

Asymmetric territorial contests in the European robin: the role of settlement costs

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Abstract. A widespread feature of territorial systems is that residents almost invariably defeat challengers. This phenomenon has been explained by the existence of value asymmetries, variations in resource-holding potential or an 'owners always win' convention. Removal–replacement experiments were performed on 75 robins, *Erithacus rubecula*, to test these hypotheses. The settling behaviour of newcomers was also examined in order to identify energetic costs incurred during territory establishment. In winter, dominance shifted gradually from removed owners to newcomers with increasing time of newcomer residence, and there was a peak in contest duration at 4–7 days. Removals of newcomers, followed by replacement with another newcomer, confirmed that dominance was determined by the time newcomers were in residence rather than the time original owners were absent. These results support the hypothesis that asymmetries in territory value govern the outcome of contests. It is proposed that high singing rates and low foraging rates of newcomers settling boundaries with neighbours contribute to this asymmetry, skewing outcomes in favour of original owners until replacements are fully established. The key result in this study is that the time at which dominance tends to reverse (5–6 days in winter) is predicted by the time taken for newcomers to settle territory boundaries and achieve base-line foraging effort. In spring, original owners become subordinate almost immediately after removal. Reductions in settlement cost for newcomers, and increases in territory value, are proposed to accelerate dominance reversal. Age and sex effects on dominance suggest that the value asymmetry rule is modified by variations in resource-holding potential.

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Territory holders are usually dominant over non-territory holders when they compete for a resource (Rohwer 1982). This rule generally holds without the need for escalated contests to settle disputes. Three general hypotheses have been proposed to explain this circumstance (Maynard Smith & Parker 1976; Maynard Smith 1979; Parker & Rubenstein 1981).

The resource-holding potential hypothesis states that residents acquire territories because they are of higher intrinsic quality than non-residents. Their superior competitive ability explains their dominance. The value asymmetry hypothesis draws attention to the greater investment (Beletsky & Orians 1989) and local experience of a resident compared with a challenger. Knowledge of a territory improves a competitor's

chances of territory acquisition (Stamps 1987), and reduces their likelihood of predation (Metzgar 1967). Awareness of food sources (Davies 1981), established boundaries with neighbours (Beletsky & Orians 1987) and reproductive investment (Hatchwell & Davies 1992) are all further potential factors underlying value asymmetries between owners and intruders. Finally, the uncorrelated asymmetry hypothesis proposes the existence of arbitrary conventions in settling contests. Simple conventions such as 'owners always win' (Davies 1978) are, however, unlikely to be stable (Grafen 1987), particularly if contestants can control their risk along a continuum (Hammerstein & Parker 1982).

Previous experimental fieldwork attempting to clarify the relative importance of these ideas has been divided in its conclusions. Some studies apparently lend support to the resource-holding potential hypothesis (Rohwer 1982; Petrie 1984),

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while some uphold both this and the value asymmetry hypotheses, or fail to exclude either (Beletsky & Orrians 1987; Jakobsson 1988), and others indicate that asymmetries in value provide the best predictions of contest outcome or intensity (Krebs 1982; Brodsky & Montgomerie 1987; Beletsky & Orrians 1989). This latter conclusion is consistent with theoretical analysis of the effects of variations in resource value (Hammerstein 1981; Enquist & Leimar 1987).

In this paper I present the results of a series of removal-replacement experiments using European robins, *Erithacus rubecula*. I consider what information these manipulations provide concerning the advantages experienced by established owners defending their territories against prospective owners. In particular, I investigate the role of cost during the settlement of territories. The effects of variation in individual quality and environmental conditions on the outcome of contests are also explored.

The European robin is a partially migratory territorial passerine. Both males and females sing and aggressively defend individual territories in winter. Pairs then form in January–March, after which only the males sing in defence of shared territories. Around 20% of males fail to breed annually (Lack 1965; Harper 1985), remaining unpaired despite advertising for mates. Competition for females is thus intense. Because of the clear constraints of space and breeding opportunities, and the unusual role of females as resources in the breeding season and territorial competitors in winter, the species provides an ideal system for investigating the questions outlined above.

The removal-replacement experimental procedure simulates the temporary disappearance of a territorial robin. On its return, the original owner discovers a newcomer in residence. I expected the outcomes of ensuing contests to be governed by one of the three hypotheses explaining the advantages experienced by owners. The generation of exclusive prediction allows these alternatives to be differentiated.

The resource-holding potential hypothesis predicts that no reversal of dominance will occur (Krebs 1982; Beletsky & Orrians 1987). Established owners should be intrinsically superior and thus always successful with minimum escalation. The value asymmetry hypothesis predicts that dominance will reverse gradually (Krebs 1982).

A relationship is predicted between the time newcomers are allowed to settle and the duration or outcome of contests. An intermediate peak in the escalation of contests should occur, coinciding with symmetrical pay-offs. The uncorrelated asymmetry hypothesis, relying on the existence of overriding ownership conventions, predicts no relationship between the duration of removals and the escalation of contests. Dominance will be immediately reversed as soon as a newcomer arrives.

When analysing results, several confounding factors need to be taken into account. Birds lose weight when kept in captivity (Krebs 1982) and levels of circulating testosterone drop (Beletsky & Orrians 1989). Moreover, stress-related secretion of corticosterone (a steroid hormone) during the handling and release of removed birds (Wingfield 1985) is likely to suppress their territorial behaviour. These effects might severely diminish the resource-holding potential of individual robins and it is important to establish that their influence does not invalidate results.

