



## Female control of copulations to maximize male help: a comparison of polygynandrous alpine accentors, *Prunella collaris*, and dunnocks, *P. modularis*

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**Abstract.** Alpine accentors and dunnocks bred in polygynandrous groups in which two or more unrelated males shared two or more females. In both species, a female solicited actively to both alpha and subordinate males whereas an alpha male attempted to guard the female to monopolize paternity. Females combated the restrictions imposed by alpha male guarding by increasing their solicitation rate to males who had gained less mating access. Males increased their copulation rate in response, but alpha males ignored more of the offers. In both species, even when a female mated with both alpha and beta males she often gained just one male's help with chick feeding. Under these conditions, alpha male alpine accentors reduced their amount of help with a decreased mating share, whereas beta males did not. In dunnocks, however, neither alpha nor beta males reduced their help provided a critical share of the matings was exceeded. As predicted if females attempted to maximize male help, female alpine accentors preferred to give more matings to the alpha male while female dunnocks preferred alpha and beta equally. There was no evidence for either species that alpha males sired fitter offspring; within broods of mixed paternity, there was no difference in the weights of chicks sired by alpha versus subordinate males. Female dunnocks competed with other females by territory defence whereas female alpine accentors had overlapping ranges and competed directly for male attention, increasing their solicitation rate to the alpha male if other females in the group were fertile. We suggest that the extraordinarily high rates of solicitation by females, refusal by males and copulation rates (up to a thousand per clutch) in the two species are the outcome of sexual conflict over the control of mating.

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Conflicts of interest have a profound effect on breeding systems. Competition among males leads not only to a battle for access to females (Darwin 1871) but also to male adaptations that enhance success in sperm competition, such as mate guarding and frequent copulation (Parker 1970). Competition may also occur among females when males provide parental care or nuptial gifts, or monopolize resources which influence female reproductive success, such as food or nest sites (Gwynne 1991; Berglund et al. 1993; Slagsvold & Lifjeld 1994). These conflicts within the two sexes generate conflicts between them when an advan-

tageous character in one sex causes a selective disadvantage to the other sex (Parker 1979). For example, whereas a male might gain from frequent copulation to assure paternity, a female might suffer from the extra time or harassment involved.

Parker (1979, 1984) has argued that asymmetries in selection for securing matings (stronger in males) and ability to manipulate the other sex (less costly for females) might balance each other, so the resolution of the conflict may be a compromise between the interests of the two sexes. However, the asymmetries may act in opposite directions in different cases. Where females gain increased male help from sharing matings between several males, selection on females for multiple mating may be as strong or stronger than that on males (Davies 1992) and whereas females may

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often seem to control matings and sperm usage, in many cases males can force copulations and manipulate sperm storage inside the female (Thornhill & Alcock 1983; Smuts & Smuts 1993; Clutton-Brock & Parker 1995).

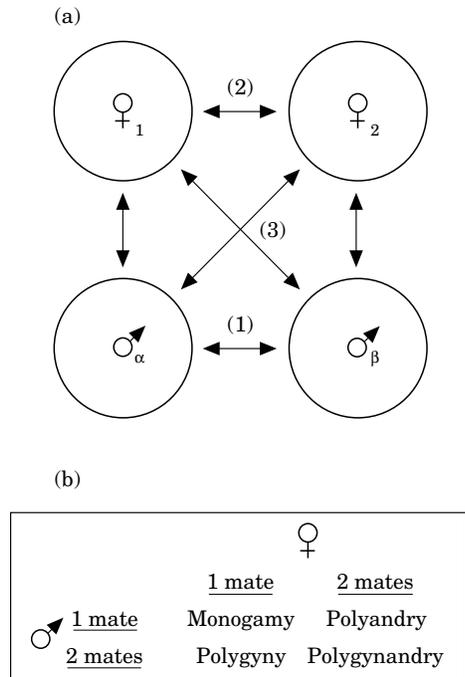
Although general theoretical predictions might be hard to make, we clearly need to consider the dynamic interplay of decisions by both sexes. Whereas ecological factors such as food and predation certainly influence breeding systems (Emlen & Oring 1977), the counterstrategies played by members of the opposite sex may be just as important. Males can be as much of a nuisance to females as predators, and breeding systems may reflect the abilities of one sex to resist or manipulate the other (e.g. Alatalo et al. 1981; Davies 1989; Rowe et al. 1994).

In birds, sexual conflict can result in high levels of extra-pair paternity, even in apparently monogamous species (Birkhead & Møller 1992; Gowaty, in press), but it is often hard to observe the behaviour involved because of the surreptitious way in which males and females seek extra-pair matings. However, in polygynandrous mating systems, where several males share several females, there is a good opportunity to study behavioural conflicts because individuals interact openly with rivals of the same sex and also have a choice between mates. All of the interactions shown in Fig. 1a may involve various degrees of conflict or cooperation.

(1) Two males may agree to share matings if their cooperation is needed to defend the females against other males (Jamieson et al. 1994; Packer et al. 1991), or if their joint help is necessary for rearing offspring (Gowaty 1981). Alternatively, the dominant male may attempt to monopolize the matings if the gain from the subordinate male's assistance does not compensate him for the costs of shared paternity (as in dunnocks and alpine accentors, see below).

(2) Two females may cooperate if their alliance protects them from predators (Robinson 1986) or males (Packer et al. 1990; Smuts & Smuts 1993), but there will be conflict if these benefits are outweighed by the costs of polygyny (e.g. shared male help or increased female infanticide; Veiga 1990).

(3) Finally, these interactions within the sexes can create conflicts between them if the dominant male gains by excluding the subordinate male but the female gains from multiple paternity, or if the



**Figure 1.** (a) A polygynandrous group of two males and two females. Each of the relationships within the sexes (1 and 2) and between the sexes (3) can involve varying degrees of conflict and cooperation. (b) Different mating systems emerge depending on the ability of individuals to exclude rivals or form alliances with members of the same sex, and to monopolize members of the opposite sex.

males benefit from polygyny but the females suffer. The various mating outcomes (Fig. 1b) may then reflect different resolutions to these conflicts, depending on which individuals can gain their best option (Davies 1989).

In this paper we describe the behavioural conflicts involved in the solicitation of copulations by females and their acceptance by males in two congeneric polygynandrous birds. In dunnocks, polygynandry usually involves two males with two females whereas in alpine accentors up to four males share four females. Mating combinations do not involve close relatives and there are clear dominance hierarchies among the males with older individuals usually being more dominant. Our previous work showed that in both species males help to feed the young only if they gain a share of the matings, which is correlated with paternity share measured by DNA fingerprinting (Davies et al. 1992; Hartley et al. 1995).

In both species all the relationships in Fig. 1a involve reproductive conflicts, which stem from two sources. First, the increased production of young arising from a second male's help does not compensate the alpha male for shared paternity, so whereas a female benefits from sharing matings between the males so as to gain increased male help, the alpha male does best by monopolizing exclusive paternity. Second, a female suffers reduced reproductive success from the presence of another female because of the costs of shared male care, but the males benefit because the combined output of two females exceeds that of one. The resulting behavioural conflicts are that the alpha male guards the female while she attempts to escape and solicit matings from the beta male, and the females are aggressive to each other while the males attempt to keep between them so as to maintain peace (Davies 1992; Davies et al. 1995).

The main questions we address here are: (1) to what extent can a female control male mating share by varying the rate at which she solicits copulations from alpha and beta males; and (2) how do males vary their acceptance of a female's offers in relation to their conflicting needs to assure paternity and conserve sperm for other females? We first discuss alpine accentors and then show how the contrasting behaviour of dunnocks supports the view that females of both species use solicitations to maximize the parental help they gain from males. In the discussion we consider to what extent the observed behaviour concerning the offers and acceptance of copulations reflects a compromise between the conflicting interests of the two sexes.

## ALPINE ACCENTORS: RESULTS AND DISCUSSION

### Study Area and Sample Sizes

A colour-ringed population of ca 30 breeding adults was studied during five breeding seasons, 1990–1994, in the Réserve Domaniale du Mont Valier, Ariège, central Pyrénées, France. The birds lived on the mountain tops (1950–2410 m), well above the tree line (ca 1500 m), in a habitat of steep cliffs and grassy meadows strewn with boulders and stones. We studied from three to five polygynandrous groups each year, in which an alpha male and from one to three subordinate males (beta, gamma, delta) shared a large range

within which from two to four females had overlapping ranges. For further details see Davies et al. (1995) and Hartley et al. (1995).

Females were observed as often as possible from ca 7 days before the first egg was laid to the day of clutch completion. Observation times lasted from 10 min to 3 h and the total times per female per breeding attempt varied from 1.0 to 17.3 h (mean 4.5 h). Every minute we recorded the distance between the female and any males, and the participants and outcome of any solicitations, copulations or chases. The data analysed here comprise a total of 216.4 h observation of fertile females in 48 breeding attempts, involving 23 different females and 28 different males (11 alpha, 17 subordinate). Fifty-six per cent of the females and 50% of the males provided data for more than one breeding attempt, which raises the problem of pseudoreplication; it would be unjustified to regard the 48 breeding attempts as independent if individuals were consistent in their performance. However, in our previous analyses we found no significant effects of individual male or female identity on behaviour or reproductive success (Davies et al. 1995; Hartley et al. 1995) and this was true for the behavioural measures studied in this paper. Thus, there were no significant effects of individual or year, nor any interaction between them for any of the following; % mating access with a female (for males) or with alpha versus subordinate male (for females), % solicitations ignored or copulation rate (two-factor ANOVAs:  $P=0.12-0.85$ ). Only solicitation rate was close to being significantly variable between females ( $F_{12,39}=2.21$ ,  $P<0.1$ ), but there were no male effects ( $P=0.64$ ). We conclude that variation within individuals across different nesting attempts was as great as that between individuals, so we can use each attempt as an independent sample. The large variation in individual performance was not surprising given that they interacted with different competitors and mates in different years and that mate guarding varied greatly depending on the activities of other females in the group (Davies et al. 1995, and below).

### Mate Guarding, Solicitations and Copulations

A female began to solicit matings once she had finished her nest, usually 3–7 days before she laid the first egg. From this time on, right up to the completion of the clutch and the onset of

incubation, the males competed for copulations. There was no significant variation during this period in the proportion of time the female spent exclusively with the alpha male or with a subordinate male (no other male within 10 m), nor in the proportion of time several males were with her (<10 m; Hartley et al. 1995). Female solicitation rate to alpha or subordinate males also did not vary during this time, nor did male copulation rate (one-way ANOVAs:  $P=0.35-0.75$ ). Therefore, as in other polygynandrous species (Briskie 1992; Hatchwell & Davies 1992), females solicited and males competed for matings throughout the female's fertile period. There was no diurnal variation in the proportion of time the alpha male spent with the female, nor in female solicitation rate to him, nor in his copulation rate (21 cases where we had data at three times of day, 0600–1000, 1000–1400 and 1400–1800 hours local time; Friedman two-way ANOVAs:  $P>0.1-0.8$ ). We therefore lumped data on mating behaviour for the whole mating period.

