

## Female dunnocks use vocalizations to compete for males

N. E. LANGMORE & N. B. DAVIES

Department of Zoology, University of Cambridge

(Received 5 March 1996; initial acceptance 19 April 1996;  
final acceptance 17 May 1996; MS. number: 5181)

**Abstract.** In songbirds, males are usually the more competitive sex and they use vocalizations to attract females and to compete with rival males. When levels of female–female competition were experimentally increased in a population of dunnocks, *Prunella modularis*, females were predicted to increase their vocalization rates and to use vocalizations in comparable ways to competing males. Females produced tseep calls in territorial conflicts with rival females, and trill calls during the pre-breeding and fertile periods when they were left alone by their mate. Males were more likely to approach trills than tseeps, and females were more likely to trill than tseep in response to the song of their mate. Removal experiments to increase polygyny showed that females produced both types of call more when they were competing for male attention. Three out of 13 polygynous, fertile females also produced complex songs when their mate left to join another female. Songs were produced in the same context as the songs of female alpine accentors, *P. collaris*, a congener which breeds in large, polygynandrous groups where female competition for mates is intense, and females attract males with song. The possible functions of the mate-attracting trills and songs of females are discussed; in dunnocks they may (1) attract mates away from other females to reduce the likelihood of polygyny, (2) ensure that the male copulates sufficiently to cross a helping threshold, and (3) enable the female to assess future levels of parental care from her mate.

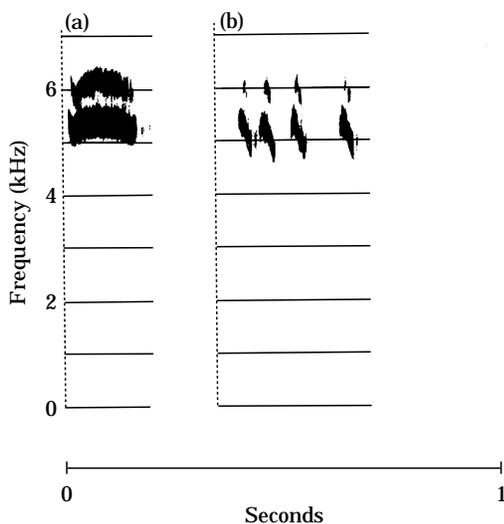
© 1997 The Association for the Study of Animal Behaviour

The complex vocalizations of oscine birds function mainly in the attraction of mates and repulsion of rivals (Catchpole 1982). In general, competition for mates is more intense between males (Emlen & Oring 1977; Clutton-Brock & Vincent 1991), and consequently sexual selection has led to the evolution of more complex vocalizations in males than in females. However, where females compete for mates they are likely to evolve vocalizations that serve analogous functions to those produced by males. First, vocalizations may deter rival females. For example, in the red-winged blackbird, *Agelaius phoeniceus*, polygynous females suffer reduced paternal care (Yasukawa & Searcy 1981) and they produce a ‘teer’ vocalization that may delay nest initiation in late-arriving females (Beletsky 1983; Yasukawa et al. 1987). Second, female vocalizations may evolve for mate attraction. In the sex-role reversed Eurasian dotterel, *Charadrius morinellus*, females

produce a simple ‘peep’ call as part of a flight display that advertises their receptivity to new mates (Kålås & Byrkjedal 1984). The polygynandrous alpine accentor, *Prunella collaris*, provides the first evidence of female songbirds producing complex songs for mate attraction (Langmore et al. 1996).

In this study we investigated the role of female vocalizations in dunnocks, *Prunella modularis*. The mating system is variable: one male may defend one female territory (monogamy) or two or three adjacent female territories (polygyny), or two, occasionally three, unrelated males may defend one female territory (polyandry) or two or three adjacent female territories (polygynandry). The reproductive success of males is highest in polygyny, whereas females do best in polyandry, where they receive most male help, and worst in polygyny where they receive least help (Davies 1992). Thus there is a conflict of interest between males and females. Our first aim was to investigate whether female vocalizations play a role in this conflict. We predicted that when levels of female competition were experimentally increased,

Correspondence: N. E. Langmore, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K. (email: nel10@hermes.cam.ac.uk).



**Figure 1.** Sonograms of female dunnoek calls: (a) tseep and (b) trill.

females would increase their vocalization rates and would use vocalizations in comparable ways to competing males.

