

Food availability as a determinant of pairing behaviour in the European robin

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Summary

1. Male and female European robins, *Erithacus rubecula*, defended separate territories from August to January. Pairs formed between January and March.

2. The benefits of early pairing were twofold: first, as 20% of males failed to pair there was strong competition for females; second, although pairing was initially costly in terms of individual foraging success, bachelors invested more time advertising in the long term.

3. Birds on individual territories encountered large food items more frequently than those on pair territories. This decrease in foraging success within pairs was identified as a cost of territory sharing.

4. To test the hypothesis that food availability underlies the defence of individual territories in winter, and the timing of switches to pair territoriality, I manipulated food supply and recorded individual behaviour.

5. Compared to controls, males provided with extra food were forced to repel intruders more frequently, yet advertised for mates earlier and paired earlier.

6. Pair members whose supplementary food supply was temporarily withdrawn spent less time consorting than controls. This suggests that an elevated food supply helped individuals to afford the costs of sharing their food resources, and thus to pair and lay clutches early.

7. The influence of food supply and territoriality on population density and social behaviour is discussed.

Key-words: competition, *Erithacus rubecula*, food, foraging success, pairing.

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Introduction

The availability of food has been found to shape many behavioural, physiological and demographic phenomena in animals; for example, food supply underlies mating success in red-winged blackbirds, *Agelaius phoeniceus* L. (Whittingham & Robertson 1994), influences population density in nuthatches, *Sitta europaea* L. (Enoksson & Nilsson 1983; Enoksson 1990), and determines whether rutting red deer, *Cervus elaphus* L., are territorial (Carranza, Garcia-Muñoz & de Dios Vargas 1995). An abundance of food improves defence against parasitism yet reduces adult survival in song sparrows, *Melospiza melodia* Wilson (Arcese & Smith 1988). Food supply affects important elements of reproductive success, such as laying date (Svensson & Nilsson 1995) and clutch size (Perrins 1991) in tits Paridae, and variations in male paternal care in red-winged blackbirds (Whittingham & Robertson 1994). In many cases the process by which food availability produces these effects remains

unclear. In this paper, I clarify the role of food in dictating territorial strategy and pairing behaviour in the European robin, *Erithacus rubecula* L.

In British robin populations, both sexes begin to sing and defend individual territories in August or September, with almost all males being resident and 60–70% of females being migratory (Lack 1965; Cramp 1988; Harper 1989). This social organization persists until between January and March, during which time migrant females return and pairs form shared territories that only the male defends. Advertising males produce large amounts of song from high perches until a female joins them on their territory (East 1982). In each breeding season around 20% of males advertise unsuccessfully for a mate (Lack 1965; Harper 1985).

If individual territoriality and partial migration evolved as adaptive responses to competition for limited food at low temperatures (East 1980; Harper 1984, 1989), it remains to be explained why individual territories are occupied when food is relatively abun-

dant and temperatures high (early autumn), and why pairing then occurs when food is most scarce and temperatures are at their lowest (midwinter).

The main questions considered in this paper are as follows:

1. What is the cost of pairing?
2. How does food limitation affect the ability of males to share territories with females?
3. What are the ecological effects (laying date and clutch size) of food supply?

To address these issues critically it is necessary to manipulate food availability and generate appropriate predictions; for example, if the occupation of pair territories is costly in terms of foraging time and foraging success, I expect to observe reduced foraging and increased singing when extra food is provided. Similarly, if supplementary food enables pairs to share territories, I predict that individual territoriality will resume if food supplies are withdrawn. If food determines the time invested in singing to attract mates, I predict that its addition will raise song output independent of intruder pressure. Further, if food limits laying dates or clutch sizes, they will vary according to manipulations of food supply. In general, I investigate the relationship between food availability and breeding behaviour, and discuss the potential influence of this relationship on the density and composition of populations.

Methods and materials

The study was conducted during the winters of 1992/93 and 1993/94 on a colour-ringed population of 45–60 robins in the Cambridge University Botanic Garden, Cambridge, England.

The location of individuals was routinely recorded on maps during site transects. The first day that a pair were observed to share similar territories was recorded as the pairing date. Pairing behaviour is conspicuous (Harper 1985; Cramp 1988), hence recorded dates are considered accurate to within 24 h. It was difficult to determine the sex of individuals in winter as there is an overlap in body size, as well as vocal and plumage characteristics (Cramp 1988). Sexes were clearly differentiated only after the commencement of pairing behaviour.

Continuous watches were made of focal individuals for periods of 20–60 min. During these time-budgets I quantified foraging efficiency by noting each occasion that food was located and consumed. When food items were visible (large invertebrates), recording was straightforward. However, as it was often difficult to distinguish the result of pecks to ground, I included cases where no food item was seen but an obvious swallowing action was observed ('invisible items'). In addition, I quantified song output by recording whether males were engaged in song bouts at sampling intervals of 30 s. Intrusions onto the territory were recorded, and whether aggressive chases ensued. A

minimum 180 min data in each period were required for individuals to be included in analyses. All behavioural observations were conducted between 0800 and 1400 GMT. Minimum daily temperatures were made available by the Cambridge University Botanic Garden Meteorological Station.

In spring, nests were located and then checked regularly to record first egg laying dates and clutch sizes. When nests were discovered after clutch completion, a standard 14-day incubation period (Cramp 1988) plus one day per egg was used to calculate the date of clutch commencement.

