

## Owner and floater red-winged blackbirds: determinants of status

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**Summary.** We used sequential removal experiments to test whether the resource-holding potential (RHP) of territory “owner” red-winged blackbirds, *Agelaius phoeniceus*, was superior to that of their first replacements (“shallow floaters”) and subsequent replacements (“deep floaters”). Among the removals were second-year males, which were morphologically inferior to adults and which also tended to be competitively inferior in aviary contests. The highest proportion of second-year males occurred in the deep floater class. Thus, the RHP of some deep floaters was inferior to that of owners and shallow floaters. However, among adults, owners, shallow floaters, and deep floaters had equivalent morphological and competitive RHP. Furthermore, replacement males that had defended territories for many days were neither morphologically nor competitively superior to males that had defended territories for only a few days. Our results suggest that RHP distinguishes adults from second-year males, but does not separate owners from floaters. The only hypothesis that is potentially supported by our observations is that owners have a greater expected payoff from their territory than intruders, and in this way owners are able to maintain site dominance. The nature of that payoff remains to be determined.

### Introduction

In the competition to breed, some individuals are temporarily or permanently thwarted in their efforts. This can occur in territorial systems where there are fewer suitable territories than there are individuals willing to defend them. Such territorial systems separate individuals into territory “owners” and non-territorial “floaters.” In this paper, we examine the factors that determine which individuals are owners and which are floaters among male red-winged blackbirds, *Agelaius phoeniceus*.

Many male passerines defend breeding territories against conspecific neighbors and floaters. Because females mate almost exclusively with territory owners (e.g., Searcy 1979a; Monnett et al. 1984; Smith and Arcese 1989), males are strongly selected for their ability to become territory owners. The resource-holding potential (RHP) hypothesis proposes that owners have an advantage over floaters in size, weaponry, display, etc. (Darwin 1871; Parker 1974). These types of RHP advantages are sufficient to explain the outcome of some male red-winged blackbird interactions. Males with larger epaulets (patches of red shoulder feathers used in display) are more effective in repelling floaters (Peek 1972; Roskoff and Rohwer 1987) and have greater success in aviary contests (Searcy 1979b; Eckert and Weatherhead 1987a). Similarly, larger males may dominate in aviary contests (Searcy 1979b). Finally, the plumage color of second-year males is intermediate between that of females and adult males (Rohwer et al. 1980) and is also associated with low RHP. For example, Laux (1970) performed removal experiments and found that after several adult males had been removed from a territory, second-year males were able to establish themselves as owners. However, these second-year males were usually driven off by adult males within a few days.

Parker (1974) recognized that intrinsic RHP does not always explain why some individuals win contests. For example, in many passerines, the morphology of owners is indistinguishable from that of adult floaters (e.g., Eckert and Weatherhead 1987a; Hogstad 1989; Smith and Arcese 1989). Also, owners temporarily removed from their territories are often unable to oust replacements (Krebs 1982; Beletsky and Orians 1987, 1989) that, according to the RHP hypothesis, should have less RHP. Similarly, the dominant-subordinate relationship between two individuals can change when they move to a new location (e.g., Desrochers and Hannon 1989; Piper and Wiley 1989), which is clearly independent of intrinsic RHP. Finally, the RHP hypothesis predicts that individuals with the highest RHP will get the best territories. However, Eckert and Weatherhead (1987b, c)

found that males from poor and good quality habitats had similar morphological and competitive RHP.

In cases where asymmetries in RHP do not explain the differences between owners and floaters, the principle alternative explanation for owners winning avian territorial contests is the "value asymmetry hypothesis." [Beletsky and Orians (1989) suggest that "arbitrary asymmetries" are not important in avian territorial systems.] The value asymmetry hypothesis was proposed to explain the observation that the owner usually wins contests with intruders irrespective of small differences in RHP (Maynard Smith and Parker 1976; Davies 1978; Krebs 1982). The value asymmetry explanation for this "site dominance" is that the territory has greater future value to the owner than to the intruder. As a result of this value asymmetry, owners are more willing to invest in territorial contests and thus are more likely to win these contests. This asymmetry in value may arise because the owner has better knowledge of the location of resources, or of territory boundaries and neighbors (Getty 1981, 1987; Stamps 1987), or because the owner will obtain more reproductive return from the territory than floaters (Beletsky and Orians 1987). The asymmetry in territory value may be related to the amount of time invested in acquiring information about resources and neighbors. Thus, the first floater to discover a vacancy may become the owner, even though subsequent challengers have similar RHP (Eckert and Weatherhead 1987a).

