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Surplus territory contenders in male red-winged blackbirds: where are the desperados?

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Summary. We tested whether payoff asymmetries could explain why "floater" red-winged blackbirds seldom escalate contests to acquire territories. We removed territorial male "owners" and allowed floater replacements to claim territories. We then released owners to see how three currencies of payoff asymmetries (replacement occupancy time, owner familiarity with neighbors, and owner reproductive investment) affected owners' likelihood and speed of reclaiming their territories (owner success). Neither the duration of an owner's internment nor the amount of time that a floater replacement had held the territory affected owner success (Figs. 1 and 2). Owner success was also not affected by the number of neighbors that they had (Fig. 3). Finally, owner success was the same irrespective of whether or not he was the likely sire of offspring on the territory, or the size of his harem (Fig. 4). Although these results are consistent with the proposal that payoff asymmetries will be irrelevant in contests for valuable resources, they are inconsistent with the proposal's corollary that excluded individuals should become "desperados" and escalate or even fight to the death in contests for those resources. Expected payoffs for passive acquisition of territories in this species may be higher than from a more aggressive desperado strategy.

Introduction

Maynard Smith and Parker (1976) proposed that contests between equally matched contestants will be decided in favor of the contestant that fights the hardest. Contestants may differ in their willingness to fight if there is an asymmetry in how much they value a contested resource (a payoff asymmetry). In this paper, we test whether payoff asymmetries explain site dominance in red-winged blackbirds (*Agelaius phoeniceus*).

Before considering payoff asymmetries, we must consider the evidence for two other asymmetries Maynard Smith and Parker (1976) described that can decide the outcome of territorial contests. The first asymmetry occurs when contestants are not equally-matched in fighting ability, i.e. "resource-holding potential" (RHP). In this case, individuals that win contests for resources such as territories do so because of their superior size, strength, etc. (Darwin 1871; Parker 1974). RHP asymmetries appear to be sufficient to explain the outcome of many contests (e.g., Arak 1988; Piper and Wiley 1989; Rowland 1989; Poole 1989). However, in red-winged blackbirds, there is little evidence for RHP differences between *adult* floaters and owners (Eckert and Weatherhead 1987a, b, c; Beletsky and Orians 1989a; Shutler and Weatherhead 1991a, b; but see Rohwer 1982). In general, RHP asymmetries do not appear to explain the red-winged blackbird owner-floater dichotomy.

A second asymmetry that may decide contest outcomes is an uncorrelated asymmetry (Maynard Smith and Parker 1976). In this case, the contestants use some arbitrary rule to settle contests, thereby avoiding escalated aggression. Escalation of contests is assumed to be undesirable for both participants because they both risk injury. In territorial situations where there are no RHP asymmetries, theory about uncorrelated asymmetries proposes that "the owner wins over the intruder" (Tinbergen 1953; Davies 1978; Krebs 1982; Desrochers and Hannon 1989) is the usual arbitrary rule by which contestants avoid escalation [but see Burgess (1976) for a rare example of the rule operating in the opposite direction]. The generality of this rule in nature is not known, but the citations above suggest that it is common. Grafen (1987) argued that arbitrary rules should only apply to contests where the value of the contested resource is low. Thus, if vacancies occur frequently enough that all contestants are likely to obtain a territory, and the costs of waiting are not greater than the costs of fighting to obtain a territory, then a territory would have a rela-

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tively low resource value (e.g., Davies 1978). However, red-winged blackbird populations often have large numbers of floaters that are unable to find vacant territories (Orians and Christman 1968; Laux 1970). Furthermore, floaters without territories probably do not breed (Gibbs et al. 1990). These factors presumably make territories valuable resources, and Grafen (1987) predicted that in this situation, floaters will become "desperados," and frequently escalate contests rather than forego breeding. If Grafen's arguments apply to red-winged blackbirds, then uncorrelated asymmetries are unlikely to decide contests for territory ownership (also see Beletsky and Orians 1987, 1989a).

The remaining alternative so far proposed for explaining the outcome of territorial contests is a payoff asymmetry (Maynard Smith and Parker 1976). In this case, owners are presumed to have more to gain from winning a contest for territory ownership than floaters, and consequently owners fight harder. Payoff asymmetries may explain why, when RHP asymmetries are not evident, one individual wins a contest for a valuable resource (Krebs 1982; but see Grafen 1987).

There are several currencies that Maynard Smith and Parker suggest may contribute to payoff asymmetries in contests for territory ownership. We group them into three general currencies. The first is occupancy time. Owners invest time in learning the location of resources such as food, or escape routes from predators. Furthermore, experience on the territory may allow owners to become more efficient in defending their territory (Copenhaver and Ewald 1980). In making these investments, owners create an asymmetry in knowledge that makes the value of the territory greater for them than for the less knowledgeable floaters; this is consistent with the findings of Beletsky and Orians (1989a). In some species, greater occupancy time may also allow owners to become familiar with individual floaters. However, few floater red-winged blackbirds remain in the vicinity of a given territory for more than a day (Shutler 1991).

