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## **Recognition of Individual Males' Songs by Female Dunnocks: a Mechanism Increasing the Number of Copulatory Partners and Reproductive Success**

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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.

### **Abstract**

Previous studies have shown that a female dunnock *Prunella modularis* increases her reproductive success on average by copulating with more than one male resident on her territory and thereby obtaining extra help in raising offspring. Here we document behavior by females that affects which males copulate with them. During her period of receptivity to copulation, a female in a territory shared by two males often left the dominant (or alpha) male, which guarded her most of the time, and approached the subordinate (or beta) male when he sang. A female's responses to individual males thus tend to increase her own reproductive success by increasing her chances for copulation with both males sharing her territory. Playbacks of tape-recorded songs in the field showed that females approached only songs of resident males, not neighbors. They can therefore discriminate individual males by their songs alone, a capability not previously established for female songbirds. Despite intensive guarding of females by males, mating success among male dunnocks depends in part on female choice.

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### **Introduction**

Although evolutionary biologists have speculated for over a hundred years on the role of females' responses in the evolution of bird song (DARWIN 1871; CATCHPOLE 1980; SEARCY & ANDERSSON 1986), few experiments in natural conditions have shown that female songbirds respond to males' songs (ERICKSSON & WALLIN 1986), and none has shown that they discriminate songs of different males. The clearest way to demonstrate response to song in the field is to present playbacks of tape-recordings. Male songbirds not only respond reliably to playbacks of conspecific songs in the field, they also recognize the songs of

individual territorial neighbors (FALLS & BROOKS 1975; WILEY & WILEY 1977; FALLS 1982; GODARD 1991). In contrast, female songbirds generally do not respond to playbacks of conspecific song in the field. Our studies, however, have revealed that female dunnocks approach singing males during several days of receptiveness for copulation prior to incubation. Furthermore, they respond to songs of different individual males in a way that tends to increase their reproductive success.

The dunnock, a common bird of forests, hedgerows and gardens in Europe, has unusually complex mating behavior (DAVIES 1985, 1986; DAVIES & HOUSTON 1986; TUOMENPULO 1989; DAVIES 1990). During the spring, males defend territories which include the ranges of one or more females. A second, unrelated (beta) male often joins the first (alpha) male on a territory but remains subordinate to the alpha in competition for food and access to females (DAVIES & LUNDBERG 1984; DAVIES 1985). A territory can thus contain a pair or various other combinations of one or two males and one or two females. Occasionally even three birds of the same sex share a territory.

This diversity of possible mating arrangements creates a conflict of interest between the sexes over the optimal situation for reproductive success. Females achieve their highest average reproductive success when they copulate with both alpha and beta males in polyandrous combinations. In this situation, both males help to feed the young and, consequently, more young fledge (DAVIES 1986; DAVIES & HOUSTON 1986; DAVIES 1990). Females average two copulations per hour during a 6–10-d period from the completion of the nest to the start of incubation (DAVIES 1985). As revealed by DNA fingerprinting, a beta male that obtains some exclusive access to a female (no other male within 10 m) during this period is likely to fertilize some of her eggs. In addition, males feed a female's young only if they have some exclusive access to her during her copulatory period (BURKE et al. 1989). For an alpha male, the increased productivity of a trio-fed brood does not compensate for shared paternity. Instead, an alpha male achieves greater reproductive success by sole paternity of a less productive, pair-fed brood (BURKE et al. 1989). An alpha male thus does better when he can maintain sole access to a female during her copulatory period.

These reproductive conflicts give rise to a behavioral conflict: an alpha male attempts to guard a female to prevent any other male from copulating, while a female attempts to escape the alpha male's attentions to allow a beta male to copulate (DAVIES 1985). The present study examines the female's part in regulating her access to copulatory partners.

