ARTICLES

Territoriality as a paternity guard in the European robin, *Erithacus rubecula*

JOE TOBIAS & NAT SEDDON

Department of Zoology, University of Cambridge

To investigate the relative importance of paternity defences in the European robin we used behavioural observations, simulated intrusions and temporary male removal experiments. Given that paired males did not increase their mate attendance, copulation rate or territory size during the female's fertile period, the most frequently quoted paternity assurance strategies in birds were absent. However, males with fertile females sang and patrolled their territories more regularly, suggesting that territorial motivation and vigilance were elevated when the risk of cuckoldry was greatest. In addition, there was a significant effect of breeding period on response to simulated intrusions: residents approached and attacked freeze-dried mounts more readily in the fertile period. During 90-min removals of the pair male in the fertile period, neighbours trespassed more frequently relative to prefertile and fertile period controls and appeared to seek copulations with unattended females. When replaced on their territories, males immediately increased both song rate and patrolling rate in comparison with controls. We propose that male robins sing to signal their presence, and increase their territorial vigilance and aggression in the fertile period to protect paternity.

© 2000 The Association for the Study of Animal Behaviour

Despite the apparent social monogamy of the majority of bird species (Lack 1968) and a minority of mammal species (Kleiman 1977), studies over the last two decades have revealed that extrapair copulations (EPCs) are frequently sought to augment reproductive output (Parker 1984; Birkhead 1987; Westneat et al. 1990). The success of EPC as a reproductive strategy in birds (Birkhead et al. 1988; Gomendio & Roldan 1993) has meant that sperm competition has played a vital role in shaping avian behaviour. For example, in response to the serious costs of provisioning unrelated offspring, males have evolved behavioural adaptations that serve to maximize their confidence of paternity (Birkhead & Møller 1992). A wide variety of paternity assurance mechanisms have been identified, including direct mate attendance or physical mate guarding (e.g. in magpies, *Pica pica*: Birkhead 1979), frequent copulation (e.g. in fulmars, *Fulmaris glacialis*: Hunter et al. 1992), removal of sperm from the female's reproductive tract (e.g. in dunnocks, *Prunella modularis*: Davies 1983) and acoustic guarding (e.g. in bay wrens,

Correspondence: J. Tobias, BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 ONA, U.K. (email: joe.tobias@birdlife.org.uk). N. Seddon is at the Department of Zoology, Downing Street, Cambridge CB2 3EJ, U.K.

Thryothorus nigricapillus: Levin 1996). Territorial site defence by males may also have evolved in response to sperm competition (Birkhead & Møller 1992). This may function through territory expansion during the fertile period (Møller 1990, but see Rodrigues 1998), increased territorial aggression (e.g. in red-backed shrikes, *Lanius collurio*: Jakober & Stauber 1989) or increased male song output (e.g. wheatears, *Oenanthe oenanthe*: Currie et al. 1998; but see Gil et al. 1999). In this study we evaluated the relative importance of various paternity guards in the European robin, a socially monogamous territorial passerine in which males in the breeding season sing in defence of shared, multipurpose territories. As competition for females is intense, with ca. 20% of territorial males failing to pair annually (Lack 1965; Harper 1985), we predicted that paternity guards are important in robins.

To investigate different paternity guards, we measured levels of intrusion, patterns of pair proximity, rates of copulation, song output and intensity of territorial defence during different stages of the breeding cycle. In addition, we conducted experiments involving male removal and replacement and simulated male intrusion and quantified the behavioural responses of both sexes to these manipulations.

METHODS

Behavioural Observations

We studied a population of ca. 25 pairs of individually colour-ringed robins in the Cambridge University Botanic Garden, U.K., between 1993 and 1995. During study site transects we routinely recorded the location of individuals and mapped territories by drawing minimum convex polygons (Odum & Kuenzler 1955) around registrations made whenever a bird moved more than 20 m or every 30 min. As the number of registrations influences calculated territory size, we used 30 registrations (the minimum number for our sample) to generate territory maps for each individual. This figure gave a mean ± SE of 71 ± 6.0% of the final calculated territory size for eight individuals with over 100 registrations. When territory sizes at different stages of the breeding cycle were compared, we used the first 30 registrations prior to, during, or subsequent to the female's fertile period. During watches of 20–60 min of each focal pair per day between 0700 and 1800 hours we recorded the following.

(1) Intrusions by males: individuals observed within the resident male's territory; intruders were frequently revealed by the response of resident males. Although we occasionally encountered interlopers before residents detected them, it is likely that we consistently underestimated intrusion rates.

(2) Pair proximity: whether pair members were within 5 m of each other at 30-s sampling intervals; males within this distance have been shown in several species to be almost certain of discouraging or disrupting EPC attempts (e.g. Alatalo et al. 1984).

(3) Move initiation: number of moves by both sexes more than 10 m away from their mate during 30-s sampling periods.

(4) Pursuit: moves were defined as having been followed if individuals pursued their mates (± 45°) within 5 s of the initial move.

(5) Copulation: this was noted only if cloacal contact was apparent; it was not possible to discern successful insemination. Copulations often took place in dense cover and were sometimes difficult to observe, although copulation calls (Cramp 1988) were often audible. We therefore also scored potential copulations (i.e. if focal individuals were temporarily lost from view after solicitation by male or female was observed, or if a copulation call was uttered).

(6) Song output: whether individuals were engaged in song bouts at point sampling intervals of 30 s (time singing); the number of songs delivered for each 30-s period in which singing occurred (song rate); and the proportion of 30-s periods in which singing occurred (periods with song).

(7) Patrolling: an independent and uninterrupted movement of more than 15 m made by either sex.

