Behav Ecol Sociobiol (1989) 24:333–339

Behavioral Ecology and Sociobiology

Territoriality among male red-winged blackbirds

III. Testing hypotheses of territorial dominance

L.D. Beletsky and G.H. Orians
Department of Zoology, NJ-15, University of Washington, Seattle, WA 98195, USA

Received October 21, 1988 / Accepted January 31, 1989

Summary. We tested two hypotheses to explain territorial dominance in male birds. Male red-winged blackbirds were removed from their territories for 7 d and then released after replacement owners had held their territories 2 to 7 d. Original owners regained territories from short-term replacements, but could not defeat 6 to 7 d replacements. This outcome suggests that replacement males relinquished their territories to persistent original owners after 2 to 3 d of ownership because the territory lacked sufficient value to them, but not after 7 d, when its value was greater. This result supports the Value Asymmetry Hypothesis of territorial dominance and provides strong evidence in birds that differences in the extent of knowledge of or investment in an area and, hence, willingness to escalate contests, contribute to territorial dominance.

Introduction

Several hypotheses to explain animal contest strategies (Maynard Smith 1974; Parker 1974; Maynard Smith and Parker 1976; Parker and Rubinstein 1981) are now being tested as they apply to dominance and territoriality (e.g., Krebs 1982; Rohwer 1982; Petrie 1984; Barlow et al. 1986; Beletsky and Orians 1987b). Two of these hypotheses are especially applicable to many avian territorial systems, where owners normally defeat all challengers, usually without having their fighting abilities seriously tested. The *Value Asymmetry Hypothesis* (VA) asserts that owners win because the territory has greater value to them than to challengers (e.g., because owners know the location of resources and escape routes or have stable relationships with neighbors). Therefore, payoffs for owners are potentially greater and they are motivated to escalate contests further than are challengers. The *Resource Holding Potential Hypothesis* (RHP) states that residents hold territories because they are better fighters than challengers. Relatively high RHP could arise from combinations of genetic, experiential, and situational factors. The *Arbitrary Rule Hypothesis*, which suggests that there is a simple arbitrary rule (e.g., "the owner always wins") that is respected by all contestants, is more likely to function when territories are short-lived and there is always a surplus of suitable breeding habitat. This hypothesis is not considered here because neither of these conditions is met among most territorial birds.

Previously (Beletsky and Orians 1987b) we evaluated these hypotheses of territorial dominance in red-winged blackbirds (*Agelaius phoeniceus*) by removing territorial males, retaining them in captivity for up to 49 h, and then releasing them to challenge their replacements. We found that original owners nearly always regained their territories and suggested that VA explained the results better than RHP. However, RHP could not be ruled out completely because both hypotheses predicted that removed males should regain territories under the conditions of those experiments. The purpose of the present study was to extend testing of VA and RHP by performing two additional types of removal experiments. In the first experiment we held males off their territories for up to 7 d, long enough to reduce their chances of recovering their territories. VA and RHP make different predictions about contest outcomes in this case. If dominance is due predominantly to RHP, then, because of condition loss, the probability of an original owner regaining a territory shortly after

Offprint requests to: L.D. Beletsky

release should decline with time in captivity. However, if males are able to regain lost condition after release, they should *always* recapture their territories from replacements who have lower RHP, which is why they did not hold territories in the first place.

If dominance is due primarily to VA, then the probability that a male recaptures his former territory should also decline with time in captivity because the territory becomes more valuable to the new owner as a result of his acquisition of knowledge, better relations with neighbors, and, eventually, genetic investments. Even if original owners regain their condition after release, they might *not* be able to recapture their territories because their improved condition may not offset the increased value of the territory to the new owner. Of course, both VA and RHP could contribute to territorial dominance, but one may have the more dominant role.