METHODS

Study Population

I studied a colour-ringed population of ca 55 European robins in the Cambridge University Botanic Garden, Cambridge, U.K. between 1992 and 1995. During the course of this study, I routinely recorded the location of individuals on maps during study site transects. Registrations were considered independent if 30 min had elapsed between recordings, or a movement exceeding 20 m was observed. There were significant effects on territory size estimates when different numbers of registrations were analysed. Therefore, I calculated areas using minimum convex polygons with matched numbers of registrations (30 or 60). For eight individuals with over 100 registrations, 30 points represented $71 \pm 6.0\%$ ($\bar{X} \pm \text{SE}$) of the final calculated territory size, and 60 points represented $92 \pm 4.5\%$. In a few cases insufficient data were available to include individuals in this analysis.

Birds were aged using a combination of palate coloration, greater covert tip pattern and rectrice shape (Svensson 1992). On the few occasions when this was not possible I assumed newcomers to the population were first year birds. These

immigrants have dispersed very short distances from their natal sites (Cramp & Simmons 1988). Winter settlers that disappeared before pairing remained unsexed because it was virtually impossible to distinguish between males and females on individual territories (Cramp & Simmons 1988).

Removal-Replacement Experiments

I experimentally removed 37 territorial males and 13 territorial females in November-December 1993 and 1994 (winter), and 19 territorial males and six females after they had paired in February-March 1994 and 1995 (spring). In spring, only paired birds were used so as to eliminate pairing status effects (Björklund 1989). The removed birds' mates either remained on the territory or settled nearby.

I captured individuals before midday using either mist-nets or Potter traps baited with bread. I immediately removed them from their territories and housed them in wooden cages with wire fronts ($0.40 \times 0.35 \times 0.30$ m) 0.5 km from the study site. Captive birds experienced room temperature and normal daylight, and were disturbed only twice a day for feeding. Durations of captivity varied from 1 to 14 days, after which the birds were released on their territories. Minimum temperatures (to nearest °C) on capture days were supplied by the Cambridge University Botanic Garden meteorological station. Captive individuals were provided with Haith's soft-bill food-mixture, live mealworms and water. A sample of adult ($N=19$) and first year ($N=15$) males were weighed with a Pesola balance after capture and immediately prior to release.

Newcomers were allowed to settle on the vacated territories, an event that always occurred between 20 min and 30 h after removals. The timing of newcomer arrivals dictated captivity times of original residents because the parameter being varied was the duration of settlement rather than the duration of captivity. To control for variations due to captivity times, I conducted double removals such that second newcomers settled on territories before the release of original owners. This allowed contests to take place between birds removed for 10 days and birds settled for 1 day. All newcomers were caught, aged and individually marked before the original owners were released.

I calculated territory sizes of removed birds using the 30 coordinates immediately prior to capture. For successful settlers, incompletely usurped original owners and 'bereaved' males, I used the first 30 registrations after settlement or release, excluding contest data.

I released original owners between 0900 and 1030 hours at the centre of their territories while new owners were not visible. This was intended to allow levels of stress to decrease before the released birds encountered their rival. I recorded the time of first and last aggressive interaction between competitors, and I considered the period between these times to be the duration of the contest. Close counter-singing, chasing and fighting were considered aggressive interactions. A fight usually consisted of two individuals grappling and, while thus locked together, fluttering to the ground and pecking at each other. Fights sometimes lasted for several minutes and at such times the birds could be approached very closely. Despite the frequent violence of these territorial struggles, no visible injuries occurred.

Behavioural Observations

I quantified the behaviour of newcomers during their settlement of territories. Using point-sampling techniques with 30-s intervals I recorded whether focal individuals were singing, foraging or neither (the latter category included comfort behaviour and resting). Taking into account all 75 removals, the observation time of newcomers or neighbours expanding their territories varied from 32 min to 130 min per day (mean=66 min) except for the rare occasions when inclement weather prevented data collection. Anomalous observations on the first day of residency in winter arise from time-budgets completed while individuals were still behaving as non-territorial floaters (i.e. foraging secretly and remaining silent; it sometimes took a few hours before birds began tentatively signalling ownership of territories). I thus eliminated activity patterns recorded on this day from analyses of settlement behaviour.

I conducted further time-budgets on a sample of neighbours in order to quantify their song output on the third day of newcomer settlement. To determine mean population song output, I collected similar time-budget data on pre-removal or non-removal individuals for a minimum total of 5 h per bird. I took care to exclude all unpaired

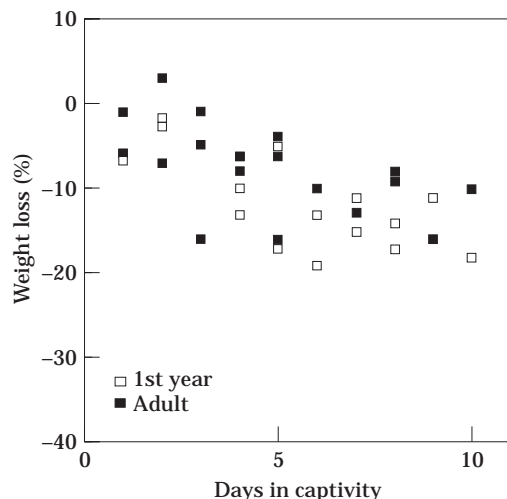


Figure 1. Percentage weight loss of adult and first year males versus duration of captivity. Weight loss was significantly correlated with captivity time for adults (Spearman rank correlation: $r_s = -0.615$, $N=19$, $P<0.01$) and first years (Spearman rank correlation: $r_s = -0.644$, $N=15$, $P<0.05$).

males from these samples in spring to eliminate the confounding influence of advertising song.