## Methods

We studied a population of about 80 dunnocks marked for individual recognition with colored bands in the Cambridge University Botanic Garden, Cambridge, an area of 16 ha. When two males shared the same territory, we could easily identify the alpha and beta by priority of access to females and food. In these contexts, the alpha male regularly supplanted the beta male (DAVIES 1985). Territories were similar in size to those measured by DAVIES & LUNDBERG (1984) (0.1–1.3 ha). Neighbors trespassed only infrequently on each other's territories.

The responses of females to singing males were summarized from watches of females during their copulatory periods (from completion of the nest to initiation of incubation, 6–10 d) in 1982, 1983, 1988 and 1989). Observations of each female, combined across nesting attempts, totaled 1–15 h. Each individual counted only once in statistical tests.

Singing males were tape-recorded in the field with a Sony TC-D5M cassette recorder and Sennheiser K3U/ME88 directional microphone. Songs were later analyzed with a Uniscan II real-time spectrum analyzer (10 kHz analysis range, 6 ms resolution) interfaced with a microcomputer. 22 males were recorded for at least 1 h on each of at least three mornings in March and April 1989, before and during the period that females were beginning their first nests.

We presented tape-recorded songs to females in the field during a 3-d period during which each subject's mate or alpha male was temporarily removed from the territory and kept in an aviary away from the study site. Each trial consisted of two brief presentations of tape-recordings in randomized order 15 min apart at a location 20–30 m from a female and within the territorial boundary of the missing male. First, a location was selected at least 10 m within the territorial boundary of the removed male, approximately 3 m from the nearest shrubs or other dense cover, and within 5 m of a location frequently used by the missing male for singing. The speaker-amplifier (Mineroff Electronics, Valley Stream) was placed 10–50 cm above ground and connected with a 16-m lead to the monitor output of the Sony TC-D5M cassette recorder. For all experiments, the monitor level of the recorder and the gain of the amplifier-speaker were held constant at levels set initially by ear to match the sound of singing dunnocks. With the speaker at the minimum elevation, the broadcast songs sounded similar in intensity to a singing dunnock when listening at 1.6 m above ground; at ground level, the songs were just audible at a distance of 25 m across grass, as a result of ground attenuation. Measurements with a sound-level meter were not informative because of the unusually brief elements that predominate in the songs of this species.

Once a location had been selected, a flip of a coin determined whether the missing mate's or the nearest neighbor's song would be presented first. After a 10-min wait, during which any known movements or vocalizations of the female were noted, the first stimulus was presented. During and following the stimulus, the time of occurrence of any movements and vocalizations by the female were recorded to the nearest 5 s by reference to a watch. These observations employed three categories of distance from the speaker,  $\leq 3$ ,  $\leq 10$  and  $> 10$  m. 15 min after the first stimulus began, the second stimulus was presented and the female's behavior noted as before. Provided no response was noted to either presentation, the same female was tested a second time either the same morning (at least 30 min later) or the following morning. These repeated tests involved selecting a new location within the territory and again randomizing the order of presentation of stimuli. Of 7 trials that evoked responses, three involved presenting the mate's or alpha male's song first, 4 the neighbor's song first.

Each playback included four consecutive songs in a natural sequence from field recordings of either the female's mate (for females of pairs) or alpha male (for females of trios) or a neighboring male. Each stimulus consisted of 8 songs, two repetitions of a natural sequence of 4 songs taken from a field recording made with the same Sony TC-D5M. The songs, selected for their clarity on the field recordings, were twice re-recorded, once to a scratch tape on a second cassette recorder and then to a playback tape on the same Sony TC-D5M, in order to insure that any minor variations in tape-speed on different machines did not alter frequencies in the playbacks. During preparation of playback tapes, recording levels were adjusted to levels of  $-6 \pm 1$  on the VU meter, in order to prevent overloading by the brief, intense elements in the songs. Altogether, the experiments included playback tapes of 25 males' songs.

We conducted trials between 7.00 and 9.30 h from 19 April to 13 June 1989, in each case on the first or second day after the female's mate or alpha male had been captured and removed (these males were returned after three days in captivity). In most cases, following removal of the mate or alpha male, either the beta male or a male from another territory began to guard the female within 1 h.