However, even if VA is supported by the result of this type of experiment, RHP might still operate if original owners suffered some long-term but undetectable loss of RHP while in confinement. Therefore, we designed a second type of removal to separate the strong correlation in all of our previous removal experiments between the length of time original owners were off their territories and the length of time replacement males were on them. Our method was a double removal experiment, in which we removed initial replacement males 4 to 5 d after they had taken over the territories, so that the original males held for 6 to 7 d in captivity faced replacements who had held their territories for periods no longer than 48 h.

If the original owners held 7 d were unable to regain their territories, it would suggest that they did, indeed, lose condition in captivity (RHP), because males held for only 2 d and replaced for 1 to 2 d do recover their territories (Beletsky and Orians 1987b). If the original males were successful in regaining their territories, however, it would indicate that the new owners did not yet value the territory enough after 1 to 2 d to raise their willingness to defend it sufficiently to overcome the higher VA of the original owners. This result would also show that the RHP/VA of original owners was not affected sufficiently by 7 d in captivity to prevent their regaining their territories.

A bird in captivity may suffer deterioration in body weight and muscle tone, attributes that must contribute to RHP and territorial dominance under natural conditions. Another factor that may influence dominance, but that has not been evaluated in removal experiments, is circulating hormone levels. Testosterone (T) is a steroid hormone known to affect aggressive behavior and dominance in birds and other animals (Searcy and Wingfield 1980; Moore 1984; Wingfield et al. 1987). Territorial male redwings have significantly higher circulating T levels than floaters during the breeding season (Beletsky et al. 1989). It is plausible that circulating T levels contribute to determining which males are capable of holding territories (RHP). We took blood samples from some of our captive males and measured plasma T levels to determine the effects of caging during removal experiments on hormone levels.

Methods

Removal experiments were conducted on marshes on the Columbia National Wildlife Refuge in south-central Washington State during the breeding seasons of 1986 through 1988. The area and the breeding biology of redwings are described in detail by Orians and Christman (1968) and Orians (1980). A map of the study area is provided by Beletsky and Orians (1987a). A complete description of male territories, our removal procedures, and descriptions of territorial contests, are found in Beletsky and Orians (1987b).

The present set of removals were performed early in the breeding season before any females arrived in the study area or, if they were already present, before they settled permanently on male territories. At this time of year, vacated territories are occupied quickly by adult, non-territorial replacement males. By completing all current removals and releases prior to nesting, we eliminated any influence of relative parental investments by original and replacement owners on contest outcomes.

All original owners were marked for individual identification with U.S.F.W.S. bands and unique combinations of colored legbands. Replacement males that were not already banded were captured in seed traps and banded prior to the releases of original owners.

Males were removed from their territories in mid-March, after boundaries had stabilized. Males removed each year held contiguous territories and all or most males on a given marsh were removed during a single 3-hour period. By removing most males on a marsh, few neighbors remained to expand their territories. Almost all territories were claimed by new replacement males, sometimes within 30 minutes of a removal, but always by dawn of the following day.

Males were held in outdoor cages (66 cm × 73 cm × 78 cm) out of sight of and 300 to 500 m from their home marshes. They were given water, sunflower seeds, cracked corn, and cereal ad libitum and mealworms each morning. Each male was weighed at the time of capture and at the time of release. Males were released at their cages, and observers were stationed at their territories to determine if they returned immediately (within 15 to 30 minutes) and to record contests if they occurred.

Because original owners held 7 d in 1986 and 1987 failed to regain their territories from 6 to 7 d replacement males, we trapped and removed as many of the replacement males as possible either 8 weeks (1986) or 4 weeks (1987) after original males were released (see below). The replacement males were held for 4 d, giving the original males still present in the area opportunities to reclaim territories.

In 1988, the first set of 11 replacement males were removed from territories 2 d before the original owners were released.

These replacement males were held for 13 d, giving the original owners and the second set of replacement males sufficient time to settle their contests without interference from these males, and then released.

