

Female begging in European robins: do neighbors eavesdrop for extrapair copulations?

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Female European robins beg for food from their mates throughout the breeding season using far-carrying “seep” calls which resemble the begging calls of fledglings. We investigated the possibility that these calls are eavesdropped by neighboring males and used as cues to target intrusions during the fertile period. Female seep calling and male courtship feeding peaked in the fertile period, and males appeared to modify provisioning rate in relation to seep calling rate. Further, there was a positive correlation between rate of courtship feeding and clutch size, both of which tended to be inversely related to seep calling rates. These observations imply that the seep call is a hunger signal directed at pair males. As the signal is loud and given most frequently during the fertile period, it must also contain information about fertility and location. Playback experiments suggested that this information is eavesdropped by neighboring males, who responded to rapid rates of seep calling more readily than slow rates and to calls broadcast at the edge of territories rather than their center, presumably in search of extrapair copulations. Pair males can reduce the intensity of the female’s signal by courtship feeding, and thus male provisioning may protect paternity. *Key words:* courtship feeding, eavesdropping, *Erithacus rubecula*, female begging, robins. [*Behav Ecol* 13:637–642 (2002)]

Traditionally, studies of animal communication have considered a receiver–signaler dyad (Johnstone, 1997). However, many animal signals, especially far-carrying sounds, involve several potential signalers and receivers in a communication network, one consequence of which is that receivers may gain information by monitoring interactions between signalers without being directly involved, a process called “eavesdropping” (McGregor, 1993; McGregor and Dabelsteen, 1996; McGregor and Peake, 2000). Eavesdropping is important in intrasexual territorial contexts: individuals may monitor male–male interactions and adjust subsequent behavior in response to their outcomes (Oliviera et al., 1998; Otter et al., 1999; Naguib et al., 1999). However, eavesdropping potentially operates in intersexual signaling: individuals may gain information by eavesdropping exchanges between males and females, a possibility that no previous study has investigated. In particular, if an intersexual acoustic signal contains fertility information, neighboring males might use it to determine the optimal time for seeking extrapair copulations (EPCs).

We tested this hypothesis in the European robin *Erithacus rubecula*. Previous work showed that extrapair males target intrusions onto neighboring territories during the female fertile period, and that, when resident males are temporarily removed at this time, unattended females are invariably approached by other males and presented with food, behavior that usually precedes copulation (Tobias and Seddon, 2000). Throughout the breeding season females give loud “seep” calls resembling the begging calls of fledglings. These calls are thought to function in maintaining contact with mates and stimulating courtship feeding (East, 1981), but they might also convey information about her location, fertility status, and the attentiveness of her mate. As seep calls can be audible to humans > 70 m, well beyond robin territory boundaries, all neighboring robins are likely to receive the signal. By eaves-

dropping, a neighboring male seeking EPCs could obtain this information without risk of injury, an important consideration given that intruders are aggressively expelled, and sometimes killed, by resident robins (Cramp, 1988). In a concurrent study (Tobias and Seddon, 2000) we revealed that territoriality is the primary paternity guard in robins. Courtship feeding, however, may also serve to guard paternity if it minimizes the information received by neighboring males.

Here we describe behavioral observations that investigate the information content of female seep calls and explore their relationship with male courtship feeding during the breeding season. In the light of these observations, we investigated the possibility that intrusion by neighboring males is related to female begging by measuring female seep calling and mobility during temporary removal of their mates and using playback to investigate whether seep calls attract neighboring males. We discuss the role of courtship feeding in the protection of paternity and discuss the relationship between blackmail and eavesdropping in the context of communication networks.

METHODS

Study site and species

A population of 20–25 pairs of color-ringed European robins was studied in the Cambridge University Botanic Garden, Cambridge, UK, in 1993–1995. The robin is a socially monogamous, territorial passerine, both sexes sing and defend individual territories in winter. Pairing takes place between January and March in southern England, after which only males sing in defense of shared, multipurpose territories, and competition for females is intense; around 20% of males fail to pair annually (Harper, 1985; Lack, 1965).

