

FACTORS AFFECTING WHICH MALE RED-WINGED BLACKBIRDS ACQUIRE TERRITORIES¹

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Abstract. We use data from a 14-year study of dispersal, territoriality, and breeding success to investigate territory acquisition in male Red-winged Blackbirds (*Agelaius phoeniceus*). Males born in our study area that we later detected breeding had dispersed an average of about 1,400 m and had traversed an average of 25 territories between natal and breeding sites. Our data indicate that all or most males that bred within our study area were probably born no more than 5 km away. Some natal-year cohorts contributed disproportionately to the population of male breeders, suggesting that population structure influenced territory ownership. Most males that obtained territories did so when two years old (their first adult year), but a significant fraction spent at least one adult year as nonterritorial floaters. Our results are consistent with the hypothesis that familiarity with particular areas contributes to territory ownership, but we found no evidence that Resource Holding Potential is a prime determinant of territory acquisition. Chance events may also strongly influence ability to gain a territory.

Key words: Territory acquisition; natal dispersal; floaters; Red-winged Blackbirds; *Agelaius phoeniceus*; birth date.

INTRODUCTION

In many bird species only males that succeed in establishing and maintaining breeding territories normally reproduce. The population of Red-winged Blackbirds (*Agelaius phoeniceus*) that we study, in which there are usually many more potential breeders than available territories, provides one such example. Lifetime reproductive success (LRS) among males in the population depends primarily upon the number of years they hold territories; the number of offspring fledged per territory owner apparently increases, on average, roughly linearly with number of breeding years (Orians and Beletsky 1989). This simple relationship between territory tenure and LRS raises two basic questions: (1) What determines which individuals obtain territories?, and (2) How are territories maintained for long periods? Although these questions are related, the second is concerned with site dominance and inter-year site fidelity and territory retention. In this paper we concentrate on the first question.

To determine which male Red-winged Blackbirds obtain territories we monitored the movements and behavior of marked individuals, either from birth or after we captured them as nonbreeding subadults or adults, to determine

their natal sites, patterns of territory acquisition, and other attributes. In addition, we use information on natal dispersal, date of birth, the ages at which males obtain territories, and territory tenure. Our objectives are to describe attributes of a population of breeding males, and to test two hypotheses of territory acquisition. "Natal dispersal" is used here in the sense recommended by Greenwood and Harvey (1982): dispersal from the site of birth to that of first reproduction.

Four hypotheses, not all of which are mutually exclusive, have been advanced to explain which individuals get territories. They are as follows.

Hypothesis 1. Only genetically or phenotypically superior individuals obtain territories. This is a "Resource Holding Potential" explanation (RHP; Parker 1974), which argues that individuals able to acquire territories are bigger, stronger, or more vigorous than their competitors. Hence, they are successful because they are better fighters.

Hypothesis 2. Males more familiar with an area and its resources are better competitors and thus are able to establish territories (e.g., Nolan 1978, Stamps 1987). Relative knowledge is therefore paramount.

Hypothesis 3. Males that gain and hold territories are more motivated than their competitors, perhaps owing to greater value attached to the territory. That is, they have more to gain and

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more to lose during territorial contests than competitors ("Value Asymmetry," or VA, Hypothesis; Maynard Smith and Parker 1976).

Hypothesis 4. Chance largely determines territory ownership (Eckert and Weatherhead 1987a).

In this paper, we test aspects of the first two of these hypotheses. The resource holding potential of an individual is influenced by its morphology, physiology, and behavior. Also, because RHP must be evaluated relative to that of other individuals, it is also influenced by local population structure. Morphological and behavioral correlates (Searcy 1979a, 1979b; Eckert and Weatherhead 1987a, 1987b; Shutler and Weatherhead 1991), and hormonal correlates (Searcy and Wingfield 1980; Searcy 1981; Beletsky et al. 1989, 1990), of dominance and territoriality among Red-winged Blackbirds, have been investigated. Here we focus on population dynamics and their consequences for individual territory ownership. Specifically, we examine the hypothesis that males that get territories are individuals of high RHP, by evaluating the predictions that males that get territories at age two, their first year in adult plumage (and the modal age for establishment), should obtain territories at higher-quality sites and hold territories for longer periods than males that obtain territories at later ages. Because LRS is strongly positively correlated with the number of years a male holds a territory, and because there is a 30% to 40% annual mortality (Orians and Beletsky 1989), males that obtain territories when they are younger should have higher LRS than males that obtain territories when they are older. Males should therefore attempt to establish territories as early as possible and those that are successful should be those with high RHP.

