Movement patterns and territory acquisition by male red-winged blackbirds

DAVE SHUTLER[1] AND PATRICK J. WEATHERHEAD[2]
Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada

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Movements of nonterritorial ("floater") male red-winged blackbirds (*Agelaius phoeniceus*) were monitored to test the hypothesis that floaters enhance their chances for territory acquisition by becoming familiar with a specific area, i.e., by restricting their geographical movements and monitoring only a few occupied territories. Intensive observations from two separate study areas did not support the hypothesis. Only 8% of the 410 males banded as floaters in an unmanipulated study area claimed territories or were ever recaptured on that study area, suggesting that floaters visited a very large number of territories. When territory owners were experimentally removed in a second study area, a greater proportion of floaters remained in the vicinity (29% of 80 males), indicating that one proximate control of floater dispersal was the availability of vacancies. Radiotelemetry confirmed that floaters ranged widely. Floaters continued to disperse as they aged, and most floaters that acquired territories probably did so outside the study areas. These patterns of dispersal and territory acquisition suggest that familiarity with a small number of territories and their owners is not a better strategy than continual dispersal for most floater red-winged blackbirds in these populations. Once adulthood was reached, younger floaters were not less successful than older floaters at claiming vacancies. This, combined with the effects of mortality, results in the majority of floaters and the majority of new territory claimants being young adult males.

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Les déplacements des Carouges à épaulettes (*Agelaius phoeniceus*) mâles non territoriaux (« reproducteurs non cantonnés ») ont été suivis dans le but d'éprouver l'hypothèse selon laquelle les reproducteurs non cantonnés augmentent leurs chances de s'approprier un territoire en se familiarisant avec une région spécifique, i.e., en restreignant leurs déplacements et en explorant seulement quelques territoires occupés. L'observation intensive d'oiseaux dans deux zones distinctes n'a pas permis de corroborer l'hypothèse. Seulement 8% des 410 mâles bagués et reconnus comme des reproducteurs non cantonnés dans une zone d'étude non perturbée ont usurpé des territoires ou ont été recapturés dans la même zone, ce qui semble indiquer que ces oiseaux visitent un très grand nombre de territoires. Dans une seconde zone d'observation, les propriétaires des territoires ont été enlevés expérimentalement et une plus grande proportion des reproducteurs non cantonnés sont restés dans le voisinage (29% de 80 mâles), ce qui indique que l'un des facteurs immédiats de la dispersion de ces oiseaux est la disponibilité des territoires non occupés. La radiotélémétrie a confirmé que les mâles non cantonnés se déplacent sur de grandes distances. Les reproducteurs non cantonnés ont continué de se disperser à mesure qu'ils vieillissaient et la plupart de ceux qui se sont approprié un territoire l'ont probablement trouvé hors des limites des régions d'étude. Ces modèles de dispersion et d'acquisition d'un territoire indiquent que la familiarisation avec un petit nombre de territoires et avec leurs propriétaires ne représente pas une meilleure stratégie que des déplacements continuels pour la plupart des carouges reproducteurs non cantonnés de ces populations. À l'avènement de l'âge adulte, les jeunes « non cantonnés » n'ont pas moins de succès que les reproducteurs non cantonnés plus âgés à s'approprier des territoires non occupés. Ce phénomène, combiné aux effets de la mortalité, a pour résultat que la majorité des reproducteurs non cantonnés et la majorité des nouveaux prétendants à un territoire sont de jeunes mâles adultes.

[Traduit par la Rédaction]

Introduction

Although the presence of surplus territory contenders (floaters) has been documented or suggested for many bird species (reviewed in Brown 1969), there are few species for which patterns of floater movement have been determined. In species in which reproductive success is predicated on territory ownership, a floater's movement patterns may be critical to its success at acquiring a territory (Yasukawa 1979; Stamps 1987). The paucity of information regarding how and where floaters acquire territories represents an important gap in our understanding of essential aspects of gene flow and of the reproductive biology of many birds. The importance of this gap to conservation biology has also been recognized (Verner 1992). In this paper, we examine movements of floater red-winged blackbirds, *Agelaius phoeniceus*, and the spatial pattern of territory acquisition by those floaters.

Patterns of territory acquisition have been determined for three passerines. Smith (1978) monitored the movements of floater rufous-collared sparrows, *Zonotrichia capensis*. She found that floater home ranges encompassed four territories or less, and that floaters that eventually claimed territories did so within three territories of where they were originally banded. Subsequent studies revealed that floater black-capped chickadees, *Parus atricapillus*, and song sparrows, *Melospiza melodia*, also had home ranges that included 10 or fewer territories (Smith 1984; Arcese 1987, 1989). Males of each of these species often spend half of their lives as floaters.