Male and female robins revealed their location by frequent vocalizations and this, together with the relatively open habitat of the study site, meant that we could usually locate both pair members during focal watches. On the few occasions when this was not possible, or when the female was incubating, data collection for patrolling and categories 2–4 was discontinued. Most behavioural observations were made preceding first broods because individuals were less easily observed during subsequent nesting attempts.

We separated data collected from each pair into the prefertile, fertile and postfertile phases of the female's breeding cycle. While there is no information on sperm storage in robins, a median of 10 days storage is reported in female zebra finches, *Taeniopygia guttata*, a duration comparable to most species currently studied (Birkhead et al. 1989). Nevertheless, the fact that sperm from the most recent mating has precedence in birds (Birkhead et al. 1988) means that copulations occurring early in the fertile period have little chance of fertilizing eggs. Although robins occasionally copulate up to 15 days before laying (Cramp 1988), almost all copulations recorded in this study (31 of 32) were detected within 8 days of the first egg. We therefore defined the fertile period as extending from day -8 to the day before clutch completion (where day 0 refers to the day of clutch commencement). This accommodates the majority of copulations within the probable length of time in which females may be fertilized. Clutch size was three to six eggs ($\bar{X} \pm SD = 4.93 \pm 0.8$; $N = 45$). A 30-day prefertile period (days -39 to -9) was chosen because several birds were unpaired before that time, with different implications for behaviour. Postfertile period data were collected largely in the incubation phase, although some were derived from chick-provisioning stages. Although this period is heterogeneous, we are principally concerned with changes in male behaviour in relation to female fertility, and, while the inclusion of some posthatching data was unavoidable, we are confident that it does not bias the results. For individuals or pairs to be included in analyses, a minimum of 150 min of data were required for each behavioural category and phase in the breeding cycle.

Simulation of Intrusions

Two male robins (both found in the Botanic Garden, one killed by a cat and another found dead during cold weather) were freeze dried on wire frames in standard upright posture and presented conspicuously in the centre of pair territories when residents were not visible. Mounts were attached to a polystyrene base and placed at least 3 m from cover. We randomized the use of the two mounts, to investigate whether they had different effects. Since in other passerine bird species intruders seeking EPCs are invariably silent and furtive (e.g. Westneat 1987; Evensen 1994) we did not play vocalizations to alert residents to the mounts. We conducted presentations between 0800 and 1100 hours, as territorial intrusions in most bird species tend to occur in the morning, although this is not necessarily the optimum time for copulations to result in fertilization (see Birkhead et al. 1996). As a control, we replicated the experiments using a freeze-dried mount of a male chaffinch, *Fringilla coelebs*. Presentations were conducted during each stage of the breeding cycle. One sample of pairs ($N = 12$) experienced simulated intrusions at all three stages, while others received

Table 1. Comparison of fertile period data from three seasons ($\bar{X}\pm$SE)

Sample	1993 (N=9)	1994 (N=13)	1995 (N=9)	H_2§	P§
Territory size (m^2)	2372±163	2420±198	2050±243	2.47	0.3
Intrusions/h	1.5±0.2	1.1±0.2	1.5±0.2	2.97	0.2
Pair proximity*	44.0±4.6	42.8±5.0	31.5±2.4	3.06	0.2
Time singing†	26.1±2.6	23.8±2.5	22.4±3.6	0.72	0.7
Periods with song‡	41.2±6.9	53.8±4.6	54.3±7.7	3.45	0.2
Patrol flights/min	0.48±0.1	0.59±0.1	0.59±0.1	0.97	0.6

Samples refer to the first year in which sufficient data were obtained for each pair.
*Percentage of 30-s point intervals at which pair members were within 5 m of each other.
†Percentage of 30-s point intervals at which individual was singing.
‡Percentage of 30-s periods in which individual was singing.
§Kruskal–Wallis tests.

presentations only during the fertile period (N=8) or during incubation (N=7), to control for the effects of habituation. Observing responses from at least 20 m away, we recorded the time to detect the mount, the closest approach to it, the song rate and the subsequent response of territory owners for a period of 5 min. The experiment was discontinued if no response was observed after 10 min, and arbitrary values of 600 s for time to detect the mount and 10 m for closest approach were recorded.

Male Removal Experiments

To mimic short-term absences by the territorial male, 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 released after 90 min (treatment A). For 1 h after their release we recorded behaviours 1–7 described above. Fertile period means for behaviours were also collected for the removed individuals more than 24 h before and after the manipulation (treatment C). All these data were then compared with those yielded by identical removals of eight males in the prefertile period (treatment D). As a further control, five additional males were captured and then immediately released during the fertile period (treatment B). No individual received more than one treatment.

Ethical Note

The removal experiments were conducted under licence from English Nature. To ensure that they did not impinge on the welfare of males, only healthy individuals were selected and the retention period was kept brief. During this period birds did not show any obvious signs of stress, tending to remain motionless, and after release no adverse effects on health or territorial ownership were noted (see Tobias 1997).