As newcomers settled in different seasons, they experienced dissimilar environmental conditions. First, minimum air temperatures on the first day of settlement in winter ($\bar{X} \pm SE = 1.43 \pm 0.33^\circ\text{C}$, $N=51$) were significantly colder than in spring ($4.95 \pm 0.74^\circ\text{C}$, $N=19$; Mann-Whitney U -test: $z = -3.148$, $P<0.01$). Second, a longer period of daylight was available in spring (ca 11 h) than winter (ca 9 h), allowing settlers more daily foraging time.

All statistical analyses are corrected for ties; standard errors of means are given where appropriate.

RESULTS

Removal of Original Owners: Effects of Captivity

Although captive robins were provided with food ad libitum, their percentage weight loss was significantly correlated with duration of captivity (Fig. 1). It is important to establish whether a loss of condition was thus responsible for any failure of original owners to regain territories. A 'double removal' control was designed to test whether

Table I. Variation in the number of neighbours adjoining the territories of robins in winter

Owner	Number of neighbours			
	2	3	4	5
Adult male	3	8	7	2
1st year male	4	6	6	1
Female	4	4	5	0

Chi-square test (2/3 versus 4/5): $\chi^2_2 = 0.14$, $P=0.9$.

individual robins were capable of challenging successfully for their territories when released after prolonged captivity.

Of six birds removed for 9–10 days during the course of standard manipulations, none succeeded in dispossessing newcomers resident for the entire period of their absence. By contrast, when birds removed for 9–10 days faced newcomers who had been allowed to settle for only 1 day ($N=4$) the original owners always ousted the newcomer, a significantly different proportion of cases (Fisher's exact test: $P<0.01$).

Settlement of Newcomers

If high-quality newcomers tended to choose high-quality territories on which to settle, this may confound results. Using age as a general indicator of individual quality, the proportion of adult male newcomers that settled on the territories of adult males (4/6) was not significantly different from the proportion of adult male newcomers settling on the territories of first year males (7/13; Fisher's exact test: $P>0.5$). Newcomer quality is impossible to standardize, but its variability is unlikely to undermine the conclusions of this study as settlement patterns were apparently random.

If high-quality residents tend to occupy territories contiguous with more neighbours this could affect the ease with which newcomers settle. However, there was no difference in the number of neighbours adjoining territories defended by adult males, first year males and females (Table I).

Newcomers were either non-territorial 'floaters' or neighbouring territory owners who shifted or expanded their ranges to occupy vacant territories. 'Floaters' formed the bulk of settling individuals in winter (17/20 in adult male removals,

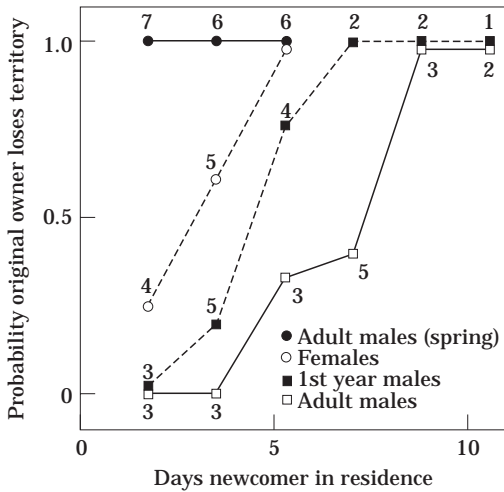


Figure 2. The probability that newcomers would resist eviction versus the length of time they were allowed to settle in the absence of different categories of original owner. These data are grouped by 2-day intervals; numerals beside data points are sample sizes.

15/17 in first year male removals; Fisher's exact test: $P=1.0$) but the minority in spring (2/19; significantly different from combined winter totals: Fisher's exact test: $P<0.0001$).

Replacement of Original Owners: Contest Behaviour

Outcome of contests

Winter. The least ambiguous aspect of contest behaviour in these experiments was the dichotomy of winners and losers. Plotting the likelihood of original owners being losers against the period of newcomer settlement in winter (Fig. 2) shows a distinct alteration in fortunes after a few days. Initially (phase 1), original owners always won contests. When newcomers were allowed to settle for longer periods they became increasingly likely to resist eviction (phase 2), until finally they were consistent winners (phase 3). Phase periods for each sample can be determined from Fig. 3. Such time-dependent reversals of dominance are contrary to the predictions of the resource-holding potential and uncorrelated asymmetry hypotheses but consistent with those of the value asymmetry hypothesis.

The outcomes of winter contests of removed adult males and first year males (Fig. 2) differed

between days 4 and 8. Contests appeared to be more frequently lost by young males (6/9) than adults (3/10) during this period, although this was not significant (Fisher's exact test: $P=0.18$). Phase 2 for young males (days 4–5) began and ended earlier than the same phase for adult males (days 6–8).