There were five themes underlying the conflicts over mating.

#### (1) Alpha males guarded females

The alpha male followed the female closely, usually feeding within 2 m or perching on a rock nearby and keeping between her and the subordinate males. Beta males followed a few metres behind and gamma and delta males (if present) still further away. When the female flew off, all the males followed in hot pursuit and sometimes they flew in a group all around the cliffs for half a minute or more, calling loudly. Subordinate males approached the female in an attempt to gain matings, either by flying in suddenly to catch the alpha male unaware or by creeping up towards her behind the rocks. Each male chased those who were lower in rank and attempted to keep them at bay. The beta male, in particular, was often very persistent and approached the female every minute or so. The alpha male usually displaced him to 5–10 m, but sometimes this escalated into a long aerial chase for up to a minute, with the alpha dive-bombing his rival in mid air and pursuing him for up to 400 m. After these long flights the beta male sometimes simply followed the alpha male back to the female and their cat and mouse chases in her vicinity began all over again. On average, the female spent 29% of her time

accompanied by more than one male ( $SE=3$ , range 1–65%,  $N=48$  breeding attempts) and the males spent on average 46% of this time chasing. Males tolerated independent juveniles who fed near fertile females, including those who had dispersed from neighbouring groups, so their aggression was restricted to sexual competitors.

#### (2) Most copulations were initiated by the female

The female actively solicited copulations with an extraordinary display in which she approached a male, crouched with her breast touching the ground and lifted her tail vertically to expose her bright red, swollen cloaca, quivering her tail from side to side and shivering her wings. Of a total of 889 solicitations, 93% were initiated by the female approaching the male and only 7% by the female responding to an approach by the male. Considering 23 different females, the mean % initiated by the female was  $95 \pm 2\%$  (see also Nakamura 1990). There was no difference between the proportion of solicitations initiated by females to the alpha male ( $\bar{X} \pm SE = 95 \pm 1\%$ ,  $N=23$  females), the beta male ( $94 \pm 3\%$ ,  $N=17$  females) or the gamma male ( $88 \pm 7\%$ ,  $N=9$  females; Kruskal–Wallis one-way ANOVA:  $P>0.9$ ).

The female often solicited repeatedly to a male, moving ahead of him if he hopped away so as to present her cloaca right in front of his face. Prior to copulation, the male stood upright behind her and then jumped at her obliquely, cloacal contact lasting just a fraction of a second (Aichorn 1969; see drawings in Nakamura 1990). Sometimes the female then immediately presented to the male again and he made up to seven cloacal contacts in quick succession. Unlike dunnocks, there was no cloaca-pecking prior to copulation (see below).

We scored a bout of female presentations to a male as one solicitation and a sequence of cloacal contacts by the male as one copulation. Female solicitation rate to the alpha male, and his copulation rate, did not differ between times when he was alone with the female and when subordinate males were nearby because subordinates rarely interrupted (Table I). By contrast, alpha males always tried to interrupt female solicitations to subordinate males. Therefore a female was only freely able to solicit to subordinates, and subordinates to copulate, when they were alone together (Table I). On average, the female solicited 7 times per h, or every 8.5 min, an extraordinarily high rate.

**Table I.** Influence of the presence of other males nearby (<10 m) on a female alpine accretor's solicitation rate to alpha versus subordinate males, and on the male's copulation rate

Male	Female solicitation rate ( $\bar{X} \pm SE$ ) per h		Copulation rate ( $\bar{X} \pm SE$ ) per h	
	Male alone with female	Other males nearby	Male alone with female	Other males nearby
Alpha ( $N=26$ )	$6.2 \pm 1.4$	$6.3 \pm 1.5$	$1.6 \pm 0.4$	$1.6 \pm 0.4$
	$P=0.89$		$P=0.97$	
Beta or gamma ( $N=18$ )	$8.4 \pm 1.7$	$0.8 \pm 0.4$	$5.4 \pm 1.3$	$0.3 \pm 0.2$
	$P<0.001$		$P<0.001$	

Paired *t*-tests, two-tailed. Comparing alpha and beta/gamma males when they were alone with the female, there was no difference in female solicitation rate ( $t=1.02$ ,  $df=42$ , ns) but beta/gamma copulation rate was higher ( $t=2.77$ ,  $df=42$ , two-tailed  $P<0.01$ ).

### (3) Females encouraged subordinate males to mate

As well as soliciting actively to subordinate males, females used three other tactics to encourage them to copulate. First, they attempted to escape the alpha male's close guarding and approached the subordinate males, often when the males called or sang from up to 200 m away. The female sometimes flew off suddenly and the alpha male failed to see her go, or if the alpha followed she doubled back behind a rock while he overshot and lost her. On two occasions, the female crept away from the alpha while he was busy catching a moth. Second, once the female was with a subordinate she sometimes stayed with him and they crouched, motionless, whenever the alpha male came by looking for them. Third, females sang or trilled loudly during their fertile period, especially when they were accompanied by a male (usually the alpha) who had monopolized most of the matings. This attracted other males in the group and so increased the chance that they gained access to her (Langmore et al., in press). Indeed, the penetrating calls of a fertile female often enabled us to find her for our behavioural observations.

### (4) Males ignored many of the female solicitations

Of the 889 solicitations observed, 68% were ignored by males, often after several presentations in the bout. In many cases a male hopped away as if to escape the female's harassment, and eventually she would give up and they resumed feeding

together. On average, alpha males rejected a greater proportion of the female offers ( $\bar{X} \pm SE=67 \pm 5\%$ ,  $N=26$ ) than did subordinate males ( $27 \pm 8\%$ ,  $N=18$ ,  $P<0.001$ ; cases in Table I, male alone with female). Thus, whereas average female solicitation rate did not differ when she was alone with subordinate or alpha males, subordinates copulated at a significantly higher rate (Table I). This is what would be predicted if males varied their copulation rate in relation to paternity chances (see below).

### (5) Females competed for male attention

When two or more females in a group were fertile at the same time they competed for males in three ways. First, if the males were with other females, a lone fertile female increased her trill or song rate to attract male attention (Langmore et al., in press). Second, females increased their solicitation rate if other females in the group were also soliciting matings (see below). Third, because female ranges overlapped extensively they also often came into direct competition, especially when the whole group fed together in a snow clearing. Sometimes, while one female was soliciting to a male another female pushed in front of her and solicited in her place. This could escalate into fights, with two females grappling on the ground for up to 25 s. Sometimes the alpha male kept between the females and chased each one away from the other in turn, as if to reduce the squabbling.

**Table II.** Influence of the activity of other females in the group on a focal female alpine accentor's time spent with males

Activity of other females in group	Mean ( $\pm$ SE) % time focal female		
	Alone	With alpha male	With subordinate male
Fertile ( $N=28$ )	13.6 $\pm$ 2.9	64.4 $\pm$ 5.5	22.0 $\pm$ 4.3
Not fertile ( $N=18$ )	4.1 $\pm$ 1.9	84.3 $\pm$ 3.4	11.5 $\pm$ 2.3
	$P<0.01$	$P<0.01$	$P<0.05$

Statistics refer to Mann-Whitney  $U$ -tests, two-tailed. % Time with males refers to time male able to copulate with the female: for alpha males this is all time with female (including time subordinate males present too), for subordinate males this is only time that they are alone with the female (see text).

### Variation in Alpha Males' Ability to Monopolize Females

We considered three factors which might influence an alpha male's ability to monopolize matings. (1) The number of subordinate males in the group. (2) The % days of the female's fertile period which overlapped the fertile periods of other females in the group. The actual fertile period ends the day the penultimate egg is laid, as eggs are fertilized 24 h before they are laid. However, although copulations throughout the last day before clutch completion are worthless, males continued to guard females and compete for matings right up to the laying of the last egg (Hartley et al. 1995). So we have scored the fertile period as that perceived by the males, from 7 days before the first egg to the day of clutch completion. (3) The proportion of the fertile period when the female's range was engulfed by low cloud (when we, at least, found them difficult to follow, so the males might have too). Each day was scored as 1 (all day low cloud), 0.5 (part of day) or 0 (no low cloud) and the total was divided by the number of days in the fertile period to give a mean cloudiness score.

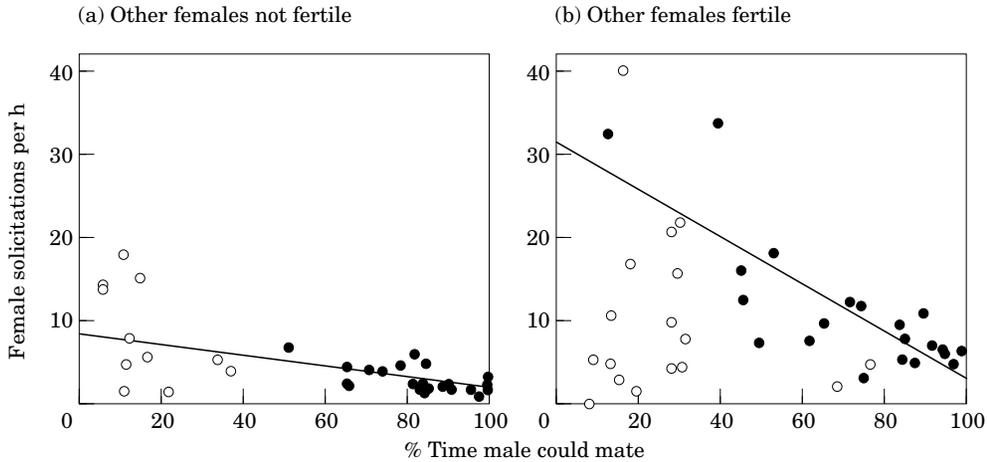
An alpha male's success in guarding a female was assessed in two ways: the % total time the female was observed that he gained exclusive access (i.e. was the only male within 10 m) and the % time he gained exclusive or shared access (time within 10 m, including time subordinates were present too). A multiple regression showed that neither the number of subordinate males, nor cloud, influenced alpha male guarding success ( $P=0.11-0.97$ ) but that an alpha male gained less mating access to a focal female the greater the

overlap of her fertile period with other females in the group ( $P<0.01$  for both measures of guarding). When other females in the group were fertile at the same time, a focal female spent more time alone, less time with the alpha male and more time with subordinate males than if she was the only fertile female available (Table II). Female synchrony increased the chance that subordinate males could mate because females usually fed apart from each other, so an alpha male could not guard more than one at a time. There was no tendency for females within a group to synchronize or stagger their fertile periods so as to manipulate male access; variation in female synchrony arose through age differences in the onset of breeding and chance predation, which affected the timing of repeat clutches (Davies et al. 1995).