The data for these three passerines indicate that floaters are relatively sedentary, suggesting some advantage to restricted home ranges. However, the benefits of restricted home ranges are not well understood. Furthermore, the generality of sedentary strategies for other passerines is not known, particularly

[1]Present address: Department of Zoology, Oregon State University, Cordley Hall 3029, Corvallis, OR 97331-2914, U.S.A.
[2]Author to whom all correspondence should be addressed.

as none of the three species studied to date is migratory. In terms of potential benefits, it has been suggested that sedentary floaters have better information than more vagrant floaters about which territory owners are in failing health, or about the location of territory boundaries (Stamps 1987). Better information may save sedentary floaters energy both in finding suitable territories and, on the territories they claim, in disputing territory boundaries (Nolan 1978; Stamps 1987). Alternatively, floaters may form a hierarchical queue waiting for a territory (Smith 1978), and individuals are only able to maintain their rank in the queue by regular interactions with its members. Additional advantages proposed for area familiarity include better knowledge of predator locations, escape cover, or foraging areas (Nolan 1978; Smith 1978). These latter advantages may not apply to species such as red-winged blackbirds that are preyed on by predators with large home ranges, that occupy open habitats where escape cover is limited, and that frequently forage off their territories (see Orians and Beletsky 1989).

If area familiarity provides sedentary floaters with an advantage, they need to visit territories repeatedly within their home range to update their information, or else they would lose their advantage over vagrant floaters. Small advantages in anticipating or recognizing vacancies may be tremendously important to territory acquisition because owners that disappear are usually replaced within minutes (Eckert and Weatherhead 1987*b*; Beletsky and Orians 1989; Shutler and Weatherhead 1991*a*). Floaters that visit only one territory probably do not maximize the number of territories for which they can remember and (or) update information. On the other hand, floaters cannot maintain current information for an infinite number of territories. Given this trade-off between the number of territories visited and the quality of information that is retained for each territory, there may be an optimum number of territories that a floater should monitor. For the species for which data exist (see above), that optimum may be quite small.

In this context, we analyzed movements of floater red-winged blackbirds. The red-winged blackbird is a common breeding passerine of open marshes and uplands of North America (Orians 1980). Males of migratory populations return to the northern breeding grounds where they defend territories against conspecific males. The species sex ratio at hatching and laying is equality (Fiala 1981; Weatherhead 1983), fledgling sex ratios are slightly female-biased (Weatherhead and Teather 1991), and survival of adult males and females is roughly equivalent (Searcy and Yasukawa 1981). All females mate (Holcomb 1974), but all males do not. Many populations are polygynous; in eastern North America harem sizes for males holding territories average between two and three (Eckert and Weatherhead 1987*a*). These data imply that at least 50% of male red-winged blackbirds in this area are floaters (also see Beletsky 1992). Because male reproductive success in red-winged blackbirds is predicated on territory ownership (Gibbs et al. 1990), there is intense selection for males to acquire territories.

One might expect that fighting ability would be more important to territory acquisition than area familiarity for red-winged blackbirds. However, fighting appears to be of limited importance for this species (Nero 1956; Yasukawa 1979; Eckert and Weatherhead 1987*b*; Shutler and Weatherhead 1991*a*). In addition, once a territory is acquired, owners rarely need to be aggressive in defending it against floaters because most floaters wait until an owner disappears rather than using aggression to claim a territory (Nero 1956; Yasukawa 1979; Picman 1987). Together, these observations suggest that floaters which are successful in acquiring territories are simply the first ones to discover a vacancy. This reinforces the suggestion that area familiarity is important to red-winged blackbird strategies for territory acquisition. If this is so, we expect that floater red-winged blackbirds would have home ranges that encompass a limited number of territories both within and between years, and that the same floaters should be detected repeatedly and eventually claim territories within the same area. We monitored the movements of floater red-winged blackbirds over several breeding seasons to determine whether these predictions were met. We also increased the number of vacancies available in one area to increase the rate at which floaters could claim territories, thereby enhancing our opportunities to observe floater territory acquisition.

Study areas and methods

We studied red-winged blackbirds near the Queen's University Biological Station (45°37′N, 76°13′W; Fig. 1). We used a woodland study area where data on floaters have been gathered opportunistically as part of a larger study begun in 1985, and a roadside study area where data were gathered from 1988 to 1990 specifically for the purpose of studying floaters. The two study areas were separated by approximately 7 km, and birds banded in one study area have not been seen in the other study area in this or previous investigations (Eckert and Weatherhead 1987*a*; Muma and Weatherhead 1989). The data we report are for marked floaters that were identified when they visited a territory, were recaptured, or acquired a territory. Data were obtained between early April and mid-July in each year. Procedures differed between the two study areas, so we present the respective methods separately.