## Results

### 1. Females' Responses to Males

As in previous studies (DAVIES 1985), females during their copulatory periods were closely followed most of the time by their mates or alpha males.

These males supplanted any others attempting to approach the females. A female guarded by an alpha male nevertheless often behaved as if she were trying to evade him (DAVIES 1985). As evidence of this evasiveness, the present study showed that a female guarded by an alpha male often flew toward the beta male when the latter began to sing (Table 1). In contrast, no female accompanied by a beta male ever approached the singing alpha male. Females in this situation instead remained quietly with the beta male, often hidden under shrubs, until the alpha male found them. On such occasions, females copulated with beta males (DAVIES 1985; BURKE et al. 1989). When alone, a female approached either the alpha or beta male, whichever began singing, or her sole mate in the case of monogamous females. In contrast, they never approached singing neighboring males, even when they trespassed and sang within the female's territory (Table 1).

Table 1: Responses of female dunnocks in their copulatory periods to singing males. Observations for each female totaled 1 to 15 h during the period between finishing a nest and beginning to incubate. Numbers of females for each case differed because not all situations occurred during observations of each female

Territorial occupants	Female's social context	Singing male	No. of females observed	Proportion observed approaching
Trios (2 males, 1 female)	with alpha male	beta male	38	0.26*
		neighbor	21	0 *
	with beta male	alpha male	29	0
		neighbor	6	0
	alone	alpha male	51	0.25**
		beta male	40	0.25**
neighbor		15	0	
Pairs (male, female)	with male	neighbor	9	0
	alone	mate	17	0.59***
		neighbor	4	0 ***

\* Responses to beta and neighboring males differ ( $p < 0.01$ , Fisher's exact probability test).

\*\* Responses to alpha and beta males do not differ ( $\chi^2 = 0.04$ ).

\*\*\* Responses to mate and neighboring male differ ( $p = 0.055$ , Fisher's exact probability test).

## 2. Characteristics of Males' Songs

Male dunnocks sing from conspicuous perches in their territories throughout most of the breeding season (SNOW & SNOW 1983). In this population, males singing alone from perches in their territories used repertoires of up to 7 different song patterns, each consisting of a stereotyped sequence of unique notes, which altogether can last 4 s or more (10, Fig. 1). A male usually sang the same pattern repeatedly before eventually switching to another pattern. Successive songs of the same pattern, however, differed in how much of the complete sequence was sung before stopping, so most songs lasted only 1.5–2.5 s. Males that shared the same

territory and males on neighboring territories often shared portions of one or more of their song patterns, but in these cases males sang individually distinctive variants of the shared pattern (Fig. 1). Our preliminary analyses suggest further that males sharing a territory were no more likely to share songs than were neighbors. In general, these observations resemble those of SNOW & SNOW (1983).