Behavioral observations

During 20- to 60-min watches of each focal pair per day between 0700 and 1800 h, we calculated rates of courtship feeding (number of feeds/hour), where a courtship feed consisted of a male presenting the female with invertebrate prey (see Cramp, 1988), which she invariably accepted. Using a Sennheiser MKH 416 condenser microphone and a WMD6C Sony Walkman, we made recordings of female seep calls from

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Received 26 June 2000; revised 1 July 2001; accepted 19 December 2001.

which we produced and analyzed sonagrams using a Kay Ele-metrics Co. Digital Sonagraph, model 7800. We found that although rate of calling varied at different stages of the breeding cycle, there were no consistent differences in call quality. Seep calls were not produced in clusters but as isolated single calls interspersed by silences of varying duration; thus we calculated the number of seep calls per 30-s sampling period rather than the number of bouts per unit time. Immediately before, during, and subsequent to feeds, females invariably produced a burst of high-pitched calls that were similar to seep calls but so rapidly uttered as to be difficult to quantify. These calls (which we term "feeding" calls) were only given in the presence of a male with food and as such contained different information from seep calls and were excluded from analysis. Feeding calls were easily identifiable at fairly long range by humans (at least 50 m), and it is thus likely that their context was obvious to neighboring males. Data collection was discontinued when the location of focal birds was unknown or when females were incubating. We separated data into the prefertile phase (days -39 to -9, where day 0 refers to the day of clutch commencement) and the fertile phase (day -8 to the day before clutch completion) of the female's breeding cycle (see Tobias and Seddon, 2000).

During the postfertile phase, the female only produced seep calls when off the nest between prolonged bouts of silent incubation. At these times, seep calls were given at high rates, presumably because of high hunger levels. Calling and feeding data for this phase were thus not included in analyses because comparison with previous periods is confounded by differences in motivation and behavior. For individuals or pairs to be included in analyses, a minimum 150 min data were required for each phase.

Mate removal experiments

We removed nine paired males from their territories using baited Potter traps during the morning after the second eggs were laid. Removed males were retained in cloth bags within their territories and were released after 90 min had elapsed. During this period of absence, we recorded the resident female's seep calling rate and closest approach to the territory boundary. These data were compared to those yielded by identical removals of eight other males in the prefertile period. As a further control, five males were captured and immediately released during the fertile period. In each trial, different individuals were selected. We selected only apparently healthy individuals (e.g., those with tidy plumage and no visible defects). During this period birds did not exhibit any obvious signs of stress, tending to remain motionless, and following release no adverse effects on health or territorial ownership were noted (see also Tobias, 1997).

Playback experiments

Using a microphone and Walkman (as detailed above), we made original recordings of female seep calls and "tic" calls given in the fertile phase. Female seep calls consist of a single high-pitched element with a band width of about 1300 Hz (7500–8800 Hz) and a duration of about 0.1 s, whereas fledgling begging calls are slightly lower pitched, longer, and more sibilant, having a band width of about 2250 Hz (6400–8650 Hz) and a duration of about 0.2 s. These calls do not lend themselves to representation using sonagrams because they are relatively high pitched and diffuse. Tic calls are given by both sexes year-round and mainly function in territory defense (Reed, 1996); the single element has a band width of about 3300 Hz (4770–8000 Hz) and a short duration of 0.03 s. Playback loops were compiled by editing original recordings