The woodland study area

The woodland study area contained a series of cattail (*Typha* sp.) and willow (*Salix* sp.) marshes with areas of intervening woodlands and uplands in which red-winged blackbirds did not occur (Fig. 1). Some of the marshes were studied from 1985 to 1990; study on the remaining marshes began in 1987 or 1988. In the woodland study area, observations were collected for 245 territory-years. Owners were banded in 237 (97%) of those territory-years.

Three different methods were used to capture owners and floaters in the woodland study area. First, floaters that were trespassing on territories were sometimes caught inadvertently in mist nets that were being used to capture territory owners (only territory owners were given unique colour-band combinations in this area). Second, floaters were captured in 3.5 × 3.5 × 2.5 m feed traps (Weatherhead and Greenwood 1981) baited with corn and live decoys (a brown-headed cowbird, *Molothrus ater*, and (or) an adult male red-winged blackbird). These traps were run continuously from April to June in each year. Third, birds were captured in mist nets as they entered one of the study marshes to roost at night. For all capture methods, floaters were given single, numbered aluminum bands. Thus, subsequent identification of these birds was restricted to recaptures. Because more than 96% of the owners in this study area were banded in each year and only 5 of these owners were caught using the methods we used to catch floaters, we appear justified in assuming that the unbanded birds we captured were floaters.

In each year in this study area, all nestlings were banded just before they fledged. This allowed us to determine whether floaters and territory claimants had been produced locally.

The roadside study area

In the roadside study area, red-winged blackbird territories were spaced irregularly along 30 km of paved highways (Fig. 1). Males in

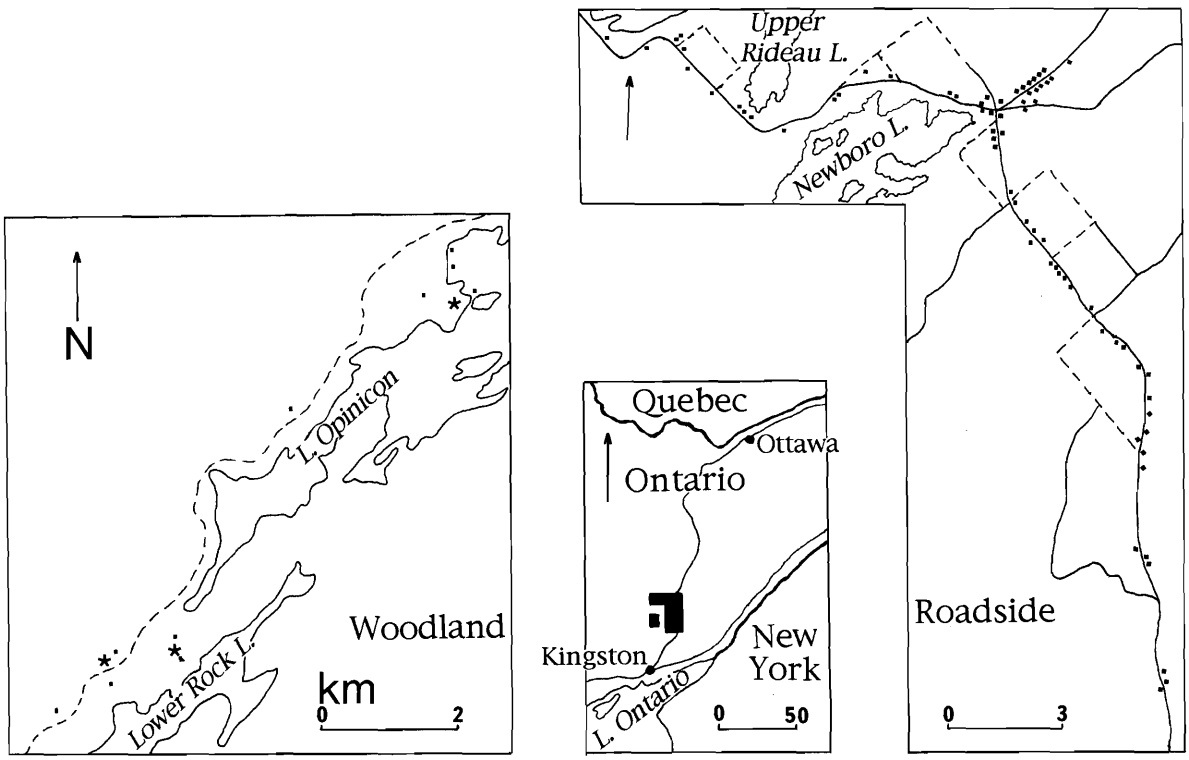

FIG. 1. Location of the woodland (left) and roadside (right) study areas relative to each other (center). Solid squares denote the location of marsh and isolated territories. In the roadside study area each solid square represented an average of 1.3 territories (range 1–7), whereas in the woodland study area the number of territories per solid square averaged 3.9 (range 1–15). The asterisks denote the positions of feed traps. Solid lines denote principal roadways and shorelines. Broken lines indicate unpaved roads.

this study area occupied either isolated territories that were separated by areas of habitat unsuitable for breeding (i.e., plowed fields or forest) or contiguous territories on small roadside cattail marshes of between 8 and 20 territories. Our protocol in this study area was to band and release as many floaters as possible. We did this with sequential removals. Male territory occupants were trapped (Smith 1972) or mist-netted using stuffed male decoys and tape recordings of territorial song. Vacancies were often claimed within minutes of removal of the previous occupant.