RHP and value asymmetry are the extremes of a continuum from intrinsic to extrinsic determinants of territory ownership. There are two situations where the importance of RHP versus value asymmetry has not been evaluated. First, Laux's (1970) removal experiments indicated that second-year males are low in the hierarchy for territory acquisition (i.e. they are "deep floaters"). The female-like morphology of second-year males suggests that they have low morphological RHP. Therefore, adult deep floaters may also have low morphological RHP. This has been tested only for adults that first replace a removed owner ("shallow floaters"). Second, although red-winged blackbird owners and shallow floaters are morphologically equivalent (Eckert and Weatherhead 1987a, b), there is no evidence that they are competitively equivalent. Using the red-winged blackbird, we address both of these issues.

The red-winged blackbird is a common breeding passerine of marshes and other open habitats over much of North America (Godfrey 1986). Sexual dimorphism is pronounced; adult males are black with red epaulets and weigh 50% more than females. The smaller females are cryptic and gray-brown. Males defend breeding territories whereas females build nests, incubate eggs, and account for most of the feeding of nestlings (Orians and Christman 1968).

The species' sex ratio at laying and hatching is equality (Fiala 1981; Weatherhead 1983), and survival rates of adult males and females are roughly equivalent (Searcy and Yasukawa 1981). Territorial males in eastern populations have harem sizes averaging between two and three (Eckert and Weatherhead 1987a). Because

these data imply that approximately 50% of male red-winged blackbirds do not hold territories, the species is well-suited to studies on floaters.

To address the hypothesis that owners have superior morphological RHP to deep floaters, we compared morphological characteristics associated with red-winged blackbird territorial behavior. These included epaulets, which are important to territorial maintenance (e.g., Peek 1972); size and physical condition, which can be related to the rate at which territorial behaviors are performed (e.g., Searcy 1979c; Tatner and Bryant 1986; Santee and Bakken 1987; Reid 1987); and bills and tarsi, which can be used as weapons in territorial contests (Rohwer 1982). We predicted that owners would have larger epaulets, would be in better condition, and would have better weaponry than adult deep floaters.

Males that have only recently acquired territories ("replacements") are intruded on more frequently than established owners (Peek 1971). If replacements with low RHP are driven off early, we predicted that replacements that had occupied a territory longer would, on average, have superior RHP to more recent replacements.

To address the hypothesis that owners have superior competitive RHP to floaters, we had to eliminate extrinsic factors associated with territory ownership. We predicted that, in aviaries away from the birds' territories, owners would outcomplete floaters for food.

## Methods

*General methods.* We studied a migratory population of red-winged blackbirds near the Queen's University Biological Station, located 50 km north of Kingston in southeastern Ontario, Canada. The males in the population defended territories that were either isolated from one another or were contiguous with other territories on small marshes. The isolated territories generally consisted of small (50–200 m<sup>2</sup>) patches of cattail (*Typha* sp.). Some isolated territories were within sight of one another, but no suitable breeding habitat existed between these sites. The marsh territories also had cattails and shared boundaries with up to three neighbors. Territories were adjacent to, and were irregularly spaced along, 30 km of highways.

We removed birds sequentially from these territories to take morphological measurements and to obtain individuals for aviary experiments. We use stuffed decoys (Smith 1976) or mist nets to capture birds between early April and mid-July in 1988 and 1989. Both capture methods relied on playback of territorial song, which evokes the strongest reaction from the current territory owner. The first male captured on a territory was defined as the owner. The first bird to replace a removed owner was defined as a shallow floater. The first bird to replace a shallow floater was defined as a deep floater, as were individuals that replaced deep floaters. We continued to remove birds from a territory until either no replacement appeared or we were unable to capture the replacement within 12 days of the previous removal. Occasionally, males of unknown owner-floater status were accidentally captured in mist nets. These males were not included in the analysis.