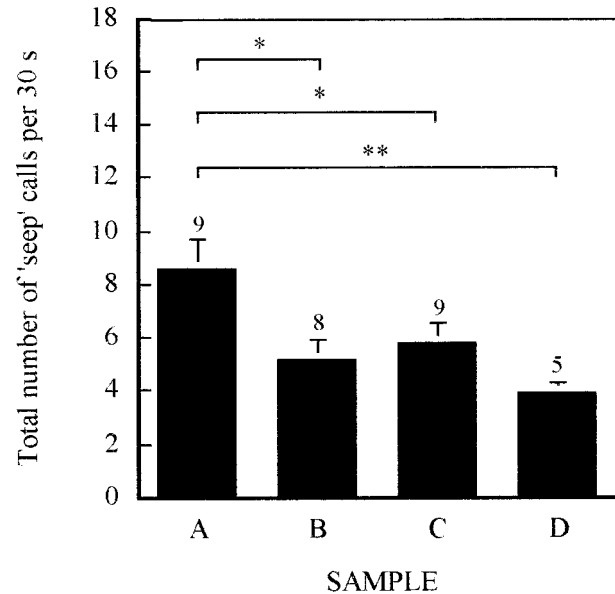


Figure 1

Number of seep calls given by females in sample A (during 90 min male removals in the female fertile period), B (prefertile period controls), C (fertile period means for females in A, >24 h before and after manipulation), and D (fertile period catch-and-immediate-release controls). Bars show means \pm SE; sample sizes are given above error bars. Statistical tests compare sample A with other samples; all significant results are shown. A versus B and A versus D are Mann-Whitney *U* tests; A versus C is a Wilcoxon-signed ranks test; * $p < .05$, ** $p < 0.01$).

using SoundEdit 16 version 2f. For each individual only five separate calls were used, these being copied in the same sequence where necessary; the rate of natural sequences was altered by deleting sections of pauses or pasting in extra pauses. To ensure that each replicate was of comparable quality, we only used those recordings made < 10 m from vocalizing birds. We adjusted sound intensity to give an amplitude of approximately 90 dB at 15 m, matching the sound pressure level of natural robin vocalizations.

We conducted playback experiments under standard weather conditions between 0900 and 1300 h on 10–14 March 1995. We carried out 4 10-min trials on each of 10 territories during the resident female's prefertile period. In each trial we broadcast recordings through a Sony SRS-57 loudspeaker, using: (1) female seep calls at a rate of 5 per 30 s (modal rate in prefertile phase), (2) female seep calls at a rate of 15 per 30 s (modal rate in fertile phase), (3) female tic calls at a rate of 15 per 30 s (control), and (4) seep calls at a rate of 15 per 30 s at the center of the territory. In 1–3 we broadcast the recordings at approximately 5 m from a territory boundary, and a different location was used in each trial; the fourth trial was designed to ascertain the influence of speaker position on the likelihood of approach. The modal values we used to generate the upper and lower rate in trials 1 and 2 exceed the mean seep calling rates (see Figure 1) because females tended to either remain silent or call frequently.

To avoid pseudoreplication and the potentially confounding effects of stranger recognition, we used the prefertile calls of the female that occupied the experimental territory. Resident females never approached the speaker nor responded vocally during playbacks; therefore, male response is not likely to have been influenced by resident female behavior. Each experimental territory received all four treatments, with the sequence of treatments effectively randomized to eliminate

order effects; no territory received more than one stimulus per day.

During the 10 min of playback, we recorded three male responses: (1) whether there was a flight toward the speaker ($\pm 45^\circ$, ending < 10 m from speaker), (2) approach latency in seconds (time taken for both residents and neighbors to fly to approach < 10 m from speaker), and (3) closest approach (minimum distance in meters between subject and speaker). When there was no response, we assigned arbitrary values of 600 s for latency to approach and 10 m for closest approach to allow statistical analysis.

Sample sizes and statistics

Data were derived from 37 breeding attempts of 31 pairs, and each data point refers to the first year in which adequate data were collected, although subsequent recombinations were treated as independent samples. As this was the case for only $< 10\%$ of pairs, this approach is unlikely to have exerted a confounding influence on the results.

Most behavioral observations were made preceding first broods. Apart from playbacks (conducted in 1995) and male-removal experiments (conducted in 1994 and 1995), data were gathered in three different breeding seasons (1993, 1994, and 1995). We pooled data for behavioral traits as single samples because there were no consistent significant differences between the years (Kruskal-Wallis tests: seep calling rate, $n_1 = 9$, $n_2 = 13$, $H_2 = 1.74$, $p = .400$; clutch size, $H_2 = 3.51$, $p = .200$). Means ± 1 SE are given; all statistical tests are two-tailed and corrected for ties where appropriate.