Phase 1 for females was truncated to just 1 day (see Fig. 3c) and phase 2 ran from days 2 to 4. During the latter period contests tended to be more frequently lost by females (4/7) than adult males, although this was not quite significant (0/5; Fisher's exact test: $P=0.08$). Females thus appeared most liable to forfeit their territories after brief absences. These results imply that while value asymmetries govern contest outcomes, the competitive ability of individuals (determined in these cases by age and sex) also modifies the rate of dominance reversal.

Spring. Even after a single day of absence, an original owner never regained the bulk of his territory in spring (Figs 2 and 4) and always lost his mate. In general, however, original owners were able to defend a small portion of their prior home ranges, as territories at this time of year were large enough to absorb a degree of partial resettlement. As these small areas were usually insufficient to allow subsequent pairing, I treated these cases as territory losses.

Changes in territory size

For males in winter, there was no significant difference in territory sizes of original owners before capture ($1386.6 \pm 113.3 \text{ m}^2$, $N=15$) and after resettlement ($1330 \pm 110.7 \text{ m}^2$, $N=15$; Wilcoxon signed-ranks: $Z = -1.45$, $P>0.1$). In spring, however, the territories of original owners were significantly larger before removal ($2106 \pm 165.2 \text{ m}^2$, $N=16$) than after ($734 \pm 93.7 \text{ m}^2$, $N=16$; $Z = -3.52$, $P=0.0004$). Furthermore, the proportion of territory area that an original owner was able to re-establish decreased with the duration of newcomer settlement in spring but not in winter (Fig. 4). This presumably reflects the reluctance of wintering neighbours to expand their territories, coupled with higher food availability and contender pressure in spring (Eberhard & Ewald 1994).

As birds invading vacated spring territories were most frequently established neighbours

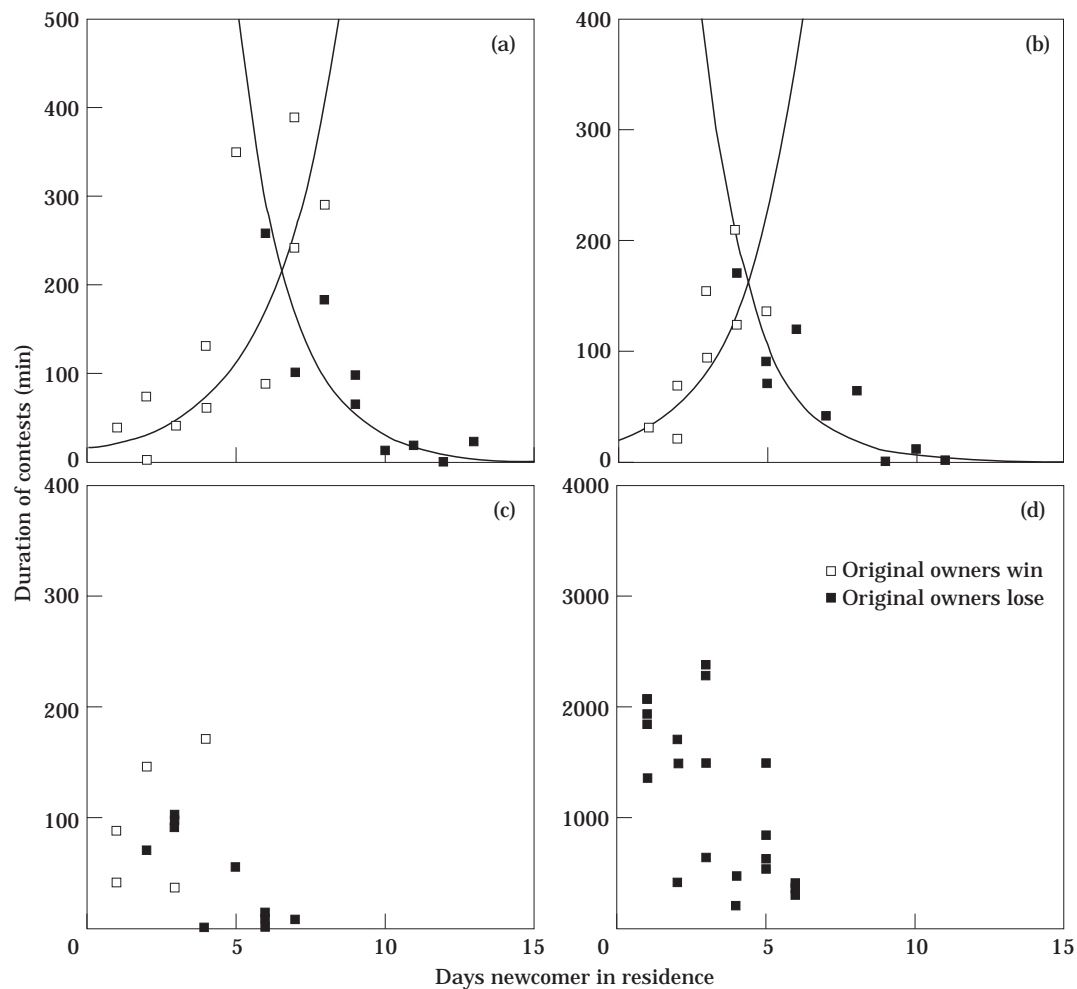


Figure 3. Duration of territorial contests in winter between newcomers and original territory owners versus the period of time newcomers are allowed to settle in the absence of the original owner; (a) when adult males were removed in winter; (b) when first year males were removed in winter; (c) when females were removed in winter; and (d) when males were removed in spring. Best fit curves are exponential through plots of winners and losers.

expanding their ranges, territories of newcomers were significantly larger after settlement ($3346 \pm 268.6 \text{ m}^2$, $N=13$) than before ($2588 \pm 238.6 \text{ m}^2$, $N=13$; $Z = -3.11$, $P < 0.01$). Evaluation of territory size effects at this time of year are complicated by the fact that vacated territories are sometimes split between two new individuals, and there is often slight encroachment by others.