Sample Sizes and Statistics

Data were derived from 45 breeding attempts of 36 pairs and each data point refers to the first year in which sufficient data were collected for each pair, although subsequent recombinations of pairs were treated as independent samples. As this was the case for less than
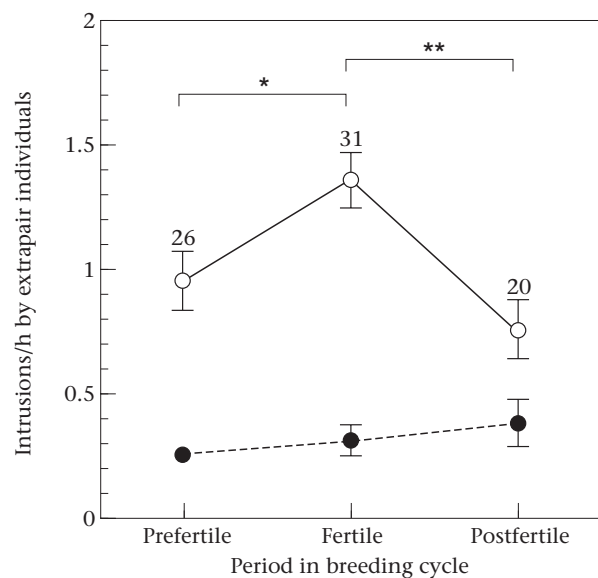

Figure 1. Rate of intrusion ($\bar{X}\pm$SE) by extrapair males (○) and females (●) in relation to stage of the female's breeding cycle. Variation between stages: Kruskal–Wallis test: males: H_2=12.22, P=0.01; females: H_2=0.41, P=0.8. Mann–Whitney U tests between adjacent periods for males: *P<0.05; **P<0.01. Sample sizes are given above the error bars.

10% of pairs it is unlikely to have had a confounding influence on the results.

Apart from mount presentations (conducted in 1994) and male removals (conducted in 1994 and 1995), data were gathered in three breeding seasons. As there were no consistent significant differences for behavioural traits between years (Table 1), we pooled them as single samples in the following analyses. Means are given ± SE; all statistical tests are two tailed and corrected for ties where appropriate.

RESULTS

Behavioural Observations

Frequency of intrusion

Male intrusions were observed most frequently during the fertile period (Fig. 1) and primarily involved

Table 2. Comparison of mate attendance behaviour and song output between three stages of the breeding cycle

Stage in breeding cycle	Mate attendance behaviour			Song output			N	U†	P†
	Proximity of pair members (% time <5 m)	Moves initiated by females (%)	Female moves pursued (%)	Time singing (%)	Song rate (songs/30 s)	Periods with song (%)			
Prefertile	42.8±2.46	0.460±0.03	0.421±0.04	28.1±1.95	2.60±0.14	41.3±2.20	26	231	<0.05
Fertile	39.9±2.70	0.409±0.02	0.425±0.04	24.1±1.62	2.19±0.12	55.3±3.61	31	148	<0.01
Postfertile	33.6±2.88	0.499±0.04	0.362±0.03	20.4±2.27	2.47±0.11	38.3±3.20	20		
H_2*	5.99	4.62	4.67	6.18	4.96	14.6			
P*	<0.05	<0.1	<0.1	<0.05	<0.1	<0.001			

*Kruskal–Wallis tests.
†Mann–Whitney U tests between adjacent breeding stages for periods with song.

neighbouring resident males. As the majority of recorded intrusions were first detected by territorial robins, our measures of intrusion rates may simply reflect variations in their behaviour. In other words, if the mates of fertile females were more vigilant and more aggressive towards trespassers, it is likely that intrusions proved easier to record at that time. However, no variation in intrusion by females was observed across the same periods (Fig. 1), suggesting that males specifically target intrusions on to territories with fertile females.

Mate attendance

There was no evidence that males spent more time accompanying females during the fertile period (Table 2). Moves were initiated at more or less equal rates by both pair members, females showing no signs of attempting to disrupt patterns of pair proximity and males making no special effort to pursue females in the fertile period (Table 2). Females initiated more moves in the postfertile period largely while feeding actively during breaks from incubation, or because of feeding trips for nestlings or fledglings.

Copulation

During 176.5 h of observations involving 36 pairs in the fertile period, we recorded 32 copulations. This gave an overall rate of 0.18 copulations/h.

Vocalizations

Percentage time singing varied across the female breeding cycle, and although there were no significant differences between periods, time singing declined from prefertile to postfertile stages (Table 2). Whilst song rate remained relatively constant throughout the breeding cycle, the proportion of periods with song reached a maximum in the fertile period. This can be explained by the observation that male robins paired to fertile females tended not to sing in protracted song bouts (usually 8–9 songs/min), but periodically give single songs. A greater frequency of song bouts in the prefertile stage may explain why time singing and song rate were highest early in the breeding cycle.

Territory size

Male territory size varied across the female breeding cycle, although this was significant only for first broods
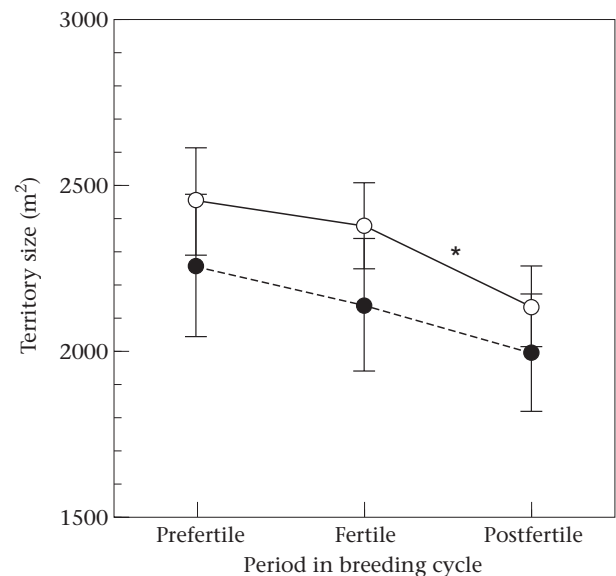

Figure 2. Male territory size ($\bar{X}$±SE) in relation to stage of the female's breeding cycle for first broods (○; N=32) and second broods (●; N=9). Variation between stages: Friedman test: first broods: χ^2_2=7.721, N=22, P<0.05; second broods: χ^2_2=3.436, P>0.1. Wilcoxon signed-ranks test between adjacent periods: *P<0.05.