We called the first males occupying territories "owners" because observations of banded individuals indicate that these males seldom change after April 1 (e.g., Eckert and Weatherhead 1987*b*). Forty-two owners were released immediately after they had been banded; these owners were monitored for natural territory turnover rates. The remaining 48 of the 90 territory owners that we captured were held temporarily (2–30 d) in outdoor aviaries to create vacancies for floaters (Shutler and Weatherhead 1992). In 15 of 152 (10%) removals (including removals of floater replacements), a vacancy was annexed by a neighbouring male. When this occurred, we terminated removals on that territory. We observed no instances where a banded territory owner relinquished a territory to claim a vacancy that we had created. Furthermore, because long-term studies have shown that territorial male red-winged blackbirds rarely switch territories during the breeding season (Beletsky and Orians 1987; data below), we assume that replacement males that were not neighbours had previously been floaters. In more than 90% of the roadside removals in this and previous studies, a floater claimed the vacancy (Eckert and Weatherhead 1987*b*; Shutler and Weatherhead 1991*a*). To create further opportunities to witness territory acquisitions, and to create a population of banded floaters, we also removed floater replacements and held these birds in aviaries as well. We continued to remove subsequent floater replacements in this manner until a replacement was not sufficiently aggressive to be captured, or until the territory remained vacant for 12 d. Overall, we captured a total of 80 floaters that had claimed vacancies we had created. Removals were done more or less continually in the breeding seasons of each of the 3 years, and were irregularly spaced geographically within the study area. In 1988, we also banded 80 nestlings just before they fledged with single, numbered aluminum bands.

All male territory occupants that we captured in this study area were given unique colour-band combinations and eventually released back to the territory from which they had been removed. Half of the owners reclaimed their territories when released, irrespective of how long they had spent in captivity or the stage of the breeding season when they were released (Shutler and Weatherhead 1992). Floaters were also released on the territories from which they had been captured, at the same time or a few days before the original owner was released. Only two floaters claimed the territory from which they had been captured, and these events were not related to when the owner had been released or to how long the floaters had spent in captivity (Shutler and Weatherhead 1992). Thus, almost all floaters returned to the floater population when released. Elsewhere (Shutler and Weatherhead 1991*b*) we provide evidence that sequential removals did not affect harem size on territories; hence, territory value to females was not changed by male removals.

We bleached two or three wing and (or) tail feathers of the birds that we held in the aviary (see Eckert and Weatherhead 1987*a*), which made these birds easier for us to detect in the field. As stated above, half of the owners were able to reclaim their territories. In comparison, Beletsky and Orians (1989) found that only 16% of territory

TABLE 1. Numbers of floaters and nestlings banded and released in the woodland study area

Method of capture	Year						Total
	1985	1986	1987	1988	1989	1990	
Second-year floaters							
Decoy	12	5	6	8	9	14	54
Feed trap	49	36	27	17	6	10	145
Roost[a]	29	44	24	43	—	—	140
Total	90	85	57	68	15	24	339
After-second-year floaters							
Decoy	1	0	4	0	0	1	6
Feed trap	12	8	4	5	0	2	31
Roost[a]	17	8	5	4	—	—	34
Total	30	16	13	9	0	3	71
Nestlings (both sexes)							
At the nest	131	158	188	284	225	301	1287

NOTE: Data for owners are given in the text.
[a]No roost captures were attempted in 1989 or 1990.

owners released after 6–7 d in captivity reclaimed their territories. The higher rate at which owners reclaimed territories in our study suggests that bleaching had no significant effect on our owners, therefore we have no reason to suspect that it affected floaters.

To monitor movements of banded floaters, we gathered over 600 h of field observations on all likely sites in the roadside study area. Although we used only territories that were adjacent to highways, territory density here was much higher than in the neighbouring agricultural and forested land and along the adjoining unpaved roads (also see Clark and Karr 1979). Based on air photographs, we estimate that roadside territories accounted for about 70% of all territories within the study area (Fig. 1). Some of the sites we used were mowed or otherwise destroyed over the course of this study, while others appeared to become suitable only after sufficient growth of vegetation. However, more than 70% of the sites were used by red-winged blackbirds in all 3 years. Hence, we were able to obtain observations of both within-year and between-years movements and patterns of settlement. In total we monitored 94 different territories over the 3 years (Fig. 1). In the roadside study area, most of these territories were observed in more than 1 year, for a total of 209 territory-years.