A second currency is familiarity with neighbors. Territory owners expend substantial effort in disputing boundaries with neighbors (Peek 1971; Jakobsson 1988), and these investments decline as neighbors become more familiar with each other (Krebs 1982). Disputes with familiar neighbors may be less expensive than trying to renegotiate boundaries with a floater that inserts himself between the owner and the owner's neighbor. It may even pay neighbors to cooperate in evicting floaters that are attempting to insert (Getty 1981, 1987; Jaeger 1981; Stamps and Krishnan 1990). As possible evidence that such "cooperation" among red-winged blackbirds is beneficial, males with one or more familiar neighbors have higher reproductive success than males with only unfamiliar neighbors (Beletsky and Orians 1989b). This implies that an owner may benefit by helping neighbors hold their territories. Thus a male with familiar neighbors may be able to hold his territory even if he is competitively inferior to some of the floaters attempting to settle. Even in the absence of cooperation among neighbors, a male that has established boundaries with his neighbors has an advantage over a floater by knowing the exact location of those boundaries. A male new to a territory would have to pay the cost of establishing boundaries with each of his neighbors. Thus, for both of these reasons, the presence of neighbors should make territories more valuable to owners than to floaters.

The third currency Maynard Smith and Parker (1976) suggested may create payoff asymmetries is reproductive investment. Where owners have invested in site-dependent pair bonds (Verrell 1987; Sandell and Smith 1991), they stand to gain more from holding the territory than their floater counterparts. In addition, if owners have sired offspring, and owners' continued investment in the form of nest defence will improve nestling survival (Walton and Nolan 1986; Weatherhead 1990), owners will again have more to gain from the territory than floaters. We tested whether these three general currencies outlined by Maynard Smith and Parker contribute to site dominance in red-winged blackbirds.

The red-winged blackbird is a common passerine that breeds over much of North America (Orians 1980). The species is migratory in the northeastern part of its range. Males arrive in the spring before females, and begin defending territories on which females eventually nest. Because the number of territories is limited and because male reproductive success is predicated on territory ownership (Gibbs et al. 1990), there should be strong competition to become an owner. Nonetheless, escalated contests for territories are infrequent (Nero 1956; Orians and Christman 1968; Røskaft and Rohwer 1987). We endeavor here to determine whether payoff asymmetries could explain why this is so.

We tested how each currency affected site dominance by experimentally varying the value of each of the three currencies. We achieved this by capturing owners and holding them in aviaries. While owners were captive, floaters claimed the newly created vacancies. We released owners and determined whether longer internments reduced owners' success at reclaiming their territories, which would be consistent with the hypothesis that knowledge asymmetries were no longer in the owners' favor. We also tested whether the number of neighbors adjacent to a removal territory affected released owners' success in reclaiming their territory. Finally, we tested whether owners were more successful at reclaiming their territories when they were probable sires of the young on the territory than when their replacement was the more probable sire.

Methods

General methods. Our study area was near the Queen's University Biological Station in southeastern Ontario. Our population of red-winged blackbirds occupied territories spaced irregularly in ditches beside rural highways. Approximately half of the males in our population are floaters (Shutler and Weatherhead 1991a). Consequently, vacancies are usually claimed within a day.

Our protocol was to compare owners' ability to reclaim their territories relative to each of the currency values. We performed removal experiments in which male territory occupants were captured using stuffed male decoys and playback with traps (Smith 1972) or mist nets. Removals were done in the morning from early

April (pre-nesting) to late June (late nesting) in 1988, 1989, and 1990. Beyond late June there were no new nest initiations and territory occupants no longer responded to decoys. Removed males were banded, and then held captive in one of six outdoor 3 × 2 × 1.5 m aviaries at the Biological Station. A maximum of ten males occupied an aviary at any time. Captive males were supplied water and food *ad libitum* and were held for between 2 and 30 days. Removed males were usually replaced on their territories by males that had previously been floaters, and less often by neighbors (Shutler and Weatherhead 1991a). In most cases, as part of a larger study, we attempted to remove floater replacements as well. Replacements were housed with the territory owner (see Shutler and Weatherhead 1991a for details). We continued to remove males until a replacement failed to respond to a decoy, or less commonly, no additional replacements occurred within 12 days after a removal. Once either situation occurred, "final" replacements were allowed to occupy the territory undisturbed. The largest number of males removed from a territory was ten. In all cases, replacements were released back at the territory from which they had been captured before or at the same time as the owner. In all cases, released individuals flew out of sight immediately or were driven off by the territory occupant within 5 min (also see Beletsky and Orians 1987). However, in many cases released individuals did eventually reclaim their territories (see below). Because the timing of territory reclamation was unpredictable, we were unsuccessful in our attempts (15 observation periods of up to 2 h) to observe a reclamation in progress. However, we were able to determine all cases in which a released male successfully reclaimed his territory.