(Fig. 2). There was a tendency for male territory size to contract gradually from prefertile to postfertile stages, although a significant decline in size was evident only between the fertile and postfertile stages in first broods (Fig. 2).

Patrolling

Patrolling flights by males were observed significantly more frequently during the fertile period (0.46 ± 0.05 flights/min) than during the prefertile period of females (0.21 ± 0.04; Mann–Whitney U test: U=202, N_1=31, N_2=26, P=0.0012). However, there was no significant increase in the females' patrolling rate from the prefertile period (0.12 ± 0.04 flights/min) to the fertile period (0.17 ± 0.05; U=355, N_1=31, N_2=26, P=0.5). During the postfertile stages, flights were often associated with food collecting for nestlings or fledglings and therefore the data were not included in this analysis.

Response to Simulated Intrusions

Control presentations of a male chaffinch (N=12) were invariably ignored by resident robins. In comparison, all male robins (N=25) that detected freeze-dried mounts of conspecifics on their territories sang loudly, while carefully approaching the 'intruder'. On many occasions no attack took place, possibly because mounts were taken to be trespassing females. Attacks usually involved brief flights at the mount, scored as one 'strike' if physical contact was observed. Rarely, robins perched on the mount and delivered repeated blows to the head.

Presentations appeared to be most rapidly encountered in the fertile period, although variation in time to detection was not statistically significant (Fig. 3a), and fertile period manipulations incited the closest approach by resident males (Fig. 3b). In addition, 31 strikes were counted in the fertile period experiments in comparison with six in the prefertile and two in the postfertile experiments (Friedman test: χ_2^2=7.43, N=7, P=0.024). Song rate, however, did not differ significantly between periods (χ_2^2=0.667, N=7, P=0.715). In all cases, there were no significant differences between repeats and controls (Table 3). In addition, there were no differences between responses to mount 1 versus mount 2 (time to detection: 226 ± 90 versus 278 ± 69 s; Mann–Whitney U test: U=13.0, N_1=N_2=6, P=0.4; approach: 0.833 ± 0.3 versus 2.0 ± 0.9 m; U=19.5, N_1=5, N_2=6, P=0.4; song output: 3.1 ± 0.4 versus 2.9 ± 0.5 songs/30 s; U=16.5, N_1=5, N_2=6, P=0.8).

Response to Male Removals

During experimental removals, intrusion rates by extrapair males increased dramatically from mean fertile period rates of 0.99 ± 0.2 intrusions/h to 2.33 ± 0.3 intrusions/h (Wilcoxon signed-ranks test: T=0, N=9, P<0.01), and increased from prefertile period control removals (0.25 ± 0.2 intrusions/h; Mann–Whitney U test: U=2, N_1=N_2=8, P<0.001). During all removal experiments in the fertile period, one to three neighbouring male robins approached unattended females and appeared to 'solicit' copulations, usually by presenting food items which the females always accepted. Chases between females and extrapair males often occurred (females apparently attempting to escape the attentions of males) making it difficult to ascertain whether copulations took place. We observed 16 separate male solicitations, two of which resulted in apparently successful EPCs. Only one solicitation (no observed EPCs) occurred during prefertile period removals.

In the first hour after temporarily removed males were returned to their territories during the female's fertile period, the rate of intrusion by extrapair males (0.22 ± 0.15 intrusions/h) was significantly lower than the mean rate of intrusion (0.99 ± 0.2 intrusions/h) for those males during the fertile period (Wilcoxon signed-ranks test: T=1.0, N=9, P=0.01). This is perhaps because neighbours are less likely to trespass immediately after a prolonged intrusion or because newly released resident males were more intent on and effective at patrolling and repelling.
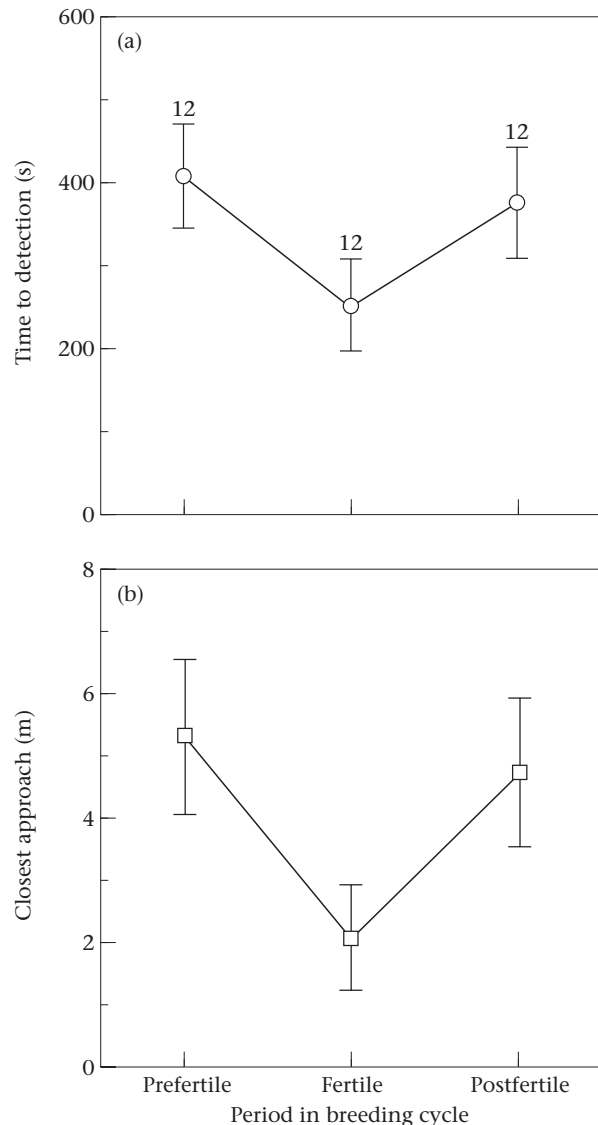