To determine testosterone levels of captive males, blood samples (200–300 µl) were taken from wing veins from 9 owners held for 7 d in 1987. Each male was bled when he was trapped, after 3 d in captivity, and after 6 d, each time between 0700 and 0800. Territorial males are apparently unaffected by this treatment because they return immediately to their territories when they are released and retain their dominance there (Beletsky et al. 1989). For a description of sampling methods and hormonal assays, see Beletsky et al. (1989).

Results

Most males held up to 49 h returned immediately to their territories and fought their replacements. In contrast, few males held for 7 d returned immediately to their territories (Table 1), and when they did, they were usually quickly chased off by their replacements. Thus, even though many males held for up to 2 d lost their first contests with replacements, their behavior at release indicates they maintained their condition and willingness to fight better than males held for the longer periods. Many males released after 7 d were not observed near their home marshes until the day after their release, suggesting that they rested and fed for a day before challenging for their territories. In fact, one male in 1988 that did not regain his territory was caught in a grain trap 3 km away only 2 h after his release, and one male that did regain his territory within 48 h was captured in a grain trap 3 km from his territory 24 h after release.

Can original owners recover their territories from 6 to 7 d replacements?

Only 2 of 18 (11%) territory owners in 1986 recovered their territories from replacement males (Table 1), one 24 h and one 48 h after release. We replicated the experiment in 1987, with a similar result; only 2 of 7 males (29%) held 7 d and whose replacements held the areas 6 to 7 d, regained territories following their releases (one in 72 h and one in 96 h). The combined percentage of males recovering territories after 7 d in captivity from long-term replacements, 16% (4 of 25), is substantially and significantly less than the percentage of males that recovered territories after only 1 to 2 d in captivity (91% (50 of 55); *t*-test of the differences between two percentages (Sokal and Rohlf 1969), $t = 7.07$, 1-tailed $P \ll 0.001$). In 1987, 2 males removed from their territories for only 4 d, facing 4-d replacements, and 3 males removed for 7 d but facing replacements who had occupied their territories for only 3 d at the time of their release (due to late insertions by floaters), had greater success (Table 1), suggesting that the duration replacement males owned territories affected the probability that the original owners could defeat them.

Are males held 7 d physically and "psychologically" capable of again holding territories?

Although a few males replaced for 6 to 7 d did defeat their replacements (as did 2 of the 3 males

Table 1. Results of experiments in which male redwings were removed from their territories, held in captivity, and subsequently released, 1983 to 1988

Year	Marsh	Date of removals	Number of males removed	Time held	x̄ weight loss in captivity (g)	x̄ weight loss in captivity (% of body weight)	*n*	Time replacement on territory at release	% returning to territory immediately after release	Number (%) recovering territories
1983–1985	varied	varied	55	7–49 h	1.0±1.5	1.4±1.9	43	3–48 h	67.5	50 (91)
1986	Unit 3	26 March	18	7 d	5.2±2.5	6.9±3.2	18	6–7 d	16.7	2 (11)
1987	Frog Lake	21 March	9	7 d	3.9±1.5	5.3±2.0	9	6=7 d 3=3 d	20.0[b]	1 (17) 2 (67)
			1	6 d	2.0	2.9	1	6 d, 2 d[a]		1 (100)
			2	4 d	1.0±1.4	1.3±1.8	2	4 d		2 (100)
1988	Hays Creek	19 March	8	7 d	3.7±2.1	4.9±2.7	11	1=24 h 7=48 h	27.3	8 (73)
			3	6 d				2=24 h 1=48 h		

[a] Two males replaced this original owner, one inserting on the territory 4 d after the other;
[b] Only males held 6 to 7 d

held 7 d who faced 3-d replacements), most could not. Loss of condition in captivity could have contributed to their failure, and explained why fewer males held for 7 d returned immediately to their territories at release (Table 1). Our main indicator of condition loss is weight loss (Beletsky and Orians 1987b). Males held 6 to 7 d in 1986 and 1987 lost an average of 4.6 ± 2.1 g ($n=28$), substantially more weight than males held only 7 to 49 h (Table 1). However, three lines of evidence suggest weight loss did not significantly change male motivations or decisively affect the final outcomes of territorial contests.