During visits to territories, we identified banded males that were occupying or visiting focal and (or) neighbouring territories. Our intensive observations were gathered during 5-min observation periods from a vehicle parked 20–30 m from a focal territory. During the breeding season, 5 min is usually sufficient to determine whether a territory is occupied and to determine the identity of the occupant if he is banded. Morning (05:00–10:00) and evening (18:00–20:30) observation periods occurred systematically (i.e., beginning one territory beyond where we had left off), except that visits were made more often to territories where we had recently captured or released males. Weather permitting, we visited on average 30 territories each day, so territories were visited 2 or 3 times per week. We made additional observations during trapping, or on foot in the middle of the day during nest searches.

In 1989, we monitored the movements of eight floaters more closely with radiotelemetry. We first captured territory owners and placed them in aviaries. The first floater replacements were then captured, at which time the owners were released. Radio transmitters (Holohil Systems Ltd., Woodlawn, Ontario) weighing 2 g (<3.3% of a male's body mass) were attached to the floaters by means of elastic harnesses (Morrison and Caccamise 1985). The transmitters had a range of approximately 1.5 km and a battery life of about 3 months. The elastic in the harnesses breaks down with exposure to the elements, and the transmitters fall off prior to migration. We held radio-equipped floaters in aviaries overnight to be certain that they could fly normally and could not remove their transmitters. These floaters were released on the territories on which they had been captured; in all cases they did not stay on the territory because they either flew off on their own or were driven off by the current territory occupant. Checks were made for the floaters' radio signals 2–5 times per week until the end of June. Three 10-min signal checks were made from each of the two points 0.5 km in either direction along the highway from the territory, and from the territory itself. Thus, signal checks should have detected radio-equipped floaters within an area of slightly less than 3 × 4 km.

TABLE 2. Numbers of birds banded and released in the roadside study area

	Year			Total
	1988	1989	1990	
Territory owners	43[a]	19	28	90
Floaters	37	23	20	80

[a]Includes 10 males banded in previous studies of Eckert and Weatherhead (1987*a*) and Muma and Weatherhead (1989).

Results

Make-up of the banded populations

Although male red-winged blackbirds mature sexually in the first breeding season after they fledge (i.e., at approximately 1 year old), they do not attain full adult male plumage until the following year (Wright and Wright 1944; Orians 1961; Payne 1969). Therefore, we could identify males as being in their second calendar year (SY) or after their second calendar year (ASY; 2 years old or more). In the woodland study area we banded 112 owners and 410 floaters. All the owners were ASY males, and 83% of the floaters were SY males (Table 1). In the roadside study area we banded 90 territory owners, all but 1 of which were ASY males (Table 2). On the 48 experimental territories, we caught a total of 80 floaters that claimed the territories when the owner or an earlier replacement had been removed. Among these floaters, only 15% were SY males. The striking difference in

the proportion of SY males caught in the two study areas can be attributed to the different methods of capturing floaters. SY males seldom claim territories (Orians and Christman 1968; Shutler and Weatherhead 1991*a*; data above), and in the roadside study area we only captured floaters when they claimed territory vacancies. In contrast, floaters in the woodland study area were captured before they had claimed territories.

Potential influences on floater data

To compare the movements of floaters from the two study areas, we needed to determine whether aviary internment of males from the roadside population affected their survival, and whether survival differed between the study areas. Because many of the interned owners reclaimed their territories after release (Shutler and Weatherhead 1992), we compared the survival rate of the interned owners that reclaimed their territories with the survival rate of banded, non-interned owners. (We assumed that any effects of internment on owners would be the same for floaters.) Of 15 interned owners that reclaimed their territories, 6 (40%) failed to return to their territories in the following breeding season. In comparison, 17 of 40 (42%) non-interned owners in the roadside study area (the territories of 2 non-interned owners were destroyed between years) and 52 of 124 (42%) in the woodland study area disappeared between the beginning of successive breeding seasons. The similar rates of return for the interned and non-interned males suggest that captivity had no effect on survival, and the identical rates of natural territory turnover (42%) in the two habitats imply that owner survival was equivalent in both habitats. Hence, males survived equally well in both habitats, and had no removals been performed, an equivalent proportion of territories would have become vacant for floaters in both habitats. It seems reasonable to assume that floaters survive equally well in the two habitats, although their survival might differ from that of territory owners.

In the woodland study area, a total of 113 vacancies occurred in 237 territory-years (0.48 per territory-year). The causes of these vacancies were owner disappearances (111) and movements by owners to new territories (2). In the roadside study area, our male removals increased the availability of vacancies to 0.97 per territory-year (201 vacancies for 209 territory-years). Of these vacancies, 75% (152) were created by our removals. Other causes of vacancies included 42 owner disappearances within or between years (21%), the appearance of 6 new territories as growth of vegetation transformed previously marginal habitat (3%), and 3 owners moving to new territories (1%). In sum, the removal experiments doubled the number of vacancies available per territory-year in the roadside study area, and this increased the probability that a floater in this area would encounter a vacancy.