RHP could also be influenced by differential juvenile nutrition. Different year cohorts could vary in average physiological condition because, for example, they were raised in unusually warm or cold breeding seasons or in low or high insect production years. This hypothesis can be tested by examining whether individuals born in some years are more likely to obtain territories than those born in other years. Similarly, males born during earlier parts of breeding seasons, because they have longer periods to develop prior to their first winter, may be more vigorous adults than later-born males (Garnett 1981, Ydenberg 1989, Harris et al. 1992). Thus, we evaluate the pre-

dictions that (1) males born early in the breeding season are more likely to obtain territories than males born later in the breeding season; and (2) of the males which succeed in obtaining territories, those born early in the season should tend to get territories at younger ages than males born later.

We evaluate Hypothesis 2 by examining natal dispersal of males and the numbers of years they spend as nonterritorial "floaters" in the study area before they acquire territories. If local knowledge is important for territory establishment, then males born locally may have the advantage of long-term site familiarity (Greenwood et al. 1979) and those obtaining territories should tend to be long-term residents of the area.

METHODS

From 1977 through 1990, we monitored breeding and dispersal in a Red-winged Blackbird population located within and adjacent to the Columbia National Wildlife Refuge, in eastern Washington state. The area and the breeding biology of Red-winged Blackbirds are described by Orians (1980) and Orians and Christman (1968). Red-winged Blackbirds breed polygynously in marshes in the region. Each year, from late February or early March through June, we studied breeding on a core group of 60 to 90 male territories on eight marshes located on five lakes along a 3 km segment of a single drainage system (for a map of the area see Beletsky and Orians 1987). Within this series of marshes we monitored all Red-winged Blackbird territories, searched them periodically for nests, and knew the identities of all breeding males and most females. Other marshes in peripheral areas at various distances from the core were censused intermittently for the numbers and identities of territory owners. We did not monitor breeding on the peripheral marshes.

All territorial males in the core area, most resident nonterritorial adult males, and most females were banded with unique combinations of colored aluminum legbands. Subadult males, one year old and with a distinctive plumage, were banded with either a single USFWS band (1977 to 1984) or a single USFWS band plus one year-coded colored band (later years). All nestlings from the approximately 350 to 600 nests located each year were marked with single USFWS bands at six to eight days of age (nestlings fledge at 11 to 12 days). Between 200 and 600 nestlings sur-

vived to banding age each year. These locally-born individuals were given unique color-band combinations only when captured as adults (females at least one year of age, males at least two years). Some nestlings were banded from 1974 to 1976, so that small numbers of banded individuals were already present at the study site in 1977.

Males were caught in small traps placed near their territories or in one of two larger, multiple-capture traps located some distance from the breeding marshes. The larger traps were operated for several hours several days per week, especially early in the breeding season when territory owners from peripheral marshes fed regularly at the traps.

Because nestlings, fledglings, and subadult males were marked with numbered USFWS bands, we knew the true ages of these males when they became territorial. For other territory owners, first captured as adults, we knew only that they were at least two years old (in adult plumage) when they received their color combinations. Because the majority of males of known age (about 80% of them; Orians and Beletsky 1989) gained territories when they were two (the modal age) or three, most of the males initially banded as adults during their first territorial year were probably two or three years old. Unless specified that only males of known age were used, analyses that include the ages of territory owners assume that males first banded as adults were two years old at that time. Most of these individuals were caught and banded during their first territorial year and, as noted above, most males of known age obtain territories at age two.

From 1985 through 1990, we censused territorial males in all marshes to distances of 4–5 km in all directions surrounding the core site. The same marshes were censused each year. The number of banded individuals we located declined with distance from the center of the core study area. Almost all territory owners more than 4 km from the core area were unbanded. Only those males with color-bands could be positively identified. This was because we did not capture males with only single USFWS bands in peripheral areas, and therefore these individuals could have been banded either as nestlings (all years) or subadults (from 1977 through 1984). Thus, their detection could not provide us with even approximate information on natal dispersal.

At the termination of each breeding season we

used a surveying instrument to prepare maps (2.54 cm = 6.1 m) of the core study area that included marsh outlines, territory boundaries, and nest positions. Additionally, territory boundaries were charted biweekly on field maps. We used an aerial photograph of the study area (2.54 cm = 170 m) for measurements of between-marsh distances.

The five north/south-oriented lakes that constituted the core site were separated from other Red-winged Blackbird breeding habitat to the east and west by several km of desert grassland unsuitable for breeding. Other clusters of territories in the region were located on very isolated marshes. Because of this clumped distribution of breeding habitat, we measured natal dispersal in several ways. When males bred on their natal marshes, the distance between a male's natal territory and his breeding territory was determined by measuring the distance between territory centers on maps of individual marshes. When males bred on other than their natal marshes, we used standard distances between the study marshes measured from the aerial photograph.