Adult male and female dunnoeks produce several different calls: a trill, a tseep, an alarm call and, rarely, a churring call (Snow 1988). Two of these calls, the trill and the tseep, are used during social interactions and can be distinguished from the other call types by context, sound and/or repetition rate (Fig. 1; for a detailed analysis see Snow 1988). The trill is a rapid three or four note 'ti-ti-ti' produced by both sexes outside the breeding season but mainly by females during the breeding season, particularly when alone and often in response to the male's song. The tseep is a loud note given singly or in short bouts, often by two individuals counter-calling.

During the breeding season, males rarely produce trills or tseeps but instead use songs in social interactions, both for territorial defence (Langmore 1996) and when searching for a fertile female (Langmore 1997). Song has also been recorded in female dunnoeks (Bartlett 1970; Snow 1988), but it is rare. In species where female song is rare, it is usually explained as being a functionless by-product of abnormally elevated androgen levels (Catchpole & Slater 1995). An alternative hypothesis is that female song is a facultative trait which is expressed only under high levels of female-female competition. In the congeneric

alpine accentor, females live in large, polygynandrous groups and have to compete for male attention with two or three other females (Davies et al. 1995). In dunnoeks, by contrast, breeding group size is limited by territoriality so there are usually only one or two females per group (Davies 1992). As a result, competition among females for access to males is not so intense, which may explain why female song is rarer than in alpine accentors. Our second aim was to test whether an experimental increase in the level of female competition in dunnoeks leads to female song.

## METHODS

### Study Species

Our study site was the Cambridge University Botanic Garden, Cambridge, U.K., where a colour-ringed population of ca 70 breeding dunnoeks has been studied since 1981 (Davies 1992). Dunnoeks start to form breeding groups in late January or early February. Females defend territories against one another, and males compete to monopolize these territories. In the early stages of breeding group formation, males who successfully obtain one or more female territories associate closely with the resident female(s) and chase them continuously for up to 10 min around the whole territory. Once groups are established, these chases become less frequent, but males often associate with females while foraging. When females enter their fertile period, intensive mate guarding commences. Males cease associating with females during incubation, the nestling period and the early fledgling period. Mate guarding commences in preparation for the next brood towards the end of the fledgling period. Females lay two to three clutches between late March and early July.

### Behavioural Observations

We studied 35 dunnoeks (19 males and 16 females) in detail from March to July 1995. We monitored female vocalizations and breeding behaviour by focal watches on most days between the beginning of April and the end of June. We followed each female for as long as possible (for up to 1 h) and every minute we recorded whether her mate was within 5 m (males who are more

than 5 m from a female are not usually aware of her location and if males are mate guarding they usually remain within 5 m, see Davies 1992, page 91), the number of trills and tseeps produced by the female, the number of male songs, and the response of the female to vocalizations by the male and other females. To control for the non-independence of data from multiple watches on the same female we calculated average vocalization rates for each female using the total number of calls divided by the total minutes that female was observed under various conditions (with male, alone, polygynous, monogamous, etc.). All statistical tests are two-tailed.

The breeding cycle of each female was divided into five stages. 'Pre-breeding' was the period up to the completion of nest building or, if the nest was not found until later, 8 days before laying commenced (including the interval between nest predation and completion of a replacement nest); the fertile period, during which females solicited matings, was from nest completion or, if the nest was not found until later, from 7 days before laying commenced until incubation commenced; 'incubation' was from the day the female commenced incubating until the day before all the chicks hatched; 'chicks' was from the day all the chicks had hatched until the day before they had all left the nest, and 'fledglings' was from the day the chicks left the nest until they no longer received feeds from their parents or until the female had completed her next nest, whichever occurred first.

### Male Removals

Under natural conditions, the frequency of polygyny in dunnocks is low (on average, 4% of groups are polygynous, from Davies 1992). To increase the level of competition between females we removed males to create a female-biased sex ratio. Males were caught by mist-net and released in suitable habitat 75 km away, under licence from English Nature. We encouraged the formation of polygynous groups in two ways: by removal of one male from a polygynandrous group, or by removal of the mate of monogamous females, inducing a neighbouring monogamous male to expand his territory to encompass the territory of the widowed female. Such changes in mating system occur naturally when males are removed by predators (Davies 1992).