When there were two synchronous fertile females, the earlier female to lay did not spend significantly more time with the alpha male ( $\bar{X} \pm \text{SE} = 64 \pm 8\%$ ) than the later female ( $44 \pm 9\%$ ,  $N=16$ ; Wilcoxon matched-pairs test:  $T=39.5$ , NS). However, 2+-year-old females did attract the alpha male more ( $\bar{X} \pm \text{SE} = 75 \pm 6\%$  time with alpha) than 1 year olds ( $32 \pm 10\%$ ,  $N=9$  cases where synchronous females differed in age;  $T=4$ , two-tailed  $P<0.05$ ). These data refer only to the period when the two females' fertile periods overlapped. Older females laid larger clutches, which may explain why alpha males regarded them as more valuable (Langmore et al., in press).

### Factors Influencing Female Solicitation Rate

For both alpha and subordinate males, there is a threshold share of the matings below which they



**Figure 2.** Variation in a female alpine accentor's solicitation rate to a male in relation to the % time he could mate with her, his dominance rank (●: alpha; ○: beta/gamma) and whether other females in the group were fertile. Analysed by ANCOVA: (a) Other females not fertile: solicitation rate declined with increasing male access ( $F_{1,32}=4.85$ ,  $P=0.035$ ) but did not vary with male rank ( $F_{1,32}=0.02$ ,  $P=0.903$ ). (b) Other females fertile: solicitation rate declined with increasing male access ( $F_{1,35}=10.49$ ,  $P=0.003$ ) and was greater to alpha males ( $F_{1,35}=6.40$ ,  $P=0.016$ ). The line is a linear regression through the alpha male points only ( $Y=31.1 - 0.28X$ ). For alpha males, both access ( $F_{1,42}=30.17$ ,  $P<0.001$ ) and the fertility status of other females ( $F_{1,42}=19.44$ ,  $P<0.001$ ) have independent effects on female solicitation rate. For beta/gamma males, neither access ( $F_{1,25}=1.09$ ,  $P=0.306$ ) nor fertility status of other females ( $F_{1,25}=0.86$ ,  $P=0.362$ ) has a significant effect.

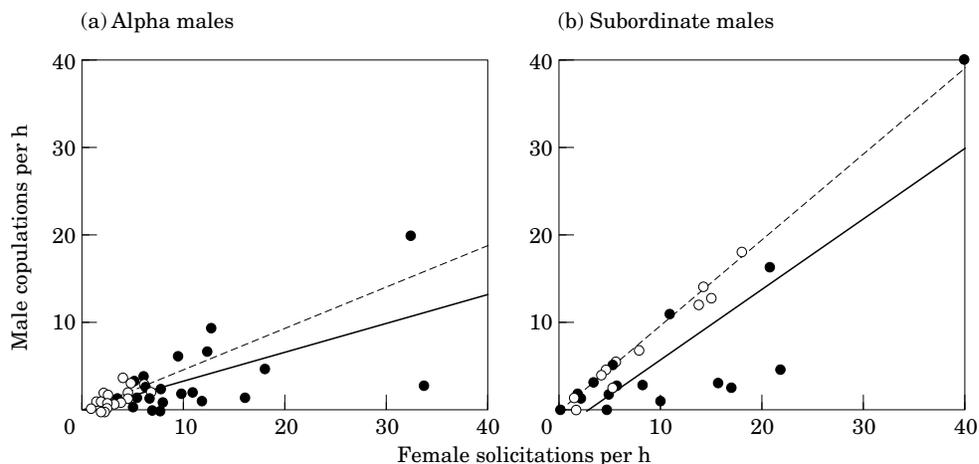
are unlikely to help feed the young (Hartley et al. 1995). One way a female could increase the chances that both alpha and subordinates cross this threshold, despite the restrictions imposed by alpha male guarding, would be to vary her solicitation rate so as to encourage matings from males who had enjoyed least access to her. We measured a male's access as the proportion of time he was able to gain matings with the female. For an alpha male, this was the % time he was with the female, including time he was the only male with her and time that subordinates were nearby, whereas for subordinate males this was only the % time they had exclusive access. For alpha males, female solicitation rate and male copulation rate were measured for all the time they were with the female, including exclusive and shared access, whereas for subordinate males these were measured only during times they were alone with the female and so free from alpha male interruptions (see above and Table I).

We had data for 22 breeding attempts where only the alpha male gained mating access, for three cases where only subordinate males did so (because the alpha spent all his time with other

females) and for 23 cases where both alpha and subordinates gained access. An overall analysis of covariance showed that female solicitation rate to a male varied with the % time he was able to gain matings ( $F_{1,68}=51.75$ ,  $P<0.001$ ), male dominance rank ( $F_{1,68}=23.67$ ,  $P<0.001$ ) and with whether other females in the group were fertile ( $F_{1,68}=7.01$ ,  $P<0.02$ ). There was also a significant interaction between male dominance and whether other females were fertile ( $F_{1,68}=42.68$ ,  $P<0.001$ ).

Figure 2 summarizes the results and shows two independent significant effects. (1) Females decreased their solicitation rate to a male the greater the share of matings he had gained. (2) When other females were fertile, and so competing for male attention, a female increased her rate of solicitation to the alpha male but not to the subordinate males. Thus females encouraged matings from males who had enjoyed less access but showed a preference for alpha males when other females were competing for matings.

In primates, younger females tend to solicit more actively, perhaps to gain the attention of males who prefer to associate with older and more fertile females (Dunbar 1988). However, the



**Figure 3.** Variation in a male alpine accentor's copulation rate in relation to female solicitation rate and whether other females in the group were fertile ( $\bullet$ , —) or the focal female was the only fertile female ( $\circ$ , ---). (a) Alpha males. Copulation rate increased with solicitation rate ( $F_{1,42}=24.9$ ,  $P<0.001$ ) but did not vary with state of other females ( $F_{1,42}=0.3$ ,  $P=0.57$ ). (b) Subordinate males. Copulation rate increased with solicitation rate ( $F_{1,25}=74.72$ ,  $P<0.001$ ) and tended to be less when other females were fertile, but not significantly so ( $F_{1,25}=3.66$ ,  $P=0.067$ ). The slope of the alpha male line was less than that of the subordinate male line both when other females were fertile ( $F_{1,35}=3.08$ ,  $P=0.088$ ) and when they were not ( $F_{1,32}=4.50$ ,  $P=0.042$ ).

analysis of covariance showed no effect of age on solicitation rate by female alpine accentors ( $F_{1,56}=2.14$ ,  $P=0.15$ ).

### Male Acceptance of Female Solicitations

How did males respond to this variation in female offers of copulations? An overall analysis of covariance revealed that a male's copulation rate varied with female solicitation rate ( $F_{1,68}=136.0$ ,  $P<0.001$ ), male dominance rank ( $F_{1,68}=6.87$ ,  $P=0.011$ ), and with whether other females in the group were fertile ( $F_{1,68}=11.69$ ,  $P<0.001$ ). There was also a significant interaction between male dominance and whether other females were fertile ( $F_{1,68}=17.70$ ,  $P<0.001$ ).

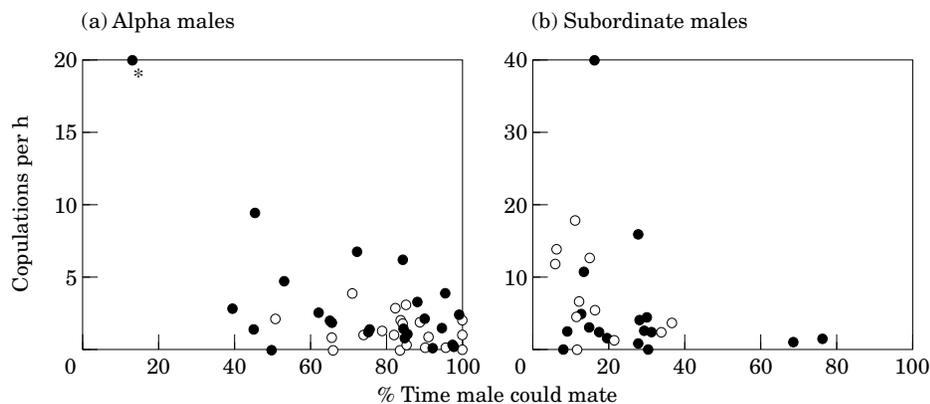
Figure 3 shows that both alpha and subordinate males increased their copulation rate in response to an increased rate of solicitation by the female, but because alpha males ignored more of the offers (see above) their rate of increase was less. Straight lines provided the best fit in both cases, which means that males rejected a constant proportion of the female solicitations. There was a weak tendency for subordinate males, but not alphas, to reduce their acceptance rate when other females in the group were fertile. In summary,

females were able to control matings and gain more copulations when they increased their solicitation rate, but they had to work harder to get copulations from the alpha male.

Given the linear increase in male copulation rate with female solicitation rate, we would expect copulations to follow the trends set by female solicitations (Fig. 2). Figure 4 shows that this was the case, though the statistical significance of the results was not so convincing. When other females in the group were also fertile, alpha males tended to decrease their copulation rate with a focal female when they had gained an increased share of the mating access, and their copulation rate was higher than when other females were not fertile. There were no significant effects of share of mating access or state of other females on a subordinate male's copulation rate.

### Number of Cloacal Contacts per Copulation

Considering all copulations observed, the number of cloacal contacts per copulation varied from one to seven and there was no difference between alpha and subordinate males in the mean or frequency distribution (Fig. 5). Comparing individual males for whom we observed at least



**Figure 4.** Variation in a male alpine accentor's copulation rate in relation to his mating access, measured as the % time he could mate with the female during her fertile period, and in relation to whether other females in the group were fertile (●) or not (○). *F*-statistics refer to ANCOVA results; % data were arcsine transformed. Excluding the data point marked \*, which was identified as the single outlier, there was no significant variation in copulation rate with % access for either alpha or subordinate males (alpha males,  $F_{1,41}=2.94$ ,  $P=0.09$ ; subordinate males,  $F_{1,25}=1.90$ ,  $P=0.18$ ). Including the outlier, alpha male copulation rate declined with increased % access when other females were fertile ( $F_{1,19}=10.9$ ,  $P=0.004$ ). For alpha males, but not for subordinate males, the copulation rate was higher when other females were fertile compared to when no other females were fertile (alpha males,  $F_{1,41}=4.65$ ,  $P=0.04$ ; subordinate male,  $F_{1,25}=0.00$ ,  $P=0.98$ ).

four copulations, there was again no difference between alpha ( $\bar{X} \pm \text{SE} = 2.18 \pm 0.17$ ,  $N=11$ ) and subordinate males ( $2.31 \pm 0.19$ ,  $N=12$ ;  $t=0.533$ , NS), nor was there any difference considering 21 breeding attempts where we could make matched comparisons between them (Wilcoxon test:  $T=36$ , NS). We consider two hypotheses for the variation.