First, many released males were observed repeatedly, over several weeks, particularly early in the morning, on their home marshes, challenging their replacements. Their behavior suggests that they were still interested in their former territories and had sufficient energy to make repeated challenges. Second, by trapping at the experimental marsh during the 12 d following releases of the males in 1986, we caught and weighed 10 of the original owners, including the 2 that regained territories. Many of these individuals had rapidly recovered lost weight. Four of the 8 males that had not recovered their territories had regained all the weight they lost in captivity (2 exceeded their initial weights) and the other 4 had gained from 1 to 5 g since their release. On average, these 8 males were at $97.4 \pm 3.6\%$ of their initial capture weights within 3 to 4 d of release. The 2 males that regained territories, trapped 2 to 3 d afterwards, weighed only 1 to 2 g less than they did when initially captured. Thus, males remained in the area following release and quickly recovered weight lost in captivity. It should also be noted that changes in redwing body weight of up to 5% within 48-h periods are common during the breeding season (4 g from a mean of 75 g; Beletsky and Orians 1987a; Orians and Beletsky, unpublished data).

Third, to determine whether original owners that did not evict replacements were still capable of owning territories, we removed a total of 14 replacements (8 in 1986 and 6 in 1987) 4 or 8 weeks following releases of original owners. By early morning the day following, 6 original owners (3 in each year) that had failed to recover their territories, had done so. (Four additional original owners from 1986 reoccupied their territories in 1987, as did one original male from the 1987 removals by 1988). Therefore, owners released after 7 d in captivity regained lost weight, were fully capable of holding territories, and were clearly very attentive to their former territories. They could not, however, defeat long-term replacements.

Can males removed 7 d recover territories from replacements owning them only 1 to 2 d?

Eight of 11 (73%) original owners held 6 to 7 d in 1988 regained their territories from replacement males that had owned them only 1 to 2 d when they were challenged by the original owners. One did so 40 min after release, 3 did so within 24 h, 3 more did so within 48 h, and one did so by evicting his replacement after 20 days. Thus, a significantly higher percentage of males held 7 d in captivity recovered their territories when they faced short-term rather than long-term replacements (73% vs. 16%, $t=-3.37$, 2-tailed $P=0.0008$). The 1988 males ($n=11$) did not lose, on average, less weight than the 1986 and 1987 males ($n=28$; absolute weight, $t=-1.13$, 1-tailed $P=0.13$; percent of body weight, $t=-1.24$, $P=0.11$). Thus, a difference in weight lost does not account for the different outcomes of the territorial contests.

Testosterone levels and removals

Average T levels for the 9 males sampled in 1987 were 0.60 ± 0.3 ng/ml plasma at the time of capture (day 0), 0.82 ± 0.97 ng/ml 3 days later (day 3), and 0.18 ± 0.15 ng/ml 6 days later (day 6; the day prior to release). T levels between day 0 and day 3 were not significantly different (Wilcoxon matched pairs test, $z=0.42$, 2-tailed $P=0.68$), but T levels declined significantly between day 3 and day 6 ($z=-2.10$, $P=0.04$) and between day 0 and day 6 ($z=-2.43$, $P=0.02$). Thus, these males at the time of their releases had significantly lower T levels than the average for territorial males in the area. Moreover, average T levels in free-living redwings tend to rise, not fall, during this part of the breeding season (Beletsky et al. 1989).

Discussion

Our removal experiments produced artificial situations in which more than one male sequentially owned the same territory. Although such situations in redwings occasionally occur naturally, they do not typify owner-challenger interactions. Therefore, results obtained with such manipulations must be interpreted cautiously. Nonetheless, we believe that our results assist us in understanding normal territory owner-replacement and owner-challenger interactions. Indeed, it is difficult to devise alternative, more powerful tests.