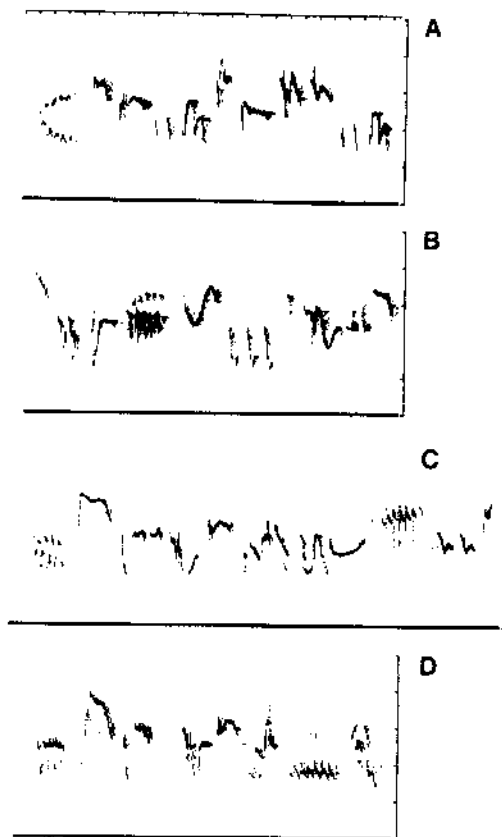


Fig. 1: Spectrograms of representative songs of male dunnocks (vertical divisions, 2 kHz; horizontal divisions, 62.5 ms). A: one of male YNL's song patterns; B, C: songs of two males on territories adjacent to YNL; D: another of YNL's song patterns to show resemblances to a pattern of one of his neighbors, as represented by song C. In an experiment conducted on 16 May 1989, two days after YNL's temporary removal, his mate approached the speaker during playback of song A and failed to respond to playback of song C; at this time she was closely guarded by one of YNL's neighbors, represented by song B.

### 3. Playbacks of Individual Males' Songs

Altogether we completed 22 playback trials (16 different females, 6 tested twice during different nesting attempts). In 8 cases (6 females, 2 twice), we discovered following the playbacks that the female had not been in her copulatory period: 7 had begun incubation earlier than anticipated; and one did not begin to lay eggs within the following 10 d. In none of these 8 trials, even in three cases in which an incubating female was known to be off the nest at the time of the playbacks, did the females respond to any stimulus. As these trials occurred outside the female's copulatory period, they were excluded from the following analysis.

The remaining 14 trials (10 females, 4 tested twice) resulted in 6 cases with closer approach or more vocalizations in response to the songs of the missing

mate than to the neighbor, one case of vocalization in response to the neighbor's songs but not to the missing mate's, and 7 cases with no response to either. The latter 7 included all 4 cases in which a female was subjected to a second trial in a subsequent nesting attempt. Thus 6 individual females responded positively to their missing mates, one responded negatively, and three failed to respond to either (binomial probability = 0.11, one-tailed).

In 5 cases, the female approached the speaker within 3 m during the playback. In three of these cases, she approached from 10 m or more away, either alone or followed by the male currently guarding her, in one case from less than 10 m away followed by her current male, and in one case from greater than 10 m with her current male closely accompanying her. If we consider only the responses that included approaches to the speaker, 5 were positive and none was negative (binomial probability = 0.03, one-tailed).

In two cases, including the one negative response, the female only uttered a single triplet call, normally used at this time of year by females separated from their mates. This negative response might also have resulted from a chance coincidence; a review of field notes indicated that on the preceding day this female had left her nest after laying an egg within 15 min of the same time as the playback to which she responded. Females in this situation have often lost track of the male associating with them and thus utter a triplet call.

Of the three females scored as failing to respond to either stimulus, one might have responded to the missing mate's song; an unidentified bird the correct size darted between two bushes from near the female's nest toward the speaker. As the bird's identifying bands could not be verified in this brief glimpse, this case was scored as no response. The other two cases of no response to either stimulus have no apparent explanation.

The females evidently responded directly to the playback. In all but one case in which the female approached the speaker, the female initiated the movement, although the guarding male always followed closely. In the one exception, in which the guarding male preceded the female as they approached the speaker, the initiation of the movement was not seen. Thus, even though we could not eliminate the possibility that the guarding male rather than the female might respond first, the evidence suggested that in all or nearly all cases the female responded first. This interpretation accords with observations that guarding males rarely leave receptive females under any provocation and instead follow them whenever possible (DAVIES 1985).

Of the 10 females tested during their copulatory periods, 4 occupied territories shared by alpha and beta males (the remaining six were monogamous). Two of these females responded to the songs of the missing alpha males and not to songs of neighboring males; two failed to respond to either stimulus.

## Discussion

Our observations of female dunnocks during their copulatory periods suggest that they approach males in a way that tends to maximize their reproductive success. It is not worth-while for a female dunnock to approach a neighbor,

because he will not provide parental care for her young even if he copulates with her (DAVIES 1985), whereas a male resident on her territory will. Furthermore, it pays a female to approach a beta male rather than an alpha male, not only to insure that the beta male copulates and so feeds her young, but also because beta males provide more food for her young the more access they have to her during her copulatory period (BURKE et al. 1989). Females maximize the amount of help they receive by allocating time equally between alpha and beta males (HATCHWELL & DAVIES 1990). Thus a female's preference for approaching a beta male might result from her attempts to equalize access to the two males under conditions in which the alpha male attempts to monopolize her.