In each year, we visited individual territories one or more times a week from early April until the first week of July, by which time most territories were deserted. Territories were visited two or more times in the first week after removals and releases. We observed territories, both before and after removals, from inside a vehicle parked approximately 20 m away. Observations usually lasted 5 min, and were carried out between 0500 and 1000 hours in the morning and 1800 to 2030 hours in the evening, providing it was not snowing or raining. Observations consisted of identifying banded territory occupants and/or neighbors, and mapping their locations. Early in the season territory occupants are on their territories about 95% of the time (Eckert and Weatherhead 1987b), and were usually detected at every visit. Later in the season, two or three visits were required to determine the identity of territory claimants.

In 6 of an initial set of 54 removal experiments, vacancies were not claimed. These six territories were excluded from our analyses. In all but two cases where a male released from captivity reclaimed a site from a final replacement, it was the original owner rather than a replacement male that we had removed from the same territory (in one case the territory was claimed by a first replacement and in the second case by the sixth replacement). Thus, we only consider owner success in our tests. An owner was deemed successful if he became the sole continuous occupant of the territory. For each currency, we evaluated the proportion of owners that reclaimed territories relative to the value of the currency at the time of their release. Second, we determined the number of days required for successful owners to reclaim their territories relative to the value of the currencies. In all cases, we observed whether an owner, a floater, a neighbor, or no individual claimed the vacancy.

Statistical tests were carried out on a microcomputer version of the Statistical Package for the Social Sciences (Nie 1988). When variables were not normally distributed, we used nonparametric statistics. All means are reported ± SD and all tests are two-tailed.

Occupancy time. We tested whether occupancy time contributed to site dominance from the final replacement's perspective. If longer occupancy time gives owners an advantage in knowledge about the location of resources (and/or about their neighbors), then longer owner absences should allow final replacements more opportunity to overcome these asymmetries. Also, independent of payoff asymmetries, increased owner weight loss from longer time in captivity may reduce their RHP (Beletsky and Orians 1987), and hence their success in reclaiming their territory. In both cases, we predicted that longer owner internments would improve final replacements' success in holding on to our artificially-created vacancies.

Because we removed replacements from some territories, and because vacancies were not always claimed immediately, owner absence time was not always indicative of how much time final replacements had occupied the territory. Therefore, we also used the number of days the final replacement had occupied a territory (at the time the owner was released) as a second index of tenure. Most final replacements were unbanded. However, observations of banded final replacements in this geographic area indicate that they turn over at a low rate (Eckert and Weatherhead 1987b; personal observation). Because our final replacements were observed for a far shorter period [i.e. usually less than 30 days compared to 90 days in the Eckert and Weatherhead (1987b) study], we assumed that a final replacement seen in one observation period was the same individual in successive visits. We predicted that final replacements that had occupied the territory longer would be less likely to be usurped by released owners.

According to our predictions, each day an owner spends in captivity and each day a final replacement occupies the territory benefits the final replacement. Therefore, in addition to considering the separate effect of these two measures, we added them together to form a combined index. We predicted that final replacements would be more likely to hold on to their territories with higher values of this index.

Familiarity with neighbors. The territories we used included isolated cattail (*Typha* sp.) patches that had no neighbors, cattail patches that had neighbors but were separated by enough space that two patches were indefensible by a single male, and territories on small cattail marshes with 8–20 contiguous territories, each with as many as three neighbors. In many cases, males on neighboring territories were unbanded, so we could not consider whether longer association periods with neighbors strengthened the owner's hold on their territories. However, the more neighbors a male has, the more likely it is that he has at least one familiar neighbor. In addition, owners should benefit from having well-established territory boundaries with their neighbors, regardless of whether or not they are familiar with those neighbors from previous years. Therefore, we predicted that owners would have more success in reclaiming their territories if they had more neighbors.

Investment in offspring. To test for the effects of investment in offspring on the owners' success at reclaiming their territories, we needed to monitor nesting activity. We checked territories for nests every 3–7 days from the date the first nest was built until the last week of June. Most nests were found at the egg stage or earlier. Harem size was defined as the maximum number of nests on a territory that simultaneously had one or more eggs or nestlings. For convenience, we refer collectively to eggs, nestlings, and fledglings as "young". We assumed that all young were sired by the territorial male that occupied the site when the eggs were laid. This appears to be a reasonable assumption, because extra-pair fertilizations in low-density red-winged blackbird populations such as ours are expected to be uncommon (Gibbs et al. 1990).

We grouped our removal experiments into three remove/release categories that reflect investment in offspring. In the control category, an owner was removed and released prior to the initiation of reproduction on his territory, so that no young were present at either time. In the second category, an owner was removed prior to the initiation of reproduction on his territory, and was released after the final replacement male had sired the young. In the third category, owners were removed after they had sired young on the territory, and were released when their young were still on the territory. We predicted that males that had sired young would have more success in ultimately claiming the territory. We also predicted that this effect would be enhanced by larger harems.

In 1990, we used 33 extra territories to increase our sample size for investigating the effects of investment in offspring on payoff asymmetries. We only removed a single male from these territories, and each of these males was held between 6 and 10 days. We did not visit these extra territories as regularly as our main territories, and we did not determine harem size on them. However, we did determine the number of neighbors associated with each territory.