At the start of the focal watches, in early April, we studied 14 females and 12 males in nine monogamous pairs, one polygynous group (one male and two females), and one polygynandrous group (two males and three females). During the week of 8–15 April, five males were removed, one new male arrived, and two females changed groups, so that there were then 14 females and eight males in three monogamous groups, five polygynous groups (one male and two females) and one unpaired female. Over the following 3 weeks two more males were removed, one male died, three new males arrived, one female moved out of the study population and a new pair was included in the focal watches, so that there were now 14 females and nine males in four monogamous groups and five polygynous groups (one male and two females). Over the next 5 weeks four males died, two males arrived, two females died, one female moved out and one female moved in, to leave 12 females and seven males in three monogamous groups and four polygynous groups (one of which contained three females) until the end of June. The end result of these experimental removals and natural removals, caused by predators (sparrowhawks, *Accipiter nisus*, and cats), was that we were able to collect data on a total of 16 females. The proportion of females experiencing polygyny increased from two out of 14 before the male removals to 13 out of 16 after the male removals. Eight of these 13 females experienced both monogamy and polygyny at different times during the breeding season, and so provide data for both mating systems.

### Playback Experiment

We recorded female vocalizations during focal watches using a Sennheiser MKH-416 microphone and a Sony Professional Walkman WM-D6C. We standardized the amplitude and sound quality of recordings of female trills and tseeps using an amplifier and a high-pass filter in the Macintosh program 'Sound Edit' before recording them on to a playback tape. For both trills and tseeps, we selected the best recording from a particular female and recorded four repeats of that call on to the playback tape, separated by intervals of 2 s. Each male was played calls recorded from his own female. Four males were presented with both trills and tseeps, on different days, and the order of presentation

was alternated. However, we did not have recordings of both call types from all the females, so three males were presented with trills only, and three males with tseeps only. This gave a total sample size of seven trill playbacks and seven tseep playbacks. To control for breeding stage, we conducted four of each type of playback during the fertile period of the female, and three when the female was not fertile.

Playbacks were conducted using a Sony Professional Walkman WM-D6C and a Sony SRS-57 speaker. A playback trial commenced when the male was solitary and within 25 m of the speakers. There was no significant difference in the distance from the subject to the speaker for playbacks of trills ( $\bar{X} \pm \text{SE} = 15 \pm 2$  m) or tseeps ( $11 \pm 2$  m; Mann-Whitney *U*-test;  $U = 17.5$ ,  $N_1 = 7$ ,  $N_2 = 7$ ,  $P = 0.37$ ). A trial consisted of a single playback of the four calls (either trills or tseeps), played at a standardized volume. Response variables were approach versus no approach, latency to approach and song versus no song. An approach was defined as a flight towards the speaker of at least 1 m.

## RESULTS

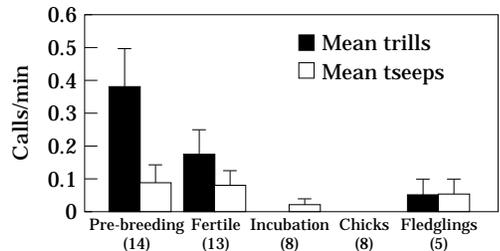
### Timing of Female Vocalizations

Trill rates varied significantly between different stages of the breeding cycle (Fig. 2). Females produced trills mainly during the pre-breeding and fertile periods. One female also produced trills during the fledgling period; however, the male had already commenced mate guarding in preparation for the next brood, so all trills occurred during stages of the breeding cycle in which males associated with females.

By contrast, tseep rates did not vary significantly between different stages of the breeding cycle (Fig. 2). Females produced tseeps both during stages when males were associating with them and when they were not.

### Responses to Female Vocalizations

Females were significantly more likely to respond to tseeps than trills, and males were significantly more likely to approach trills than tseeps (Table I). Females often replied to one another's tseeps, in bouts of 'counter-tseeping', where a bout is a continuous series of calls



**Figure 2.** Rate of trilling and tseeping ( $\bar{X} \pm \text{SE}$ ) by female dunnocks at each stage of the breeding cycle. Data collection commenced on 1 April. Sample sizes (number of females) are given in parentheses. Trill rates varied significantly between different stages of the breeding cycle (Kruskal-Wallis:  $H_4 = 25.42$ ,  $P = 0.0001$ ). Excluding the chick and incubation stages, when females did not trill, there was still significant variation (Kruskal-Wallis:  $H_2 = 6.97$ ,  $P = 0.03$ ). Tseep rates did not vary significantly between the different stages of the breeding cycle (Kruskal-Wallis:  $H_4 = 7.52$ ,  $P = 0.11$ ). In these analyses some but not all females appeared in more than one stage. A further analysis was conducted on a subset of eight females that were recorded at all three of the following stages: pre-breeding, fertile and the other three stages lumped (Incubation, Chicks, Fledglings). Trill rates still varied significantly across the breeding cycle and tseep rates did not (Friedman two-way ANOVAs:  $df = 2$ ,  $N = 8$ ; trills  $\chi^2 = 9.17$ ,  $P = 0.01$ ; tseeps  $\chi^2 = 2.7$ ,  $P = 0.26$ ).