We had to be certain that all replacements were floaters rather than owners. This was easy for the 20% of the cases where neighbors adjacent to removal territories were banded. In the remainder of the cases, we observed whether replacement males annexed the vacancies we created to adjoining, pre-existing territories. Annexing was only observed on contiguous marsh territories. Where annexing occurred, removals were terminated.

In 1988, we removed birds as quickly as they responded to decoys and were captured. This occurred in as little as 15 min

after the capture of the original occupant. In 1989, we waited a minimum of 2 days between removals to allow more time for ownership to be contested.

**Morphological comparisons.** All measurements were taken when the birds were captured. We took two measures of epaulet length (length of red and length of yellow were the distance from the bend of the folded wing to the furthest extent of red and yellow feathers in the wing, respectively; Searcy 1979b). As indices of body size and weaponry, we measured unflattened wing length, tarsus length, bill length, and bill depth. We weighed birds and computed body condition as weight divided by the cube of wing length (Searcy 1979a). We then used discriminant function analysis to attempt to separate owners from floaters based on overall morphology (see Freeman and Jackson 1990).

**Behavioral comparisons.** Birds captured from the same territory were housed together in a  $3 \times 2 \times 1.5$  m compartment of an outdoor roofed, mesh aviary. Birds were provided food (cracked corn, millet, and Purina chick starter) *ad libitum* in long troughs with a divider down the middle and always had access to two water dispensers.

To aid in the identification of individual birds on videotape, we bleached approximately 5 cm of the end of three or four feathers on the wing and/or tail in unique combinations. Bleaching was done by massaging a commercial hair dye powder and 20–30% peroxide into the feathers until most of the feather pigment came out. The feathers were then rinsed with water. Further details of these and other aviary methods are given in Eckert and Weatherhead (1987a).

We removed from one to nine birds from individual territories, but only 15 territories yielded two or more males, i.e., enough for comparisons of competitive ability in aviary trials. A day or more before aviary experiments were initiated, we placed all captured birds from a given territory in an unfamiliar aviary compartment. This was done to overcome any established site dominance for a particular compartment. The night before an aviary trial, all food was removed from the compartment. The next morning, we provided a single food dish that allowed only one bird to feed at a time. Interactions at the food dish were videotaped for later analysis. After approximately 2 h, the trial ended, and the long food troughs were returned to the aviary compartment. Three to ten trials were run (depending on the group size and the frequency of interactions during videotaping) so that most dyads had interacted a minimum of 10 times.

Competitive interactions at the food dish varied from threat displays to outright attacks. The victory was assigned to the bird retaining possession of the food dish following the interaction. At the end of the trials, we totalled the number of victories and losses within dyads and, using binomial tests, tested whether the ratio of victories to losses was significantly different from random.

All statistics were analyzed on a microcomputer using the Statistical Package for the Social Sciences (Nie 1988).

## Results

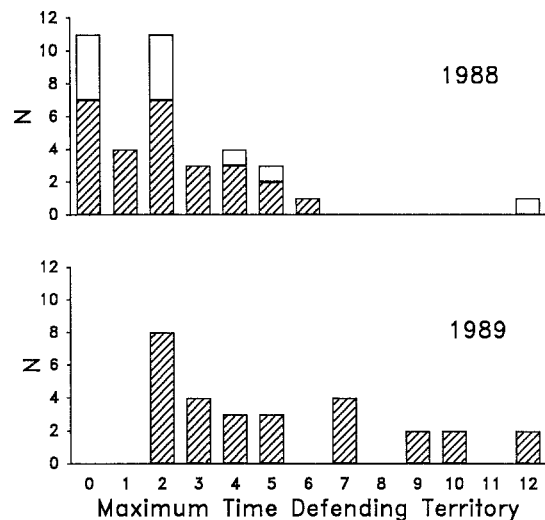
### Morphological comparisons

Our experimental design required that, on average, we capture owners earlier in the season than floaters. This could potentially bias our results if any of the morphological features we were measuring varied seasonally. To assess this possibility, we examined morphology versus capture date among territory owners. We used only owners because their date of capture was independent of when they became resident on the territory (i.e., early in the spring). Among owners, we found that birds had shorter wings, longer and deeper bills, and weighed less