Balancing the design. Unpredictable events, including predation, unclaimed vacancies, and absence of breeding activity on a territory, caused some data to fall outside some of the categories we used for some currencies. This caused sample sizes to differ between tests. It also affected our planned, balanced design so that tests for the importance of one currency might be confounded with respect to the remaining currencies. However, the only significant deviation from a balanced experimental design was that territories with larger harems also had more neighbors. We consider the potential confounding effects of this in our results.

To maintain a balanced design, we could not include the 33 extra territories we used to test for effects of investment in offspring on payoff asymmetries. Thus, in our initial tests, these territories are considered separately.

Results

Covariates

We removed more males from some territories than from others. Late floater replacements, i.e., those that did not claim a territory until after we had removed the owner and some of the owner's replacements, may have lower RHP than the initial replacements that were faster to capitalize on the appearance of a vacancy. Thus, released owners may have more success at driving off late replacements than early replacements. We tested whether owners were more successful at reclaiming territories from final replacements on territories where more males had been removed. The average number of males removed from territories that owners successfully reclaimed (mean $= 2.9 \pm 2.2$ males removed, $n = 23$ territories) was slightly greater than the average number of males removed from territories that owners did not reclaim (mean $= 2.0 \pm 1.6$, $n = 25$; Mann-Whitney U-test, $U = 213.5$, $P = 0.10$). In addition, we also held owners captive longer when we removed more replacements ($r_s = 0.62$, $P < 0.001$). Finally, we were able to remove more replacements on territories where we released owners back to territories where final replacements had sired young than in any other remove/release category (categories explained above; Kruskal-Wallis test, $\chi^2 = 12.9$, $P = 0.002$). We thus repeat subsequent analyses controlling for the number of males removed.

We tested whether the percent of weight lost in the days between initial capture and eventual release affected owners' success at reclaiming territories. Average weight loss was approximately 12% for both successful (mean $= 8.4 \pm 5.5$ g, $n = 21$) and unsuccessful males (mean $= 8.5 \pm 5.8$ g, $n = 24$; t-test, $t = 0.11$, $P = 0.92$). (Initial or final weights were not obtained for 3 of the 48 owners.) However, successful males required more time to reclaim their territories when they lost more weight, although this relationship was not strong ($n = 21$, $r_s = 0.30$, $P = 0.10$). Nonetheless, we repeat subsequent analyses controlling for weight loss where we tested for the effects of each currency on time for owners to succeed.

Occupancy time

We had predicted that final replacements would repel original owners more often when the final replacements had spent more time as occupants of a territory, and also when the original owners had spent more time in captivity. However, the occupancy time of final replacements that were usurped by released owners did not differ from that of final replacements that managed to hold territories against released owners (Table 1). Furthermore, final replacements were not more successful in holding their territories if the original owners were held captive longer. Finally, the effects of these two factors combined did not affect owner success (Table 1).

We performed separate discriminant function analyses for each occupancy time index including as a variable in each case the number of males removed from the territory. The proportion of cases where owner success could be correctly predicted using these variables was never higher than 65% (Fig. 1; all P's testing Wilk's Lambdas > 0.25). Thus, the combined effect of occupancy time and the number of males removed had no significant effect on final replacements' success at retaining territories.

Table 1. Comparison of the occupancy time indices of unsuccessful ($n = 23$) and successful final replacements ($n = 25$)

Occupancy time index	Mean ± SD (days)		U^1	P
	Unsuccessful replacements	Successful replacements		
Time owners spent in captivity	18 ± 10	15 ± 7	238.0	0.31
Time replacement occupied territory	8 ± 8	8 ± 7	245.5	0.50
Combined index	25 ± 16	23 ± 13	273.5	0.77

[1] Mann-Whitney U-tests

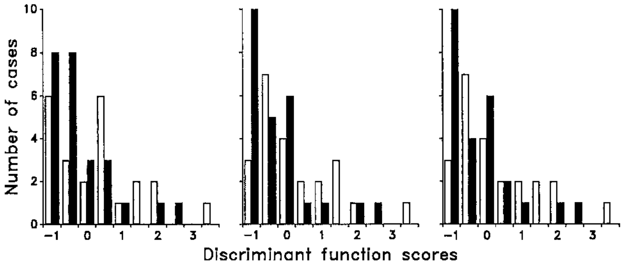

Fig. 1. A comparison of the discriminant function scores for unsuccessful ($n = 21$; *open bars*) and successful final replacements ($n = 24$; *shaded bars*) relative to occupancy time and the number of males removed. *From left to right*, respectively, the figures depict the frequency distributions from owner captivity time, replacement occupancy time, and the combined index

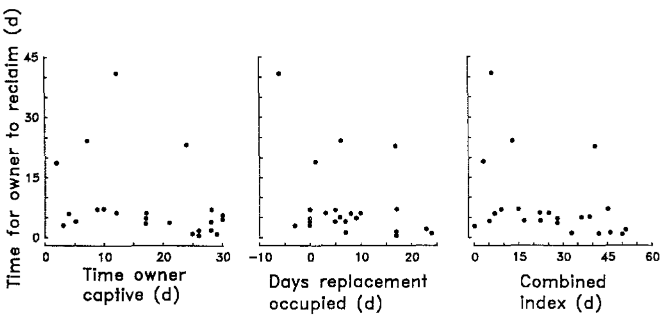

Fig. 2. The time that successful owners required to reclaim their territories relative to the amount of time they had spent in captivity, the amount of time a final replacement had occupied the owner's territory (*negative values* indicate that the territory was not claimed by a final replacement until the owner was released), and the combined effects of these factors