RESULTS

Behavioral observations

The rate of female seep calling was significantly greater in the fertile than in the pre-fertile phase (5.31 ± 0.38 versus 2.19 ± 0.30 calls/30 s, Wilcoxon signed-rank test; $z = -4.00$, $n = 26$, $p < .0001$). Similarly, rates of courtship feeding were higher in the fertile phase (3.93 ± 0.213 vs. 2.10 ± 0.202 feeds/h, $z = -4.23$, $n = 26$, $p < .0001$). The inverse relationship between seep calling rate and rate of courtship feeding was weakly significant during the fertile phase but not during the pre-fertile phase (Spearman rank correlations; fertile phase: $r_s = -.354$, $n = 31$, $p = .05$; pre-fertile phase: $r_s = -0.235$, $n = 26$, $p = .240$).

Females with large clutches (five to seven eggs) had a seep calling rate that tended to be lower than that of females with small clutches (two to four eggs; Mann-Whitney U test; $U' = 60.5$, $n_1 = 21$, $n_2 = 10$, $p = .056$). These results imply that better fed and hence less vociferous females laid larger clutches. In support of this idea, we found that clutch size was positively correlated with courtship feeding rate (Spearman rank correlation; $r_s = .519$, $n = 31$, $p = .004$) and tended to be negatively correlated with seep calling rates ($r_s = -.311$, $p = .089$).

Response to male removals

In comparison with mean rates, females begged at significantly higher rates when their mates were removed in the fertile period (Figure 1, A vs. C). Similarly, females begged at higher rates during fertile period removals than during pre-fertile and fertile period controls (Figure 1, A vs. B and A vs. D). Furthermore, solitary females approached territory boundaries more closely during fertile period removals (2.44 ± 0.87 m) than during catch-and-immediate-release controls (6.8 ± 1.43 m) (Mann-Whitney U test; $U' = 6.5$, $n_1 = 9$, $n_2 =$

5 , $p = .032$). In contrast, there was no significant difference between boundary approaches during fertile period removals and pre-fertile period controls (2.44 ± 0.868 vs. 4.38 ± 1.30 m, $U' = 25.5$, $n_1 = 9$, $n_2 = 8$, $p = .308$), suggesting that unpaired, fertile females (rather than paired, fertile females, or unpaired, nonfertile females) are more likely to seek copulations with neighboring males.

Playback experiments

Although seep calling almost always began before the intrusion of neighboring males, we cannot eliminate the possibility that increased seep calling is a response to intrusion itself. We therefore conducted playback experiments to test whether seep calling can incite intrusion and whether seep calls are received and assessed by neighboring males. We found that for resident and neighboring males, high seep calling rates elicited a stronger response than low seep calling rates (Figure 2), whereas high seep calling rates were equally likely to elicit responses from neighbors as from residents (Table 1). However, neighboring males tended to approach slow seep calling less frequently than residents, and residents responded to tic calls, but neighbors appeared to ignore them (Table 1). Neighbors never approached seep calls when they were broadcast from the center of territories, this being significantly less often than their approach to playbacks from the edge (Table 2). As seep calls are quite far-carrying, this result is unlikely to be related to audibility. On two occasions neighbors approached the signal carrying food items, behavior characteristic of natural EPCs (Tobias and Seddon, 2000). Residents responded more strongly than neighbors in each treatment (Figure 2). Approaches by residents occurred more promptly than those by neighbors (Figure 2a; Mann-Whitney U test; 5 calls/30 s: $U' = 20.5$, $n_1 = n_2 = 10$, $p = .024$; 15 calls/30 s: $U' = 27.5$, $p = .036$), and residents approached more closely than neighbors (Figure 2b; 5 calls/30 s: $U' = 27.5$, $n_1 = n_2 = 10$, $p = .089$; 15 calls/30 s: $U' = 24.5$, $p = .050$).