FOOD PROVISION EXPERIMENT

Supplementation of food began after the full establishment of individual wintering territories. Supplementation entailed daily provision of 150 g of Haith's softbill food mixture to one location (1 × 1 m) in the centre of selected territories. Provisioning was terminated in April (1993) or late March (1994) when almost all pairs had formed. In both seasons, 12 feeder territories were randomly chosen. In the 1992/93 season these were derived from the entire population before the sex of birds had been identified (one fed bird disappeared before this was possible), whereas in the second season only adult male territories were selected. Feeders occasionally caused alterations in territory configuration such that they were eventually located near boundaries. The original owner always remained dominant. I quantified the attendance of owners, nonterritorial individuals and neighbours at feeders during 60 min observation periods.

FEEDER DISCONTINUATION EXPERIMENT

For a period of three weeks (6–26 February 1994) the behaviour of 12 feeder pairs and six nonfeeder pairs was observed during 20–120 min time-budgets (weekly minimum of 120 min per pair). In the second week (13–19 February) six feeders were discontinued while normal food supplementation proceeded on the remaining six. Discontinued feeders were covered with soil to prevent birds from feeding on remnants of the provisioned food. In the third week, provision of food was resumed on experimental territories.

During each stage of the experiment, I recorded male song during time-budgets as above, and whether individuals of the pair were within 10 m of each other at each 30 s time interval. Territories of males and females in separate weeks were calculated as previously. Because of time constraints, 30 registrations were used rather than 60.

SAMPLE SIZES

As data analysed in this paper are derived from two study seasons, it is necessary to justify their treatment as single samples. Data have been combined in this

way because in all cases when comparisons were possible, there was strong similarity between years.

To avoid the problem of pseudoreplication, all males were provided with food for one season only. Similarly, as range size and pairing date were significantly consistent for individuals between years, data for unfed birds are derived from one season per individual. All statistical analyses are corrected for ties, and means are presented with one standard error where appropriate.

Results

POPULATION STRUCTURE

The incidence in both sexes of individual and pair territoriality encountered throughout the study is presented in Table 1. During early winter, 70–80% of individuals in the population were male (Fig. 1a). Maintenance of pair territoriality was very rare at this season: only one pair was recorded amongst 106 overwintering individuals. In the breeding seasons, after females had returned to the population, around 55% of individuals were male (Fig. 1a). On two occasions males were temporarily polygynous, but one female invariably left to join an unpaired male.

After moulting in July and August, many females settled outside the study area. Plotting the sex ratio of territory occupants each month reveals a gradual reduction in the predominance of males from January to March as females returned from their wintering grounds (Fig. 1a). While almost all individuals of both sexes defended individual territories in winter, they switched to pair territoriality at different rates (Fig. 1b). Most resident females paired before the end of January, but many males had to await the return of migrant females before they shared territories. The skewed operational sex ratio resulted in 20% of males remaining unpaired while all females found mates.

USE OF SUPPLEMENTARY FOOD BY TERRITORY OWNERS AND INTRUDERS

It is important to establish that the intended recipients of supplementary feeding utilize their extra resource,

Table 1. Population details (number of colour-ringed individuals belonging to each category for majority of given period) over the two study years. Feeder territories are included and nonterritorial birds excluded

	Totals recorded			
	1992 Aug–Dec	1993 Jan–Jun	1993 Aug–Dec	1994 Jan–Jun
Lone male	33	7	35	6
Lone female	14	0	11	0
Pairs	0	26	1	23
No. males	33	33	36	29
No. females	14	26	12	23
Total	47	59	48	52

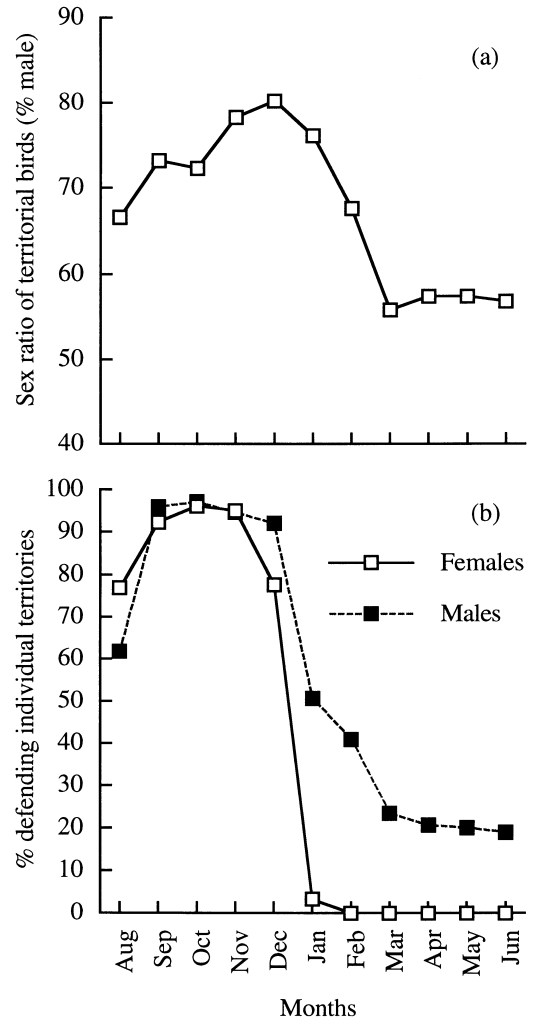


Fig. 1. Population structure. Graph (a) traces the sex ratio of birds occupying territories in the study population throughout the year (1993 and 1994 combined) presented as the percentage of such individuals that are male, while graph (b) shows the percentage of individuals of either sex defending independent territories throughout the same period. Feeder birds are included. In July the bulk of the population is nonterritorial, comprising juveniles and moulting adults.

and that neighbouring birds experience natural conditions.