separated by intervals of less than 3 s. All counter-tseeping exchanges occurred during April, before nesting commenced, and during this period an average  $\pm \text{SE}$  of  $63 \pm 18\%$  of tseep bouts occurred as part of a counter-tseeping exchange ( $N = 7$  females). Counter-tseeping was sometimes associated with chases and physical fights between females on their territory boundaries, and all observed chases ( $N = 6$ ) and fights ( $N = 4$ ) between females occurred in conjunction with counter-tseeping. Females did not trill in response to the trills of other females, although occasionally they tseeped in reply (Table I). In three of five cases, when a female's trills elicited tseeps from another female, she then switched to tseeping herself, and a counter-tseeping exchange ensued.

These results suggest that females use trills primarily for attracting their mates, whereas tseeps are involved in female-female aggression. This was confirmed by the results of the playback experiment. Of seven males who were played the trills of their own female, all approached the speaker before the playback had ceased (latency

**Table I.** Responses of males and females to female trills and tseeps, and responses of females to male song

Stimulus	% eliciting a male approach	% eliciting a female response		
		Tseeps	Trills	Approach
Female trills ( <i>N</i> =13 females)	30 ± 6	2 ± 1	0	0
Female tseeps ( <i>N</i> =12 females)	(a) 13 ± 4	(b) 15 ± 7	(c) 0	1 ± 1
Male song ( <i>N</i> =14 females)	—	7 ± 5	(d) 26 ± 7	12 ± 4

Data on responses to female trills and tseeps are the  $\bar{X} \pm \text{SE}$  percentage of call bouts from the focal female that elicited a response. Data on responses to male songs are the  $\bar{X} \pm \text{SE}$  percentage of male song bouts in the female's territory, heard by the observer whilst watching a solitary focal female, that elicited a response from that female. A call or song was defined as 'eliciting' a response when the response occurred within 3 s of the vocalization. Statistical tests (all tests are two-tailed): (a) Comparing a subset of females who produced both trills and tseeps (*N*=11), males were significantly more likely to approach trills than tseeps (Wilcoxon test:  $Z = -2.4$ ,  $P=0.02$ ). (b) From the same subset of females, tseeps were significantly more likely to elicit a response from other females than trills (Wilcoxon test:  $Z = -1.99$ ,  $N=11$ ,  $P=0.046$ ). (c) Tseeps were significantly more likely to elicit tseeps from other females than trills (Wilcoxon test:  $Z = -2.03$ ,  $N=12$ ,  $P=0.042$ ). (d) Male song was significantly more likely to elicit female trills than tseeps (Wilcoxon test:  $Z = -2.05$ ,  $N=14$ ,  $P=0.041$ ).

<9 s), and six also sang after approaching. Males flew an average  $\pm \text{SE}$  of 10.5  $\pm$  2.5 m (range=1–18 m) during their approach. By contrast, of the seven males who were played the tseeps of their own female, only one approached the speaker (distance flown=1 m), and none sang in response (approach versus no approach and song versus no song; in both cases  $\chi^2_1=7.3$ ,  $P=0.007$ ). Although this sample size is not large, the results provide good support for the observational data that males approach female trill calls.

### Mate Attraction

The results show that female trills are effective at attracting established mates. Therefore, it is possible that females use trills to attract a new mate when they are unpaired. During male removals, five females were left without a mate for 1 or more days during their pre-breeding or early fertile period. The call rates of these five females were compared when they were paired but alone during the pre-breeding/fertile period ( $\bar{X} \pm \text{SE}$  observation time=142  $\pm$  40 min) and after male removals but before a new male had arrived on their territories ( $\bar{X} \pm \text{SE}$  observation time=147  $\pm$  41 min). The females trilled, on

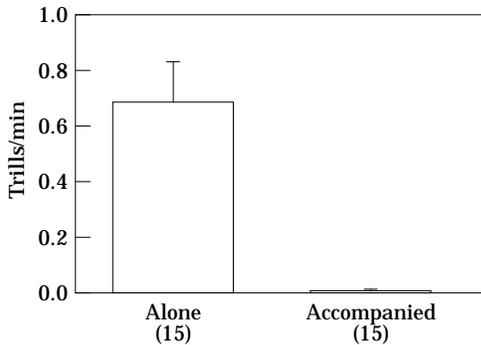
average  $\pm \text{SE}$ , 1.1  $\pm$  0.3 times/min when paired, and 0.08  $\pm$  0.05 times/min when unpaired (Wilcoxon matched-pairs test:  $Z = -2.023$ ,  $N=5$ ,  $P=0.043$ ). Trills, therefore, were used primarily by solitary females to attract an established, resident male on the female's territory, rather than by unpaired females to attract a new mate.