Figure 3. Responses of males ($\bar{X} \pm$SE) to simulated intrusions in different stages of the breeding cycle. (a) Time to detect mounts; (b) closest approach to mounts. Variation in time to detect mounts across periods: Friedman test: χ_2^2=3.65, P=0.161; variation in closest approach to mounts: χ_2^2=8.34, P=0.015. The distribution of these data did not differ significantly from normal (Kolmogorov–Smirnov tests: time lag: D=2.0, P=0.736; approach: D=3.56, P=0.338). Influence of breeding period on responses: MANOVA, Wilks' lambda: $F_{4,64}$=2.35, P=0.063; Roy's greatest root: $F_{2,33}$=5.21, P=0.011). Sample sizes are given above the error bars.

During the first hour after fertile period removals, proximity of reunited pair members did not increase (Table 4, A versus D). However, pair members tended to spend less time together subsequent to manipulation, although not significantly so, compared with fertile period controls (A versus B) or with fertile period means (A versus C). That this is not a result of female behaviour is indicated by the decrease in her moves away from the male once pairs were reunited (A versus B, C and D). Moreover, removals did not appear to affect the rate of move following by males (A versus B, C and D). During

Table 3. Results of Mann–Whitney *U* tests between controls and repeat mount presentations during the fertile and postfertile periods

Response measure	Fertile period			Postfertile period		
	U	N_1, N_2	*P*	*U*	N_1, N_2	*P*
Time lag	37.0	12, 8	0.67	39.0	12, 7	0.80
Approach	44.0	12, 8	0.76	32.5	12, 7	0.74
Song output	36.0	11, 7	0.82	14.0	8, 4	0.73
Attack	44.5	12, 8	0.79	39.0	12, 7	0.80

time budgets after all nine fertile period removals, not a single copulation was observed. In comparison, one copulation was recorded after the five fertile period control removals, a rate matching the mean value reported above. This suggests that males or females initially reduce copulation rates after a period of separation, counter to predictions of the frequent copulation hypothesis. However, the data are too few to analyse further.

The immediate response of 89% (8/9) of males released in the fertile period was to sing, whilst after prefertile controls, significantly fewer males (37.5%, 3/8) sang (Fisher's exact test: *P*<0.05). Males removed in the fertile period sang more overall than control males in the fertile or prefertile periods (Table 4, A versus B and D). Additionally, the rate of singing was highest for manipulated males. They sang significantly more rapidly during bouts of singing than they otherwise did in the fertile period, or in the prefertile period controls (A versus C and D). Perhaps surprisingly, replaced males did not appear to sing more consistently than they did after control removals, or otherwise in the fertile period (A versus B and C). During the prefertile period, removals resulted in fewer periods with song (A versus D).

While patrolling rates were highest after fertile period removals, this measure did not differ significantly from other fertile period samples (Table 4). However, rate of patrolling was significantly lower in the prefertile period (A versus D).

To summarize, a 90-min absence from the female in the fertile period, and the associated high risk of cuckoldry, did not increase a male's copulation rate nor his efforts to attend his mate. In fact, these behaviours appeared to be supplanted by an increased territorial motivation, characterized by increases in song output, as measured by proportion of periods with song, and maintenance of high patrolling rate during the hour after his release back on to the territory.

Table 4. Comparison of mate attendance, song output and male patrolling behaviour between the four experimental treatments

Behaviour	Treatment*			
	A	B	C	D
Mate attendance				
Proximity of pair members (% time <5 m)	27.4±5.48	43.8±4.15	45.6±7.35	28.8±6.12
U/T		8.00	6.00	35.5
P		<0.1	<0.1	NS
Moves initiated by females (%)	0.234±0.04	0.470±0.09	0.431±0.04	0.428±0.07
U/T		6.50	3.00	15.0
P		<0.05	<0.05	<0.05
Female moves followed by male (%)	0.478±0.07	0.466±0.09	0.434±0.85	0.469±0.06
U/T		22	22.0	35.5
P		NS	NS	NS
Song output				
Time singing (%)	34.6±4.77	15.4±3.40	22.9±2.88	19.1±4.66
U/T		6.50	37.0	13.5
P		<0.05	NS	<0.05
Song rate (songs/30 s)	3.01±0.12	2.38±0.29	2.23±0.28	1.86±0.22
U/T		9.50	40.0	5.5
P		NS	<0.05	<0.01
Periods with song (%)	50.0±5.31	28.4±8.18	41.8±7.17	22.5±4.09
U/T		20.5	26.0	8.00
P		NS	NS	<0.01
Male patrolling				
Flights/min	0.489±0.08	0.360±0.13	0.378±0.08	0.138±0.05
U/T		15.0	28.0	8.00
P		NS	NS	<0.01

All statistical tests compare sample A with other samples. A versus B and A versus D are Mann–Whitney *U* tests (*U* statistic given) while A versus C is a Wilcoxon signed-ranks test (*T* statistic given).
*A: Resident male replaced after 90-min removal in fertile period (*N*=9); B: fertile period controls (*N*=5); C: fertile period means for males in A, >24 h before and after manipulation (*N*=9); D: prefertile period removals (*N*=8).