Individual or pair territories containing feeders suffered higher intrusion rates than territories where no food was provided (Fig. 2a). This effect may be slightly exaggerated because of the ease with which trespassers were detected during feeder watches, but the fact that nonfeeder individuals travelled up to 100 m to raid feeders indicated that provisioning was indeed likely to increase contender pressure. This entails a disadvantage to high food availability. In addition, the rate of intrusion was significantly inversely related to temperature, with trespassing being particularly frequent below freezing point (Fig. 2b). Conversely, plotting the proportion of intrusions that resulted in chases by territory owners reveals a positive relationship with temperature (Fig. 2c). After prolonged snow cover, up to five robins foraged simultaneously at a feeder in apparent harmony.

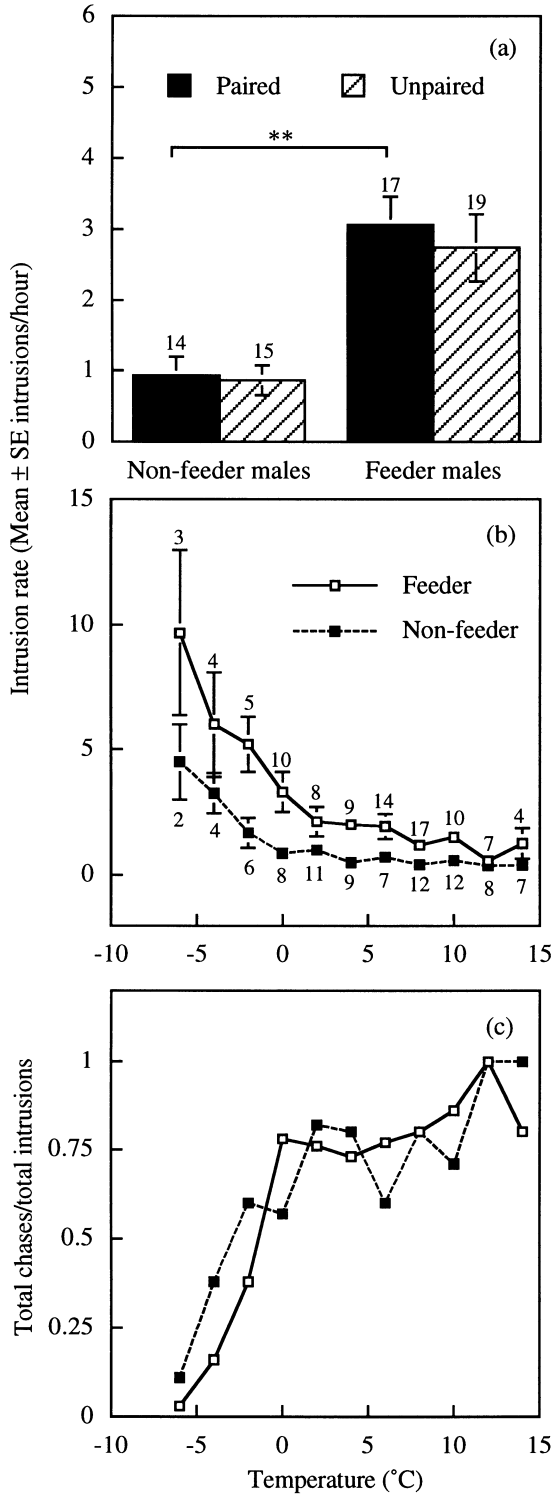


Fig. 2. Intruder pressure from December to February inclusive. (a) Comparison between frequency of intrusions on the territories of feeder and nonfeeder males when paired and unpaired. No difference between paired and unpaired values in either case. Mann-Whitney *U*-test, combining paired and unpaired males, feeder vs. nonfeeder birds: $**P < 0.01$. (b) Intruder pressure vs. temperature for feeder and nonfeeder males. Figures above or below error bars are sample sizes. Spearman rank correlation, feeder territories: $r_s = -0.532$, $P = 0.0001$; nonfeeder territories: $r_s = -0.422$, $P = 0.0001$. (c) The ratio of total chases to total intrusions vs. temperature. Samples are as in Fig. 2b. Temperatures are daily minimums subdivided into 2°C ranges and plotted above their lower limits on abscissa.