### Female–Female Competition

If trills are used by paired females to compete with rival females for male attention, we can make two predictions. These were tested using data from paired females during the pre-breeding and fertile periods only, since almost all female trilling occurred during these stages.

(1) Females should trill more when alone than when accompanied by a male. Females' trill rates were significantly higher when they were solitary than when they were within 5 m of their mate (Fig. 3).

(2) Solitary females should trill at a higher rate if they are competing for access to males. The level of competition between females can be measured in two ways. First, we can simply compare polygynous and monogamous females. Considering females who were observed for at least 1 h during

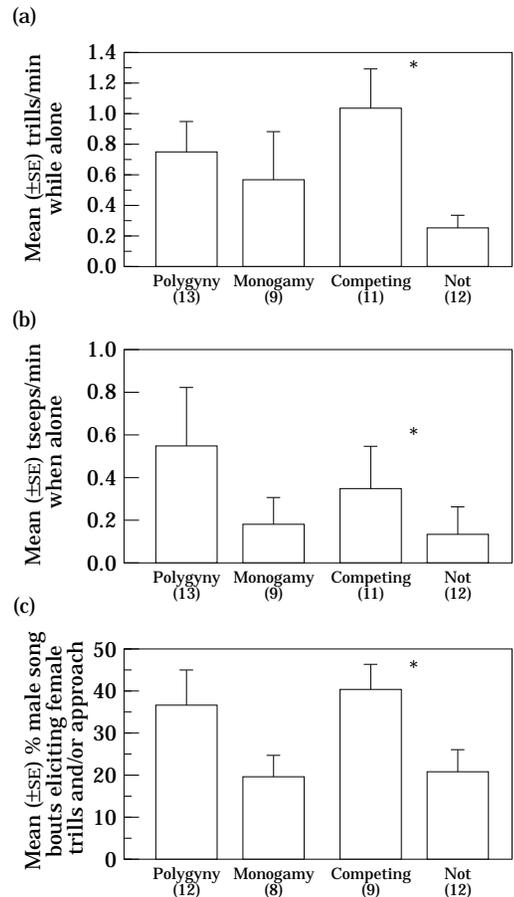


**Figure 3.** Trill rates ( $\bar{X} \pm \text{SE}$ ) of paired females during the pre-breeding and fertile periods, when females were alone versus when they were accompanied by a male less than 5 m away (Wilcoxon matched-pairs test:  $Z = -3.296$ ,  $N = 15$ ,  $P = 0.001$ ). Sample sizes are given in parentheses.

the pre-breeding and fertile periods, polygynous females ( $N = 11$ ) spent significantly more time alone than monogamous females ( $N = 6$ ; Mann-Whitney  $U$ -test:  $U = 12$ ,  $P = 0.035$ ). However, there was no significant difference in the trill rate (Fig. 4a) or the tseep rate (Fig. 4b) of solitary polygynous versus solitary monogamous females. When alone, polygynous females were more likely to trill and/or approach in response to the songs of their mate than monogamous females, but not significantly so (Fig. 4c).

However, a better measure of female competition is to consider whether the focal female is competing with another female for the attention of her mate. Males may be attracted away from a fertile or pre-breeding female both when there is another fertile or pre-breeding female in the group, and when another female in the group has nestlings or fledglings (Davies 1992). By contrast, females do not have to compete for the attention of their mate if they are the only female in the group, or if the other female in the group is incubating. Considering females who were observed for more than 1 h ( $\bar{X} \pm \text{SE}$  observation time =  $248 \pm 33$  min) during the pre-breeding and fertile periods, competing females ( $N = 9$ ) spent a significantly greater proportion of their time alone ( $\bar{X} \pm \text{SE} = 56 \pm 7\%$ ) than non-competing females ( $N = 9$ ;  $36 \pm 5\%$ ; Mann-Whitney  $U$ -test:  $U = 18$ ,  $P = 0.047$ ).

