalos caudatus* (Glen & Perrins 1988)).

Figure 1 shows that the number of helpers is less when helping depends on shared paternity rather than on collateral kinship with the brood. The species values shown in table 1 cannot be considered as independent data points because of possible effects of common phylogenetic descent. We therefore used an independent comparisons method (Felsenstein 1985; Purvis 1990; Harvey & Pagel 1991; Pagel 1992) in conjunction with Sibley & Ahlquist's (1990) molecular phylogeny. From the data in table 1 and Bennett (1986), we identified eight independent occurrences of the evolution of polyandrous cooperative breeding, and 23 independent occurrences of the evolution of monogamous cooperative breeding. We quantified the

change in the maximum number of helpers which occurs at each of these evolutionary nodes, and compared the size of changes at nodes where polyandrous cooperative breeding evolved with the size of changes at nodes where monogamous cooperative breeding evolved. We then standardized all evolutionary changes in maximum helper number to control for the phylogenetic level at which the evolutionary event occurred (Pagel 1992). The results of this phylogenetic analysis confirm that the evolution of polyandrous cooperative breeding is associated with a smaller maximum number of helpers than is monogamous cooperative breeding (figure 1*c*). Furthermore, this result was not dependent on the use of the molecular phylogeny as the same result was given when a traditional morphological phylogeny was used (for details, see Owens & Bennett 1994). The noisy miner is a clear exception (table 1), and it is difficult to believe that as many as 20 males help at a nest because all have chances of paternity. Paternity data are needed to confirm that they really belong in this category.

The distinction between the two cases analysed in figure 1 may not always be clear cut; in some species helping may be based both on paternity sharing and collateral kinship (Rabenold *et al.* 1990; Mulder *et al.* 1994), and further use of genetic parentage tests in studies of cooperatively breeding species would be useful. Nevertheless, the difference in number of helpers is striking, and recent work on lions, *Panthera leo*, shows the same result within one species; coalitions between unrelated males, which depend on paternity sharing, are smaller than those involving relatives, where males who fail to mate can gain indirect fitness from helping their kin to breed (Packer *et al.* 1991).

We suggest that the key difference between the two

Table 1. Numbers of helpers (*n*) who help the female and sole (or alpha) male breeders to feed the brood in cooperatively breeding birds

(This compares (A) cases where the helpers are additional breeding males in a polyandrous mating system, and thus potential fathers of the brood, and (B) cases where the helpers are collateral kin of the brood (e.g. siblings, uncles, aunts). The table includes only cases where there was apparently just a single breeding female at the nest, and is based on the list of species in Brown (1987, table 2.2, excluding *Sitta pygmaea* and *S. pusilla* (origin of helpers unknown), *Geospiza scandens* and *G. fortis* (helping thought to be misdirected care), and all species for which mating system is unknown, or sex of helpers unknown, so that helpers could not be categorized) and studies since his review.)