**Table 1.** Seasonal change in morphological measures for adult owners ( $N=56$ ). Values shown are the correlations between the morphological measure and Julian date

Morphological measure	$r$
Length of red	-0.08
Length of yellow	-0.02
Wing length	-0.38**
Tarsus length	-0.08
Bill length	0.34**
Bill depth	0.50***
Weight	-0.58***
Condition	0.03

\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$



**Fig. 1.** Maximum time in days a male occupied a territory before being captured in 1988 (mean =  $2.0 \pm 1.8$  days) and 1989 (mean =  $5.2 \pm 3.2$  days; Mann-Whitney  $U$ -test,  $Z = -3.9$ ,  $P < 0.001$ ). Hatched areas represent adults and unshaded areas represent second-year males

when they were captured later in the season (Table 1). In subsequent analyses, in order to control for these seasonal changes, we used the residuals from regressions of morphological data against Julian date for each year. So as not to weaken our test of the prediction that inferior males would be captured later in removals, we used the regression equations for owners to calculate residuals for all males.

We captured a total of 127 males. Fifty-seven were owners, 25 were shallow floaters, and 45 were deep floaters. In 1988, 13 second-year males were captured (Fig. 1). Only 1 was an owner (2 were shallow floaters, and 10 were deep floaters). By comparison, in the same year, 28 of 57 adults were owners (chi-square = 5.88,  $P = 0.02$ ). This suggests that second-year males were unable to hold territories as long as adults. Furthermore, second-year males weighed less and had smaller epaulets and wings than adults (Table 2). In summary, the morphology of second-year males was related to lower RHP.

We did not capture any second-year males in 1989 (Fig. 1). This could be due to our sampling method:

**Table 2.** Comparisons of the morphology of second-year males ( $N=13$ ) and adult males ( $N=114$ ). Values shown are means ( $\pm$ SD) in mm except where indicated;  $t$ -values are based on a comparison of the residuals following regression against Julian date

Morphological measure	Adults	Second-year males	$t$
Length of red	37.4 $\pm$ 2.1	35.1 $\pm$ 0.9	6.2***
Length of yellow	43.2 $\pm$ 2.6	39.4 $\pm$ 2.8	4.2***
Wing	121.3 $\pm$ 3.1	117.4 $\pm$ 3.8	3.6***
Tarsus	25.5 $\pm$ 1.4	25.7 $\pm$ 0.7	-1.2
Weight (g)	68.5 $\pm$ 3.5	64.7 $\pm$ 5.1	2.4*
Condition (g/mm <sup>3</sup> $\times$ 10 <sup>5</sup> )	3.8 $\pm$ 0.3	4.1 $\pm$ 0.3	-1.9
Bill length	22.9 $\pm$ 1.1	23.0 $\pm$ 0.6	-0.5
Bill depth	11.6 $\pm$ 0.6	11.9 $\pm$ 0.6	-1.8