There was a significant difference between the trill rates when alone of pre-breeding/fertile



**Figure 4.** Female vocalization rates and responses to male songs during the pre-breeding and fertile periods, when females were alone, of polygynous versus monogamous females and females who were competing with another female for the male's attention (see text) versus females who were not competing. Sample sizes are given in parentheses. Statistics refer to Mann-Whitney  $U$ -tests. (a) Trill rates of polygynous versus monogamous females ( $U = 44$ ,  $N_1 = 13$ ,  $N_2 = 9$ ,  $P = 0.33$ ); and competing versus non-competing females ( $U = 28$ ,  $N_1 = 11$ ,  $N_2 = 12$ ,  $P = 0.019$ ). (b) Tseep rates of polygynous versus monogamous females ( $U = 38$ ,  $N_1 = 13$ ,  $N_2 = 9$ ,  $P = 0.16$ ); and competing versus non-competing females ( $U = 27$ ,  $N_1 = 11$ ,  $N_2 = 12$ ,  $P = 0.01$ ). (c) Percentage of male song bouts eliciting female trills and/or approach for polygynous versus monogamous females ( $U = 27$ ,  $N_1 = 12$ ,  $N_2 = 8$ ,  $P = 0.1$ ); and competing versus non-competing females ( $U = 23$ ,  $N_1 = 9$ ,  $N_2 = 12$ ,  $P = 0.026$ ).

females who were competing for the male's attention and females who were not competing (Fig. 4a). Competing females also produced tseeps

at a significantly higher rate than non-competing females (Fig. 4b), and were more likely to trill and/or approach in response to male songs (Fig. 4c). Competition was quite apparent during focal watches; females often commenced trilling immediately after a male left to join another female, and ceased as soon as he returned. When competition between two females was intense, the male flew to and fro in response to their trills, sometimes as often as every 10 or 20 s.

### Female-Female Competition and Female Song

Thirteen females were polygynous for at least part of the breeding season. Three of them produced complex songs as well as simple calls. The songs were produced in a similar context to those of female alpine accentors (Langmore et al. 1996); all three females were in their fertile periods, and all sang when their mate left them alone to associate with another female in his group. One female sang a total of 60 songs in six song bouts over 2 days (total length of focal watches=93 min). Three song bouts elicited an approach from her male. The other two females sang one and two songs each (length of focal watches=24 and 31 min respectively), and neither elicited an approach from her male. Nine females were monogamous for at least part of the breeding season, and none produced complex songs. Given the small number of females who sang, the difference between the proportion of females that sang in polygyny (3/13) and monogamy (0/9) was not significant ( $\chi^2_1=0.55$ ,  $P=0.46$ ).

## DISCUSSION

### Trills and Tseeps

We predicted that when levels of female competition were experimentally increased, female dunnoeks would increase their vocalization rates and use vocalizations in comparable ways to competing males. Our results show that female dunnoeks did use their vocalizations for similar functions to competing males. The aggression observed between females, comprising counter-tseeping, chases and fights, is analogous to the counter-singing and territorial conflicts of competing males. Aggression and tseep rates were highest when females were competing for male

attention during the pre-breeding and fertile periods, suggesting that, as in red-winged blackbirds (Yasukawa & Searcy 1982), intra-sexual aggression is a strategy used by female dunnoeks to deter rival females and thereby ensure male parental investment.

Furthermore, females produced trills to attract males. However, this was not strictly analogous to the mate-attraction song typical of many male oscines. Trills were produced by paired females to attract an established mate, rather than by unpaired females to attract a new mate. This suggests that trills might be used by females to influence the outcome of the conflict between the male and female of a pair. Females trilled during their fertile period when they were left alone by the male, and trills often elicited an approach from males, but never from females. To this extent, increasing the level of female-female competition in dunnoeks led to alpine accentor-like behaviour. In alpine accentors, there is more intense competition among females for males because the patchy food supply on the bare mountain tops where they live causes individuals to have large, overlapping home ranges. This creates polygynandrous groups in which a female has to compete with up to three other females for male attention (Davies et al. 1995, 1996). Female alpine accentors sang and trilled only during their fertile period, and they sang at a greater rate when alone than when they were accompanied by one or more mate-guarding males. Female songs and trills elicited approaches from males, but not from other females (Langmore et al. 1996). Thus, trilling in female dunnoeks may serve a similar function to the trills and songs of female alpine accentors. However, female dunnoeks differed from female alpine accentors in two main ways; they trilled at a significantly higher rate during the pre-breeding stage than the fertile stage, and they rarely produced complex songs.

Why trill to attract males? We consider three hypotheses.

(1) Females may trill to ensure that males copulate sufficiently to cross a helping threshold. In both dunnoeks and alpine accentors, males helped provision offspring only if a minimum share of mating access was exceeded (Davies et al. 1992; Hartley et al. 1995). In alpine accentors, females used trills and songs to attract absent males, perhaps as a means of ensuring that males cross this threshold (Langmore et al. 1996).