Table 2. Relationship between the time required for owners to reclaim territories relative to each of our final replacement occupancy indices, controlling for the number of males removed from the territory and owner weight loss during his internment. Results are presented for multiple regressions

Variable in equation	Beta	*T*	*P*
Time owner spent captive (days)	−0.36	−1.19	0.25
Number of males removed	−0.03	−0.09	0.93
Owner weight loss	−0.05	−0.20	0.84
Regression statistics: Multiple $R=0.40$; $F=1.05$; $df=3,17$; $P=0.40$			
Time replacement occupied (days)	−0.36	−1.65	0.12
Number of males removed	−0.22	−0.99	0.34
Owner weight loss	−0.11	−0.51	0.62
Regression statistics: Multiple $R=0.46$; $F=1.52$; $df=3,17$; $P=0.25$			
Combined index (days)	−0.38	−1.56	0.14
Number of males removed	−0.09	−0.37	0.72
Owner weight loss	−0.07	−0.31	0.76
Regression statistics: Multiple $R=0.45$; $F=1.41$; $df=3,17$; $P=0.27$			

We next considered whether our three measures of occupancy time predicted the speed with which successful owners would reclaim their territories. Counter to prediction, final replacements were more rapidly usurped by owners that had spent longer in captivity (Fig. 2; $r_s=-0.42$, $P=0.02$, $n=23$). Final replacements that had occupied territories longer also tended to be usurped more rapidly ($r_s=-0.30$, $P=0.08$). Thus, the relationship between replacement usurpation speed and the combined occupancy index was also significant (Fig. 2; $r_s=-0.45$, $P=0.02$). We then controlled for potential effects caused by differences in the number of males removed from a territory and owner weight loss. Again, counter to prediction, these multiple regressions indicated that increased occupancy time by final replacements resulted in faster usurpation by released owners, although the results were no longer significant (Table 2). Furthermore, neither the number of males removed from the territory nor owner weight loss contributed significantly to the speed at which final replacements lost their territories (Table 2). In sum, we have no convincing evidence that occupancy time affected site dominance in the predicted fashion.

We are left with the counterintuitive result that longer periods of captivity helped owners recapture their territories more rapidly. However, among successful owners, longer periods of captivity were associated with *less* weight loss ($n=21$, $r=0.35$). Although this relationship was not significant ($P=0.15$), it suggests that successful owners acclimatized to the aviary, and thereafter their weights began to recover. When released after this period of acclimatization, they were thus in better shape for reclaiming their territories than had they been released shortly after internment.

Four owners took far longer to reclaim their territories than the other successful owners (Fig. 2). The currency values at the time of release of these owners did not differ significantly from those of the other 19 males (Mann-Whitney *U*-tests comparing the two groups of males, all *P*'s>0.10). The only thing these four males had in common was that they all reclaimed their territories late in the season after nest initiations had ceased (Mann-Whitney *U*-test comparing the dates the territories were reclaimed, $P=0.06$). We repeated the previous analyses excluding these males. Doing so made the multiple regression for final replacement occupancy time significant ($R=30.67$, $F=3.57$, $df=3, 13$, $P=0.04$) but still counter to what was predicted. In the analyses that follow, the results were not significantly different if these males were exluded. Thus they are retained in the results we present below.

Neighbor familiarity

Our second currency was the number of neighbors with which an owner had to negotiate boundaries. Owners released on territories that had been claimed by either floaters or neighbors were not more successful if they had more neighbors (Table 3, log-likelihood $G=0.5$, $df=2$, $P=0.80$). This conclusion was the same if we included the number of males removed as a covariate ($G=0.4$, $P=0.81$).

There was also no relationship between the time required for successful owners to reclaim their territories and the number of neighbors they had (Fig. 3, Kruskal-Wallis $\chi^2=0.30$, $P=0.86$). This result was still not signif-

Table 3. Success of owners at reclaiming their territories relative to the number of neighbors they had. Values are the number of territories

Territory ultimately claimed by:	Number of neighbors		
	0	1	2+
Owner	8	8	7
Floater or neighbor	11	7	7

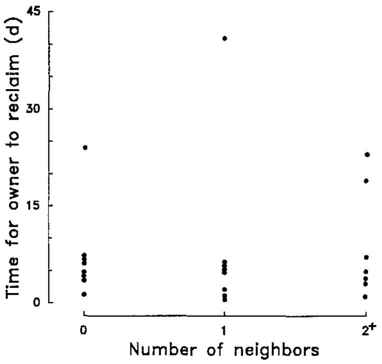

Fig. 3. The time required for successful owners to reclaim their territories relative to the number of neighbors they had