There was no significant difference between territory size of pairs before female removals in spring ($2275 \pm 295.7 \text{ m}^2$, $N=6$) and the territory

size of 'bereaved' males ($2391.7 \pm 167 \text{ m}^2$, $N=6$; $Z = -0.95$, $P = 0.3$). This indicates that females play a negligible role in territory defence during the breeding season.

Duration of contests

Winter. When adult male owners were released after 1–4 days of newcomer settlement they won relatively short contests (Fig. 3a). When they were released after 9–13 days of newcomer settlement the contests were also brief but newcomers were

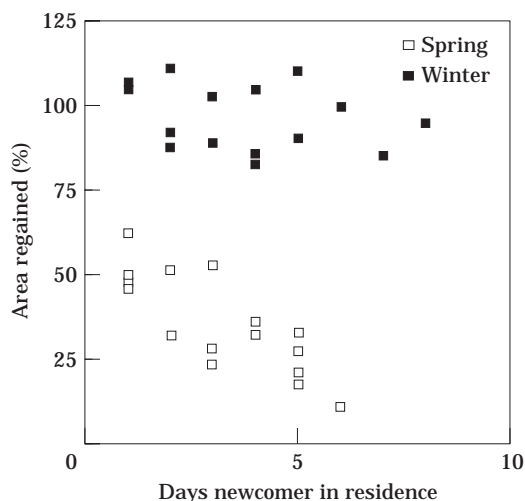


Figure 4. Percentage of original territory area regained by replaced males who kept at least some of their territory versus length of time newcomers were settled in their absence. Ability to regain territory area is negatively correlated with newcomer settlement time in spring (Spearman rank correlation: $r_s = -0.755$, $N=16$, $P<0.01$), but not in winter ($r_s = -0.3030$, $N=15$, $P=0.25$).

invariably victorious. Between these periods (5–8 days) a conspicuous peak in contest duration was apparent. These events closely match the three phases of contest outcomes. The intersection of exponential curves for contests won by original owners or newcomers, occurring around the seventh day of settlement, gives an approximate measure of where the peak in duration lay. The pattern was similar for first year males (Fig. 3b) but the approximate peak lay around day 4.

Because of a paucity of overwintering females it was necessary to lump the contest data of adults and first winters (Fig. 3c). Results from this sample were less clear, and data were too scattered to fit curves. There was no clear intermediate maximum contest duration (although contests were still longest in phase 2) and most struggles were relatively short. Females thus tended to relinquish winter territories after brief contests and then disappear, suggesting that they are closer to the behavioural or conditional threshold beyond which non-residency is the adopted strategy.

With the exception of spring contests, duration data can be arranged into the three phases of contest outcomes (Table II). Significant differences arose between phases for adult males and young males in winter, but these were not apparent in the sample of females or in spring. Similarly, analyses of variance indicated significant differences across phases for adult and first year males in winter, but not for other samples. The difference between phase 2 contest durations of adult males and females in winter is significant (Mann–Whitney U -test: $Z = -2.36$, $N_1 = N_2 = 7$, $P < 0.05$), while the difference between adult male and first year male phase 2 contests approached significance ($Z = -1.71$, $N_1 = 7$, $N_2 = 6$, $P = 0.08$). These results suggest that adult male owners participate in the longest contests and females in the shortest contests. In winter, the longest contests occurred in phase 2, as did the largest differences between samples. Ideally, the age and sex of the newcomer should be taken into account but insufficient combinations of interactions were available to carry out this analysis.

Table II. Comparisons of contest durations observed at different phases of newcomer residency

Owner/season	Phase 1 (n_1, N_2, N_3)	Mean (\pm SE) duration of contests (min)			P †		
		Phase 2	Phase 3				
Adult male/winter	(7, 7, 6)	99.4 \pm 44.3	*	222 \pm 40.5	**	36.7 \pm 14.9	<0.01
1st year male/winter	(5, 6, 6)	73.8 \pm 23.9		134.2 \pm 20.7	*	40.7 \pm 18.9	<0.05
Female/winter	(2, 7, 4)	63.5 \pm 23.5		87.8 \pm 22.4		19.7 \pm 12.1	0.14
Male/spring	(7, 6, 6)	1540.8 \pm 209		1240.8 \pm 386		701.6 \pm 175	0.20

For winter samples (see Fig. 2): Phase 1 = 100% probability of newcomer losing; Phase 2 = period of mixed outcomes; Phase 3 = 100% probability of newcomer winning. For spring sample: Phase 1, less than 2 days; Phase 2, 3–4 days; Phase 3, 5 days or more. Asterisks indicate results of Mann–Whitney U -tests between adjacent columns.

* $P < 0.05$; ** $P < 0.01$.

†Kruskal–Wallis one-way ANOVA across phases.