However, this seems unlikely to be the sole explanation for trilling in dunnocks because females trilled at a higher rate in the pre-breeding period than during their fertile period.

(2) Females may trill to reduce the likelihood of polygyny. A second possibility is that a female dunnock attempts to monopolize male attention during the early stages of the breeding season so that the male is less able to defend other females, thus reducing the likelihood of polygyny. This strategy could work in dunnocks because, unlike alpine accentors, they are territorial. Thus a male must devote time to defending each female territory before breeding commences if he is to have mating access, and the female he defends first may disrupt his attempts to defend the territories of other females (Davies 1992).

(3) Females may trill to predict the level of paternal care. A third hypothesis is that a female dunnock uses trills as a means of assessing the level of paternal care she can expect from her mate. A male provides parental care only to the offspring of females with whom he has copulated, and previous studies have shown that a female will seek copulations only with those males who can provide parental care (i.e. males resident on her territory). A female will reject advances from unfamiliar males (Hatchwell & Davies 1992) and does not copulate with extra-pair males (Burke et al. 1989). Furthermore, Wiley et al. (1991) found that females responded to playback of the songs of their own mates with approaches and trills, but not the songs of neighbouring males.

The most reliable way for a female to determine whether a male is permanently resident on the territory, and if so, whether his time is divided between multiple females, is by testing his 'commitment' prior to nesting. A male who spends a substantial amount of time with a female, and always approaches in response to her trills, is likely to provide substantial parental care at the nest. By contrast, a male who is often absent, and is less responsive to female trills, may be dividing his time between two or more females, and is likely to provide less parental care. In this case, the female may benefit by shifting her territory to find a different mate (or possibly by forcing one of the other females to disperse through intra-sexual aggression). This was the response of two of the females in the three-female polygynous group in this study, who had remained together in the same group while there were two resident males, but

dispersed after one of the males was removed. By using trills females could actively assess male 'commitment', rather than passively observing his attendance time. This would facilitate a more accurate assessment of whether he was spending time with other females when he was absent, because a male would be less likely to respond to trills if he was mate guarding another female than if he was engaged in other activities (e.g. foraging, preening, singing). Such assessment by females would prevent the type of deception suggested for pied flycatchers, *Ficedula hypoleuca*, where females may be unable to detect whether a prospective mate is already paired, and consequently risk suffering the reduced level of male help at the nest experienced by secondary females (Alatalo et al. 1982).

These hypotheses are not mutually exclusive, and female dunnocks could benefit by trilling to attract males for all three reasons.

### Female Song

Complex songs were produced by three females while competing for male attention during their fertile period. Thus, the context of female song was the same as in the alpine accentor, but the frequency was much less. In species where female song is rare, it is often attributed to abnormally high testosterone levels early in the breeding season (Catchpole & Slater 1995). Females of several species have been induced to sing by injections of testosterone (e.g. white-crowned sparrows, *Zonotrichia leucophrys*: Kern & King 1972; chaffinches, *Fringilla coelebs*: Kling & Stevenson-Hinde 1977). This suggests a possible mechanism by which female song could arise under high levels of female-female competition. In male birds, circulating levels of testosterone increase during periods of heightened aggression, and are possibly stimulated by male-male interactions (Wingfield 1985; Wingfield et al. 1990). Polygynous females in this study were more aggressive than monogamous females, and if aggressive interactions elevate testosterone levels, this may 'switch on' the ability to sing in polygynous females. Our sample sizes were insufficient to conclude that female dunnock song occurs under conditions of high female-female competition, although the trend was in that direction.

The greater frequency of female song in the alpine accentor than in the dunnock may be

the result of higher levels of female–female competition in alpine accentors. Alpine accentors form larger groups than dunnocks, so the chances that two or more females will be competing for male attention at any particular time are higher in alpine accentors than in dunnocks. Furthermore, in our study (Langmore et al. 1996) alpine accentor groups were always polygynandrous, whereas most dunnock groups contain only one female (mean = 70% of groups from 10 years data in Davies 1992). Therefore, the selection pressures favouring the evolution of a mate-attraction song were higher in our population of alpine accentors than in dunnocks. Some indirect support for this comes from a study of alpine accentors in Switzerland, where males and females defended territories and the sex ratio was male biased, so competition between females was low, and female song was uncommon (Heer 1994, 1996).