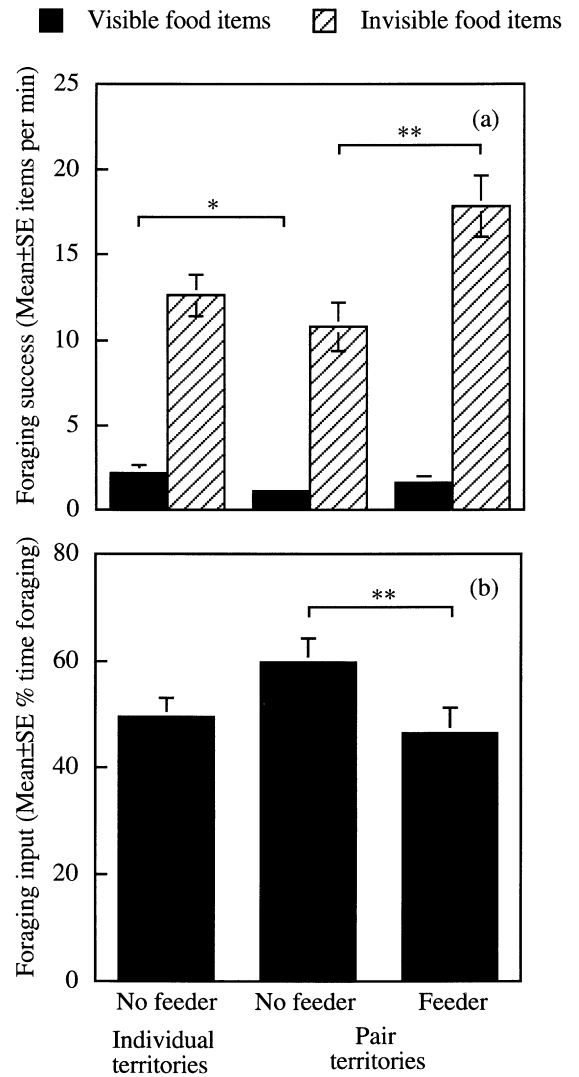


Fig. 3. Graph (a) shows foraging success on visible and invisible food items in January and February for males defending individual territories ($n = 10$), males defending pair territories ($n = 13$) and males provided with additional food on pair territories ($n = 12$). Invisible items included the softbill food provided at feeders. Data are per time spent foraging; 30 s intervals in which no foraging occurred are excluded from analysis. For the same samples, graph (b) shows proportion of total time allocated to foraging. Mann-Whitney *U*-tests: $*P < 0.05$; $**P < 0.01$.

The fact that feeders were persistently visited by neighbouring individuals somewhat reduces the efficacy of this manipulation. Although access to feeders was not exclusive, the percentage of time spent by owners at their resource ($16.16 \pm 2.0\%$ time, $n = 19$) far exceeded the time spent at feeders by trespassing neighbours ($1.53 \pm 0.3\%$ time, $n = 19$; Wilcoxon signed ranks: $z = -3.82$, $P = 0.0001$). The total proportion of time spent foraging is given in Fig. 3b. This indicates that feeders are an important asset to experimental birds, and that neighbours receive little benefit. Nevertheless, feeder ownership does increase the cost of territory defence.

The proportion of time spent at feeders by unpaired

Table 2. A comparison of percentage time ($X \pm SE$) spent at feeders by males and females when territories were individual or shared

	Nov-Dec (N)		Jan-Feb (N)	
	Unpaired ♀ (19)	Unpaired ♂ (4)	Paired ♀ (12)	Paired ♂ (12)
>1°C	12.58 ± 1.6	20.25 ± 3.2	18.00 ± 2.0	14.50 ± 1.8
<1°C	20.42 ± 2.7	25.50 ± 3.7	24.91 ± 2.8	20.50 ± 2.4
*P	<0.01	0.068	<0.05	<0.05

*Wilcoxon signed ranks test.

males during November and December was temperature dependent. To explore this relationship, behaviour above and below 1°C was compared, as below this temperature the frequent occurrence of frosts or snow-cover rendered natural foods more difficult to obtain, and birds appeared to spend a greater proportion of their time at feeders (Table 2). This result implies that supplementary resources were a more important commodity at low temperatures, presumably because food was otherwise harder to find and because each individual required more food in total.

COSTS OF PAIRING

Attraction of mates

The proportion of time allocated to singing by males without feeders was much higher before pairing

(43.38 ± 2.5% time, $n = 21$) than after pairing (25.81 ± 2.1% time, $n = 21$; Wilcoxon signed ranks: $z = -3.77$, $P < 0.001$). This difference relates largely to the enormous amount of time invested by bachelor males in advertising song. It may also derive from reduced foraging success after pairing which potentially decreases the time available for singing.

Males tended to spend more time singing in their month of pairing than in preceding or subsequent months (Fig. 4). By March, the time spent singing by bachelors was double that invested by birds paired in January or February (Fig. 4). The quantity of song produced by paired males declined markedly in the first 4 months of the year, regardless of whether they were provided with food (Fig. 5). By contrast, unpaired males sing more as the breeding season continues. In effect, each individual male appeared to raise song output as early in winter as possible until a