DISCUSSION

Is the seep call a signal of hunger?

From the perspective of cooperation between paired individuals, seep calls may be intended as honest signals of the hunger and whereabouts of females. Although confounding factors such as female age may have influenced the result, provisioning of females by males appears to have direct reproductive benefits to both individuals by increasing clutch size, a result found in previous studies (e.g., Neuman et al., 1998; Nisbet, 1973). To this end, females must signal the extent of their need for food. Moreover, seep calling may incur energetic and predation costs (Haskell, 1994; Leech and Leonard, 1996; Redondo and Castro, 1992), and thus, if seep calls are hunger signals, females should use them only when they are not receiving enough food. The inverse relationship between seep calling rate and provisioning rate in the fertile period therefore suggests that the seep call functions, at least partly, as a hunger signal. In addition, the positive correlation between courtship feeding and clutch size and the strong resemblance of female seep calls to those of begging fledglings also suggest that the calls might function primarily as informative signals of hunger that have direct benefits to both pair members. However, other processes invoking conflict may also operate: females might beg vociferously so that males are prevented from seeking EPCs or from advertising for further mates (Hunter et al., 1992), to enforce honest advertisement through feeding (Johnstone, 1995), or to inform neighboring males of their fertility and location.

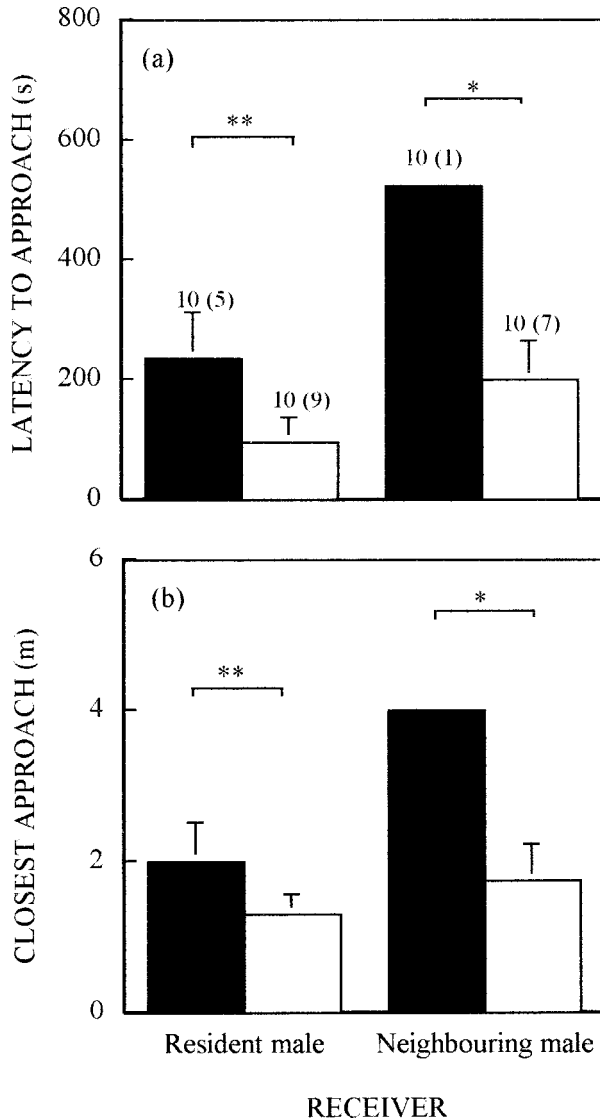


Figure 2
 (a) The latency to approach by receiver males to slow (5 calls/30 s, filled bars) and fast (15 calls/30 s, open bars) stimuli; (b) the minimum distance between receiver males and stimulus during the same trials. Bars show means \pm SE; sample sizes are given above error bars, with actual numbers of individuals responding in parentheses. Receiver males showed stronger responses to high rates of seep calling than to low rates (Wilcoxon-signed ranks tests; * $p < .05$, ** $p < .01$).

To whom is the seep call directed?