These differences in females' responses to singing alpha and beta males also suggest that females can discriminate males by their songs. More definite evidence for discrimination of males by their songs comes from our experiments with playbacks. The results show that a female dunnock can discriminate at least between the songs of males resident on her territory and those of neighboring males. In these experiments, females only approached songs of males with which they had associated until one or two days earlier.

The perceptual basis for the females' discrimination remains uncertain. They might have responded on the basis of associations between the songs and individual males, or they might have responded to differences in the familiarity of songs. Because territories in this population were small, the females had routinely heard both the missing alpha males' songs and their neighbors' songs for more than a month before the experiments. A simple discrimination between familiar and strange songs thus seems unlikely. This possibility cannot be definitely excluded, however, because of uncertainty about the exposure of females to these songs. Regardless of the basis for the discrimination, the experiments demonstrate that female dunnocks can distinguish between songs of different males. Because female dunnocks do not normally sing, their neural mechanisms for recognition of songs cannot depend on active mechanisms for production of song.

Two results from these experiments require special note. First, when another male had primary access to a female after removal of the alpha male, the female then approached the songs of the missing alpha male. In normal situations this behavior did not occur (Table 1). However, if females attempted to equalize their time with both males, one would expect such behavior in the experiments. Second, females from neighboring territories never approached or otherwise responded to any playback. From the point of view of a female in a neighboring territory, the playbacks represented either songs of neighbors or of her own mate or alpha male. As mentioned, a female could not expect that copulation with these males would increase paternal care for her young.

By approaching only the songs of males that represented additional copulatory partners in her own territory, and thus ultimately additional paternal care for her offspring, a female behaved in a way that tended to increase her own reproductive success. These responses by females to individual males partially circumvented the intensive mate-guarding by alpha males. Mating success of male dunnocks thus depended both on their success in guarding females and on females' preferences for particular partners.

The dunnoek's complex mating system created unusual opportunities for demonstrating females' responses to males' songs. Two features of the experimental design probably also increased the probability of females' responses. First, careful timing was required. Playbacks not conducted during the female's copulatory period failed to elicit responses, and females' responses were never repeated. Second, removal of the male mimicked by the playback probably increased the probability of a response by the female. A female might often know the location of a male on her territory and thus be confused by a playback of his song from somewhere else. It seems possible that similar experiments might show that females of other species of songbirds recognize and approach their mates' songs.

Previous evidence that females respond to males' songs comes in part from captive birds. In such situations, it has been demonstrated that conspecific song can promote ovarian development (NOTTEBOHM & NOTTEBOHM 1971; HINDE & STEELE 1976) and, in addition, that females primed with implants of estradiol perform copulatory solicitation displays when they hear recordings of conspecific males' songs (WEST et al. 1979; WEST et al. 1981; SEARCY & MARLER 1981, 1984; CATCHPOLE et al. 1984, 1986; BAKER et al. 1986, 1987). In the field, evidence for responses by females to males' songs comes from correlations between singing and mating success of males (CATCHPOLE 1980, 1986; GOTTLANDER 1987; RADESÄTER et al. 1987) and from one previous field experiment (ERICKSSON & WALLIN 1986). The present study, however, provides the first experimental evidence for any songbird that females can recognize the songs of individual males and actively approach those that can contribute to their reproductive success.

### Acknowledgements

We thank Dr. C. D. PIGOTT, the Director, for allowing us to work in the Cambridge University Botanic Garden, J. TUOMENPURO for help in the field, R. GODARD and M. GREEN for suggestions on the manuscript, the University of North Carolina for granting R. H. WILEY a research leave of absence, and the Natural Environment Research Council for helping to fund this work.

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Received: October 1, 1990

Accepted: March 25, 1991 (G. Barlow)