species	family	<i>n</i>	reference
(A). Polyandry: female and alpha male plus <i>n</i> additional breeding males			
Tasmanian native hen (<i>Tribonyx mortierii</i>)	Rallidae	1–2	Ridpath (1972)
brown skua (<i>Catharacta lombergi</i>)	Laridae	1–3	Millar <i>et al.</i> (1992)
Galapagos hawk (<i>Buteo galapagoensis</i>)	Accipitridae	1–3	Faaborg (1986)
noisy miner (<i>Manorina melanocephala</i>)	Meliphagidae	3–21	Dow & Whitmore (1990)
black tit (<i>Parus niger</i>)	Paridae	1	Tarboton (1981)
Henderson reed-warbler (<i>Acrocephalus vaughani</i>)	Sylviidae	1	Brooke & Hartley (1995)
dunnock (<i>Prunella modularis</i>)	Passeridae	1	Davies (1992)
alpine accentor (<i>Prunella collaris</i>)	Passeridae	1–2	Davies <i>et al.</i> (1995); Hartley <i>et al.</i> (1995)
Smith's longspur (<i>Calcarius pictus</i>)	Emberizidae	1–2	Briskie (1992)
(B). Monogamy: breeding pair with <i>n</i> helpers who are collateral kin of the brood			
(1) Helpers predominantly or entirely males			
red-cockaded woodpecker (<i>Picoides borealis</i>)	Picidae	1–4	Walters (1990)
superb fairy wren (<i>Malurus cyaneus</i>)	Maluridae	1–4	Mulder <i>et al.</i> (1994)
purple-crowned fairy wren (<i>Malurus coronatus</i>)	Maluridae	1–5	Rowley & Russell (1994)
pinyon jay (<i>Gymnorhinus cyanocephalus</i>)	Corvidae	1–2	Marzluff & Balda (1990)
Galapagos mockingbird (<i>Nesomimus parvulus</i>)	Sturnidae	1–3	Curry & Grant (1990)
long-tailed tit (<i>Aegithalos caudatus</i>)	Aegithalidae	1–8	Glen & Perrins (1988)
common babbler (<i>Turdoides caudatus</i>)	Sylviidae	1–9	Gaston (1978)
(2) Helpers are of both sexes			
green woodhoopoe (<i>Phoeniculus purpureus</i>)	Phoeniculidae	1–7	Ligon & Ligon (1990)
red-throated bee-eater (<i>Merops bullocki</i>)	Meropidae	1–3	Fry (1972)
white-fronted bee-eater (<i>Merops bullockoides</i>)	Meropidae	1–4	Emlen (1990)
white-throated bee-eater (<i>Merops albicollis</i>)	Meropidae	1–5	Fry (1972)
pie kingfisher (<i>Ceryle rudis</i>)	Alcedinidae	1–2	Reyer (1990) (primary helpers only)
kookaburra (<i>Dacelo gigas</i>)	Alcedinidae	1–4	Parry (1973)
hoatzin (<i>Opisthocomus hoazin</i>)	Opisthocomidae	1–6	Strahl & Schmitz (1990)
moorhen (<i>Gallinula chloropus</i>)	Rallidae	1–3	Gibbons (1987)
purple gallinule (<i>Porphyryla martinica</i>)	Rallidae	1–8	Hunter (1985)
splendid fairy wren (<i>Malurus splendens</i>)	Maluridae	1–4	Rowley & Russell (1990)
bell miner (<i>Manorina melanophrys</i>)	Meliphagidae	4–10	Clarke (1984)
buff-rumped thornbill (<i>Acanthiza reguloides</i>)	Pardalotidae	1–5	Bell & Ford (1986)
striated thornbill (<i>Acanthiza lineata</i>)	Pardalotidae	1–2	Bell & Ford (1986)
grey-crowned babbler (<i>Pomatostomus temporalis</i>)	Pomostomatidae	1–8	Brown <i>et al.</i> (1978)
yellow-billed shrike (<i>Corvinella corvina</i>)	Laniidae	3–10	Grimes (1980)
white-winged chough (<i>Corcorax melanorhamphus</i>)	Corcoracidae	2–18	Heinsohn (1992)
Florida scrub jay (<i>Aphelocoma coerulescens</i>)	Corvidae	1–6	Woolfenden & Fitzpatrick (1990)
chestnut-bellied starling (<i>Spreo pulcher</i>)	Sturnidae	1–12	Wilkinson & Brown (1984)
stripe-backed wren (<i>Campylorhynchus nuchalis</i>)	Certhiidae	1–7	Rabenold (1990)
bicolored wren (<i>Campylorhynchus griseus</i>)	Certhiidae	1–3	Austad & Rabenold (1985)
black-capped donacobius (<i>Donacobius atricapillus</i>)	Certhiidae	1–2	Kiltie & Fitzpatrick (1984)
Arabian babbler (<i>Turdoides squamiceps</i>)	Sylviidae	1–6	Zahavi (1990)
Seychelles brushwarbler (<i>Acrocephalus sechellensis</i>)	Sylviidae	1–11	Komdeur (1994)
White-browed sparrow weaver (<i>Plocepasser mahali</i>)	Passeridae	1–6	Lewis (1982)