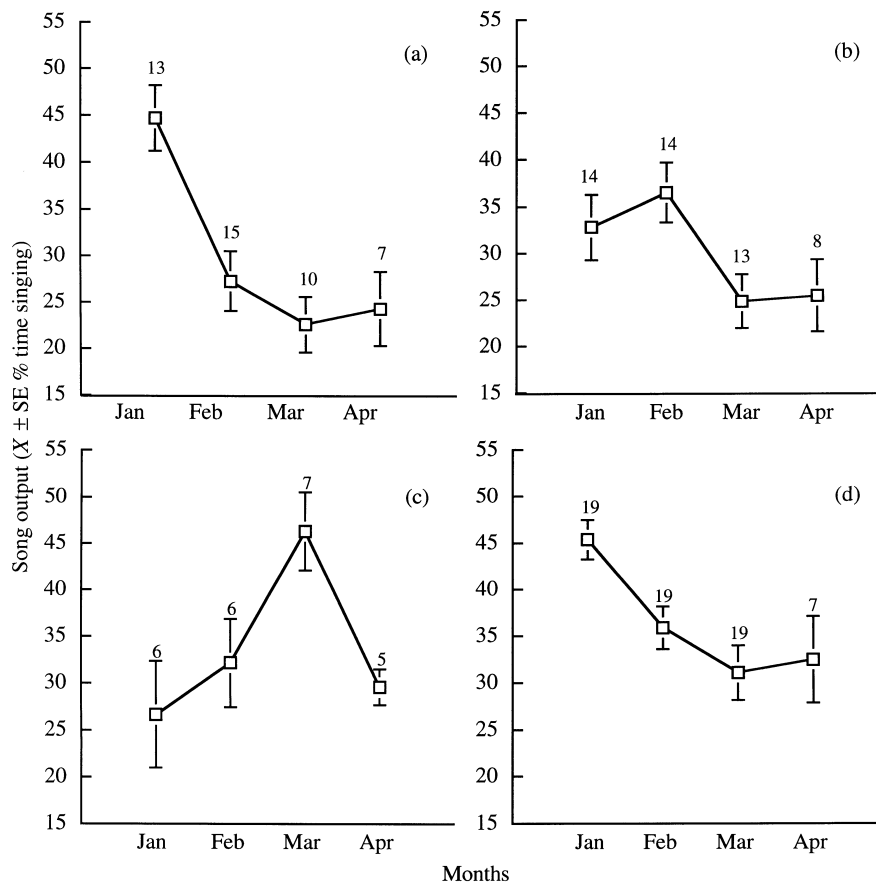


Fig. 4. Monthly song output ($X \pm SE$ percentage time) from January to April by males that paired in (a) January, (b) February, (c) March, and (d) all feeder males. In months of pairing, only data gathered before pairing date are included.

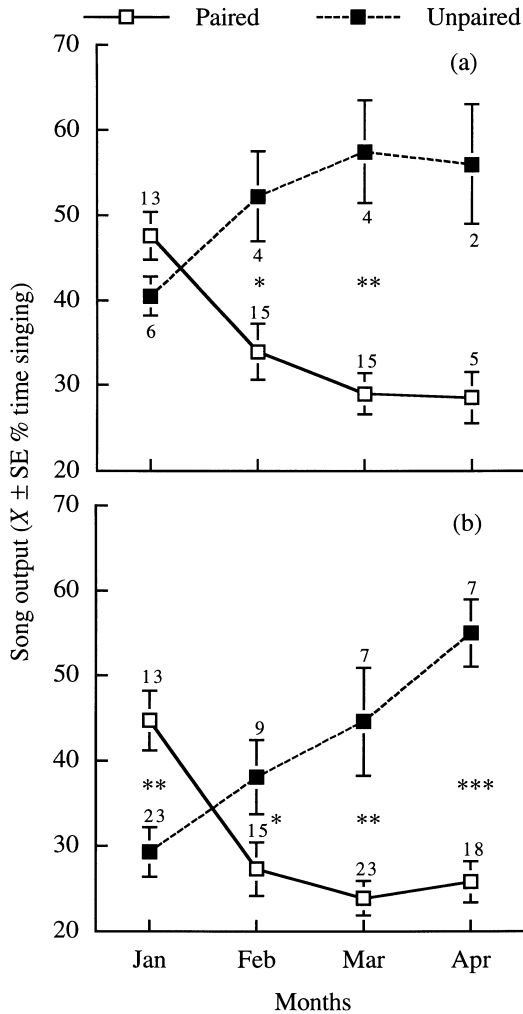


Fig. 5. Song output ($X \pm SE$ percentage time) on individual and pair territories. Graph (a) shows this relationship with and graph (b) without the provision of extra food. Figures by error bars are sample sizes. Mann-Whitney U -tests between monthly means within graphs: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

mate was successfully attracted, after which point song output declined.

In January, males that are unpaired and have no feeder produce less song ($30.45 \pm 5.5\%$ time, $n = 20$) than males receiving supplementary food ($45.63 \pm 2.6\%$ time, $n = 19$; Mann-Whitney U -test: $z = -2.87$, $P < 0.01$). This indicates that, while bachelors need to advertise for mates, they also require an adequate food supply to afford the cost of mate attraction.

In midwinter, when energy demands are high and food availability low, song output may serve as an honest signal of individual quality or territory quality. Plotting the foraging success of unpaired male robins in January against their song rates in the same month suggests a weak positive relationship between these factors for birds without feeders (Fig. 6; Spearman rank correlation: $r_s = 0.38$, $P < 0.1$), but not for those with feeders ($r_s = 0.12$, $P > 0.5$).

Several conclusions can be drawn from these results. First, mate attraction is costly. Second, the

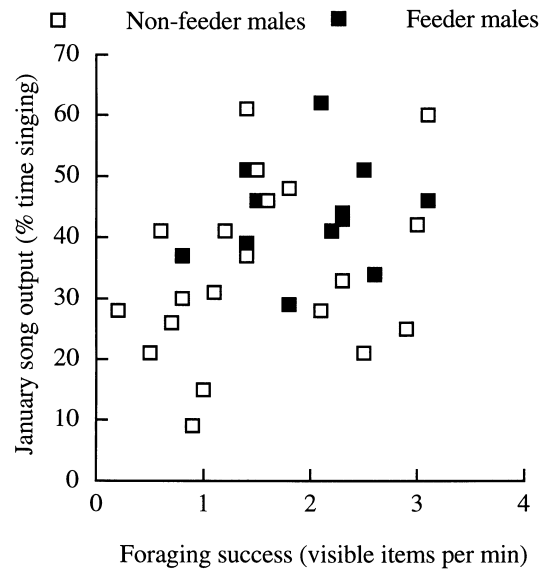


Fig. 6. Foraging rate on large food items by unpaired males in January vs. their pre-pairing song output in the same month.

output of advertising song is mediated by food availability. As predicted, males direct surplus time and energy that is made available by improved foraging efficiency to advertising. Third, the effects of food limitation decrease as spring approaches and the abundance of natural food rises. Intruder pressure is of secondary importance in predicting singing behaviour, as revealed by the decline in song output after pairing.