If RHP governed territorial possession and dominance, and if physical condition (hence, RHP) deteriorated in captivity, released males should

have recaptured their territories when they recovered lost weight. Additionally, replacement males, presumably of lower initial RHP than original owners, should not have been able to retain dominance on territories once the original owners regained their RHP. This was clearly not the case in our first set of 7-d removals (1986 and 1987) because most males could not evict their replacements even after they regained lost weight. Therefore, the RHP Hypothesis cannot explain our results unless we postulate that the original owners never regained their high RHP even though they recovered lost weight.

When replacement males held territories for 1–4 d, they usually could not prevent original owners from regaining dominance. When replacements owned territories for 6–7 d, they usually defeated former owners. Changes in the original or replacement owners, or in both, could account for this difference. The evidence presented here suggests that the key change occurs in the replacement males.

The motivation of released owners was apparently no different in 2-d and 7-d removals. Males released after 7 d remained in the area and persistently tried to recover their territories; in a few cases they succeeded. Even though the condition of removal males, as measured by weight, was negatively affected by captivity, it rapidly improved. As demonstrated by our secondary removals in 1986 and 1987, these males were fully capable of re-establishing and defending their territories. Thus, the key factor in our experiments that affected whether owners could recover their territories was the length of time replacement males owned territories, not motivational or conditional changes of original owners. On this basis we conclude that the VA Hypothesis of territorial dominance better explains our 1983 through 1987 results than does the RHP Hypothesis.

The results of our 1988 removals further strengthen the conclusion that value asymmetries play an important role in territorial dominance. If loss of RHP in captivity affected our results, then the males held 7 d but facing 2-d replacements should have failed to regain territories. However, most of these males did defeat their replacements, most of the time within 48 h, indicating that changed RHP of original owners played little or no role in the final outcomes of these experiments. Rather, the length of time replacement males held territories determined the outcomes, as predicted by the VA hypothesis. Our results suggest that a territory rapidly gains in value to a replacement so that within 6 or 7 d any prior VA has disappeared, at which point the current resident may have a tactical advantage.

Our conclusion that differences in RHP between owners and replacements had little effect on the final outcomes of our contests is supported by a recent study of redwing territoriality by Eckert and Weatherhead (1987a). They found that replacement males from the floating population did not differ from original owners in body or epaulette size. They concluded that differences in morphological factors that may be associated with competitive ability (RHP) do not determine which males obtain territories. Their study did not address the question of value asymmetries. In contrast, Rohwer (1982) scored territorial redwings and their replacements for fighting ability, and concluded that original owners were, on average, better fighters, supporting the RHP hypothesis. However, he found that some "inferior" males did hold territories. Our results suggest that new territory owners, regardless of their RHP, might not vigorously attack a mount (Rohwer's assay) during their first few days of occupancy because their dominance is not yet complete.

We can only speculate about the basis of value asymmetries that affect redwing dominance. Parental investment was ruled out as a possible contributing factor in our study because experiments were conducted before nesting started. The knowledge differential between replacements owning territories 2 d or 7 d could involve a combination of factors such as increased knowledge of territorial escape routes and hiding places, predator activity patterns, feeding areas on and near territory, the quality and location of nest sites, etc., and increased familiarity with neighbors (Krebs 1982). These territorial attributes could be learned within a week but might be difficult to learn within 2 or 3 d. Preliminary bonds with females may also strengthen, increasing the value of a territory. Loss of information might also affect motivation and the valuing of a territory by original and replacement owners.