As we have suggested that seep calls function primarily as a hunger signal, it follows that they are probably directed mainly at the pair male. Further, if females intended to attract extrapair males and promote male–male competition (a proposed function of copulation calls; Birkhead and Møller, 1992; Cox and La Boeuf, 1977), we would expect seep calling to cease during EPCs to disguise them so that physical retaliation by mates (Gowaty, 1981) or deleterious effects on paternal care (Hatchwell and Davies, 1992) are avoided. It is interesting that, during the two observed EPCs, seep calling continued but copulation calls (see Cramp, 1988) were absent. This also implies that seep calls are an honest hunger signal, but it is impossible to establish whether they are exclusively di-

Table 1
 Comparison between approaches of 10 resident and 10 neighboring males to playbacks 5 m from the territory boundary of three separate stimuli

Signal	Receiver response (approach/no approach)		<i>p</i>
	Resident	Neighbor	
(1) 5 seep calls/30 s	5/5	1/9	.076 (.051)
(2) 15 seep calls/30 s	9/1	6/4	.303 (.121)
<i>p</i> (1 vs. 2)	.076 (.051)	.056 (.019)	
(3) Tic calls	7/3	0/10	.003 (.001)
(2) 15 seep calls/30 s	9/1	6/4	.303 (.121)
<i>p</i> (3 vs. 2)	.334 (.264)	.005 (.003)	

p values are derived from Fisher's Exact tests; values from chi-square tests in parentheses.

rected at the pair male, as females might intend the signal to be overheard.

Do seep calls contain information of interest to extrapair males?

First, the higher seep calling rate in the fertile phase and the conspicuous increase between the pre-fertile and fertile phases potentially allow neighboring males to identify the breeding condition of females. Second, neighboring males appeared to distinguish between calls broadcast from the center and those from the edge of territories, suggesting that these calls, like most others, contain location information. Third, increased rates of seep calling during male removals suggest that extrapair males might judge female availability by listening to their vocalizations. Finally, a male's quality could correspond to his provisioning rate, and female robins may use this rate as an honest signal of, for example, foraging ability (e.g., Hill, 1991). Thus, as seep calling rate is inversely related to provisioning rate, seep calling could signal the quality or attentiveness of a mate to its neighbors. A male may thus gain information about a rival male by listening to the vocalizations of that male's mate, in contrast to previous studies that have shown males or females assessing the quality of rivals or potential extrapair mates by attending to their vocalizations directly (e.g., Naguib et al., 1999; Otter et al., 1999). Thus, seep calls not only allow the fertility and location of a female to be assessed, but perhaps also the quality of a rival male and his attentiveness. Such information is of high potential value to males seeking EPCs.

Table 2
 Comparison between approaches of neighboring males to female seep calls broadcast 5 m from the edge and from the center of territories

Signal	Neighbor response (approach/no approach)		<i>p</i>
	Territory edge	Territory center	
15 calls/30 s	6/4	0/10	.011 (.003)

p value is derived from Fisher's Exact test; value from chi-square test in parentheses.

Do extrapair males act on the information in seep calls?

Intrusion and approach to females by neighboring males, extrapair courtship feeding, and hence potentially EPC rates, were all apparently highest during the fertile period, both under natural circumstances and during male removals (see also Tobias and Seddon, 2000). Playback experiments showed that female seep calls are used as cues, as neighboring males approached simulated fertile period seep calling rates more readily than prefertile period seep calling rates. Thus, males use the information provided by female vocalizations to target their intrusions. As all playback tapes were recorded during the prefertile period, the response of neighboring males must be dictated by the rate of calling rather than any distinctive change in the structure of fertile period calls.

Does provisioning by males reduce seep calling?

High provisioning rates reduced seep calling rates in the fertile period: well-fed females called less. The apparent lack of this relationship in the prefertile period is difficult to explain but may relate to reduced motivation of females to signal their need, or of males to respond to these signals. Feeding may serve to provide the fertile female not only with food, but a reminder of the male's continued attendance. Such reminders are important because females will re-pair quickly in the absence of their mates (Tobias, 1997).