cases is as follows. When helpers are collateral kin, their relatedness to the brood remains the same irrespective of the number of helpers ($r = 0.5$ for full sibs and 0.25 for half sibs, uncles and aunts). The number of helpers may then be limited simply by the diminishing benefits to the brood from increased care. By contrast, when communal breeding is based on shared paternity, average male relatedness to the brood decreases with the number of males ($r = 0.5/n$ where n males share

paternity equally). There are two ways in which this could reduce the number of helpers.

1. Male–male competition may restrict access to fertile females such that subordinate males in a group stand to gain very few matings.

2. Female choice may limit the number of polyandrous males for two reasons: (i) more males may lead to more sexual chases and harassment, which causes stress and may reduce hatching success (Davies

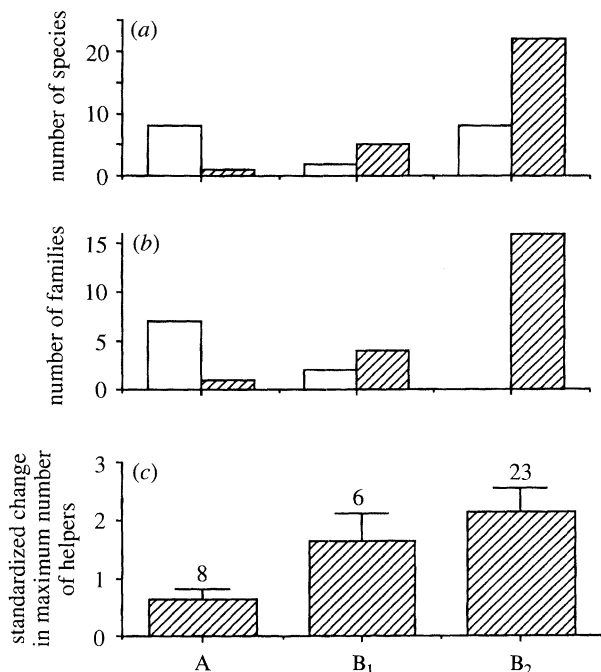


Figure 1. Maximum number of helpers (< 4 , open columns: ≥ 4 , shaded columns) who help the female and sole (or dominant) male breeders to feed the brood (a) by species and (b) by family. Data are from species listed in table 1. Two cases are compared: A, helpers are additional males in a cooperative polyandrous breeding system, and so potential fathers of the brood. B, helpers are collateral kin of the brood, either previous offspring of one or both breeders (hence half-siblings or full-siblings of the brood), or siblings of one of the breeders (hence uncle or aunt to the brood); B₁ (collateral kin, male helpers), B₂ (collateral kin, all cases). *G*-tests at the family level: (A against B₁), $G_1 = 4.58$, $p = 0.04$; (A against B₂), $G_1 > 17.0$, $p < 0.0001$. (c) A phylogenetic analysis (based on a molecular phylogeny) of the maximum number of helpers associated with the evolution of communal breeding is summarized, which shows mean (+s.e., n) standardized changes in helper number associated with independent occurrences of the evolution of cooperative breeding. Comparing the two cases as above: (A against B₁), $t_{12} = 2.23$, $p < 0.05$; (A against B₂), $t_{29} = 2.05$, $p < 0.05$. Similarly, if a morphological phylogeny is used: (A against B₁), $t_{12} = 3.28$, $p < 0.01$; (A against B₂), $t_{29} = 2.16$, $p < 0.05$.