(1) If a male had a constant probability,  $p$ , of successful insemination each cloacal contact ( $p=1/\text{mean}$ ), and made a succession of contacts until he achieved success, then the number of contacts per copulation would follow a geometric distribution. The distribution for all the copulations observed was significantly different from this (Fig. 5c). Lumping all the data would be unjustified if  $p$  differed between individuals. However, considering four males for whom we observed 15 or more copulations with a particular female, three showed significant ( $P<0.01$ ) differences from a geometric distribution.

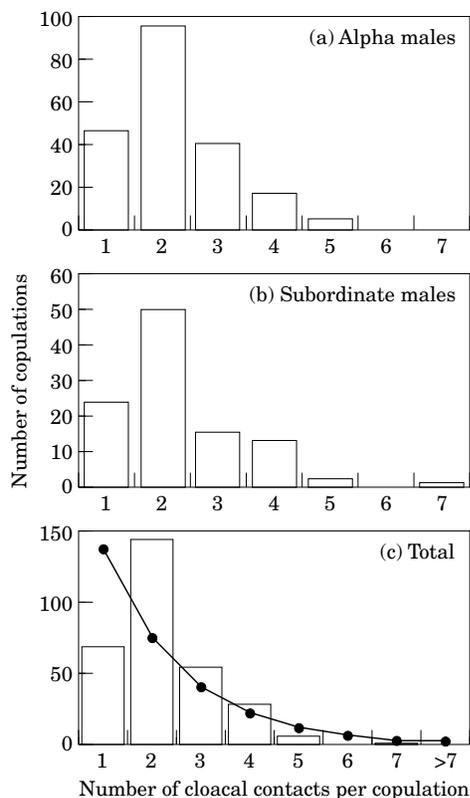
(2) If more cloacal contacts led to increased sperm transfer, then the variation could reflect strategic choices by individuals in relation to sperm competition (Parker 1990). For example, a male might make more cloacal contacts per copulation if his chance of gaining access to the female was lower. The lack of difference between alpha

and subordinate males (above) suggests this is unlikely, and there was only weak support for the idea that cloacal contacts per copulation increased with decreasing mating access (ANCOVA: significant effect for subordinate males,  $F_{1,25}=4.33$ ,  $P=0.048$ , but not for alpha males,  $F_{1,38}=0.00$ ,  $P=0.97$ ). Alternatively, males may be expected to make fewer cloacal contacts with a focal female if other females in the group were fertile at the same time, so as to conserve sperm for other matings. However, there was no evidence for this idea either (alpha males,  $F_{1,38}=2.20$ ,  $P=0.15$ ; subordinates,  $F_{1,25}=0.02$ ,  $P=0.88$ ). There was a weak positive correlation between overall copulation rate and mean number of cloacal contacts per copulation (alpha,  $r=0.320$ ,  $N=41$ ,  $P<0.05$ ; subordinate,  $r=0.114$ ,  $N=27$ , NS), so males did not reduce the apparent amount of sperm inseminated each copulation when overall copulation rate was higher.

In conclusion, we are unable to explain the variation in cloacal contacts per copulation. Until we know how these reflect sperm transfer, further speculation seems pointless.

### Why do Females Prefer Alpha Males?

We consider three hypotheses for why female alpine accentors solicit most strongly to alpha males (Fig. 2).



**Figure 5.** Frequency distribution of the number of cloacal contacts per copulation in alpine accentors, considering all copulations observed. No difference between means ( $\pm$  SE) for (a) alpha males,  $2.19 \pm 0.07$ ,  $N=201$ , and (b) beta/gamma males,  $2.27 \pm 0.11$ ,  $N=105$  ( $t=0.611$ ,  $df=304$ , ns), nor in their distributions ( $\chi^2=2.83$ ,  $df=3$ ,  $P>0.3$ ). Similarly, no differences when means per individual male are considered (see text). The overall distribution (c),  $\bar{X} \pm SE=2.22 \pm 0.06$ ,  $N=306$ , differs from a geometric distribution, shown by the line ( $\chi^2=119.2$ ,  $df=5$ ,  $P<0.001$ ), which is what would be expected if all males had a constant probability of successful insemination each cloacal contact ( $p=1/\text{mean}=0.451$ ), and continued until this had been achieved. See text for this comparison within individual males.

### (1) To reduce male harassment

In some primates (Manson 1994) and ungulates (Clutton-Brock et al. 1992), females may suffer less sexual harassment if they associate with dominant males, who act as better protectors. Female alpine accentors, however, were chased more by males during periods when they were guarded by

the alpha male rather than by the beta male (Table III). This difference simply reflects the fact that beta males were able to guard only when alpha males had temporarily lost the female or were associating with other fertile females, so fewer males were competing when beta males guarded. Considering only times when there was one or more other males present too, there was no difference in female harassment comparing periods when alpha and beta males guarded (Table III). This hypothesis also seems unlikely given the fact that when females were guarded by alpha males, they actively encouraged approaches by subordinates, which led to increased male harassment.

### (2) To gain genetic benefits

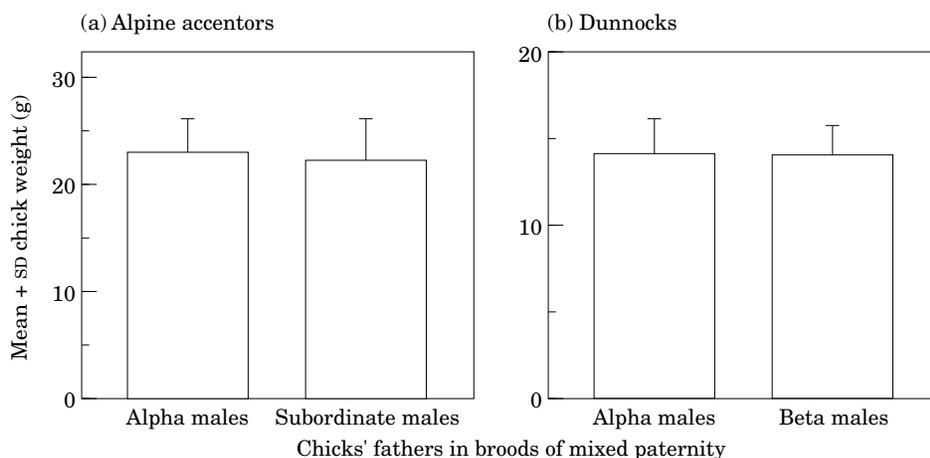
Females may gain better quality offspring by mating with males who are dominant or more vigorous in their displays (Alatalo et al. 1991; Petrie 1994). According to this hypothesis, young fathered by the alpha male would be fitter.

We were unable to measure offspring survival to independence or beyond because they dispersed soon after fledging. Provided the brood escaped predation, all the chicks were likely to fledge successfully (Davies et al. 1995) so the best fitness measure we could obtain was nestling weight at 6–7 days after hatching, which is known to influence juvenile survival in a number of species (Magrath 1991). To control for female quality, brood size, number of provisioning adults (which varied from one to four) and environmental effects (food available, season, habitat, etc.), we analysed broods of mixed paternity and compared chicks sired by alpha versus subordinate males (beta/gamma) within broods (see Hartley et al. 1995 for details of samples used and paternity assessment). There was no tendency for alpha males to dominate mating access at particular times of the mating period (see Hartley et al. 1995), so no hint that alpha males were more likely to sire early-laid eggs, which would be likely to hatch first and so give the chicks a competitive advantage in the nest. Thus our matched comparisons within multiply sired broods seem to be an unbiased measure of fitness.

Figure 6a shows no significant difference in chick weight in relation to alpha versus subordinate male paternity. In 10 broods the chicks sired by the alpha male were heavier and in eight

**Table III.** Harassment of female alpine accentors by males during the mating period, measured as the proportion of the time the female was chased, comparing occasions when she was guarded by the alpha male and the beta male

Period measured	Mean ( $\pm$ SE) % time female chased		Wilcoxon matched-pairs test, two-tailed
	Guarded by alpha male	Guarded by beta male	
Total time female observed ( $N=21$ females)	15.9 $\pm$ 3.3	6.2 $\pm$ 1.6	$z=3.14$ , $P<0.001$
Only times when one or more other males <10 m ( $N=9$ females)	35.3 $\pm$ 8.4	37.3 $\pm$ 10.4	$T=4$ , NS

**Figure 6.** Matched comparisons of the mean ( $\pm$ SD) weights of chicks sired by alpha males and subordinate males in broods of mixed paternity. Weights refer to 6–7 days after hatching. Significance tested by paired  $t$ -tests, two-tailed. (a) Alpine accentors:  $t=0.87$ ,  $df=17$ ,  $N=18$ ,  $P=0.4$ . (b) Dunnocks:  $t=0.56$ ,  $df=15$ ,  $N=16$ ,  $P=0.6$ .