Within-year floater movements

If floaters have restricted home ranges, they should be seen repeatedly in the same locale and many should eventually establish territories in that locale. To assess this prediction, we first consider within-year resightings of floaters and within-year territory acquisition by floaters. In the woodland study area we could "resight" a floater only if he was recaptured because floaters all had only plain leg bands. We recaptured only 13 of 410 (3%) floaters within the same year they were banded as floaters. In the roadside study area, where floaters were given unique colour-band combinations and had bleached feathers, we observed 13 of the 80 (15%) floaters trespassing in the same year they had been banded as floaters. We should note that we regularly observed trespassing by unknown floaters, so the low resighting rate of banded floaters is not a reflection of infrequent trespassing or cryptic behaviour by floaters. The proportion of SY and ASY floaters that we resighted was roughly equivalent in the two study areas. In the woodland area we resighted 1 of 71 (1.4%) ASY floaters and 12 of 339 (3.5%) SY floaters. In the roadside area, 11 of 68 (16%) ASY floaters and 1 of 12 (8%) SY floaters were resighted.

TABLE 3. Percentage of time during which floaters with radio transmitters were detected relative to the interval since their release

Date male released	Total time spent checking for radio signals (min)	Percentage of time male detected after: 0 d	1 d	10 d
12 May	580	8	5	0
17 May	235	45	52	80
18 May	350[a]	—	0	0
24 May	300	57	32	36
25 May	165	50	21	0
28 May	215	14	10	0
5 June	125[a]	—	28	0
7 June	105[a]	—	0	0
Average	259	34.8	18.5	14.5

[a]No signal checks were made on the day of release.

The radio transmitters provided additional information about within-year floater movements. Although floaters with or without radios usually flew out of sight when released back to a territory (Shutler and Weatherhead 1992), all radio-equipped floaters stayed within the 1.5-km range of the receiver for the first hour after their release (Table 3). One day after the radio-equipped floaters were released, 6 of 8 were still near their territory, but most were detected during less than half of the time spent searching for them (i.e., they were probably moving in and out of receiver detection range). After 10 d, only two males could be located (Table 3). One of these two males disappeared after 18 d. The second male remained in the vicinity of his original territory after 18 d and claimed the site when the territory owner was removed. This male also reclaimed the territory in the subsequent year. This floater was exceptional, since all the remaining floaters dispersed from the focal territory. Our low success rate at detecting radioed floaters suggested that we should widen our search area. Beginning 9 June, as part of the regular search routine, we checked for all eight of the transmitter signals (2 min per signal) at each territory where a radio-equipped floater had been released. On the 10 d when this was done, we failed to detect any radio-equipped males. Thus, most of the radio-equipped floaters had evidently left the study area completely.

We have no evidence that floaters' movements were affected by the radios. First, 89% of the non-radio-equipped floaters in both study areas also disappeared after they were released, and few were ever resighted. Second, two radio-equipped males (one of which disappeared after release) were able to return a year later and claim territories. Thus, the radiotelemetry data provide further evidence that floater

TABLE 4. Original status of banded males in the woodland study area that claimed vacancies

	Year						
	1985	1986	1987	1988	1989	1990	Total
	Number of vacancy claimants in the year[a]						
Unbanded males	8	9	12	19	15	15	78
Males banded as:							
owner or neighbour	0	4	2	0	5	5	16
floater	0	3	1	3	5	1	13
nestling	—	—	1	3	1	2	7
	Estimated number of between-years survivors						
Males in floater population banded as:							
floater	—	72	104	104	109	74	463
nestling	—	—	16	28	40	58	142
No. of territories observed	30	31	48	48	43	45	245

NOTE: See text for explanation of survival estimates.
[a]All vacancies were claimed and all vacancy claimants were adults.

TABLE 5. Original status of banded males in the roadside study area that claimed vacancies relative to their estimated abundance in the population

	Year			
	1988	1989	1990	Total
	No. of vacancy claimants in the year			
Unbanded males[a]	48	57	52	157
Males banded as:				
owner or neighbour (released)	5	5	13	23
floater	1	4	4	9
nestling	—	—	2	2
	Estimated no. of between-years survivors			
Males in floater population banded as:				
floater	—	22	27	49
nestling	—	—	10	10
No. of territories observed	65	75	69	209

NOTE: Vacancy claimants were after-second-year males except where noted. See text for explanation of survival estimates. Eleven territories remained vacant in 3 years.
[a]Includes 10 second-year males.

red-winged blackbirds seldom stay within a small, restricted area, and this explains why we saw so few of our banded floaters.