1985; Lifjeld 1994); or (ii) a male may reduce his parental effort in relation to a reduction in paternity (Møller 1988; Davies *et al.* 1992; Wright & Cotton 1994), so a female may suffer a reduction in the total amount of help she gains from males if she spreads matings too thinly.

We examined these hypotheses by manipulating experimentally the availability of males to polyandrous female dunnocks.

2. COOPERATIVE POLYANDRY IN DUNNOCKS

We have studied a colour-ringed population of dunnocks since 1981 in the Cambridge University Botanic Garden (Davies 1992). The mating system is variable; one male may defend one female territory (monogamy) or two adjacent female territories (polygyny), or two, occasionally three, unrelated males may defend one female territory (polyandry) or two or

three adjacent female territories (polygynandry). From 1981 to 1990, 29% of the mating combinations at the start of the breeding season were polyandrous and 24% polygynandrous. Almost all of these involved just two males, and there was a clear dominance hierarchy with alpha males (usually older) displacing beta males from food and from the vicinity of the female. Of the 75 cases of polyandry, only one involved three males, and the third male was a weak competitor and failed to gain matings. Of the 60 cases of polygynandry, only six involved three males. In five cases the pattern of overlap between male and female territories was such that each female had just two males. This arose either because an alpha male defended two adjacent female territories, each of which was encompassed by a different beta male, or because two adjacent female territories were each overlapped by a different alpha male with a beta male encompassing them both (see figure 3.3 of Davies 1992). Only in one case did three males compete for matings with a female and the gamma male failed to mate. In summary, the number of males sharing matings with a female and helping her to raise a brood seems to be limited to two.

During each breeding season, 15–35% of the females were killed by predators (cats *Felis catus*, tawny owls *Strix aluco*, kestrels *Falco tinnunculus*, and sparrowhawks *Accipiter nisus*). When one female was killed in polygynous or polygynandrous mating systems, the males stayed with their remaining females. However, the death of the female in monogamous and polyandrous systems left the males without a mate, and they then attempted to settle on neighbouring territories (Davies 1992). We followed the behaviour of 15 such widowed males (data from 1981 to 1990). All 15 had the choice between settling on a neighbouring territory defended by one male and a territory defended by two males. Neighbouring territories were defined as those whose boundaries abutted that of the widowed male. Of these males, 14 settled on the one-male option whereas just one settled, as a gamma male, on the two-male option (a polygynandrous combination of two males and three females). Considering the choices available to each male (the number of neighbouring territories varied from two to four), the probability that just one or fewer chose to settle on the two-male defended option was less than 0.001.

These choices by widowed males make good sense because they have greater chances of gaining matings with a female if she is defended by just one male rather than two (see below). However, they do not allow us to distinguish between the two hypotheses in section 1. A widowed male may not join a system with two males because he is excluded either by male–male competition (hypothesis 1) or by female choice (hypothesis 2).

3. CAN EXPERIMENTAL REMOVALS OF FEMALES INCREASE POLYANDRY BEYOND TWO MALES?

We removed some females to create a male-biased sex ratio so that widowed males only had the option of settling on territories defended by two males. We

removed 23 females during the early part of the breeding season (4 April–6 May) in 1992 and 1993. They were caught by mist net and released in suitable habitat 75 km away, under licence from English Nature. This resulted in 25 males being left without a mate. The removals were done so that all the neighbouring territories to these widowed males were defended by two males (either polyandry or polygynandry). The result of the removals was that from two to six extra males were made available as potential settlers on each of these two-male defended territories. Territories were plotted before and after the removals by using minimum polygons drawn around the map registrations of each individual, and the number of registrations was matched for the two time periods (see Davies (1992) for details). To assess the success of widowed males in gaining matings with neighbouring females, focal watches of females were done during the mating period (from nest completion to the beginning of incubation, which occurs when the clutch is complete, a period of *ca.* 5–10 days). Females were observed for, on average, a total of 8.6 hours each ($n = 15$), and we made continuous observations of which males were with them (within 10 m). A male's mating success was measured as the percentage of total time for which he gained exclusive access to the female, i.e. was the only male within 10 m of her. Only when a male has such exclusive access is he able to copulate, uninterrupted by other males. Previous work has shown that these behavioural measures and observation times give a good measure of a male's paternity share, as assessed by DNA fingerprinting (Davies *et al.* 1992).