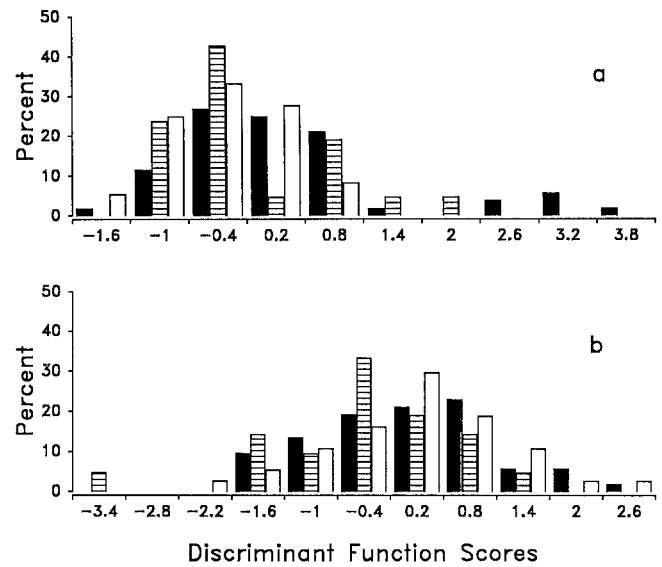
\*  $P < 0.05$ , \*\*\*  $P < 0.001$

**Table 3.** Comparison of the morphology of adult owners ( $N=56$ ), shallow floaters ( $N=23$ ), and deep floaters ( $N=35$ ). Values are means in mm except where indicated and are for data pooled from both years. There were no significant differences between groups either within years or with data from both years pooled (based on seasonally adjusted residuals, ANOVA,  $P > 0.10$ )

Morphological measure	Owners	Shallow floaters	Deep floaters
Length of red	37.7 $\pm$ 1.9	37.9 $\pm$ 1.7	37.1 $\pm$ 1.9
Length of yellow	43.6 $\pm$ 2.9	43.7 $\pm$ 1.9	43.0 $\pm$ 2.7
Wing length	122.1 $\pm$ 3.4	121.4 $\pm$ 3.4	120.9 $\pm$ 2.8
Tarsus length	25.6 $\pm$ 1.3	25.4 $\pm$ 1.1	25.3 $\pm$ 1.3
Bill length	22.8 $\pm$ 1.2	22.7 $\pm$ 1.0	22.9 $\pm$ 0.9
Bill depth	11.6 $\pm$ 0.6	11.6 $\pm$ 0.6	11.8 $\pm$ 0.6
Weight (g)	68.7 $\pm$ 3.4	68.6 $\pm$ 2.9	68.5 $\pm$ 4.1
Condition (g/mm <sup>3</sup> $\times$ 10 <sup>5</sup> )	3.8 $\pm$ 0.3	3.8 $\pm$ 0.3	3.9 $\pm$ 0.3

in 1988 we removed males as quickly as possible, but in 1989 we waited at least 2 days between captures on a territory (see "General methods"). This longer interval in 1989 could have resulted in more competition among replacements, thereby preventing any second-year males from holding territories long enough for us to capture them. However, 8 of the 11 second-year males captured in 1988 were caught 2 or more days after the previous male had been removed (Fig. 1). Thus, the difference in the methods between the 2 years would seem not to account for the differences in captures of second-year males. Possibly, the floater population was smaller in the first year of the study, and thus second-year males were able to hold territories longer than they could in 1989. The reasons the floater population would have been smaller are unknown, which points out our incomplete understanding of this segment of the population.

Among adults, we found no morphological differences between owners, shallow floaters, or deep floaters in univariate measures (Table 3). A discriminant function analysis was able to classify only 44% of adults as either owners, shallow floaters, or deep floaters (Fig. 2). Similarly, adult shallow floaters were morphologically indistinguishable from adult deep floaters (Ta-



**Fig. 2.** Comparison of the morphology (adult males only) of owners (solid bars), shallow floaters (hatched bars), and deep floaters (unshaded bars) for the first (a) and second (b) discriminant functions ( $N=110$ ). There were no differences between the three groups in discriminant function scores for the first (chi-square = 13.4,  $df=16$ ,  $P=0.64$ ) or the second discriminant function (chi-square = 3.6,  $df=7$ ,  $P=0.82$ ).