#### ACKNOWLEDGMENTS

We thank the staff of the Cambridge University Botanic Garden for the use of the study site, I. Hartley, R. Lein and H. Nakamura for help with colour-ringing, R. Kilner and two anonymous referees for comments on the manuscript, and NERC for funding this work through a Small Research Grant.

#### REFERENCES

- Alatalo, R. V., Lundberg, A. & Ståhlbrandt, K. 1982. Why do pied flycatcher females mate with already-mated males? *Anim. Behav.*, **30**, 585–593.
- Bartlett, E. 1970. Song of the female dunnock. *Br. Birds*, **63**, 179–180.
- Beletsky, L. D. 1983. Aggressive and pair-bond maintenance songs of female red-winged blackbirds (*Agelaius phoeniceus*). *Z. Tierpsychol.*, **62**, 47–54.
- 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.
- Catchpole, C. K. 1982. The evolution of bird sounds in relation to mating and spacing behavior. In: *Acoustic Communication in Birds I: Production, Perception and Design Features of Sounds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 297–317. London: Academic Press.
- Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Clutton-Brock, T. H. & Vincent, A. C. J. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature, Lond.*, **351**, 58–60.
- Davies, N. B. 1992. *Dunnock Behaviour and Social Evolution*. Oxford: Oxford University Press.
- 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.
- 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., Hartley, I. R., Hatchwell, B. J. & Langmore, N. E. 1996. Female control of copulations to maximize male help: a comparison of polygynandrous alpine accentors, *Prunella collaris*, and dunnocks, *Prunella modularis*. *Anim. Behav.*, **51**, 27–47.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- 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. 1992. An experimental study of mating competition in monogamous and polyandrous dunnocks, *Prunella modularis*: II. Influence of removal and replacement experiments on mating systems. *Anim. Behav.*, **43**, 611–622.
- Heer, L. 1994. Zur sozialen Organisation und Brutbiologie der Alpenbraunelle (*Prunella collaris*). Ph.D. thesis, Zoologischen Institut, Universität Bern.
- Heer, L. 1996. Cooperative breeding by alpine accentors *Prunella collaris*: polygynandry, territoriality and multiple paternity. *J. Ornithol., Lpz.*, **137**, 35–51.
- Kålås, J. A. & Byrkjedal, I. 1984. Breeding chronology and mating system of the Eurasian dotterel (*Charadrius morinellus*). *Auk*, **101**, 838–847.
- Kern, M. D. & King, J. R. 1972. Testosterone-induced singing in female white-crowned sparrows. *Condor*, **74**, 204–209.
- Kling, J. W. & Stevenson-Hinde, J. 1977. Development of song and reinforcing effects of song in female chaffinches. *Anim. Behav.*, **25**, 215–220.
- Langmore, N. E. 1996. Song and territoriality as flexible paternity guards in dunnocks and alpine accentors. *Behav. Ecol.*, **7**, 183–188.
- Langmore, N. E. 1997. Song switching in monandrous and polyandrous dunnocks. *Anim. Behav.*, **53**, 757–766.
- Langmore, N. E., Davies, N. B., Hatchwell, B. J. & Hartley, I. R. 1996. Female song attracts males in the alpine accentor *Prunella collaris*. *Proc. R. Soc., Lond. Ser. B*, **263**, 141–146.
- Snow, D. 1988. Family Prunellidae: accentors. In: *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic. Vol. V. Tyrant Flycatchers to Thrushes* (Ed. by S. Cramp), pp. 547–560. Oxford: Oxford University Press.
- Wiley, R. H., Hatchwell, B. J. & Davies, N. B. 1991. Recognition of individual males' songs by female dunnocks: a mechanism increasing the number of

- copulatory partners and reproductive success. *Ethology*, **88**, 145–153.
- Wingfield, J. C. 1985. Short term changes in plasma levels of hormones during establishment and defense of a breeding territory in male song sparrows, *Melospiza melodia*. *Horm. Behav.*, **19**, 174–187.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M. & Ball, G. F. 1990. The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.*, **136**, 829–846.
- Yasukawa, K. & Searcy, W. A. 1981. Nesting synchrony and dispersion in red-winged blackbirds: is the harem competitive or cooperative? *Auk*, **98**, 659–668.
- Yasukawa, K. & Searcy, W. A. 1982. Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.*, **11**, 13–17.
- Yasukawa, K., Boley, R. A. & Simon, S. E. 1987. Seasonal change in the vocal behaviour of female red-winged blackbirds, *Agelaius phoeniceus*. *Anim. Behav.*, **35**, 1416–1423.