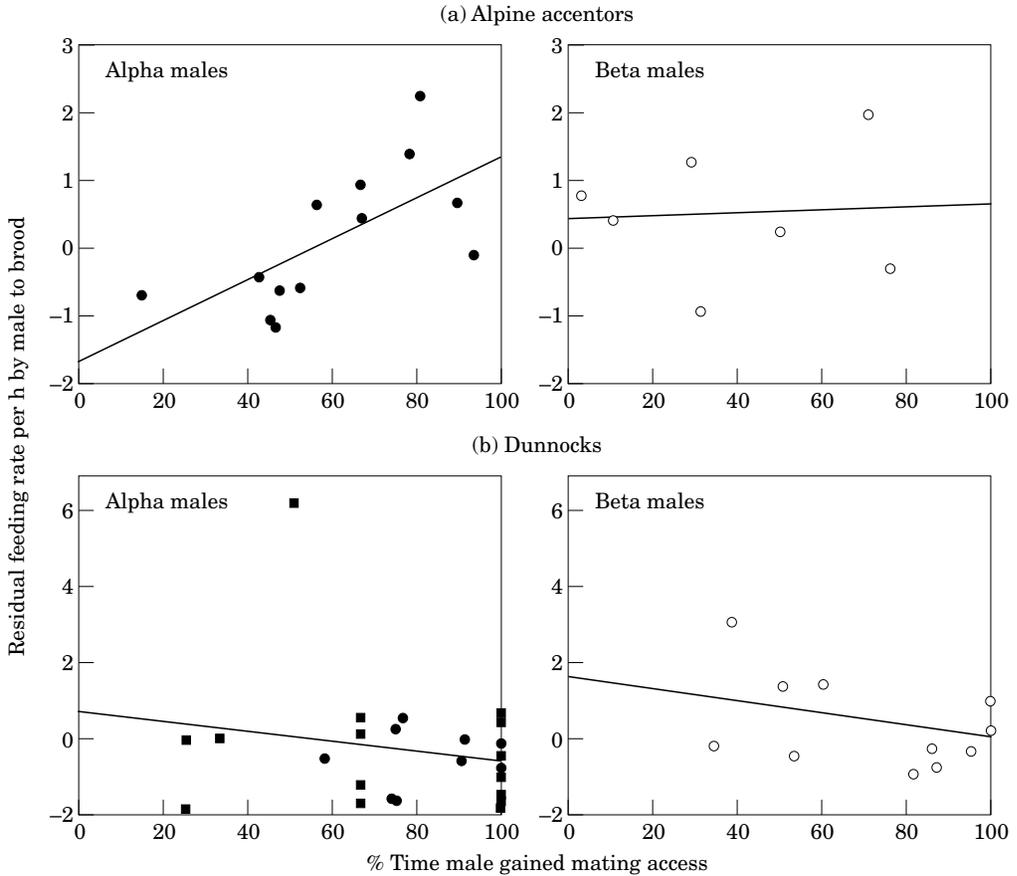
broods those sired by the subordinate male were heavier. Furthermore, this hypothesis alone cannot explain why females prefer to give some matings to subordinate males too.

### (3) To maximize parental care

We have shown previously that it would be risky for a female to give all the paternity to the alpha male because she would lose his help in parental care if other females were attracting him, either through being fertile or having broods at the same time (Davies et al. 1995). By giving more than a critical threshold of the matings to subordinate males, she increases the chance that a male will be available to help her even when other females have synchronous young. Females are usually helped by just one male, and in these cases alpha males decreased their amount of help with

decreased mating share, whereas beta males did not (Fig. 7a; Hartley et al. 1995). This difference may arise because alpha males have greater chances of mating with other females, so the opportunity costs of helping are greater for them.

Given these different male responses, the observed female preference for multiple mating, but with a bias to alpha males, would make good sense in terms of maximizing parental care. Females need give only a small threshold mating share to secure full help from subordinate males and should give the rest to the alpha to maximize his contribution. At first, it seems that this would not explain why females prefer alpha males only when other females in the group are competing for matings (Fig. 2). However, when other females are not fertile the alpha male is better able to monopolize a female (Table II), so she



**Figure 7.** Differences between alpine accentors and dunnocks in the ways alpha versus beta males vary their parental effort in relation to their mating access with a female (which correlates with paternity). All data refer to a single male helping a female feed a brood of nestlings. Lines are linear regressions. (a) Alpine accentors, from Hartley et al. (1995). Feeding rate measured as residual feeds per h, controlling for chick age. Alpha males,  $r_s=0.742$ ,  $N=13$ ,  $P<0.01$ . Beta males,  $r_s=-0.214$ ,  $N=7$ , ns. (b) Dunnocks. Feeding rate measured as residuals from that expected for a monogamous male with full paternity, controlling for brood size and chick age. Alpha (●) and beta (○) males from polygynandry where just one male helped (from Davies & Hatchwell 1992), and from polyandry where just one male helped because the other was removed (from Hatchwell & Davies 1990). ■: Cases where a monogamous male was removed for 3 days either during the mating period or during incubation, and then replaced on his territory (from Davies et al. 1992). There was no difference between solid circles and solid squares for alpha male dunnock plot (ANCOVA:  $F_{1,23}=0.50$ ,  $P=0.49$ ), nor any effect of mating access on feeding rate in dunnocks for either alpha males ( $F_{1,23}=0.43$ ,  $P=0.52$ ) or beta males ( $F_{1,10}=1.40$ ,  $P=0.26$ ).

would not need to show a preference for him to secure his attention. In theory, the female behaviour could also minimize infanticide by males (negative care) if males who did not mate destroyed eggs or young, and if alpha males demanded a greater mating share to desist. However, we found no evidence for infanticide in alpine accentors.

It could still be argued that our fitness measure to test hypothesis (2) is weak and that the female preference for alpha males is selected for by genetic benefits, with some matings given to subordinate males either to ensure sufficient parental care (Mulder et al. 1994) or as an insurance against alpha male infertility (Sheldon 1994a). A comparison with dunnocks

provides an opportunity to test hypothesis (3) further.

## DUNNOCKS: RESULTS AND DISCUSSION

### Chick Weight in Relation to Paternity

Our study site was in the Cambridge University Botanic Garden, where a colour-ringed population of ca 80 breeding adults was studied from 1980 to 1990 (for details see Davies 1992). As with the alpine accentors, we tested hypothesis (2) above by comparing the weights of chicks sired by alpha versus subordinate (beta) males within broods of mixed paternity. Once again there was no tendency for alpha males to dominate mating access at particular times of the mating period (Hatchwell & Davies 1992), so matched comparisons within multiply sired broods seem to be an unbiased measure of fitness. For details of the 1988 breeding season samples used and paternity assessment, see Burke et al. (1989), to which we added five more cases from the 1989 breeding season. All cases involved multiple paternity which arose naturally through shared matings. We did not include any cases created experimentally by removals of the alpha male during the mating period (Davies et al. 1992) as these caused biased alpha versus beta access at particular stages, and hence biased chances of fathering early versus late hatched chicks, likely to differ in weight.

There was no significant effect of paternity on chick weight (Fig. 6b). In 11 broods the chicks sired by the alpha male were heavier and in five broods those sired by the beta male were heavier. Thus once again there was no suggestion that alpha males sired fitter offspring. We return, therefore, to hypothesis (3).

### Male Parental Effort in Relation to Mating Share

In polygynandry, alpha and beta males usually helped to feed different broods so, like alpine accentors, there was usually just one male helping at a nest. However, in contrast to alpine accentors, neither alpha nor beta male dunnocks showed a reduction in parental effort in relation to a reduced mating share, provided a minimum threshold was exceeded (Davies & Hatchwell 1992). Short-term removal experiments also showed that although a reduction in mating share

led to reduced paternity, it did not cause reduced parental effort by a single male helping at a nest, provided he gained at least some matings during the egg-laying period (Davies et al. 1992). These results (Fig. 7b) contrast with the alpha versus beta male differences for alpine accentors (Fig. 7a). Two factors probably contribute to the different alpha male responses in the two species. First, male dunnocks usually have, at most, just two females compared to up to four females for a male alpine accentor. Thus the opportunity costs of helping, in terms of mating and chick-feeding demands elsewhere, are less for a male dunnock. Second, male help has a much larger effect on chick survival in dunnocks, so the benefits of helping are greater (Davies & Hatchwell 1992; Davies et al. 1995).

According to hypothesis (3), the different chick-feeding responses in the two species should lead to differences in female preferences. If female solicitation behaviour is selected to maximize male parental care, then polygynandrous female dunnocks should show equal preference for alpha and beta males, in contrast to the greater preference for alpha males shown by female alpine accentors. Dunnocks also breed in polyandrous mating systems, where two males share just one female. Here the response to paternity loss is different; where two males both help at the same nest then they each vary their parental effort in relation to mating share. However, alpha and beta males respond in the same way (Davies et al. 1992) and polyandrous females maximize the total help they gain from two males if they share the matings equally between them (Hatchwell & Davies 1990). So again we predict that a female should prefer alpha and beta males equally.

### Female Solicitation Behaviour

As with the alpine accentors, we observed female dunnocks during their mating period, from the time they finished their nest (usually 3–7 days before the first egg) up to the completion of the clutch and the onset of incubation. There was no significant variation in mate guarding, solicitations or copulations during this time (Hatchwell & Davies 1992), so data were lumped for the whole period. Mating behaviour was observed for a total of 233 h during the six breeding seasons, 1981–1983 and 1988–1990, comprising 24 breeding attempts in polyandry and 23 in

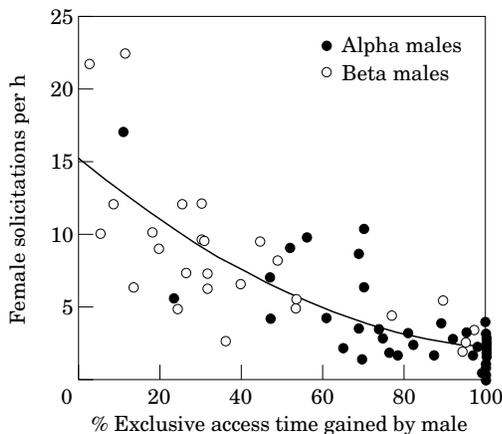
polygyny and involving 32 different females, 29 alpha males and 30 beta males. The total time of observation per female per breeding attempt varied from 1.9 to 12.1 h (mean 5.0 h). We have shown previously that variation in behaviour and reproductive success within individuals across different breeding attempts is as great as that between individuals, so it is justified to regard breeding attempts as independent samples (Davies & Hatchwell 1992). In any case, most attempts involved different individuals, or if the same individuals were observed in several attempts they were often with different mates or in different mating combinations.

Whereas almost all the solicitations by alpine accentors were initiated by the female (see above), only half the dunnoek solicitations were female-initiated ( $\bar{X} \pm \text{SE}$  for 31 females =  $46.6 \pm 4.2\%$ ; total of 459 solicitations observed) either by the female approaching the male or soliciting while he fed or perched nearby. The remainder were initiated by the male approaching the female and she then solicited in response. The proportion of female-initiated solicitations did not differ to alpha, beta or monogamous males (Kruskal–Wallis one-way ANOVA:  $H=2.40$ ,  $df=2$ ,  $P>0.30$ ). Female-initiated solicitations were less likely to lead to copulation ( $19.9 \pm 6.9\%$ ) than those initiated by a male ( $48.9 \pm 9.5\%$ ;  $N=12$  females where we observed five or more solicitations of each type; Wilcoxon matched-pairs test:  $T=1$ , two-tailed  $P<0.01$ ). There was no variation in the % solicitations initiated by the female in relation to a male's mating access, male status or the mating system ( $F_{1,47}=0.29$ – $1.59$ ,  $P=0.21$ – $0.59$ ), so there was no obvious variation in which sex controlled the mating offers in relation to mating access or sperm competition.