Spring. In spring, when territorial behaviour is largely confined to males, contest duration was negatively correlated with duration of newcomer residency (Fig. 3d; Spearman rank correlation: $r_s = -0.57$, $N=19$, $P<0.05$), although differences between phases were not significant (Table II). The other remarkable feature of spring contests was their extended length: aggressive interaction was regularly recorded on the second day after replacement of the initial owner. Phase 2 contests were significantly longer for adult males in spring than in winter (Table II; Mann-Whitney U -test: $Z = -2.43$, $N_1=6$, $N_2=7$, $P<0.05$).

Of six females removed in spring, two were replaced by newcomer females. After release of the original bird, temporary and uneasy coalitions existed between new and old females (3–6 days) while the male attempted to attend both. On both occasions the newcomer female eventually departed and paired with a solitary male elsewhere.

The main conclusion of the first part of this paper is that newcomers are more likely to win contests if they have been allowed to settle for 3–7 days, depending on their quality and the identity of the original owner whom they face. I now look at settlement behaviour in more detail to determine how it might generate this delayed reversal of dominance, and accelerate the process in spring.

Settlement Costs

Singing

During territory establishment, newcomers competed with neighbours to settle boundaries. Although birds often counter-sang from a distance, territorial contests were infrequent and usually brief, consisting primarily of close-range counter-singing interspersed with occasional chases. I witnessed only one escalated fight. After a hesitant first day, newcomers in winter initially spent more of their time singing than residents (Fig. 5; Kruskal-Wallis: $H_8=36.22$, $P<0.001$). This high output declined to mean population levels after 6 days (Fig. 5).

In contrast, newcomers in spring did not significantly vary song output between days 1 and 6 of settlement (Kruskal-Wallis: $H_5=2.87$, $P=0.7$). By the third day there was no significant difference between newcomer song output and the population mean (Fig. 5). The required expenditure of

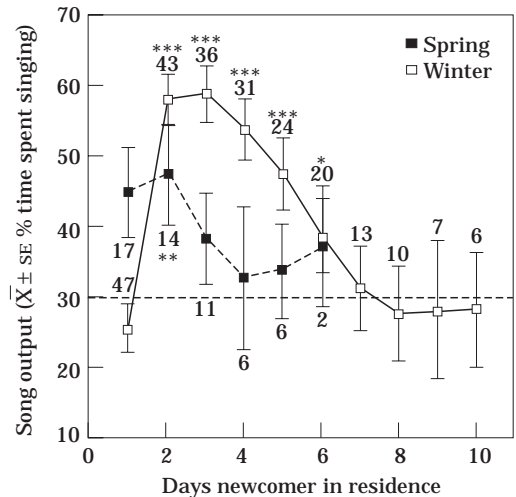


Figure 5. Proportion of time allocated to singing by newcomers during settlement and before the release of original owners. Winter sample sizes are given above error bars, spring sample sizes below error bars. Horizontal line represents mean percentage time spent singing by pre-removal or non-removal controls in both winter and spring ($29.9 \pm 1.0\%$, $N=67$). Control data from both seasons are lumped because there was no significant difference between the former ($29.5 \pm 1.3\%$, $N=41$) and the latter ($30.5 \pm 1.5\%$, $N=26$; unpaired t -test: $t_{27} = -0.052$, $P=0.6$). Asterisks indicate significant differences between daily behaviour and population means: * $P<0.05$; ** $P<0.01$; *** $P<0.001$ (Mann-Whitney U -test).

energy for singing is thus lower for spring settlers than for winter settlers.

Although the percentage of time spent singing by a sample of established neighbours in winter was not significantly higher during the third day of settlement ($40.4 \pm 4.6\%$, $N=25$) than the population mean ($29.5 \pm 1.3\%$, $N=41$, Mann-Whitney U -test: $Z = -1.71$, $P=0.09$), there was a trend towards increased song output of neighbours while newcomers were settling. This implies that neighbours play a part in generating the high song output of newcomers, thus being responsible for a quantifiable cost of settlement.

Foraging

During the period when settling birds in winter allocated a relatively large proportion of their time to singing, they spent less time foraging (Fig. 6; Kruskal-Wallis: $H_8=36.3$, $P=0.0001$).

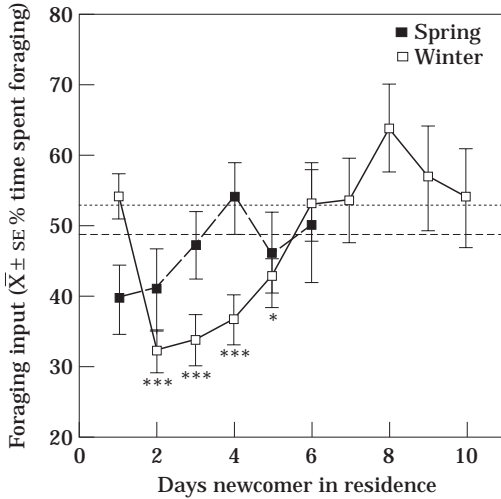


Figure 6. Proportion of time allocated to foraging by newcomers during settlement and before the release of original owners. Sample sizes are the same as Fig. 5 for each category. Dotted line represents mean percentage time spent foraging by pre-removal and non-removal controls in winter ($53.5 \pm 1.4\%$, $N=41$), hatched line represents the same value in spring ($48.6 \pm 1.9\%$, $N=26$). Control data are not lumped because they differ significantly between season (unpaired t -test: $t_{27}=2.132$, $P=0.037$). Asterisks indicate significant differences between daily behaviour and respective population means: * $P<0.05$; ** $P<0.01$; *** $P<0.001$ (Mann-Whitney U -test).