Between-years floater movements

We now consider observations of floaters between years. Note that the second year in which floaters were seen, they were all ASY males. Because observation effort differed between study sites, we estimated the cumulative number of opportunities we had to see floaters in each study area. We assumed that 60% of all males (SY and ASY, owner and floater) survived to the following year (Searcy and Yasukawa 1981) and then accumulated the expected number of floater survivors for each year (bottom of Tables 4 and 5). In the woodland study area, 14 of 463 (3%) floaters had claimed territories, and 5 were recaptured as floaters. In the roadside study area, of an estimated 49 ASY male floaters that would have been part of the floater population a year or more after banding, 8 (16%) had claimed territories, and 1 was still a floater. The higher territory claim rate in the roadside study area is likely due to the higher proportion of vacancies we created there.

The bottom line is that despite our having banded 490 floaters and accumulated hundreds of hours of territory observation and trapping effort, only 56 floaters banded in our study areas were recaptured or seen holding territories in those study areas. Some of these floaters would have died, but it is likely that the majority dispersed beyond our study areas.

Fledglings versus floaters

For familiarity with the area to have the most benefits, it should be gained during the breeding season, when harem sizes and territory boundaries can be assessed. Because of the late stage of the breeding season at which they leave the nest, fledglings have less opportunity to obtain this information than SY or ASY floaters. Thus, we would expect that floaters would disperse less than fledglings because floaters would have more accurate information about specific areas. We thus compared the proportion of birds banded as floaters and nestlings that eventually claimed territories or were detected floating. We assumed that 50% of all nestlings were males (Fiala 1981; Weatherhead 1983), and that 20% of the nestlings banded survived to their second year (Weatherhead et al. 1982; Curio 1989) and 60% survived each subsequent year. In the roadside study area, of 10 male nestlings (fledglings) estimated to have survived to adulthood, 2 claimed territories (20%, Table 4), which is comparable to the return rate for floaters assumed to have survived (Fisher's exact test, $p = 0.44$). Similarly, in the woodland study area, 11 of 142 (8%) male nestlings that were estimated to have survived to adulthood claimed territories or were recaptured, which is also comparable to the proportion of floaters that stayed in the vicinity (Table 5; $\chi^2 = 1.1$, $p = 0.29$). These data suggest that floaters disperse at the same rate as fledglings. Seven of these 11 males banded as nestlings in the woodland study area were territory claimants, and they filled only 13% of the 54 vacancies that occurred during the study period. This indicates

TABLE 6. Number of banded nestlings, second-year floaters (aged 1), and after-second-year floaters (aged 2 or more) that eventually claimed territories in the woodland study area

	Age (years)			
	1	2	3	4
Nestlings (n = 643)				
No. of estimated survivors	129	77	46	28
No. claiming territory		5	2	0
		(6.5)	(4)	(0)
Second-year floaters (n = 339)				
No. of estimated survivors		203	122	73
No. claiming territory		8	2	0
		(3.9)	(1.6)	(0)
After-second-year floaters (n = 71)				
No. of estimated survivors			43	26
No. claiming territory			2	1
			(4.7)	(3.8)
Total		13	6	1
		(4.6)	(2.8)	(0.8)

NOTE: See text for explanation of survival estimates. n is the number of males banded. Numbers in parentheses are the percentages of estimated survivors.

that most fledglings dispersed outside the study area and that most territory claimants were newcomers and likely floaters from outside the study area (also see Beletsky and Orians 1987; Orians and Beletsky 1989). These conclusions are essentially unchanged if we increase or decrease our estimates of survival rates by 10%.

Age and territory acquisition

We examined the ages at which banded males acquired territories in the woodland study area (Table 6). Assuming the two ASY floaters in these data were 2 years old, 13 floaters claimed territories when they were 2 years old, 6 when they were 3 years old, and 1 when it was 4 years old. After accounting for dispersal prior to claiming territories and mortality, these data suggest that age does not affect success in territory acquisition once adulthood is reached. These data also show that a greater proportion of vacancies are claimed by young adults. Finally, the proportion of returning survivors decreases with each successive year (Table 6), suggesting that dispersal continues with age.

Discussion

Based on observations of other passerines (Smith 1978, 1984; Arcese 1987, 1989), we predicted that floater red-winged blackbirds would have small home ranges. Instead, we found a comparatively high rate of floater movement. Most (89%) of the 490 floaters we banded were never seen again, even when we experimentally enhanced the number of vacancies available for floaters. We had predicted that floaters would stay in a small, defined area because sedentary floaters would have an advantage over more vagrant floaters because of the sedentary floaters' familiarity with the area. However, red-winged blackbirds are flexible in their habitat requirements (Orians 1980), and this versatility may devalue the importance of familiarity with the area. Nonetheless, Yasukawa (1979) reported that floaters which were familiar with an area were more successful than newcomers at territory acquisition. We do not have the data to compare success at territory acquisition by floaters that were familiar with an area versus floaters that were new to an area, but the high proportion of vacancies claimed by males that had not previously been seen in either study area suggests that there was no advantage to being a sedentary floater (also see Orians and Beletsky 1989). Possibly, both the sedentary and dispersing strategies exist in the population; if this is the case, our data clearly indicate that the dispersing strategy predominates in our area. An alternative interpretation of our results is that floater red-winged blackbirds maintain restricted home ranges that are larger than our methods could detect. If so, this brings into question the proposed benefits to restricted home ranges. The implication is that floaters would have to remain updated on perhaps hundreds of territories and their owners. It remains to be seen whether they possess such an ability.