Average circulating testosterone levels of males declined in captivity. This decline is consistent with the "Challenge Hypothesis" of T secretion (Wingfield et al. 1987), which suggests T levels are high only when males are challenged by conspecifics. At release, then, males held 7 d were triply disadvantaged: they were not necessarily aware that they had been replaced and may have been surprised and attacked when they first returned to their territories (Beletsky and Orians 1987b); they had lost weight; and their T levels were low. Because the current view is that T facilitates ex-

pression of aggressive behaviors (Wingfield et al. 1987), the decline in T levels we found may help explain why many males that eventually recovered territories could not defeat their replacements during their initial encounters. However, T levels probably had little effect on long-term RHP or on final contest outcomes, because circulating T can rise significantly in songbirds within 10 min of aggressive encounters (Wingfield et al. 1987).

We cannot explain why a few males held off their territories 1 to 2 d and 3 of the 1988 males held 7 d failed to recover their territories. Individual differences among males, alone or in conjunction with situational factors, may have been responsible. For example, some males may be especially sensitive to being held captive and may have left the area upon release. Alternatively, some removal males may have been, by chance, individuals of relatively low RHP, capable of defending a territory once they own it, but not capable of challenging successfully as a floater (see below). Finally, because redwings inflict severe damage on one another (Rohwer 1982), some males may have been injured during early fights for their territories.

Individual differences were also apparent in the time it took original males to recover their territories. A few males removed for only 1 or 2 d, for instance, did not regain their territories for a week or more after release (Beletsky and Orians 1987b). At the extreme, one male in 1988 recovered his territory only after 20 d. In these cases a "war of attrition" (Parker and Rubinstein 1981) occurred, in which persistence by original owners finally overcame the resistance of replacements. These delayed recoveries suggest that a new owner may not be able to attain full dominance quickly on a territory, i.e., be capable of defeating all challengers, if he undergoes a serious challenge for ownership early in his tenure, of the type and intensity to which we exposed our replacements. Of course, few new owners in nature face such immediate and powerful threats to their dominance.

Our interpretation of the 1988 double removal experiment is based on the assumption that the second set of replacement males had the same RHP as the first replacements in our previous experiments. We believe this to be the case for several reasons: 1) Rohwer (1982), working near our study area, scored first and second replacement male redwings on the same territories for fighting ability, and found that second replacements were as good or better fighters as first replacements 57% of the time. 2) There were many floaters in the study area during our 1988 removals (personal observations); and 3) even if there were as few as one high RHP floater per territory in the removal area, there were at least 40 additional territories immediately adjacent to the experimental marsh, from which high quality floaters could have been drawn.

We have presented strong evidence that value asymmetries at least partially determine territorial dominance in redwings, and that these asymmetries, probably involving knowledge acquisition, develop within 7 d. However, we do not suggest that RHP plays no role in deciding territorial contests between owners and challengers. Rather, we suggest that between individuals nearly evenly matched in fighting ability, victory often may be decided by willingness to escalate. In most cases, the individual most willing is the resident, who values the territory more. Although resident redwings nearly always defeat challengers, some floaters do insert between established owners or defeat them for their territories (Nero 1956; Yasukawa 1979; Eckert and Weatherhead 1987a; Orians and Beletsky, unpublished data). These floaters may be individuals of truly superior RHP who had not yet obtained territories, or they may have injured their opponents during early clashes (Rohwer 1982; Freeman 1987). Freeman (1987) has shown that male redwings probably assess their neighbor's RHP and use the information in contests over boundary positions.

Finally, chance may influence which male redwings get territories. Where males are resident all year, as is the case in our population, most males may obtain territories by being the first to discover recent vacancies. Thus, owners may vary widely in RHP, and males of highly variable RHP may be able to maintain their territories by their willingness to escalate contests further than are most challengers. It may be difficult for challengers to assess the real RHP of territory owners, and the risk of injury may be sufficient to deter random escalated challenging. If so, there would be a poor correlation between male and territory quality, as found recently by Eckert and Weatherhead (1987b). Although claiming a territory regardless of its quality may be an important first step for many male redwings to enter the breeding population, it is not necessarily their last. These males are known to shift to higher quality territories in their areas when vacancies occur (Beletsky and Orians 1987b).