Until the sixth day of residency in winter, newcomer foraging levels differed significantly from the population mean (Fig. 6). In spring, time spent foraging did not vary significantly while individuals were establishing boundaries (Fig. 6; Kruskal-Wallis: $H_5=3.33$, $P=0.65$) and daily foraging budgets were never significantly different from population foraging budgets (Fig. 6).

Young males allocated less time to foraging during the first few days of settlement than adult males (Fig. 7). If, as is likely, this constitutes a higher settlement cost to inexperienced males, it might explain the relative ease with which they are defeated in territorial contests (see Fig. 2).

DISCUSSION

Potentially Confounding Variables

If birds released from captivity are inferior competitors any conclusions derived from

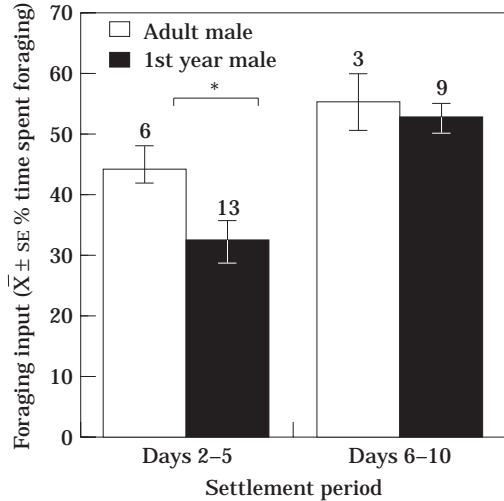


Figure 7. Proportion of time allocated to foraging by newcomers at early and late stages of territory settlement. Figures above error bars are sample sizes. * $P<0.05$ (Mann-Whitney U -test).

experimental results are confounded. Gradual weight loss through captivity suggests that loss of condition might well be a relevant consideration. Depending on the period of captivity, individual birds generally lost 1–3 g. Although this seems a considerable amount for a 20-g bird, it is likely that it can be rapidly replaced. Moreover, fat deposits tend to decrease naturally when birds experience stable environmental conditions (Bednekoff et al. 1994) and so the relative warmth and constant food supply of the aviaries might be expected to promote weight loss, but not necessarily a loss of condition.

The success of original owners after double removal controls indicates that robins held in aviaries for protracted periods remain physiologically and psychologically capable of winning territorial contests. The important factor appears to be the length of time a newcomer is allowed to settle, although minor conditional effects of captivity cannot be ruled out.

Newcomers cannot be selected in these experiments and variation in their quality is difficult to control for. High-quality newcomers perhaps settle more efficiently and make stronger opponents. In addition, birds in their first winter are presumably less experienced foragers or competitors than they become by the following spring (e.g. Desrochers 1992). Seasonal bias in animal

conflicts may thus derive to some extent from seasonal variation in the quality of contestants.

Some territories in these experiments were located at the edge of suitable habitat (e.g. alongside lawns, roads or buildings) and thus had a reduced length of boundary requiring establishment and defence. Costs involved in settling on these edge territories are theoretically lower than the costs of occupying territories in continuous suitable habitat surrounded by several neighbours. However, because neighbours are distributed similarly for each sample, variation in neighbourhood pressure should not confound my results.

Although I did not measure territory quality, it was apparent that when a resident was removed from a well-vegetated, and thus high-quality, territory (Hoelzel 1989), invasion was more rapid and neighbours more likely to abandon their own territories in favour of the vacated area. Intrinsic habitat quality presumably modified the extent to which competitors were likely to invest in the defence or acquisition of space. To refine the conditions of these removal-replacement experiments it would be necessary to standardize territory quality.

Contest Behaviour

The main results of the analysis of contest data can be summarized as follows. (1) Robins held in captivity for 10 days were fully capable of expelling newcomers. (2) Reversal of dominance in winter was gradual and depended on the time newcomers were allowed to settle on the territory. (3) By contrast, reversal of dominance was almost immediate in spring. (4) In winter there was an intermediate peak in contest duration prior to which original territory owners generally succeeded in expelling newcomers, and subsequent to which they failed to do so. (5) This intermediate maximum contest duration was reached most rapidly by females, and least rapidly by adult males. (6) Contests were longest for adult male owners and shortest for females. How can these results be interpreted so as to shed light on the mechanisms underlying territoriality?

The pattern of contest outcome and duration observed in winter has been previously reported in great tits, *Parus major* (Krebs 1982). It provides strong support for the value asymmetry hypothesis, which states that time-dependent

asymmetries in territory value govern the success of competitors. In spring, however, the immediate shift of dominance after the arrival of a newcomer is contrary to predictions of the value asymmetry or resource-holding potential hypotheses, while apparently consistent with those of the uncorrelated asymmetry hypothesis. Despite this, the existence of an ownership convention in spring seems improbable. Rather, I interpret this result as evidence of the high value of spring territories and a concomitant low cost to settlement. This combination of circumstances promotes a very rapid reversal of dominance, which nevertheless remains governed by a value asymmetry.

In winter, a male robin requires a territory in order to advertise to females in spring. Should he lose his territory to a competitor he reduces his likelihood of breeding. By contrast, a female can leave the resident population without jeopardizing her chances of returning to choose a mate. Winter territories are therefore likely to be more valuable to males than females and this might partly explain the differences in defensive motivation and performance between the sexes at that time of year (see Fig. 3a,c). Equally, higher resource-holding potential for males might lead to their greater resilience and success in defending territories.