DISCUSSION

Mate Attendance

In many studies, the patterns of pair proximity fit the predictions of the mate attendance hypothesis (e.g. Björklund & Westman 1986; Rodrigues 1998). In robins, however, these predictions were not fulfilled. The overall time spent together by males and females during the fertile period was roughly half that observed in other species with intense mate attendance (e.g. barn swallows, *Hirundo rustica*: Møller 1987; and magpies: Birkhead 1982). Although it is easier to ascertain the existence of mate attendance than its absence (Lefelaar & Robertson 1984), it seems that male robins do not allocate much time to pursuing, closely guarding or monitoring their fertile mates. Low attendance might derive from constrained visibility in woodland habitats (Björklund & Westman 1986), female control of fertilizations (Chek & Robertson 1994), or incompatibility with male and female feeding efficiency, as in dunnocks (Davies 1992). A further possibility is that females cooperate with their pair males, neither actively seeking EPCs nor requiring constant physical monitoring, as indicated in other species with low levels of mate attendance and copulation (e.g. penduline tit, *Remiz pendulinus*: Schleicher et al. 1997).

Frequent Copulation

Copulation rate during the fertile period was comparable to the 0.16 copulations/h recorded in Sussex, U.K. (Cramp 1988), but considerably lower than the 2.5 copulations/h observed by Harper (1984) in Cambridge Botanic Garden, suggesting that copulation rates in the species are highly variable. Whilst this may be in response to varying risks of cuckoldry, it could equally relate to differing criteria for categorizing copulations or to the timing of behavioural observations (e.g. crepuscular peaks in copulation rates have been recorded, Cramp 1988).

Data nevertheless suggest that copulation rate does not play a central role in guaranteeing paternity in this species. Indeed, the tree swallow, *Tachycineta bicolor*, which reportedly relies on frequent copulation as a paternity guard, copulates around three times more often (Venier & Robertson 1991). Weak or absent mate attendance has been reported in populations of tree swallows (Chek & Robertson 1994) and Norwegian pied flycatchers, *Ficedula hypoleuca* (Chek et al. 1996). In the former, EPCs are common and under apparent female control (Lifjeld & Robertson 1992); thus it is argued that frequent copulation is a more cost-effective strategy for the pair male. In pied flycatchers, neither copulation nor mate attendance is conspicuous during the female's fertile period. This is perhaps explained by low population density or female 'disinterest' reducing the risk of cuckoldry, as demonstrated by low levels of extrapair paternity in the same population (Lifjeld et al. 1991). In robins, however, some risk of cuckoldry is likely: increased intrusion rates during the fertile period, and particularly during fertile period removals, indicated that

neighbouring males are aware of both female fertility and male attendance (see Tobias 1996). Indeed, DNA fingerprinting of 25 robin nestlings from six broods revealed that one (4%) was fathered by an extrapair male (Tobias 1996). Given that copulations are reported to take place immediately after separations in various species (e.g. zebra finches: Birkhead et al. 1989; dunnocks: Hatchwell & Davies 1992), an interesting observation regarding fertile period copulations in robins was that, in common with mountain bluebirds, *Sialia mexicana* (Dickinson 1996), they did not occur during the hour after male replacement. This implies that copulation is not the priority for male robins in terms of paternity defence, despite the likelihood of EPCs occurring during their absence. This may relate to the fact that, at the time of male removal, the third egg would have already been fertilized, and sufficient time was available to ensure paternity of the fourth egg. The main threat after removal, therefore, was not so much loss of paternity, but loss of mate and hence the optimal strategy for a released robin was to increase territorial defence as opposed to mate attendance or copulation rate.

Song

The function of song in the fertile period has been postulated as mate defence (Langmore 1996), honest signalling of male quality by announcement of mate fertility (Møller 1991), or as a means of stimulating the pair female to solicit copulations (Pinxten & Eens 1998). The basic prediction of these hypotheses is that the proportion of time spent singing should be highest in the fertile period. In common with many other species (Rodrigues 1996; Gil et al. 1999), this prediction was not met in the robin. If song operates as a paternity guard in these species, it may be as a reminder to competitors of the continued presence of territorial individuals, a function suggested by the regular single songs of male robins with fertile mates. Because of the demands imposed by courtship feeding (East 1981), male robins may simply be unable to afford time or energy for protracted song bouts and respond with frequent single songs. The increased rates of intrusion by extrapair males during removal experiments suggests that males are nevertheless effective at deterring rivals. Immediate singing by males after release on familiar territories is found in several other species (e.g. mountain bluebirds: Dickinson 1996). The relative increase in this behaviour during the fertile period suggests that it is modified by the urgency of territory maintenance, or resumed contact with mates. The latter function can be achieved through tic calling (a low-intensity contact call; Cramp 1988) and paired male robins often use this form of vocalization after release when the female is not fertile, implying that territoriality is more important within the fertile period.

Territory Expansion

If large territories serve to protect the reproductive investment of males, territory size might be expected to

reach its maximum during the period of greatest risk (Møller 1990, 1992). In common with chiffchaffs, *Phylloscopus collybita* (Rodrigues 1998), this temporal pattern of territory size did not occur in robins, apparently refuting the suggestion that territoriality might function as a paternity guard, at least in these species. A recent review of the literature showed little evidence for territory expansion during the fertile phase in a variety of species (Rodrigues 1998), putting into question its importance as a paternity assurance mechanism. Instead, Rodrigues found evidence for a peak in territorial aggression during the fertile period. Robins would thus appear to conform to an emerging pattern amongst territorial passerines of heightened defence of a normal-sized territory as a paternity guard, rather than territory expansion per se: an adaptive situation given that a normal-sized territory is likely to be more effectively defended than an expanded territory (Langmore 1996).