Table 4. Success of owners at reclaiming their territories relative to their reproductive investment, and relative to their harem size

Situation when owner released:	Outcome		Totals
	Owner reclaimed	Final replacement held	
Young not present	3	9	12
Young sired by replacement	6	4	10
Young sired by owner	4	7	11
Harem size 0	6	3	9
Harem size 1	8	11	19
Harem size 2+	6	10	16

In the former analysis, we excluded territories on which predation removed young from territories ($n=6$) and territories that attracted no females ($n=9$). In the latter analysis, we excluded 4 territories for which total harem sizes were not obtained

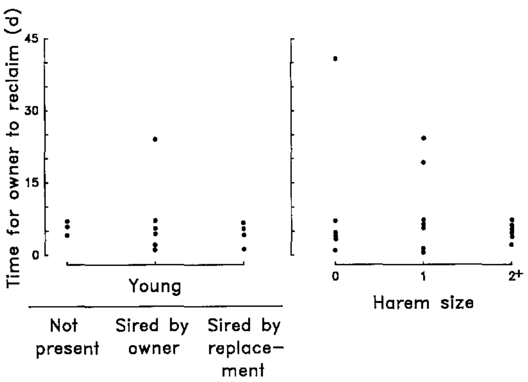

Fig. 4. The time required for successful owners to reclaim their territories relative to whether or not they had young present, and relative to their harem size

icant when both owner weight loss and the number of males removed from the territory were included in a multiple regression (ANOVA, $F=2.25$, $P=0.13$).

We found that territories with more neighbors were more likely to have larger harems ($G=9.8$, $df=4$, $P=0.04$). This is attributable to the fact that contiguous marsh territories tend to have more extensive areas of suitable nesting habitat than the isolated roadside territories. However, we predicted that owners would have more success reclaiming territories if they had larger harems; thus larger harems would complement the effect of more neighbors. However, we found no significant effect on owner success despite this confounding effect in our experimental design. This strengthens our conclusion that owners' site dominance is not enhanced by having more neighbors.

We compared the success of owners at reclaiming territories from floater replacements with their success against neighbor replacements. The proportion of territories that owners reclaimed from floater replacements (17 of 37) was similar to that reclaimed from neighbor replacements (6 of 11; $G=0.1$, $df=1$, $P=0.99$). Thus, our data indicate that floaters and neighbors are equally tenacious replacements.

Investment in offspring

Our final hypothesis was that males would be more successful at reclaiming territories on which they had sired young. However, we found no evidence for this (Table 4; $G=2.9$, $df=2$, $P=0.24$). We also found no evidence that owners with larger harems were any more successful at reclaiming their territories (Table 4; $G=2.1$, $df=2$, $P=0.34$). The number of males removed from the territory had no effect on these conclusions (statistics identical to the preceding comparison).

The time successful owners required to reclaim their territories was unaffected by investment in offspring (Fig. 4, Kruskal-Wallis $\chi^2=0.63$, $P=0.73$) or by harem size ($\chi^2=0.04$, $P=0.98$). This conclusion was not affected if we controlled for the number of males removed from the territory and owner weight loss with multiple regressions (Table 5). We thus have no evidence that investment in offspring affects site dominance. The fact that the time required to reclaim territories was independent of investment in offspring suggests that intruder pressure, which varies with the stage of the breeding season (Peek 1971), is also unimportant to site dominance.

Extra territories

For the 33 extra territories that we used to test for effects of investment in young, we also had data on the number of neighbors. However, we could not accurately assess owner's speed at reclaiming extra territories because we only visited extra territories once a week. Owners successfully reclaimed 4 of 8 of these territories that had no neighbors, 3 of 12 territories that had one neighbor, and 4 of 13 territories that had two neighbors ($G=1.4$, $df=2$, $P=0.50$). Because we have so far failed to find any evidence that our three currencies affect site dominance, we combined the results from the main and extra experiments. In total, owners reclaimed 12 of 27 territories that had no neighbors, 11 of 27 territories with one

Table 5. The effect of the number of males removed, owner weight loss, and reproductive investment on owner success at reclaiming their territories. The analysis is repeated substituting harem size for reproductive investment

Source of variation	*df*	*F*	*P*
Reproductive investment	2	0.2	0.80
Covariates:			
Number of males removed	1	0.4	0.54
Owner weight loss	1	0.9	0.39
Total for covariates	2	0.8	0.51
Total variation explained	4	0.5	0.74
Harem size	2	0.3	0.72
Covariates:			
Number of males removed	1	2.0	0.18
Owner weight loss	1	3.2	0.10
Total for covariates	2	3.0	0.09
Total variation explained	4	1.6	0.23

neighbor, and 11 of 27 territories with two or more neighbors ($G=0.1$, $df=2$, $P=0.95$). This supports our conclusion that the number of neighbors had no effect on site dominance.