**Table 4.** Factor loading of the morphological variables on the factors from a factor analysis, following varimax rotation, for 1988 ( $N=27$ ) and 1989 ( $N=28$ ). Factor loadings  $\geq 0.6$  are underlined. Correlations between the factors and the maximum time the replacement had occupied the territory are also given ( $P > 0.10$ )

Morphological measure	1988				1989		
	Factor				Factor		
	1	2	3	4	1	2	3
Length of red	-0.2	0.8	-0.1	-0.1	<u>0.7</u>	0.3	0.3
Length of yellow	-0.1	<u>0.6</u>	0.3	0.1	<u>0.5</u>	0.3	0.6
Wing length	-0.8	<u>0.4</u>	0.3	0.1	0.9	0.3	-0.2
Tarsus length	-0.1	0.2	0.8	-0.3	<u>0.2</u>	0.5	0.1
Bill length	0.1	-0.1	<u>0.8</u>	0.2	-0.1	0.1	0.6
Bill depth	0.1	0.1	<u>0.1</u>	0.9	0.1	0.6	-0.5
Weight	0.3	<u>0.8</u>	0.2	<u>0.1</u>	-0.1	<u>0.9</u>	0.2
Condition	- <u>1.9</u>	<u>0.2</u>	0.1	0.1	- <u>0.8</u>	<u>0.3</u>	0.3
Correlation of factor with time as owner	-0.1	0.1	0.3	-0.3	-0.1	-0.2	0.2

ble 3; Fig. 2). For adults then, morphology did not predict owner-floater status.

As previously argued, the time a replacement male held a territory before we caught him could reflect his RHP, since the longer a male defended a territory, the more he would have been challenged. Among adult replacements, we analyzed morphology relative to maximum possible residence time. Maximum residency for a given male was the time between his capture and that of the previous capture in that territory. We used a factor analysis to test for changes in overall morphology. We

found that there were no significant correlations between the maximum time a male had occupied a territory and his morphology (Table 4).

### Behavioral comparisons

Sixty-four birds – including 15 owners, 13 shallow floaters (2 shallow floaters escaped), and 36 deep floaters – were used in 15 aviary experiments (each experiment involved all the males removed from one territory). Of these birds, 10 were second-year males (1 owner, 1 shallow floater, and 8 deep floaters).

In most of the aviary experiments, the winner of a dyad in the first trial won in all subsequent trials. We consider only dyads where binomial tests indicated a clear victor after all trials were pooled. Adults won more contests with second-year males than they lost (17 of 21 dyads won,  $P=0.004$ ). Only 5 second-year males accounted for these dyads (one territory had 5 second-year males and no adults). Thus, these results are not completely independent. Of these 5 males, 2 won more dyads than they lost, and 3 lost more dyads than they won. Our results thus offer only weak support for the hypothesis that second-year males have low competitive RHP.

Among adults, owners did not outcompete floaters in either year, or when years were pooled (19 of 35 dyads won,  $P=0.37$ ). Similarly, owners did not outcompete either shallow floaters (6 of 11 dyads won,  $P=0.50$ ) or deep floaters (13 of 24 dyads won,  $P=0.42$ ). Finally, shallow floaters did not outcompete deep floaters (13 of 25 dyads won,  $P=0.50$ ). We thus have no evidence for differences in competitive RHP between adults.

We also tested whether males that had occupied territories for many days won a greater percentage of dyads than males that had occupied territories for a few days only. We found no relationship between the length of time a replacement had defended a territory and his success rate in the aviary (Fig. 3).

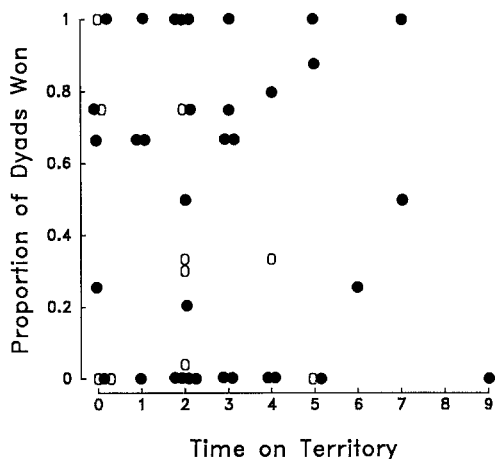


Fig. 3. Proportion of dyads won versus the number of days a replacement had occupied a territory ( $r_s = -0.07$ ,  $P=0.32$ ,  $N=45$ ). Closed circles represent adults; open circles represent second-year males

### Discussion

We have no evidence that differences in adult male RHP determine which become territory owners and which remain floaters in red-winged blackbirds. However, low RHP does hinder the majority of second-year males from becoming territory owners. In the aviaries, even unmeasured variables such as adult age, physiology, etc. did not distinguish owners from floaters. The only situation in which owners dominated adult floaters was on the territory.