Does courtship feeding guard paternity?

Direct mate-guarding is minimal in other species with high levels of female provisioning, such as shrikes (Laniidae) and raptors (Accipitridae/Falconidae), suggesting that courtship feeding may represent an alternative paternity guard (Birkhead and Møller, 1992). Although no study has demonstrated a mechanism, it is possible that high provisioning rates signal male quality to the female (Searcy, 1979), thus reducing the likelihood that she will seek EPCs or accept the solicitations of trespassing males (e.g., Kempnaers et al., 1992). When courtship feeding was regular, female robins often remained relatively static and centrally positioned in the territory, behavior that probably helps to conserve energy and facilitates her location by the returning male. In effect, by minimizing the mobility of females, courtship feeding reduces their likelihood of encountering rival males. Although territoriality is the primary paternity guard in the robin (Tobias and Seddon, 2000), we suggest that courtship feeding guards paternity by lowering the rate at which female's beg and hence the probability that an extrapair male will intrude to seek EPCs.

Blackmail or eavesdropping?

In conclusion, by increasing rates of seep calling and approaching territory boundaries, females can elevate the chance of encountering an extrapair male. Conversely, through regular provisioning, males can reduce female seep calling and mobility. Neighboring males approach seep calls given at high rates from the edge of territories, apparently in search of EPCs. As the seep call is far-carrying, containing fertility and location information, it apparently forces the pair male to be attentive or risk losing paternity.

McGregor and Dabelsteen (1996) define eavesdropping as a process whereby a third party (the eavesdropper) gains information from an interaction that could not be accrued from the signal alone. If the female is deliberately seeking to communicate with neighboring males in order to modify the behavior of her mate, the system is more akin to blackmail (see Zahavi, 1977). In robins, the seep call appears to be directed

at the pair male, and although in isolation it may allow female fertility and location to be assessed, it is the interaction with the male, whose behavior is correlated with the intensity (or rate) of the signal, that provides a neighbor with the key information relating to how successful an intrusion is likely to be (see McGregor and Peake, 2000). From this viewpoint, the evidence implies a case of eavesdropping rather than blackmail. In either case, it is the first indication in any species that female vocalizations may be used by neighboring males to target intrusions for EPCs. Future studies should consider the influence of within-pair communication on neighbors and hence on sperm competition (see McGregor and Peake, 2000).

The situation is partly analogous to that found in bronze-winged jacobins *Metopidius indicus*, a species in which the sex roles are reversed and male vocalizations force (i.e., blackmail) females to attend their mates as they otherwise encourage intrusions and increase the likelihood of takeovers by other females (Butchart et al., 1999). Unlike the "yell" call of male jacobins, however, the seep call of female robins appears to be directed primarily at the mate and relates to hunger. In reality, the roles of eavesdropping and blackmail in natural communication systems are difficult to disentangle because they lie at opposite ends of a continuum, and the former may function as a component of the latter. For example, if the seep calls communicated by female robins to their mates are eavesdropped by neighboring males such that the pair-male risks losses in paternity, there may be selection pressure on the female to exploit this risk because it forces her mate to cooperate. In this way, the eavesdropping of vocalizations might act as a precursor in the evolution of blackmail.

We are indebted to Mike Brooke, Nick Davies, Rebecca Kilner, and two anonymous reviewers for advice and comments on the manuscript, and we thank the staff of the Cambridge University Botanic Garden for their cooperation. This work was supported by a studentship from the Natural Environment Research Council, for which we are grateful; the temporary removal experiments were conducted under license from English Nature.