Territorial Aggression and Vigilance

The strongest observational evidence suggesting an increase in territorial motivation in the fertile period is that males increase their rate of patrolling whereas females do not. It is improbable that courtship foraging flights, which occur at a comparatively low rate (Tobias 1996), account for the tendency of males with fertile females to patrol the territory regularly. Such increased patrolling and vigilance explains why simulated intrusions were approached more closely in the fertile period. The presentation experiments suggest an increase in territorial vigilance and aggression in the fertile period, as has been found in other species (e.g. red-backed shrikes: Jakober & Stauber 1989). The aggressive response of male robins to mounts was highly variable, perhaps because they were unable to distinguish the sex of the 'intruder', but significantly more 'strikes' were recorded in the fertile period than outside it. In sexually dimorphic species, fertile period presentations of males often elicit strong responses, including aggression directed towards mates (e.g. in mountain bluebirds: Barash 1976). The increase in intrusions by extrapair males and rise in rate of EPC solicitation seen after the removal of male robins has also been found in other species (e.g. wheatears: Currie et al. 1999). The prominent increase in such behaviour by extrapair males during fertile period removals gives credence to the idea that males sing to remind neighbours of their presence, and patrol their territory boundaries to detect or dissuade intruders. It reveals to what extent neighbours are aware of the predicament of females and the whereabouts of males. It also shows how quickly neighbours can respond to a relaxation of male defences. That males can reduce intrusion rates in the fertile period by territorial presence rather than direct mate guarding has been shown in removals of yellowhammers, *Emberiza citrinella* (Sundberg 1994).

Conclusions

In comparison with other small passerines, male robins did not appear to protect their paternity by closely attending their mate, nor through frequent copulation or territory expansion. Instead, it appears that during the fertile period males increased their territorial vigilance and aggression, using song as a signal of presence, to guard their mates. In robins, the constraints of courtship feeding, the poor visibility in their preferred forest habitat (Hoelzel 1989), or the intensity of competition for space (Tobias 1997), might have rendered direct female defence less tenable than exclusion of competitors from territories. However, the lack of mate attendance may also be related to female cooperation with their mates over paternity. For example, it may be that if risks of cuckoldry are lowered by female behaviour, it might benefit males to pursue a territorial strategy, rather than to expend time and energy on direct mate defence, or frequent copulations. In this way, whilst breeding territories confer an array of advantages, such as reduced predation through spacing, and resource defence, sperm competition is clearly an important factor underlying and modifying avian territoriality.

References

Alatalo, R. V., Gottlander, K. & Lundberg, A. 1984. Extra-pair copulations and mate guarding in the polyterritorial pied flycatcher, *Ficedula hypoleuca. Behaviour*, **101,** 139–155.

Barash, D. P. 1976. Male response to apparent female adultery in the mountain bluebird *Sialia currucoides*: an evolutionary interpretation. *American Naturalist*, **110,** 1097–1101.

Birkhead, T. R. 1979. Mate guarding in the magpie, *Pica pica. Animal Behaviour*, **27,** 866–874.

Birkhead, T. R. 1982. Timing and duration of mate guarding in magpies, *Pica pica. Animal Behaviour*, **30,** 277–283.

Birkhead, T. R. 1987. Sperm competition in birds. *Trends in Ecology and Evolution*, **2,** 268–272.

Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.

Birkhead, T. R., Pellat, J. & Hunter, F. M. 1988. Extra-pair copulation and sperm competition in the zebra finch. *Nature*, **334,** 60–62.

Birkhead, T. R., Hunter, F. M. & Pellat, J. E. 1989. Sperm competition in the zebra finch, *Taeniopygia guttata. Animal Behaviour*, **38,** 935–950.

Birkhead, T. R., Cunningham, E. J. A. & Cheng, K. M. 1996. The insemination window provides a distorted view of sperm competition in birds. *Proceedings of the Royal Society of London, Series B*, **263,** 1187–1192.

Björklund, M. & Westman, B. 1986. Mate guarding in the great tit: tactics of a territorial forest-living species. *Ornis Scandinavica*, **17,** 99–105.

Chek, A. A. & Robertson, R. J. 1994. Weak mate guarding in tree swallows: ecological constraint or female control? *Ethology*, **98,** 1–13.

Chek, A. A., Lifjeld, J. T. & Robertson, R. J. 1996. Lack of mate-guarding in a territorial passerine bird with a low intensity of sperm competition, the pied flycatcher (*Ficedula hypoleuca*). *Ethology*, **102,** 134–145.

Cramp, S. 1988. *Handbook of the Birds of Europe, the Middle East and North Africa, Vol. V.* Oxford: Oxford University Press.

Currie, D. R., Burke, T., Whitney, R. L. & Thompson, D. B. A. 1998. Male and female behaviour and extrapair paternity in the wheatear. *Animal Behaviour*, **55,** 698–703.

Currie, D. R., Krupa, A. P., Burke, T. & Thompson, D. B. A. 1999. The effect of experimental male removals on extrapair paternity in the wheatear *Oenanthe oenanthe. Animal Behaviour*, **57,** 145–152.

Davies, N. B. 1983. Polyandry, cloaca-pecking and sperm competition in dunnocks. *Nature*, **302,** 334–336.

Davies, N. B. 1992. *Dunnock Behaviour and Social Evolution.* Oxford: Oxford University Press.