4. TERRITORY CHANGES

We compared territories before and after the experimental female removals by using two-tailed Wilcoxon matched pairs tests. Widowed males soon began to trespass on neighbouring territories. Scoring the neighbouring territory which a widowed male most overlapped before his own female was removed, the percentage of this neighbouring female's territory he overlapped increased significantly after the removal of his mate (mean \pm s.e. = $4.9 \pm 3.0\%$ before, against $36.9 \pm 12.7\%$ after removal; $n = 13$, $p = 0.002$). Although some widowed males increased their territory size, there was no overall significant change in response to the removal (mean \pm s.e. territory size before removal = 0.28 ± 0.03 ha \dagger , against 0.43 ± 0.09 ha after removal; $n = 16$, $p > 0.1$). Therefore the main response to mate loss was simply a shift towards a neighbouring territory occupied by a female.

There was no indication that the neighbouring females changed their territories to encourage access to the widowed males. Female territory size did not change in response to the removal of the neighbouring female (0.31 ± 0.05 ha before, against 0.38 ± 0.08 ha after; $n = 14$, $p = 0.10$), nor did the percentage of the neighbouring female's territory that they overlapped ($1.0 \pm 0.6\%$ before, against $1.8 \pm 1.4\%$ after; $n = 13$, $p > 0.5$). All these females already had two males,

\dagger 1 ha = 10^4 m 2 .

either in polyandry or polygynandry. To test whether a female was more likely to expand or shift her territory to gain access to a widowed neighbour if she only had one male, either in monogamy or polygyny, we compared responses to natural female removals of neighbouring females who had one as against two males. There were no differences in percentage change in territory size from before to after the removal for females with one male (mean -4.0% , $n = 10$) against two males (mean -2.8% , $n = 23$, n.s.). Neither were females with one male more likely to shift their territories towards the widowed male (change in percentage overlap with neighbouring female before to after the removal, mean $+14.1\%$, $n = 10$) than females with two males (mean $+6.9\%$, $n = 23$, n.s.).

5. MATING SUCCESS OF WIDOWED MALES

When a widowed male settled on a territory defended by one male (response to natural removals), he was likely to be successful in gaining a share of the matings with the female during her fertile period and so to help with chick feeding (table 2).

Females actively solicited matings from a second resident male and thereby increased their reproductive success from gaining increased male help (Davies 1992). By contrast, when faced only with territories defended by two males (experimental removals), widowed males had little success (table 2). Of the three who gained some access to the fertile female, one settled on the territory as a gamma male and gained exclusive access for 22% of the time. In this case the female accepted the third male and solicited matings from him as well as from her original alpha and beta males. Unfortunately the nest was depredated, so there are no data on chick feeding. In the other two cases, although the males settled as gamma males they gained very little exclusive access to the female (0.4% and 0.5% of the time), and in both cases the female rejected their advances, by dipping her wings and tail, fluffing her plumage and adopting a head down posture (Davies 1992). We did not see either of them copulate and neither helped to feed the chicks.