In the extra experiments, we removed and released owners before breeding began in 18 cases, and, in 12 cases, removed and released owners after they had sired young on the territory (breeding did not occur on 3 extra territories). Owners recaptured 4 of 18 territories before breeding began, and 5 of 12 territories where the owners had sired the young ($G=1.3$, $df=1$, $P=0.26$). When we combined these results with those from the main experiments, we could still find no evidence that reproductive investment affected site dominance (7 of 30 territories reclaimed by owners before the breeding season, 9 of 23 territories reclaimed where the owner had sired young; $G=1.5$, $df=1$, $P=0.21$). This reinforces our conclusion that investment in offspring had no effect on an owner's success at reclaiming his territory.

We considered the effects of the number of males removed from a territory with the pooled results from the main and extra experiments. Significantly more males had been removed from territories that owners successfully reclaimed than those they did not (Mann-Whitney *U*-test, $U=631.5$, $P=0.05$). After controlling for the number of males removed in analyses where we could pool results (i.e. those not involving harem size, occupancy time, or time to succeed), the results were essentially the same as what we have reported above; none of the three currencies affected site dominance.

Discussion

Two general patterns emerged from our removal and release experiments. First, of all the males removed from territories (owners and their replacements), only the original owners were regularly successful at reclaiming their territories when released, but they were only successful approximately half of the time. Second, asymmetries in occupancy time, neighbor familiarity and reproductive investment between original owners and the males they had to displace did not explain why some owners were successful at reclaiming their territories and others were not. Thus, payoff asymmetries do not appear to explain site dominance in this population of red-winged blackbirds.

In two removal experiments on red-winged blackbirds in eastern Washington, Beletsky and Orians (1987, 1989a) found that occupancy time did influence site dominance. When owners were held captive for only 7–49 h, 91% (50 of 55) regained their territories while only 16% (4 of 25) regained their territories after 6–7 d in captivity. The success of the longer-term captives increased to 73% (8 of 11) when their replacements were only allowed 2–3 days occupancy, suggesting that a replacement requires 3 or more days on a territory to establish site dominance (also see Krebs 1982). These results clearly contrast with the 48% success rate that owners in our study had at regaining their territories after they had averaged 16 days in captivity and their final replacements had occupied their territories for an average of 8 days. It is possible that value asymmetries are only important while an owner occupies a territory; if an owner is absent more than 2 days, other asymmetries become more important to territorial contests. Although we do not have the data to address this point, this possibility would not explain the different results of the two studies.

One possible explanation for the different outcome of these two studies is that in our study the final replacement males (i.e., those males that owners had to displace) had lower RHP relative to owners than in Beletsky and Orians' (1987, 1989a) studies. In our main study population we continued removing males from territories until either no replacement male occupied the territory within 12 days of the last removal or the replacement male did not react strongly enough to a model to get caught. Beletsky and Orians caught all their replacement males to band them, and some of these males were caught with models (Beletsky and Orians 1987). While this difference in methods is consistent with final replacements in our study having low RHP, there are several reasons that this explanation may be inadequate. First, final replacements in our study had sufficient RHP to hold the territory in a competitive environment. Second, in related research (Shutler and Weatherhead 1991a, b) we were unable to find any evidence of RHP differences between adult floaters and owners. Third, in the 33 extra territories we used in this study we only did a single removal on each territory and yet 33% of the original owners still were successful at regaining their territories after 6–10 days in captivity. It appears that additional experiments may be necessary to understand the differences between the two studies. Some of these differences may be attributable to differences in the study areas. At any rate, within our study, we must still explain why owners were the only removed males that were regularly able to regain their territories and why differences in payoff asymmetries did not distinguish successful from unsuccessful owners.

We found that the number of neighbors that a male had did not influence the probability that he would be successful regaining his territory if he was removed. This result suggests that there was no advantage to a male from knowing his neighbors and/or from having established boundaries with those neighbors. We had predicted an advantage to neighbor familiarity because Beletsky and Orians (1989b) had shown that males with familiar neighbors had higher reproductive success than those with unfamiliar neighbors. It is possible that the final replacement males held the territories long enough for territory boundaries and neighbor familiarity to become well established. However, if familiarity could be established that quickly, then we should have found that the time an owner was in captivity or the time that his final replacement was on the territory affected the success of owners at regaining their territories. In addition, rapid establishment of familiarity would mean that Beletsky and Orians' (1989b) results do not make sense. They defined neighbors as familiar if they had shared a territory boundary for at least one previous breeding season. However, males in their study with "unfamiliar" neighbors would have certainly known their neighbours for more than a few weeks, suggesting that familiarity takes longer than a few weeks to be established. Thus, it seems unlikely that final replacements in our study were as familiar with their neighbors as were the owners they replace. Therefore, our results indicate that familiarity with neighbors is not an important currency influencing site dominance in red-winged blackbirds.

The final currency we considered was reproductive investment. Again, there was no evidence that there was a payoff asymmetry in favor of the male that had sired young on the territory. In the short term, owners may have little to gain by reclaiming a territory on which they have sired young, because females in this population feed the young almost exclusively (Muldal et al. 1986; Weatherhead 1990). However, males do defend the young and nest success increases with nest defence (Weatherhead 1990). Since replacement males are unlikely to defend young that they have not sired, it should be to the owner's advantage to regain their territories so that they can defend their young.