Dickinson, J. L. 1996. Male detention affects extra-pair copulation frequency in western bluebirds. *Behavioral Ecology*, **7,** 168–175.

East, M. 1981. Aspects of courtship and parental care of the European robin *Erithacus rubecula. Ornis Scandinavica*, **12,** 230–239.

Evensen, C. 1994. Mate guarding, song and paternity in the bluethroat *Luscinia s. svecica*. M.Sc. thesis, University of Oslo.

Gil, D., Graves, J. A. & Slater, P. J. B. 1999. Seasonal patterns of singing in the willow warbler: evidence against the fertility announcement hypothesis. *Animal Behaviour*, **58,** 995–1000.

Gomendio, M. & Roldan, M. 1993. Mechanisms of sperm competition: linking physiology and behavioural ecology. *Trends in Ecology and Evolution*, **3,** 95–100.

Harper, D. G. C. 1984. Economics of foraging and territoriality in the European robin *Erithacus rubecula*. Ph.D. thesis, University of Cambridge.

Harper, D. G. C. 1985. Pairing strategies and mate choice in female robins *Erithacus rubecula. Animal Behaviour*, **33,** 862–875.

Hatchwell, B. J. & Davies, N. B. 1992. An experimental study of mating competition in monogamous and polyandrous dunnocks, *Prunella modularis*: I. Mate guarding and copulations. *Animal Behaviour*, **43,** 595–609.

Hoelzel, A. R. 1989. Territorial behaviour of the robin *Erithacus rubecula*: the importance of vegetation density. *Ibis*, **131,** 432–436.

Hunter, F. M., Burke, T. & Watts, S.E. 1992. Frequent copulation as a method of paternity assurance in the northern fulmar. *Animal Behaviour*, **44,** 149–156.

Jakober, H. & Stauber, W. 1989. Attrapenversuche am Neuntöter *Lanius collurio. Journal of Ornithology*, **130,** 247–251.

Kleiman, D. 1977. Monogamy in mammals. *Quarterly Review of Biology*, **52,** 39–69.

Lack, D. 1965. *The Life of the Robin.* London: Witherby.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds.* London: Methuen.

Langmore, N. E. 1996. Territoriality and song as flexible paternity guards in dunnocks and alpine accentors. *Behavioral Ecology*, **7,** 183–188.

Lefelaar, D. & Robertson, R. J. 1984. Do male tree swallows guard their mates? *Behavioral Ecology and Sociobiology*, **16,** 73–79.

Levin, R. N. 1996. Song behaviour and reproductive strategies in a duetting wren *Thryothorus nigricapillus*. II Playback experiments. *Animal Behaviour*, **52,** 1107–1117.

Lifjeld, J. T. & Robertson, R. J. 1992. Female control of extra-pair fertilisation in tree swallows. *Behavioral Ecology and Sociobiology*, **31,** 89–96.

Lifjeld, J. T., Slagsvold, T. & Lampe, H. M. 1991. Low frequency of extra-pair paternity in pied flycatchers revealed by DNA fingerprinting. *Behavioral Ecology and Sociobiology*, **29,** 95–101.

Møller, A. P. 1987. Mate guarding in the swallow *Hirundo rustica*: an experimental study. *Behavioral Ecology and Sociobiology*, **21,** 119–123.

Møller, A. P. 1990. Changes in the size of avian breeding territories in relation to the nesting cycle. *Animal Behaviour*, **40,** 1070–1079.

Møller, A. P. 1991. Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *American Naturalist*, **138,** 994–1013.

Møller, A. P. 1992. Relative size of avian breeding territories and the risk of cuckoldry. *Animal Behaviour*, **43,** 860–861.

Møller, A. P. & Birkhead, T. R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour*, **118,** 170–186.

Odum, E. P. & Kuenzler, E. J. 1955. Measurement of territory and home range size in birds. *Auk*, **72,** 128–137.

Parker, G. A. 1984. Sperm competition and the evolution of animal mating strategies. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 2–60. Orlando: Academic Press.

Pinxten, R. & Eens, M. 1998. Male starlings sing most in the late morning, following egg-laying: a strategy to protect their paternity? *Behaviour*, **135,** 1197–1211.

Rodrigues, M. 1996. Song activity in the chiffchaff: mate-guarding or territory defence? *Animal Behaviour*, **51,** 709–716.

Rodrigues, M. 1998. No relationship between territory size and risk of cuckoldry in birds. *Animal Behaviour*, **55,** 915–923.

Schleicher, B., Hoi, H., Valera, F. & HoiLeitner, M. 1997. The importance of different paternity guards in the polygynandrous penduline tit *Remiz pendulinus. Behaviour*, **134,** 941–959.

Sundberg, J. 1994. Paternity guarding in the yellowhammer *Emberiza citrinella*: a detention experiment. *Journal of Avian Biology*, **25,** 135–141.

Tobias, J. 1996. Mechanisms and functions of territoriality in the European robin *Erithacus rubecula*. Ph.D. thesis, University of Cambridge.

Tobias, J. 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. *Animal Behaviour*, **54,** 9–21.

Venier, L. A. & Robertson, R. J. 1991. Copulation behaviour of the tree swallow, *Tachycineta bicolor*: paternity assurance in the presence of sperm competition. *Animal Behaviour*, **42,** 939–948.

Westneat, D. F. 1987. Extra-pair copulations in a predominantly monogamous bird: observations of behaviour. *Animal Behaviour*, **35,** 865–876.

Westneat, D. F., Sherman, P. W. & Morton, M. L. 1990. The ecology and evolution of extra-pair copulations in birds. *Current Ornithology*, **7,** 331–369.