Acknowledgements. We thank Sievert Rohwer, Bill Searcy and Jamie Smith for reviewing drafts of this paper and Tammy Olson, Mathew Titcomb, Tom Steedle, Sharon Birks, John McCarty, Glenna Stewart, and Martha Dunham for invaluable assistance during removal experiments. Refuge Manager Dave

Goeke provided permission to conduct this study at the Columbia National Wildlife Refuge. This work was supported by National Science Foundation grants BNS 8405486 and BRS 8614620 awarded to Gordon Orians. Les Beletsky was supported by NSF Post-doctoral Fellowship BSR 8600123.

References

Barlow GW, Rogers W, Fraley N (1986) Do Midas cichlids win through prowess or daring? It depends. Behav Ecol Sociobiol 19:1–8

Beletsky LD, Orians GH (1987a) Territoriality among male red-winged blackbirds. I. Site fidelity and movement patterns. Behav Ecol Sociobiol 20:21–34

Beletsky LD, Orians GH (1987b) Territoriality among male red-winged blackbirds. II. Removal experiments and site dominance. Behav Ecol Sociobiol 20:339–349

Beletsky LD, Orians GH, Wingfield JC (1989) Steroid hormones and polygyny: Relationships to territorial status, breeding experience, and reproductive success in male red-winged blackbirds. Auk (in press)

Eckert CG, Weatherhead PJ (1987a) Owners, floaters and competitive asymmetries among territorial red-winged blackbirds. Anim Behav 35:1317–1323

Eckert CG, Weatherhead PJ (1987b) Ideal dominance distributions: A test using red-winged blackbirds (*Agelaius phoeniceus*). Behav Ecol Sociobiol 20:43–52

Freeman S (1987) Male red-winged blackbirds (*Agelaius phoeniceus*) assess the RHP of neighbors by watching contests. Behav Ecol Sociobiol 21:307–311

Krebs JR (1982) Territorial defence in the great tit (*Parus major*): Do residents always win? Behav Ecol Sociobiol 11:185–194

Maynard Smith J (1974) The theory of games and the evolution of animal conflicts. J Theor Biol 47:209–221

Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:159–175

Moore MC (1984) Changes in territorial defense produced by changes in circulating levels of testosterone; a possible hormonal basis for mate-guarding behavior in white-crowned sparrows. Behaviour 88:215–226

Nero RW (1956) A behavior study of the red-winged blackbird. II. Territoriality. Wilson Bull 68:129–150

Orians GH (1980) Some adaptations of marsh-nesting blackbirds. Princeton University Press, Princeton

Orians GH, Christman GM (1968) A comparative study of the behavior of red-winged, tricolored and yellow-headed blackbirds. Univ Calif Publ Zool 84:1–81

Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223–243

Parker GA, Rubinstein DI (1981) Role assessment, reserve strategy and acquisition of information in asymmetric animal conflicts. Anim Behav 29:221–240

Petrie M (1984) Territory size in the moorhen (*Gallinula chloropus*): An outcome of RHP asymmetry between neighbors. Anim Behav 32:861–870

Rohwer S (1982) The evolution of reliable and unreliable badges of fighting ability. Am Zool 22:531–546

Searcy WA, Wingfield JC (1980) The effects of androgen and antiandrogen on dominance and aggressiveness in male red-winged blackbirds. Horm Behav 14:126–135

Sokal RR, Rohlf FJ (1969) Biometry. Freeman, San Francisco

Wingfield JC, Ball GF, Dufty AM, Hegner RE, Ramenofsky M (1987) Testosterone and aggression in birds. Am Sci 75:602–608

Yasukawa K (1979) Territory establishment in red-winged blackbirds: Importance of aggressive behavior and experience. Condor 81:358–364