Because opportunities for siring young decline with the season, the short-term value from claiming territories also declines. Owner success at reclaiming territories was roughly the same from April to July. This implies that replacements' and owners' evaluations of territory value were correlated over the course of the season. Despite declining reproductive opportunities, the strong site fidelity of male red-winged blackbirds (e.g., Picman 1987) suggests that vacancies should be claimed when available for their long term benefit, even if no breeding will occur until the next year. However, our late-season removal experiments sometimes attracted no replacements, which implies that, after breeding has ended, floater occupancy of a territory is of little benefit to site dominance in the subsequent year (contra Yasukawa 1979).

Our inability to detect any value for the currencies we tested (for the internment periods we used) supports Grafen's (1987) contention that payoff asymmetries should be irrelevant to contests for valuable resources. On the other hand, Grafen (1987) also predicted that if reproductive success can only be ensured by obtaining a territory, and if territory vacancies are rare, floaters will become desperados and fight to the death if necessary (also see Enquist and Leimar 1990). However, floater red-winged blackbirds seldom escalate contests for territory ownership (Nero 1956; Orians and Christman 1968; Røskaft and Rohwer 1987; personal observation). Where, then, are the desperados in our population? The success of a desperado relative to that of a pacifist (i.e., one who waits for a vacancy) will depend on several factors. Desperados will incur some cost (injury or death) from engaging in escalated contests with territory owners, but when successful, will have the advantage of obtaining a territory sooner than a pacifist. By contrast, a pacifist will incur no cost in actually acquiring a territory, but must survive long enough to find a vacancy. No information is available on the costs to the participants in escalated contests in red-winged blackbirds. However, from a 6-year study in eastern Ontario, we know that only 125 of 241 (52%) males holding territories in a given breeding season successfully returned to hold territories in the following breeding season (P.J. Weatherhead, unpublished). This return rate is similar to values reported for other populations (Dyer et al. 1977; Searcy and Yasukawa 1981; Picman 1987). Therefore, it seems likely that a pacifist that survives to the next breeding season should have a high probability of finding a vacant territory. If pacifists survive only as well as territory owners (i.e. 50%), then the cost to desperados must be very high for the pacifist strategy to prevail, even given that all the *surviving* pacifists obtain territories. However, pacifists will not incur any of the reproductive costs of territory owners (Partridge and Harvey 1988), and therefore may well survive at a rate substantially higher than 50%. The critical data (i.e. costs to desperados and survival of pacifists) necessary to test the hypothesis that the pacifist strategy is superior to that of the desperado, will be difficult to obtain.

If territory ownership is unrelated to RHP and/or payoff asymmetries, what determines which floaters get territories? Because vacancies occur randomly with respect to habitat quality (Eckert and Weatherhead 1987b), floaters are probably opportunistic in locating and claiming vacancies. If the first floater that locates a vacancy becomes the owner, male reproductive success would be predicated on skills at finding vacancies. After a floater has located a vacancy, other floaters respect territory ownership because they do not want to risk injury in escalated contests. This would imply that, once a vacancy is claimed, the arbitrary rule that "the owner wins over the intruder" (Davies 1978) maintains the owner-floater dichotomy. This arbitrary asymmetry did not explain the outcome of our experiments, because the released original owners did not respect the newly-acquired ownership status of replacement floaters. The approximate 50% success rate of released owners in reclaiming their territories fits expectation for a "symmetric war of attrition", where contestants are evenly matched, but they both assume that they own the territory (Maynard Smith and Price 1973; Waage 1988; Marden and Waage 1990). Our removal experiments forced owners to be absent from their territories longer than occurs in natural situations, and these artificial situations increased the frequency with which wars of attrition occurred.

The success of owners (relative to other removed males) at regaining their territories is also consistent with our hypothesis that we caused owners and final replacements to compete in a symmetric war of attrition. On territories where both owners and replacements were removed, we removed a total of 21 owners and 59 replacement males, and of the 13 males from this group that regained the territory from which they had been removed, all but two were owners. Owners and adult floaters do not differ in RHP (Shutler and Weatherhead 1991a), so the failure of replacement males to regain the territories from which they had been removed cannot be attributed to competitive inferiority. However, replacement males that we removed did differ from both original owners and final replacements in their time of tenure on the territories. We removed replacement males rapidly, resulting in a mean tenure time of 3.9 days, less that the 8 days for final replacements and months or years for owners. The failure of the replacement males to win back the territories from which they had been removed may have been a consequence of them not having held the territories long enough to establish site dominance (that they would have had to retain while in captivity), and therefore not being willing to participate in a symmetric war of attrition with either the original owners or the final replacements.

In natural situations, the arbitrary owner-floater asymmetry may be sufficient to maintain the owner-floater dichotomy, especially if the desperado route is less profitable than respecting the arbitrary asymmetry and simply awaiting opportunities to claim vacancies. The implication is that territory competition is of less importance to male red-winged blackbirds than are the stringent requirements of surviving to adulthood, locating a vacancy, and maintaining the minimum physical attributes necessary to hold the territory.

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