Female solicitations were similar to those of alpine accentors, except that the female did not raise her tail so vertically and the cloaca did not appear so bright in colour. Unlike alpine accentors, the male pecked the female's cloaca for ca 1 min prior to copulation, to stimulate her to eject any pool of sperm from recent matings and so clear the way for his own insemination. Copulation also differed in that dunnoeks performed just one cloacal contact (Davies 1983).

### Factors Influencing Female Solicitation Rate

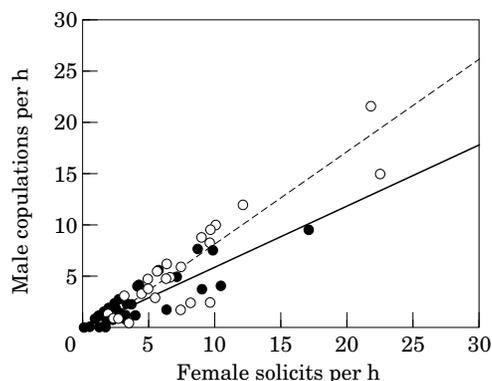
Whereas alpha male alpine accentors could copulate in the presence of subordinate males,



**Figure 8.** Variation in a female dunnoek's solicitation rate to alpha (●) and beta (○) males in relation to the % time they gained mating access to her. An analysis of covariance showed that a second-order polynomial provided the best fit ( $Y=15.17-0.23X+0.001X^2$ ) and that solicitation rate declined with male mating access ( $F_{2,63}=35.0$ ,  $P<0.001$ ), but did not differ between alpha versus beta males ( $F_{1,63}=0.15$ ,  $P=0.70$ ) and did not differ between polygyny (another female competing for male attention) and polyandry (female had both males to herself;  $F_{1,63}=0.13$ ,  $P=0.72$ ). Nor was there any interaction between mating system and male status ( $F_{2,63}=1.76$ ,  $P=0.18$ ). Note the difference compared with Fig. 2, where female alpine accentors prefer alpha males, and where competition among females increases female solicitation rate.

alpha male dunnoeks were always interrupted if a beta male was nearby, perhaps because the prolonged cloaca-pecking gave them greater opportunity for disruption. Therefore, for both alpha and beta males we scored the % time they were able to gain matings as the % of the exclusive access time they gained (% time no other male within 10 m; Davies et al. 1992). Like alpine accentors, a female dunnoek decreased her solicitation rate to a male the greater the share of the mating access he had gained (Fig. 8). Unlike alpine accentors, however, she treated alpha and beta males in exactly the same way. Female behaviour therefore encouraged an equal share of matings between them, just as we predicted if they behaved to maximize male help with parental care.

In contrast to alpine accentors, a female dunnoek did not increase her solicitation rate if she was competing for male attention with another

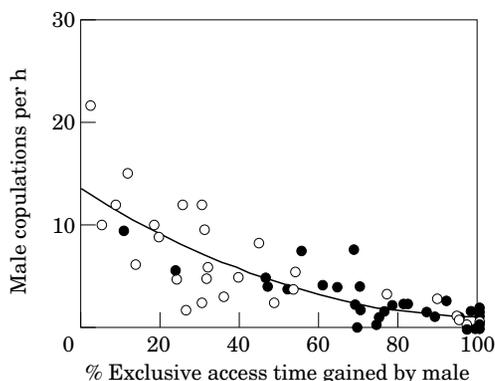


**Figure 9.** Variation in a male dunnock's copulation rate in relation to female solicitation rate. Copulation rate increased with solicitation rate ( $F_{1,65}=172.3$ ,  $P<0.001$ ) and the relationship tended to differ for alpha males (●, —) and beta males (○, ---;  $F_{1,65}=3.41$ ,  $P=0.069$ ). There was no effect of mating system (polyandry versus polygynandry,  $F_{1,65}=0.02$ ,  $P=0.89$ ), nor any interaction between this and male dominance ( $F_{1,65}=1.82$ ,  $P=0.18$ ). Second-order polynomials did not provide a better fit than straight lines.

female in a polygynandrous system, compared to polyandry where she had two males to herself (Fig. 8). The solicitation rate to beta or alpha males when they had gained 100% of the mating access (see Fig. 8) was similar to that for monogamous females ( $\bar{X} \pm \text{SE} = 3.7 \pm 0.9$  per h,  $N=16$ ). There was no effect of female age on solicitation rate (ANCOVA:  $F_{1,61}=0.39$ ,  $P=0.53$ ).

#### Male Acceptance of Female Solicitations

An analysis of covariance showed that the % solicitations ignored by males did not vary with female solicitation rate ( $F_{1,46}=0.93$ ,  $P=0.34$ ) or between polyandry and polygynandry ( $F_{1,46}=0.32$ ,  $P=0.57$ ) but there was an effect of male status ( $F_{1,46}=8.24$ ,  $P<0.01$ ), with alpha males rejecting more ( $\bar{X} \pm \text{SE} = 44 \pm 5\%$ ,  $N=37$ ) than beta males ( $28 \pm 6\%$ ,  $N=24$ ). Figure 9 shows how male copulation rate increased with female solicitation rate. The results are similar to those from the alpine accentors (cf. Fig. 3); the slope for alpha males was less than that for beta males, straight lines gave the best fit, implying that males rejected a constant proportion of female solicits, and male dunnocks did not reject more of the female offers if there were other females available (polygynandry) compared to cases where they had just one



**Figure 10.** Variation in a male dunnock's copulation rate in relation to his share of the mating access with the female during her fertile period. A second-order polynomial ( $Y=13.51-0.24X+0.0012X^2$ ) provided a better fit than a straight line. ●: Alpha males; ○: beta males. There was a significant effect of mating access on copulation rate ( $F_{1,64}=42.36$ ,  $P<0.001$ ) but no effect of male dominance ( $F_{1,64}=0.14$ ,  $P=0.71$ ), polyandry versus polygynandry ( $F_{1,64}=0.12$ ,  $P=0.74$ ), nor any interaction between them ( $F_{1,64}=1.49$ ,  $P=0.23$ ).

female (polyandry). Compared to alpine accentors, dunnock male copulation rate showed clearer variation in relation to sperm competition. Both alpha and beta males increased their copulation rate in a similar way as their share of the mating access (and hence paternity chance) was reduced (Fig. 10).

## GENERAL DISCUSSION

### Differences between Alpine Accentors and Dunnocks

In the Cambridge Botanic Garden, female dunnocks defended territories against other females and often had exclusive access to one (monogamy) or two males (polyandry). If they shared one male (polygyny) or two males (polygynandry), then this was usually with just one other female. By contrast, in the French Pyrénées the widely dispersed food patches precluded territory defence and led female alpine accentors to share large ranges with up to three other females. This led them to compete more directly for male attention by escalated displays, including song (Langmore et al., in press), more frequent solicitation and bright red cloacas, reminiscent of the sexual swellings of female primates which live in multi-male troops

**Table IV.** Comparison between mating competition in polygynandry for dunnocks in the Cambridge Botanic Garden and alpine accentors in the French Pyrénées

Measure of behaviour	Dunnock ( <i>N</i> =53)	Alpine accentor ( <i>N</i> =48)	<i>P</i> *
Female time budget, % Time			
Alone	19.6 ± 2.6	8.7 ± 1.6	<0.001
With alpha male	55.0 ± 3.8	48.0 ± 3.5	NS
With beta male	18.1 ± 3.1	11.4 ± 2.1	NS
With gamma/delta males	0	3.2 ± 0.9	<0.001
With several males	7.2 ± 0.9	28.8 ± 2.8	<0.001
% Time males chasing near female	8.1 ± 1.1	13.0 ± 1.7	<0.05
Female solicitations per h alone	4.5 ± 0.5	7.3 ± 0.9	
with any male (range)	(0.4–15.0)	(0.8–27.0)	<0.01
Female copulations per h alone	2.0 ± 0.2	3.2 ± 0.5	
with any male (range)	(0–7.3)	(0.5–16.0)	<0.05

Figures in the table are  $\bar{X} \pm SE$  and refer to the female fertile period.

\*Mann–Whitney *U*-tests (first six rows) or *t*-tests (last two rows), all two-tailed. *N* refers to the number of breeding attempts observed.

(Dixon 1983; Pagel 1994). Table IV contrasts the time budgets of fertile polygynandrous females of the two species on our two study sites. Compared to dunnocks, female alpine accentors spent less time alone and more time with several males, and they solicited and copulated at a greater rate.

The more intense direct competition for males by female display probably explains why female alpine accentors initiated a greater proportion of the solicitations (>90%, compared to ca 50% in dunnocks) and why they increased their solicitation rate in response to competition from other fertile females (Fig. 2) whereas female dunnocks did not (Fig. 8). In primates too, females are more likely to initiate the copulations when there is increased competition among females for male attention (Dunbar 1978, 1988) or when females gain from mating with multiple males (Janson 1984). The female alpine accentor's preference for the alpha male (Fig. 2) compared to the female dunnock's equal preference for alpha and beta (Fig. 8) is likely to reflect the fact that alpine accentors live in larger groups, where alpha males in particular have increased alternative mating opportunities and so demand greater paternity for a high parental effort to offset their greater opportunity costs of provisioning.

Further studies are needed to explore the variation within each species before we can say whether these are general species differences rather than differences specific to our study sites. There are suggestions of considerable flexibility

in individual behaviour in both species. For example, in parts of the Swiss Alps female alpine accentors behave like our dunnocks; they defend exclusive territories and do not sing (Heer 1994). Conversely, we have found that experimental provisioning of a patchy food supply, to mimic the conditions on the mountain tops of the Pyrénées, causes female dunnocks in our Botanic Garden site to adopt larger overlapping ranges, like our alpine accentors (unpublished data). It is possible that solicitation and copulation rates and female preferences may vary within each species depending on levels of competition for mates.

The act of copulation, however, does appear to be species-specific, with alpine accentors performing multiple cloacal contacts and dunnocks performing just one, following cloacal pecking to clear the way for the male's insemination. We suggest that this difference is related to the greater number of competing males in alpine accentors and the greater proportion of time that the female is accompanied by several males (Table IV). The more intense sperm competition in alpine accentors favours rapid mating by a male to ensure insemination before competitors can interrupt, and a series of ejaculations may permit him to transfer more sperm. In dunnocks, a male has sole access to a female or competes with just one other male, and he can more easily hide with the female in dense vegetation, away from interference. This may favour the prolonged pre-copulatory display

to ensure that there is a clear passage through to the female's sperm storage tubules.