It is still possible that, shortly after we created a vacancy, adult males with inferior RHP were intimidated by the stuffed male decoys we used for trapping, or they were driven off by contestants with superior RHP. Thus, adults with inferior RHP would not appear in our data. Nonetheless, owner and floater adults that were willing to contest the territory did not differ in any of our measures of RHP.

Our results thus only offer support for the value asymmetry hypothesis. Grafen (1987) has pointed out that value asymmetry alone is not evolutionarily stable because it always assigns the intruder a losing role, creating a “divisive asymmetry.” The value asymmetry hypothesis was based on the observation that owners consistently evicted intruders (e.g., Davies 1978), and this led to the interpretation that territory ownership consistently conferred an advantage in contests. Grafen (1987) instead suggested that floaters must test several owners to determine which owners have sufficiently low RHP to be usurped. In Davies’ (1978) study of speckled wood butterflies (*Pararge aegeria*), territory ownership had no effect on the outcomes of *escalated* contests. Thus, although owners win the majority of contests over intruders, in escalated contests owners and floaters have similar chances (Grafen 1987).

Despite the intuitive appeal of Grafen’s arguments, our evidence strongly supports a value asymmetry explanation for the differences between adult owners and floaters. Further support for the value asymmetry hypothesis was obtained by Krebs (1982) and Beletsky and Orians (1989). In both of these studies, males were removed from their territories and held captive. Replacement males were allowed to occupy the newly created vacancies for various durations. When the owners were released, replacements that had held the vacancies longer were the most likely to fend off the released owner and hold on to the territory. These results suggested that longer occupancy times shifted the value asymmetry in favor of the floater. Thus, value asymmetry has received some additional empirical support.

One possible resolution of these results with Grafen’s viewpoint is that RHP has not been adequately measured. For example, perhaps our aviary experiments placed our birds in artificially high densities or atypical circumstances (Rowell 1974). However, our aviary densities were less than those of roosting red-winged blackbird (Eckert and Weatherhead 1987a). Furthermore, dominance status in aviaries often correlates with dominance status in the wild (Rothstein et al. 1986), and, as just discussed, this applies to interactions between

second-year males and adults. Thus, we feel our aviary results are not confounded by the effects of crowding. Another potential objection to our results is that we measured dominance using food as the object of competition rather than territories or mates. Dominance with respect to food resources may not reflect dominance for more valuable resources (reviewed by Searcy 1979c). Furthermore, in a review of fatal fighting in animals, Enquist and Leimar (1990) concluded that contests for food are not likely to escalate. Thus, our aviary results may not reflect the RHP traits associated with territory acquisition.

Enquist and Leimar (1990) concluded that escalations were less frequent in species that have several reproductive opportunities in a lifetime. If younger individuals avoided risky contests because it improved their chances of reproducing later on, this would be an "undivisive asymmetry" (Grafen 1987). In contrast, older individuals have less reproductive future, and thus less to lose from escalations. This explanation can only apply if senescence occurs in the population; otherwise all individuals have the same reproductive expectations regardless of age. However, mortality in adult male red-winged blackbirds appears to be constant (Searcy and Yasukawa 1981). Thus, we have no evidence that age contributes to site dominance, and we cannot resolve our findings with Grafen's (1987) arguments.

If we have not measured RHP realistically, then the most plausible explanation of our results is that owners have superior competitive skills to floaters in escalated contests. This would imply that owners' competitive skills in unescalated contests do not correlate with competitive skills in escalated contests. Furthermore, it would predict that owners held in captivity for a few days would always regain their territory from floater replacement, which is contrary to what Krebs (1982) and Beletsky and Orians (1989) have found. If our measures of RHP are realistic, then owners hold their territories against intruders because the territory is worth more to the owner than it is to the floater. The causes for the greater relative value of the territory to owners remain to be determined.

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