Foraging success

The foraging success of males occupying individual territories in January and February was similar to that of paired males when considering only invisible food items (Fig. 3a; Mann-Whitney U -test: $z = -0.83$, $P > 0.5$). However, unpaired males ingested visible items significantly more frequently (Fig. 3a). This may be a result of decreasing prey encounter rates when two individuals forage over the same territory. Although the differences between values in Fig. 3a appear small, the cumulative effect over many hours is potentially substantial. A higher foraging success of males on individual territories (in terms of large food items) presumably underlies the tendency for unpaired males to allocate less time to foraging than paired males (Fig. 3b; Mann-Whitney U -test: $z = -1.67$, $P < 0.1$). Further, paired males provided with extra food allocated less time to foraging than paired males without feeders (Fig. 3b). These results indicate that pairing was costly because pair members experienced reduced foraging efficiency and had to spend more time foraging.

IS PAIRING LIMITED BY FOOD?

The energetic costs imposed before and after pairing, first by mate attraction and then by reduced foraging

Table 3. Song output of paired males ($X \pm SE$ percentage time singing) during different stages of the feeder discontinuation experiment, comparing data from control territories and experimental territories. A = 1†week prior to feeder discontinuation; B = 1†week of feeder discontinuation; C = 1†week subsequent to feeder resumption. Control 1 = pairs continuously fed; Stop food = pairs with discontinued feeders; Control 2 = pairs that were never provided with supplementary food

Group (<i>n</i>)	Experimental period			<i>P</i> †
	A	B	C	
Control 1 (6)	38.17 ± 4.3	35.17 ± 4.5	37.66 ± 5.5	0.9
Stop food (6)	40.67 ± 5.8 *	23.50 ± 4.5 *	36.2 ± 3.2	0.02
Control 2 (6)	–	28.83 ± 5.3	30.50 ± 4.8	–

†Friedman two-way ANOVAS across experimental periods.

Wilcoxon signed ranks test between adjacent columns: **P* < 0.05.

N.B. No data collection for control 2 in period A. Sample size of discontinued feeder group dropped to five in period C because of one pair dissociating entirely.

success, suggest that a good food supply is a vital asset for prospective breeders. Having observed the effects of increased food availability on behaviour, initial conclusions remain to be tested by observing responses to a decrease in food availability.

Table 3 compares the quantity of time allocated to singing by paired males experiencing three different experimental treatments. Males whose supplementary feeding was discontinued significantly varied their song output across the experimental periods, whereas the two control groups did not. When extra food was unavailable, males produced less song than they did prior to and subsequent to the manipulation. They also tended to sing less than males to whom food was continuously provided, although this result was not significant (Table 3; Mann–Whitney *U*-test: $z = -1.684$, $P < 0.1$). This appears to confirm that song is delivered at artificially high rates on feeder territories. There was no difference between intruder pressure where provisioning was withdrawn (2.0 ± 0.4 intrusions h^{-1} , $n = 6$) and where provisioning was continued during the same experimental period (2.83 ± 0.5 intrusions h^{-1} , $n = 6$; Mann–Whitney *U*-test: $z = -1.33$, $P > 0.1$). As temperatures were low when feeders were stopped, trespassing was generally more frequent than at other times.

Table 4 compares the proximity of pair members

during different stages of the experiment. Males and females whose supplementary resource was discontinued spent less time together than they did prior to and subsequent to the manipulation, fitting predictions of the hypothesis that pairing is food limited. Additionally, there was a trend for pairs to spend less time together when the provision of food was interrupted for 1 week, than control pairs that continued to receive supplementary food (Table 4; Mann–Whitney *U*-test: $z = -1.92$, $P < 0.1$). The variance of their proximity across experimental stages was also significant, whereas no such relationship was apparent for controls. Individuals with discontinued feeders spent less time consorting with their mates in stage B than individuals that were never provisioned (Table 4; $z = -2.24$, $P < 0.05$). No incidence of aggression between pair members was observed. Males and females simply dissociated within the pair territory, such that they effectively occupied individual territories.

In three out of six cases this took the form exemplified by Fig. 7a. Pair members tended to occupy ranges closest to their wintering territory. They retained considerable overlap, but largely avoided each other's presence until stage C in which consorting was resumed. In one case (shown in Fig. 7b), disassociation was permanent, the female accompanying

Table 4. Pair member proximity ($X \pm SE$ percentage time within 10 m) during different stages of the feeder discontinuation experiment, comparing data from control territories and experimental territories. A = 1†week prior to feeder discontinuation; B = 1†week of feeder discontinuation; C = 1†week subsequent to feeder resumption. Control 1 = pairs continuously provisioned; Stop food = pairs with discontinued feeders; Control 2 = pairs that were never provisioned

Group (<i>n</i>)	Experimental period			<i>P</i> †
	A	B	C	
Control 1 (6)	49.00 ± 8.8	44.60 ± 5.9	47.17 ± 5.7	0.8
Stop food (6)	46.67 ± 8.5 *	22.50 ± 6.7 *	40.00 ± 9.3	0.03
Control 2 (6)	–	45.83 ± 7.3	52.67 ± 11.3	–

†Friedman two-way ANOVAS across experimental periods.

Wilcoxon signed ranks test between adjacent columns: **P* < 0.05.

N.B. No data collection for control 2 in period A. Sample size of discontinued feeder group dropped to five in period C because of one pair dissociating entirely.