In spring, it is even more vital that a male successfully defends his territory against rivals and the value of his resource is multiplied greatly if he is paired with a female (e.g. Björklund, 1989). Increased territory value thus goes some way to explaining the extreme escalation observed in spring contests. Unless territories have a higher value for adult males than first year males, it is difficult to construct a value asymmetry that explains the greater success and motivation of adults. It might be that variation in resource-holding potential explains some of these differences. Do observations of settlement behaviour provide any further insight?

Settlement Costs

The main results of territory settlement analysis are as follows. (1) Newcomers settling on territories in winter allocated more time to singing and less time to foraging than established territory holders. (2) In spring, increases in song and decreases in foraging were less evident. (3) In winter, the time at which dominance was observed to switch roughly corresponds to the time taken

for singing and foraging to reach average levels for the population. The duration of this period is a measure of 'settlement cost', namely time taken to settle boundaries with neighbours and, perhaps, to learn foraging areas.

Environmental conditions (temperature, hours of daylight) favoured the original owner in winter, and the settler in spring. In winter, previously non-territorial newcomers paid a considerable energetic cost: high song output and low nutritional input. It seems reasonable to assume that this cost delayed the point at which they attained peak condition as territory owners, thus enabling removed birds to win contests after several days of absence. It is particularly significant that the 5–6 day time-lag between settlement and normal singing behaviour (Fig. 5) or normal foraging behaviour (Fig. 6) roughly equates to the window in which original owners tended to succeed in ousting newcomers (Fig. 2). Unfamiliarity with new territories probably exacerbated the energy deficit generated by insufficient foraging time.

The unlikelihood of newcomers being dislodged after full establishment might help to explain the relevance of satellite individuals on territories. For example, satellite waterbuck, *Kobus ellipsiprymus*, assist in territory defence yet appear to gain very few matings (Wirtz 1981). In this case, the benefit to subordinate satellites is their increased rate of take-over or promotion to ownership. This was interpreted as a demonstration of the importance of experience. However, as experience of an area is arguably acquired by covert intruders, the success of satellites is perhaps better explained by their circumvention of settlement costs.

Did young male robins pay a higher cost than adult males because they had to work harder to establish themselves? Age-related differences in foraging success (Marchetti & Price 1989; Desrochers 1992), and the reduced foraging input of young males (see Fig. 7) over the first few days of settlement suggest that this may have been the case.

In spring, the higher temperatures and increased hours of daylight available for foraging undoubtedly reduced the energetic cost of settlement. In addition, newcomers were primarily neighbours expanding their territories and thus had fewer new boundaries to settle. Coupled with high resource value in spring, this explains the reduced advantage conferred to prior residents in comparison with winter experiments. Seasonal

differences in behaviour appear to be governed by variations in settlement cost and territory value. This is very strong evidence for the integral role of payoff asymmetries in animal conflicts. If dominance was regulated primarily by variations in resource-holding potential we would not expect conspicuous seasonal effects in contest behaviour. More generally, these results indicate how important it is to take seasonal and environmental effects into account when investigating questions related to territorial behaviour.

Consequences for Animal Conflicts

The costly nature of interactions with new neighbours (Copenhaver & Ewald 1980; Eason & Hannon 1994) can only relate to populations of species, or related species (Robinson & Terborgh 1995), in which territories are contiguous. This condition is fulfilled only by relatively densely packed populations. As territory contiguity is a widespread phenomenon, settlement costs may help explain some of the residence effects observed in previous studies (Krebs 1982; Beletsky & Orians 1989; Sandell & Smith 1991).

In general, high settlement costs will tend to reinforce the correlation between prior residency and dominance in territorial systems. Conversely, any factor that tends to reduce time or energy expenditure for newcomers, such as an abundant food supply or an amelioration of climatic conditions, will accelerate the reversal of dominance between competitors. Settlement costs will theoretically be lower where territories do not function as a food resource (e.g. at leks) or where newcomers do not appear to fight with neighbours (e.g. at northern elephant seal *Mirounga angustirostris* colonies, Haley 1994). In these cases, contests are predicted to be more violent, and their outcomes more closely predicted by differences in resource-holding potential.

The liability of non-territorial challengers to settlement costs that do not apply to residents is not incorporated in existing models of asymmetric contests (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Leimar & Enquist 1984) and ignored in the identification of payoffs to contestants (e.g. Krebs 1982; Brodsky & Montgomerie 1987; Shutler & Weatherhead 1991; Beletsky & Orians 1993). This factor is potentially crucial in determining the outcome and dynamics of owner–intruder conflicts.

While the results of this study generally support the value asymmetry hypothesis as the primary determinant of territorial dominance in robins, Grafen (1987) has suggested that value asymmetries alone are evolutionarily unstable because they result in 'divisive asymmetries' (i.e. one class of individuals always loses). The current study, along with other recent research (e.g. Shutler & Weatherhead 1991, 1992; Beletsky & Orians 1993), has continued to indicate that resource-holding potential is of secondary importance, and that the 'desperadoes' predicted by Grafen (1987) to result from 'divisive asymmetries' do not exist. While these findings appear difficult to reconcile with Grafen's (1987) theoretical arguments, it is plausible that substantial settlement costs contribute to value asymmetries and maintain ownership dominance in many systems.

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