The limited success of the widowed males' settlement

Table 2. Comparison of a widowed male dunnock's mating success when he has the option of joining a neighbouring territory defended by one male (data from natural removals, caused by predation) and when he only has the option of joining a neighbouring territory defended by two males (data from experimental removals)

widowed male's mating options on neighbouring territories	number of cases widowed male	
	gained some access to fertile female	fed the brood
joined territory defended by one male	9/12	7/9
attempted to join territory defended by two males	3/23	0/8
	$G_1 = 13.7$ $p < 0.0005$	$G_1 = 8.0$ $p < 0.005$

on territories defended by two males was clearly partly due to defence by the resident alpha and beta males, who attempted to chase them off. However, the rejection behaviour of females in two of the three cases above suggests that females also could play an active role in limiting the share of matings to two males. During the mating period, there is a conflict of interest between the alpha male and female. The alpha male maximizes his reproductive success by preventing the beta male from mating because the increased production of a trio-fed brood does not compensate him for shared paternity. The female, however, does best by sharing matings between alpha and beta males so as to gain help from them both (Davies 1992). Females who can escape the alpha male's close guarding are more likely to mate with the beta male. A good measure of the female's ability to control the allocation of matings is the proportion of time she can escape male attention and remain alone (Hatchwell & Davies 1990). Considering the 15 females who had the opportunity, from our removals, to gain extra males in addition to their original alpha and beta, the mean percentage time alone during the mating period was 33.5% (s.e.; 4.8, range 4.5–61%). Of these, 11 were alone for 20% or more of the time or more, and nine for 30% or more, so most had ample opportunity to escape the attentions of their alpha and beta males and to solicit matings from a third male.

6. WHY DO FEMALES NOT ENCOURAGE A THIRD MALE?

We suggest two hypotheses to explain why females restrict polyandry to two males.

(a) To reduce harassment

Monogamous females usually fed quietly with their guarding male during the fertile period and suffered little in terms of male harassment (mean percentage time chased by male = 1.5 ± 0.4 s.e., $n = 14$). Polyandrous females, however, were often chased as the alpha and beta male battled for paternity (mean percentage time chased = 15.3 ± 2.2 , $n = 29$; significantly greater than monogamous females, $p < 0.01$). Such squabbles reduce the female's feeding rate and lead to an increased frequency of unhatched eggs (Davies 1985). If a female encouraged more than two males, by soliciting copulations from them, then this could lead to a further increase in harassment and a reduction in female fitness.

(b) To maximize male parental care

A female that mates with two males gains more help with parental care than a female that mates with one (Hatchwell & Davies 1990), but it does not necessarily follow that three or more males would be even better. If matings are divided too thinly between several males, then they may not all exceed a helping threshold. Furthermore, a reduction in parental effort in response to paternity loss may mean that, even if all males do help, the total amount of help may not increase beyond two helpers. Unfortunately, our

experiment failed to provide us with cases of three males helping so we have to use the relation between alpha and beta male parental effort and their mating share to predict how total help will vary as matings are shared between more males (figure 2). We used data from natural and experimental variation in mating share between alpha and beta males in polyandry (see Davies *et al.* (1992) for details).