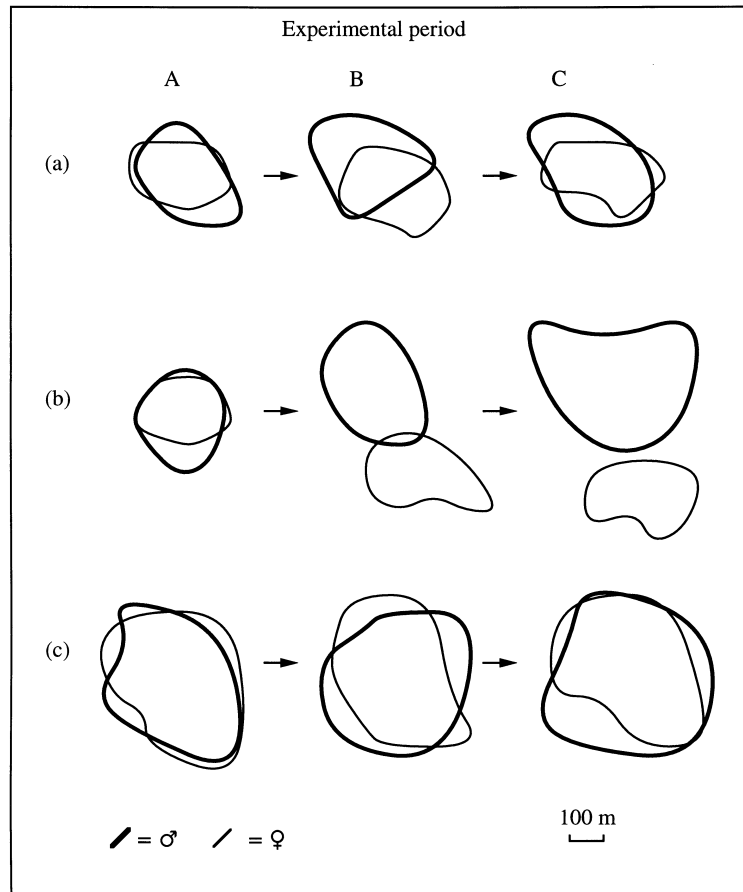


Fig. 7. Alterations in territory overlap across three periods of feeder discontinuation experiment (see Table 4). Example (a) depicts partial dissociation reverting when provisioning resumed, while example (b) depicts permanent dissociation, the female pairing with nearby male and example (c) illustrates constant overlap, pair members spending more time apart but within original ranges. These examples are roughly drawn from territory maps.

a neighbouring male even after the resumption of advertising by her original mate. In the final two cases (illustrated in Fig. 7c), there was little alteration in territory overlap from stage A to stage B, but pair members spent more time apart in the latter.

The best explanation for these observations is that feeder pairs were able to absorb the decrease in foraging success caused by territory sharing because extra food was available. When this additional resource was withdrawn, they responded by minimizing energy output by singing infrequently and maximizing energy input by foraging independently.

EFFECTS OF SUPPLEMENTARY FEEDING ON PAIRING DATE, LAYING DATE AND CLUTCH SIZE

Males with feeders paired significantly earlier than those without feeders (Table 5; Mann–Whitney *U*-test: $z = -2.0$, $P < 0.05$). However, there was no significant difference between the proportion of fed (88% of 19) and unfed (66% of 42) individuals that successfully paired (Chi-squared test: $\chi^2 = 1.01$, d.f. = 1, $P > 0.1$). In addition, pairs provided with extra food began their first clutches earlier in the season (Table

5; Mann–Whitney *U*-test: $z = -2.24$, $P < 0.05$). Although there was no evidence that extra food caused clutch size to increase (Table 5) it may have increased the relative size of early clutches. These results confirm that pairing date and laying date are strongly linked to food supply.

Discussion

THE INFLUENCE OF FOOD SUPPLY ON PAIRING BEHAVIOUR

A positive relationship between food availability and pairing success has been reported in several studies (e.g. Whittingham & Robertson 1994). In agreement with this, the switch from individual to pair territoriality in the robin is clearly associated with food. The main evidence presented here is the advance in pairing date when extra food is provided on territories, and the fact that when such food supplies are discontinued the newly formed pairs dissociate.

It can be inferred from monthly singing behaviour (see Figs 4 and 5), that many individuals appeared unable to afford the high cost of advertising until environmental conditions improved. If forced by

inefficient foraging or ownership of poor territories to delay intense advertising until March, individuals were unlikely to breed as almost all females were then settled with mates. In reproductive terms therefore it paid males to advertise as soon as possible to maximize their chances of breeding. We would thus expect males provided with enhanced resources to advertise earlier, and this is shown to be the case.

Combining time-budget data for singing and foraging behaviour does not conclusively indicate that song output is an honest advertisement of territory quality or foraging efficiency (see Fig. 6). However, although the correlations shown are not significant, the measures used to obtain them are crude, and it remains plausible that the ability to allocate large amounts of time to song is condition dependent. If individuals with favourable energetic budgets are capable of sustaining more prolonged bouts of advertising song, the logical female strategy is to choose males that succeed in doing so.