REFERENCES

- Birkhead TR, Møller AP, 1992. Sperm competition in birds: evolutionary causes and consequences. London: Academic Press.
- Butchart SHM, Seddon N, Ekstrom JM, 1999. Yelling for sex: harem males compete for female access in bronze-winged jacobins. *Anim Behav* 57:637–646.
- Cox CR, Le Boeuf BJ, 1977. Female incitation of male competition: a mechanism in sexual selection. *Am Nat* 111:317–335.
- Cramp S, 1988. Handbook of the birds of Europe, the Middle East and North Africa, vol. V. Oxford: Oxford University Press.
- East M, 1981. Aspects of courtship and parental care of the European robin *Erithacus rubecula*. *Ornis Scand* 12:230–239.
- Gowaty PA, 1981. Aggression of breeding eastern bluebirds, *Sialia sialis*, toward their mates and models of intra- and interspecific intruders. *Anim Behav* 29:1013–1027.
- Harper DGC, 1985. Pairing strategies and mate choice in female robins *Erithacus rubecula*. *Anim Behav* 33:862–875.
- Haskell D, 1994. Experimental evidence that nestling begging behavior incurs a cost due to nest predation. *Proc R Soc Lond B* 257: 161–164.
- Hatchwell BJ, Davies NB, 1992. An experimental study of mating competition in monogamous and polyandrous dunnocks, *Prunella modularis*: I. Mate guarding and copulations. *Anim Behav* 43:595–609.
- Hill HE, 1991. Plumage colouration is a sexually selected indicator of male quality. *Nature* 350:337–339.
- Hunter FM, Burke T, Watts SE, 1992. Frequent copulation as a method of paternity assurance in the northern fulmar. *Anim Behav* 44: 149–156.
- Johnstone R, 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol Rev* 70:1–65.

- Johnstone R, 1997. The evolution of animal signals. In: Behavioural ecology: an evolutionary approach, 4th ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 155–178.
- Kempenaers B, Verheyen GT, Van den Broeck M, Burke T, Van Broeckhoven C, Dhondt AA, 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature* 357: 494–496.
- Lack D, 1965. The life of the robin. London: Witherby.
- Leech SM, Leonard ML, 1996. Is there an energetic cost to begging in nestling tree swallows, *Tachycineta bicolor*? *Proc R Soc Lond B* 263:983–987.
- McGregor PK, 1993. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Phil Trans R Soc Lond B* 340:237–244.
- McGregor PK, Dabelsteen T, 1996. Communication networks. In: The ecology and evolution of acoustic communication in birds (Kroodsma DE, Miller EH, eds). Ithaca, New York: Comstock; 409–425.
- McGregor PK, Peake TM, 2000. Communication networks: social environments for receiving and signalling behaviour. *Acta Ethol* 2:71–81.
- Naguib M, Fichtel C, Todt D, 1999. Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proc R Soc Lond B* 266:537–542.
- Neuman J, Chardine JW, Porter JM, 1998. Courtship feeding and reproductive success in black-legged kittiwakes. *Colon Waterbirds* 22: 73–80.
- Nisbet ICT, 1973. Courtship feeding, egg size and breeding success in common terns. *Nature* 241:141–142.
- Oliveira RF, McGregor PK, Latruffe C, 1998. Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc R Soc Lond B* 265:1045–1049.
- Otter K, McGregor PK, Terry AMR, Burford FRL, Peake TM, Dabelsteen T, 1999. Do female great tits *Parus major* assess males by eavesdropping? A field study using interactive song playback. *Proc R Soc Lond B* 266:1305–1309.
- Redondo T, Castro E, 1992. The increase in risk of predation with begging activity in broods of magpies *Pica pica*. *Ibis* 134:180–187.
- Reed CR, 1996. Function of vocalisations in the European robin *Erithacus rubecula* (M. Phil. thesis). Cambridge: University of Cambridge.
- Searcy WA, 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds *Agelaius phoeniceus*. *Am Nat* 114:77–100.
- Tobias J, 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. *Anim Behav* 54:9–21.
- Tobias J, Seddon N, 2000. Territoriality as a paternity guard in the European robin *Erithacus rubecula*. *Anim Behav* 60:165–173.
- Zahavi A, 1977. Reliability in communication systems and the evolution of altruism. In: Evolutionary ecology (Stonehouse B, Perrins C, eds). London: Macmillan; 253–259.