It is improbable that the individuals we defined as floaters were territory owners that chose to claim a vacancy en route to their breeding area. First, territory owners exhibit strong site fidelity (Beletsky and Orians 1987; unpublished observations) and are therefore unlikely to claim unfamiliar sites south of their breeding grounds. Second, in the roadside area, more than 90% of the birds we called floaters were captured after 15 April and 71% were captured after 30 April. At these late dates it is likely that migration is complete. Third, the proportion of floaters captured before 30 April that claimed a territory or were seen floating (7 of 13) was not different from that proportion for floaters captured after 30 April (15 of 38; $X^2 = 0.07$, $p > 0.90$); hence, late-season movements were no different from movements that may have occurred during migration.

An alternative explanation for the high rate of floater dispersal in this population in inbreeding avoidance (reviewed in Greenwood and Harvey 1982). However, much less dispersal than we observed is sufficient to avoid close inbreeding (Moore and Dolbeer 1989; Payne 1990), and evidence indicates that the red-winged blackbird is highly outbred (Ball et al. 1988). Thus, inbreeding avoidance does not explain the degree of dispersal found here or in many other passerines (Weatherhead and Boak 1986; Weatherhead and Forbes 1994).

A more important cause of dispersal may be migration. Unlike previous populations for which floater home ranges have been determined (see above), the populations in this study were migratory. By migrating, birds incur whatever cost is associated with leaving an area with which they are familiar. Thus, when they return, if there is no advantage to returning to the exact location they left (as there is for owners reclaiming a territory), they should only return to the same habitat (Weatherhead and Boak 1986; Weatherhead and Forbes 1994). Beletsky and Orians (1993) reported a return rate of nestlings of about 6% in their nonmigratory red-winged blackbird population; the return rate of nestlings for our roadside study area was just over 2% and the return rate for the woodland study area was less than 1%. The significantly lower return rate for our study areas supports the idea that migration reduces the probability that individuals will return to the same area. Our study sites were arbitrarily delineated from a much larger area of suitable blackbird habitat (i.e., southeastern Canada and northeastern United States), so floaters were not constrained by habitat limitations to return

to our study areas. Although this explains why there is no cost to floaters from dispersing, it does not explain why most floaters do not benefit from returning to an area where they may more easily recognize suitable territory vacancies.

Natural turnover rates were identical in the roadside and woodland study areas despite the higher average harem size in the woodland study area (Eckert and Weatherhead 1987*c*). Other authors have failed to find a correlation between measures of territory quality (in our case, harem size) and turnover rate (e.g., Lanyon and Thompson 1986; Eckert and Weatherhead 1987*b*; Apollonio et al. 1990; Beletsky 1992). Thus, under natural circumstances, turnover rate probably does not affect floater home range sizes in red-winged blackbirds. However, comparisons between species may reveal a relationship between floater home range size and turnover rate. There are too few species for which data are available to make this comparison.

We found that among ASY male red-winged blackbirds, older floaters were not more successful than younger floaters at acquiring territories (this is also the conclusion reached by Beletsky and Orians (1993) for their Washington State population). This is in keeping with the results of our previous study (Shutler and Weatherhead 1991*a*), where we detected no intrinsic differences between ASY owners and floaters. If competitive ability does not improve once adulthood is reached, this suggests that territory acquisition depends to a great extent on chance. Thus, floaters continue to move around as they get older, presumably prospecting for vacancies. Older adult males are more likely than younger males to be territory owners, but this is due simply to the cumulative probability of locating a vacancy. This implies that where floater populations exist, one should assume that the greatest proportion of newly settling males are likely to be young individuals (also see Orians and Beletsky 1989).

The results of this study clearly did not support the prediction that floaters should have restricted home ranges. Thus, we are left with a paradox. On the one hand, all the evidence accumulated to date suggests that male red-winged blackbirds acquire territories by being the first to discover vacancies. On the other hand, males do not remain in a small restricted area, a strategy that we expected would give them an advantage in discovering vacancies and establishing themselves on territories. It remains for future research to explore why familiarity with a small area and its territorial residents is apparently not advantageous to floater red-winged blackbirds looking for territories.

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