Large food items such as adult or larval beetles (Coleoptera), larval Lepidoptera, millipedes (Diplopoda) and earthworms (Oligochaeta), provide the greatest energetic returns to a foraging robin. It appears reasonable to assume that competition for such items will impinge directly on the ability of individuals to coexist on shared territories. The apparent contradiction that many individuals are solitary when temperature and food availability are high in September, and then share territories when resources are depleted and temperatures low in January can be reconciled by the variable costs and benefits of individual territoriality. In September, there is little benefit to sharing a territory, and the cost of intrapair competition dictates that it pays to be solitary. In January, although the cost of territory sharing is greater than in September, it is presumably exceeded by the cost of remaining unpaired. At this time of year therefore individuals should fuse territories as promptly as individual or territory quality allows. The cost of pairing declines as summer approaches because of increased daylight foraging time, increased temperature and abundant prey (in March and April feeders were used infrequently).

The main advantage of early pairing for males has already been mentioned: it ensures an opportunity to breed that is otherwise by no means guaranteed. As

females that pair in January are invariably resident females, they are thus perhaps the highest quality individuals of their sex (Tobias 1997). This might constitute an additional incentive for males to advertise as early as possible. The advantage of early pairing for females is threefold. First, it maximizes the availability of high quality males. Second, the energetic constraints on males in winter ensure that signalling of quality is most likely to be honest. Third, it minimizes the energetic requirements of territory defence.

In effect, the switch from individual territoriality to pair territoriality appears to be adjusted to the equilibrium between the opposing forces of intrapair competition for food and intrasexual competition for mates. The former drives the system towards later pairing, while the latter drives the system towards earlier pairing. Provision of food reduces the impact of intrapair competition, thus advancing pairing dates.

THE INFLUENCE OF FOOD SUPPLY ON LAYING DATE

Post-fledging survival rates sometimes decline with hatching date (Smith *et al.* 1980). As this temporal variation appears to relate to breeding time *per se* rather than underlying factors (Norris 1993), it follows that females will rear more offspring if they breed earlier (Svensson & Nilsson 1995). Also, once paired, the advantage of nesting early is probably that it increases the likelihood of accommodating a second or third clutch in a single season. This final point perhaps explains the lack of difference in clutch size between feeder and nonfeeder pairs. It is worth bearing in mind that clutch size might have increased in relation to natural variation in the early breeding season (Dijkstra *et al.* 1982), and that the type of food used in supplementation experiments can affect whether egg production is enhanced (Ewald & Rohwer 1982; Arcese & Smith 1988).

The addition of food to territories has been previously shown to advance the onset of breeding (Ewald & Rohwer 1982; Davies & Lundberg 1985; Dhindsa & Boag 1990). Furthermore, increases in nestling weight gain and fledgling success have been reported (Dhindsa & Boag 1990). In the majority of species tested, supplemental feeding advances laying

Table 5. Breeding season data ($X \pm SE$) for combined study seasons

	Male pairing date† (<i>n</i>)	Laying date† (<i>n</i>)	Clutch size§ (<i>n</i>)
With feeder	21.8 ± 6.7 (17) *	95.2 ± 3.2 (14) *	4.7 ± 0.2 (14)
Without feeder	42.5 ± 6.2 (31)	104.5 ± 2.4 (21)	4.9 ± 0.2 (35)

†Jan 1st = 1; pairing dates refer to first female if subsequent switches occurred; laying dates refer to first egg of first clutch.

§First clutch only; 1 data point per female. Mann-Whitney *U*-test: **P* < 0.05.

date by only 3–6 days, regardless of the quantity of extra food supplied (Svensson & Nilsson 1995). This suggests that, beyond a certain degree, laying date is not energetically constrained but is determined by other factors. The higher magnitude of advancement in laying date recorded in robins (Table 5) indicates that, at the time of experimentation, food availability was the primary limiting factor.

CONSEQUENCES FOR SOCIAL BEHAVIOUR AND POPULATION DENSITY

At high temperatures, the clumped distribution of feeders facilitated their defence. At low temperatures, defendability was reduced because of high energetic demands and high intrusion rates. The decline in territoriality at low temperatures and the simultaneous gathering at feeders broadly reflects the dynamics of winter flocking and territoriality in the pied wagtail, *Motacilla alba yarelli* Gould (Davies 1976), and the relinquishment of territories on cold days by great tits, *Parus major* L., in winter (Hinde 1956). Social behaviour, although largely stable in the robin, may be disrupted by food supply and environmental conditions.

Regulation of population size and density through winter feeding is not a new concept (van Balen 1980; Enoksson 1990) but the behavioural foundations to these effects are unclear. By interrupting food supplementation, I have shown that food supply does not merely affect the ability of males to allocate time to advertising, but that it impinges directly on the ability of individuals to share resources in winter. Taken in conjunction with the fact that territorial behaviour can influence population density (Krebs 1971; Newton 1992), what light does this information shed on avian ecology?

Two individual territories generally encompass a larger area than a pair territory (Tobias 1996). This implies that a population comprising pairs will be more dense than a population of solitary individuals. As food availability determines the incidence and timing of pair territoriality, this relationship presumably influences breeding density (Enoksson & Nilsson 1983), productivity and the sedentary fraction of partially migratory populations (Adriaensen & Dhondt 1990; Tobias 1996). Similarly, an increase in population density will theoretically cause settlement of suboptimal habitat and increase the incidence of non-territoriality (Sutherland 1996). These processes have fundamental implications for the behaviour of individuals and the structure of populations; for example, if the Botanic Garden robin population was provided with abundant food throughout the year, we might predict that the proportion of overwintering females would increase, as would year-round pair territoriality, population density, and the average number of clutches produced per breeding season.

Unfortunately, because population effects will sel-

dom be accounted for by any one factor, the exact impact of food supply is difficult to predict or determine (Newton 1980). In general, however, the results presented in this paper support the contention that food availability is an integral component of the density-dependent processes underlying population ecology.

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