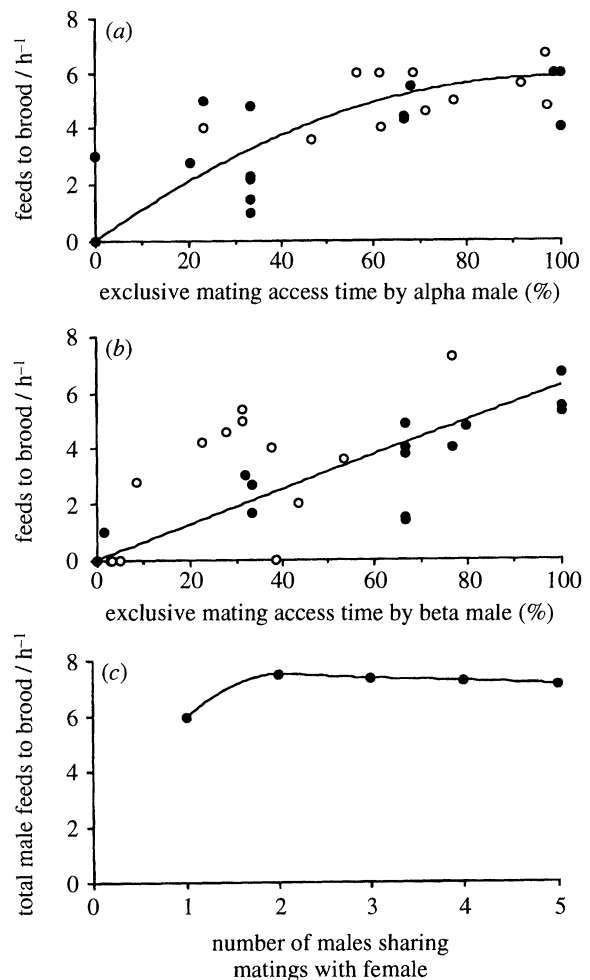


Figure 2. A male dunnock's provisioning effort to the brood in relation to the percentage of exclusive mating access time he gained with the female during her fertile period for (a) alpha males and (b) beta males in cooperative polyandry, where both males helped the female to feed the young. In both (a) and (b), the filled circles represent experimentally manipulated exclusive access time, and the open circles represent the natural variation; data are for broods of 3 or 4 nestlings (no difference between these two brood sizes, ANCOVA, $F_{1,28} = 2.02$, n.s.). The regression lines are fitted through all data; for alpha males a quadratic expression gave a significantly better fit than a linear, but not for beta males where a linear regression is used. When males gain no exclusive mating access time they provide no parental care (Davies *et al.* 1992), so the regressions are constrained to pass through the origin. The equations of the lines are: (a) $y = 0.12x - 0.00058x^2$, and (b) $y = 0.063x$. (c) These equations are used to show how total male feeding rate to the brood could vary with the number of males sharing mating with the female. We assume that the alpha male responds as in equation (a) and subordinate males as in equation (b), with all males achieving an equal share of the exclusive access time with the fertile female.

Assuming that alpha males respond to mating share as in figure 2*a*, and the beta and other subordinate males as in figure 2*b*, then the total male effort decreases slightly beyond two males, if all males share matings equally (figure 2*c*). An alternative scenario would be for the alpha male to gain most matings (say 60%, the mean observed in polyandry) and for the subordinates to share the remaining 40% equally. In this case the curve of total male effort would reach an asymptote at two males.

7. DISCUSSION

We conclude that female choice plays a major role in limiting dunnoek polyandry to two males. Under natural conditions, unpaired males usually have the option of settling on a neighbouring territory defended by one male. Our removal experiments show that their preference for this option over a two-male defended territory makes good sense. Although females encourage matings from a second male, they do not usually do so from a third male, probably because this would not increase total male help and would also bring costs of increased male harassment. Reduction of male help in relation to paternity sharing, together with the costs of sexual harassment, may explain why cooperative polyandry in other species is usually limited to a few males compared with helping based on collateral kinship where there is no such competition concerning relatedness to the brood (table 1). The limit may vary between species depending on operational sex ratios, which sex can most easily control matings, and on the alternative options for males. For example, in dunnoeks a polyandrous female can rely on help from two resident males who share her territory provided she mates with them both. However, in the congeneric alpine accentor a female usually shares two to four males with one to three other females in a large polygynandrous group. Here, females often solicit matings from three males but they are unlikely to gain parental help from all three simply because some of the males are usually busy competing for matings or feeding broods elsewhere in the group. In this case, sharing matings among three males simply increases the chance that at least one of them will be available to help feed the young, and so acts as an insurance for male help (Davies *et al.* 1995; Hartley *et al.* 1995).

We thank Ian Owens for carrying out the comparative analysis; the Natural Environment Research Council for funding our work; the staff of the Cambridge University Botanic Garden for their help, and Michael Brooke, Andrew Cockburn, Bryan Grenfell, Ben Hatchwell, Naomi Langmore and Ian Owens for their comments.

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Received 19 April 1994; accepted 25 April 1994