In alpine accentors the testes are 7.8% of the male's body weight (Nakamura 1990) whereas in dunnocks they are only 3.4% (Birkhead et al. 1991). Furthermore, testis size scales with body weight with an exponent of less than one (approximately two-thirds: Møller 1991), so the real difference in relative testes mass is even larger. This too suggests that male alpine accentors adopt more of a 'swamping' strategy whereas dunnocks save on testes costs and increase the value of each insemination. In primates, mating may also be more rapid when males have briefer opportunities to associate with a female because of increased male competition (Caldecott 1986).

This interpretation is from the male's point of view. An alternative is that female alpine accentors, who compete with more females, would benefit by depleting a male's sperm supplies so that the male would be less able to mate with other females and so less likely to spend time caring for their young. Perhaps multiple cloacal contacts are driven by the female tapping in to a receptive male? This brings us to the issue of which sex controls matings.

### Male versus Female Control of Copulations

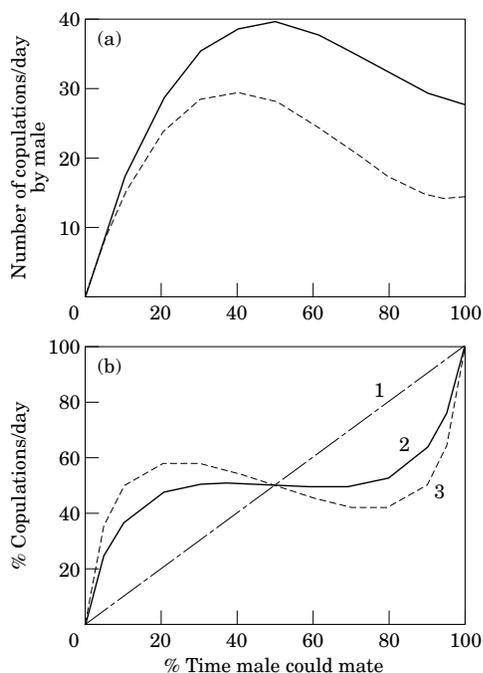
Females of both species solicited copulations for a minimum of 6 days per clutch (from 3 days before the first egg to the completion of an average clutch of four eggs). Assuming a 13-h day and the average rates in Table IV, a female alpine accentor solicited 569 times and copulated 250 times per clutch, while a female dunnock solicited 351 times and copulated 156 times. Some females had fertile periods lasting 10 days and solicited or copulated at three to five times the average rate (Table IV), so would have copulated well over a thousand times per clutch.

These extraordinary rates (see also Birkhead & Møller 1992; Briskie 1992) are far in excess of what is necessary to fertilize the eggs. In other passerines, a single insemination can fertilize an entire clutch (Birkhead et al. 1989) and even if only two-thirds of copulations are successful in transferring sperm (Birkhead 1991), a female would need just a few copulations to ensure fertilization. There are numerous hypotheses for why a female may mate frequently with the same male or several males (Petrie et al. 1992; Hunter

et al. 1993). At one extreme, females may accept multiple matings simply because this is less costly than to resist. Even active solicitations by females in the presence of males does not necessarily indicate that females benefit from multiple matings; solicitation may simply be a way of reducing male harassment. According to this view, high rates of solicitation and copulation evolve entirely through male-male competition as males battle for paternity.

This idea clearly cannot explain why female dunnocks and alpine accentors seek matings with several males despite the resulting increase in male harassment and despite the potential for a female to reject males and so limit the number who mate with her (Hartley & Davies 1994). The different way in which females of the two species vary their solicits to alpha versus beta males makes good sense in terms of the benefits females gain from increased male care through shared paternity. Instead, we suggest that the conflicting interests of the female and alpha male, who does best with full paternity, generate a series of ploys and counter-ploys as each attempts to manipulate the behaviour of the other. Females increase their solicitation rate first to improve the chance that males who have enjoyed less access gain copulations, and so cross the threshold share for helping, and second, as an attempt to lure males away from other fertile females (see also Summers 1989; Petrie 1992). Although females gained more copulations from an increased solicitation rate, males did not submit entirely to female control; they ignored many of the offers and ignored more if they were alpha males. We suggest that the resulting feedback between the sexes, involving increased solicitation and rejection, has led to the behaviour we now observe. The outcome of sexual conflict is a compromise in the sense that a male has to copulate more than he would need to if the female was faithful to him, whereas the female has to solicit more than she would need to if the male did not guard, or if there were no other females attracting him.

In Fig. 11 we have calculated to what extent the decline in female dunnock solicitation rate in relation to increased male access (Fig. 8) is successful in combating alpha male guarding, so as to promote an equal paternity share between alpha and beta male and thus maximize male help. A male performs most copulations per day if he has intermediate levels of % access to the female



**Figure 11.** Calculations of the number and share of copulations per day by alpha and beta male dunnocks in relation to their share of the mating access. (a) The number of copulations by a male (either alpha or beta) per a 13-h day, in relation to the % time the male spent with the female. The solid line assumes that a male accepts every female solicitation, at the rate given by the curve in Fig. 8. The dashed line assumes the actual copulation rate in relation to % access, the curve in Fig. 10. (b) The % of the day's total copulations performed by a male in relation to his share of the mating access. It is assumed that the female spends all her time either with one male or the other male. Curve 1 is the relationship if the males simply copulated at the same fixed rate, irrespective of their % access. Curve 2 assumes they accept every female solicitation at the rate given in Fig. 8 and curve 3 assumes they copulate at the observed rate in relation to % access, the curve in Fig. 10.

(Fig. 11a). At low shares of access he does not associate with the female for long enough to achieve many copulations, despite the highest rate of female solicitation. At higher shares, he has a reduced number of copulations because although he is with the female for more time she solicits at a much lower rate to him.

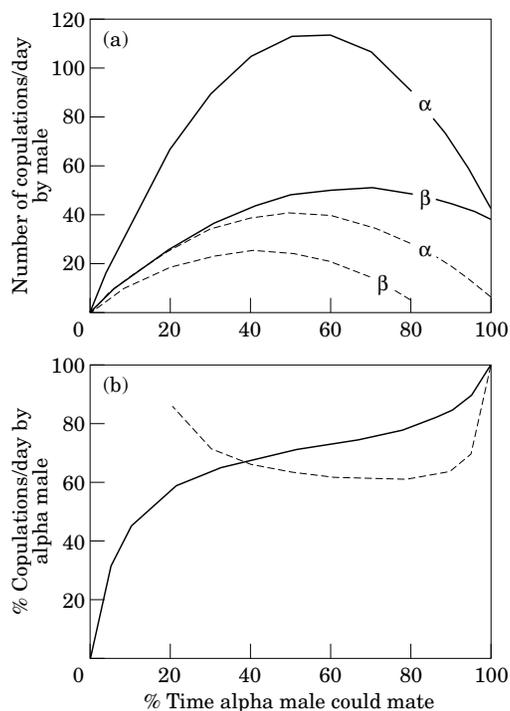
The variation in female solicitation rate promotes a 50% share of the total matings by a male over a wide range (ca 20–80%) of the share of

mating access time he gains (Fig. 11b, curve 2). The observed copulation share (curve 3) follows a similar trend. Thus the female is able to control copulation share and encourage a 50:50 paternity split between alpha and beta even when alpha males guard the female for up to 80% of the time. If females solicited at a fixed rate irrespective of male access, then a male's share of the copulations would simply increase linearly with his % access (curve 1). The way in which curves 2 and 3 deviate from this gives a measure of the extent to which a female can exert control and gain her optimum.

Similar calculations are presented for alpine accentors in Fig. 12 for cases where several females in the group are fertile at the same time. Here, the combination of a preference for the alpha male, together with a decline in female solicitation rate when he has increased access (Fig. 2b), encourages mixed paternity, but with a bias to alpha males, again over a wide range of alpha male % share of the mating time.

Our previous work has shown that although there are strong correlations for both species between a male's % access time and his paternity, there is wide scatter in % paternity at intermediate shares of access, and over the range 20–80% access share the correlation with paternity is weak (for dunnocks, see Figure 2 in Davies et al. 1992; for alpine accentors, see Figure 5 in Hartley et al. 1995). The findings here that females are able to control copulation share over a wide range of intermediate % access time may help to explain this result. Nevertheless, share of access time may still be used by males as a simple rule of thumb to predict paternity and so guide their parental effort (Davies et al. 1992).

Sexual conflict over the control of copulation is likely to be widespread in birds. High rates of female-initiated solicitations and high male rejection rates occur not only in other polygynandrous species (Briskie 1992) but also in some monogamous species where female solicitations may signal fertility to encourage extra-pair matings (Sheldon 1994b). In monogamous species the benefit to females from mating with multiple males is not increased male help, as with the accentors, but probably improved genetic quality of offspring (Kempnaers et al. 1992) or perhaps fitness benefits through multiple copulation itself, if the attributes that make males successful at sperm competition are heritable (Keller & Reeve 1995).



**Figure 12.** Calculations of the number and share of copulations per day with a focal female by alpha and beta male alpine accentors when other females in the group are also fertile. (a) The number of copulations per a 13-h day in relation to the % time the male spent with the female. The solid lines assume that the males accept every female solicitation, at the rates given in Fig. 2b; for alpha males rate,  $Y$ , in relation to % time could mate,  $X$ , is given by  $Y=31.1-0.28X$  and for beta males,  $Y=11.5-0.08X$ . The dashed line assumes that the males copulate at the observed rate in relation to % time with the female (see Fig. 4, ●); for alpha males,  $Y=11.8-0.11X$ ; for beta males,  $Y=8.8-0.10X$ . (b) The % of the day's total copulations performed by the alpha male in relation to his share of the mating access. The solid line assumes the males accept every female offer (Fig. 2b) and the dashed line assumes the observed copulation rate (Fig. 4), using the regressions above.

A better analysis of the outcome of sexual conflict requires a more detailed knowledge of the mechanisms involved in sperm competition. Male alpine accentors (Nakamura 1990) and dunnocks (Birkhead et al. 1991) have unusually large testes and cloacal protuberances which contain the seminal glomera, packed with sperm. These have presumably evolved to meet the demands of a high copulation rate under intense sperm competition.

However, the high rejection rates of female solicits suggest that males may still have to conserve sperm. The next step must be to quantify the parameters involved in sperm transfer by males (ejaculate size, sperm store depletion and renewal; see Birkhead et al. 1994; Birkhead & Fletcher 1995), together with those involved in sperm reception by females (constraints on solicitation, how sperm compete in the female reproductive tract), in order to understand how the conflicts between and within the sexes are resolved.

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## REFERENCES

- Aichorn, A. 1969. Lautäusserungen des Schneefinken (*Montifringilla nivalis* Linnaeus) und Begattungsverhalten der Alpenbraunelle (*Prunella collaris* Scopoli). *Verh. dt. zool. Ges.*, **32**, 690–706.
- Alatalo, R. V., Carlson, A., Lundberg, A. & Ulfstrand, S. 1981. The conflict between male polygamy and female monogamy: the case of the pied flycatcher. *Am. Nat.*, **117**, 738–753.
- Alatalo, R. V., Höglund, J. & Lundberg, A. 1991. Lekking in the black grouse: a test of male viability. *Nature, Lond.*, **352**, 155–156.
- Berglund, A., Magnhagen, C., Bisazza, A., König, B. & Huntingford, F. 1993. Female–female competition over reproduction. *Behav. Ecol.*, **4**, 184–187.
- Birkhead, T. R. 1991. Sperm depletion in the Bengalese finch *Lonchura striata*. *Behav. Ecol.*, **2**, 267–275.
- Birkhead, T. R. & Fletcher, F. 1995. Depletion determines sperm numbers in male zebra finches. *Anim. Behav.*, **49**, 451–456.
- Birkhead, T. R., Hatchwell, B. J. & Davies, N. B. 1991. Sperm competition and the reproductive organs of the

- male and female dunnoek, *Prunella modularis*. *Ibis*, **133**, 306–311.
- Birkhead, T. R., Hunter, F. M. & Pellatt, J. E. 1989. Sperm competition in the zebra finch, *Taeniopygia guttata*. *Anim. Behav.*, **38**, 935–950.
- Birkhead, T. R. & Møller, A. P., 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.
- Birkhead, T. R., Veiga, J. P. & Møller, A. P. 1994. Male sperm reserves and copulation behaviour in the house sparrow, *Passer domesticus*. *Proc. R. Soc. Lond. B*, **256**, 247–251.
- Briskie, J. V. 1992. Copulation patterns and sperm competition in the polygynandrous Smith's longspur. *Auk*, **109**, 563–575.
- Burke, T., Davies, N. B., Bruford, M. W. & Hatchwell, B. J. 1989. Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature, Lond.*, **338**, 249–251.
- Caldecott, J. O. 1986. Mating patterns, societies and the ecogeography of macaques. *Anim. Behav.*, **34**, 208–220.
- Clutton-Brock, T. H. & Parker, G. A. 1995. Sexual coercion in animal societies. *Anim. Behav.*, **49**, 1345–1365.
- Clutton-Brock, T. H., Price, O. F. & MacColl, A. D. C. 1992. Mate retention, harassment, and the evolution of ungulate leks. *Behav. Ecol.*, **3**, 234–242.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- Davies, N. B. 1983. Polyandry, cloaca-pecking and sperm competition in dunnocks. *Nature, Lond.*, **302**, 334–336.
- Davies, N. B. 1989. Sexual conflict and the polygamy threshold. *Anim. Behav.*, **38**, 226–234.
- Davies, N. B. 1992. *Dunnoek Behaviour and Social Evolution*. Oxford: Oxford University Press.
- Davies, N. B., Hartley, I. R., Hatchwell, B. J., Desrochers, A., Skeer, J. & Nebel, D. 1995. The polygynandrous mating system of the alpine accentor, *Prunella collaris*. I. Ecological causes and reproductive conflicts. *Anim. Behav.*, **49**, 769–788.
- Davies, N. B. & Hatchwell, B. J. 1992. The value of male parental care and its influence on reproductive allocation by male and female dunnocks. *J. Anim. Ecol.*, **61**, 259–272.
- Davies, N. B., Hatchwell, B. J., Robson, T. & Burke, T. 1992. Paternity and parental effort in dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Anim. Behav.*, **43**, 729–745.
- Dixon, A. F. 1983. Observations on the evolution and behavioural significance of 'sexual skin' in female primates. *Adv. Study Behav.*, **13**, 63–106.
- Dunbar, R. I. M. 1978. Sexual behaviour and social relationships among gelada baboons. *Anim. Behav.*, **26**, 167–178.
- Dunbar, R. I. M. 1988. *Primate Social Systems*. London: Croom Helm.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, **197**, 215–223.
- Gowaty, P. A. 1981. An extension of the Orians-Verner-Willson model to account for mating systems besides polygyny. *Am. Nat.*, **118**, 851–859.
- Gowaty, P. A. In press. Battles of the sexes and origins of monogamy. In: *Partnerships in Birds* (Ed. by J. Black). Oxford: Oxford University Press.
- Gwynne, D. T. 1991. Sexual competition among females: what causes courtship-role reversal? *Trends Ecol. Evol.*, **6**, 118–121.
- Hartley, I. R. & Davies, N. B. 1994. Limits to cooperative polyandry in birds. *Proc. R. Soc. Lond. B*, **257**, 67–73.
- Hartley, I. R., Davies, N. B., Hatchwell, B. J., Desrochers, A., Nebel, D. & Burke, T. 1995. The polygynandrous mating system of the alpine accentor, *Prunella collaris*. II. Multiple paternity and parental effort. *Anim. Behav.*, **49**, 789–803.
- Hatchwell, B. J. & Davies, N. B. 1990. Provisioning of nestlings by dunnocks, *Prunella modularis*, in pairs and trios: compensation reactions by males and females. *Behav. Ecol. Sociobiol.*, **27**, 199–209.
- Hatchwell, B. J. & Davies, N. B. 1992. An experimental study of mating competition in monogamous and polyandrous dunnocks *Prunella modularis*: 1. Mate guarding and copulations. *Anim. Behav.*, **43**, 595–609.
- Heer, L. 1994. Zur sozialen Organisation und Brutbiologie der Alpenbraunelle (*Prunella collaris*). Diplomarbeit, Zoologischen Institut, Universität Bern, Switzerland.
- Hunter, F. M., Petrie, M., Otronen, M., Birkhead, T. & Møller, A. P. 1993. Why do females copulate repeatedly with one male? *Trends Ecol. Evol.*, **8**, 21–26.
- Jamieson, I. G., Quinn, J. S., Rose, P. A. & White, B. N. 1994. Shared paternity among non-relatives is a result of an egalitarian mating system in a communally breeding bird, the pukeko. *Proc. R. Soc. Lond. B*, **257**, 271–277.
- Janson, C. H. 1984. Female choice and mating system of the brown capuchin monkey, *Cebus apella* (Primates: Cebidae). *Z. Tierpsychol.*, **65**, 177–200.
- Keller, L. & Reeve, H. K. 1995. Why do females mate with multiple males? The sexually selected sperm hypothesis. *Adv. Study Behav.*, **24**, 291–315.
- Kempnaers, B., Verheyen, G. R., Van den Broeck, M., Burke, T., Van Broeckhoven, C. & Dhondt, A. A. 1992. Extra-pair paternity results from female preference for high quality males in the blue tit. *Nature, Lond.*, **357**, 494–496.
- Langmore, N. E., Davies, N. B., Hatchwell, B. J. & Hartley, I. R. In press. Female alpine accentors *Prunella collaris* sing to attract males. *Proc. R. Soc. Lond. B*.
- Magrath, R. D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *J. Anim. Ecol.*, **60**, 335–351.
- Manson, J. H. 1994. Male aggression: a cost of female mate choice in Cayo Santiago rhesus macaques. *Anim. Behav.*, **48**, 473–475.
- Møller, A. P. 1991. Sperm competition, sperm depletion, parental care and relative testis size in birds. *Am. Nat.*, **137**, 882–906.
- Mulder, R. A., Dunn, P. O., Cockburn, A., Lazenby-Cohen, K. A. & Howell, M. J. 1994. Helpers liberate

- female fairy-wrens from constraints on extra-pair mate choice. *Proc. R. Soc. Lond. B*, **255**, 223–229.
- Nakamura, M. 1990. Cloacal protuberance and copulatory behaviour of the alpine accentor (*Prunella collaris*). *Auk*, **107**, 284–295.
- Packer, C., Gilbert, D. A., Pusey, A. E. & O'Brien, S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature, Lond.*, **351**, 562–565.
- Packer, C., Scheel, D. & Pusey, A. E. 1990. Why lions form groups: food is not enough. *Am. Nat.*, **136**, 9–19.
- Pagel, M. 1994. The evolution of conspicuous oestrus advertisement in old world monkeys. *Anim. Behav.*, **47**, 1333–1341.
- Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.*, **45**, 525–567.
- Parker, G. A. 1979. Sexual selection and sexual conflict. In: *Sexual Selection and Reproductive Competition in Insects* (Ed. by M. S. Blum & N. A. Blum), pp. 123–166. New York: Academic Press.
- Parker, G. A. 1984. Sperm competition and the evolution of animal mating strategies. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 1–60. New York: Academic Press.
- Parker, G. A. 1990. Sperm competition games: raffles and roles. *Proc. R. Soc. Lond. B*, **242**, 120–126.
- Petrie, M. 1992. Copulation frequency in birds: why do females copulate more than once with the same male? *Anim. Behav.*, **44**, 790–792.
- Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature, Lond.*, **371**, 598–599.
- Petrie, M., Hall, M., Halliday, T., Budgey, H. & Pierpoint, C. 1992. Multiple mating in a lekking bird: why do peahens mate with more than one male and with the same male more than once? *Behav. Ecol. Sociobiol.*, **31**, 349–358.
- Robinson, S. K. 1986. The evolution of social behaviour and mating systems in the blackbirds (Icterinae). In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 175–200. Princeton, New Jersey: Princeton University Press.
- Rowe, L., Arnqvist, G., Sih, A. & Krupa, J. J. 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends Ecol. Evol.*, **9**, 289–293.
- Sheldon, B. C. 1994a. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proc. R. Soc. Lond. B*, **257**, 25–30.
- Sheldon, B. C. 1994b. Sperm competition in the chaffinch: the role of the female. *Anim. Behav.*, **47**, 163–173.
- Slagsvold, T. & Lifjeld, J. T. 1994. Polygyny in birds: the role of competition between females for male parental care. *Am. Nat.*, **143**, 59–94.
- Smuts, B. B. & Smuts, R. W. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv. Study Behav.*, **22**, 1–63.
- Summers, K. 1989. Sexual selection and intra-female competition in the green poison-dart frog, *Dendrobates auratus*. *Anim. Behav.*, **37**, 797–805.
- Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.
- Veiga, J. P. 1990. Infanticide by male and female house sparrows. *Anim. Behav.*, **39**, 496–502.