However, absolute distance does not measure the amount of suitable breeding habitat between natal and settling locations. For example, because breeding habitat in the core area is nearly continuously distributed in a north-south direction, a male born there could have found a suitable breeding territory less than 100 m to the north or south, but if he dispersed east or west, no suitable breeding habitat was less than, 1,500 m away from his natal territory. Therefore, we also determined the number of territories (along a straight line) between a male's natal and breeding territories. Because the number of territories in each marsh varied from year to year, we estimated the number of intervening territories using a measure of "marsh units" as follows. During the last 10 years of our study, the eight core marshes had an annual average of about nine territories each (9.3 ± 0.8 , range 4 to 24), and thus nine territories were defined as a marsh unit. We counted the number of marshes males passed over between natal and breeding sites, and multiplied by nine to determine the average number of intervening territories. A male born on marsh A, for example, passing over marshes B, C, and D, and breeding on marsh E, was assigned 27 intervening territories (three marsh units). For males that bred on their natal marshes we determined, as closely as possible, the actual num-

TABLE 1. Natal years of male Red-winged Blackbirds born in the study area and known to have obtained territories on the core or peripheral marshes.

First year on territory	Number of males with natal year													Total
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	
1978	1													1
1979		4												4
1980		1	3	2										6
1981		1	3	15										19
1982				2		1								3
1983		1		4	1	3								9
1984			1			2	2							7
1985						1	5	2						8
1986				1	1	2		2	9	1				16
1987						2			6	8				16
1988								1	3	7	8	1		20
1989									2	1	1	15	1	20
1990								1		2		10	1	14
Total	1	7	7	24	2	11	7	8	20	19	9	26	2	143
Estimated no. of males fledged: ^a	67	127	288	197	168	140	132	216	218	205	97	305	166	2,326
% of banded nestlings known to eventually own territories:	1.5	5.5	2.4	12.2	1.2	7.9	5.3	3.7	9.2	9.3	9.3	8.5	1.2	6.1

^a Assumes a 1:1 nestling sex ratio at 6–8 days of age and 100% fledging of banded individuals.

ber of territories between their natal and settling territories.

Marshes in the area were of two types. In strip marshes, the emergent vegetation bordered lakes in thin patches only one territory wide. Pocket marshes were broader expanses of vegetation that contained many irregularly-shaped territories. Average annual fledging success for Red-winged Blackbirds, both per male territory and per female, was almost twice as high on pockets as on strips (Beletsky and Orians 1989a, 1991), perhaps owing to improved anti-nest predator effectiveness on the densely-packed pockets. Due to this consistent difference in breeding success, for this analysis we consider strip marshes to be low quality, and pocket marshes to be high quality, breeding sites.

RESULTS

From 1976 through 1988, 4,652 nestlings were banded in the study area, about half of which were probably males (Fiala 1981). By June 1990, 143 (6.1%) of the males were known to have obtained territories and bred for one or more seasons in the core or peripheral areas (Table 1). For several reasons, this is an under-estimate of the true proportion of locally-born males that bred in the area. First, because we conducted our comprehensive census of peripheral breeding

marshes only from 1985 through 1990, estimates from earlier years are lower than those of later years. Second, an unknown but significant fraction of banded nestlings do not live to fledge. Third, we have no information on the survival of fledglings during the 14–20 days they are fed by parents, a period when mortality rates could be high. Thus, the proportion of locally-born males that survive to independence which eventually obtain territories within the study area is probably much greater than 6%. The 127 of 143 locally-born males for which we knew exact natal sites traversed an average of $1,420 \pm 1,350$ m (median = 1,000 m; range 20–7,200 m, Fig. 1). 25 ± 20 territories (median = 18; range 1–72, Fig. 2), or 2.7 ± 2.3 marsh units (median = 2; range 0–8), between their natal and breeding territories.

The proportion of locally-born males that bred each year on the core area marshes varied between 8.8% and 32.0%, from 1980 through 1990 (annual $\bar{x} = 18.8 \pm 7.3$; Fig. 3).

Table 2 shows the natal years of males of known age that obtained territories on the core marshes. The years 1978, 1979, 1981, 1983, and 1986 contributed large numbers of territory owners, whereas 1980 and 1982 contributed relatively few. The eruption of Mt. St. Helens on 18 May 1980, covered the study area with several cen-

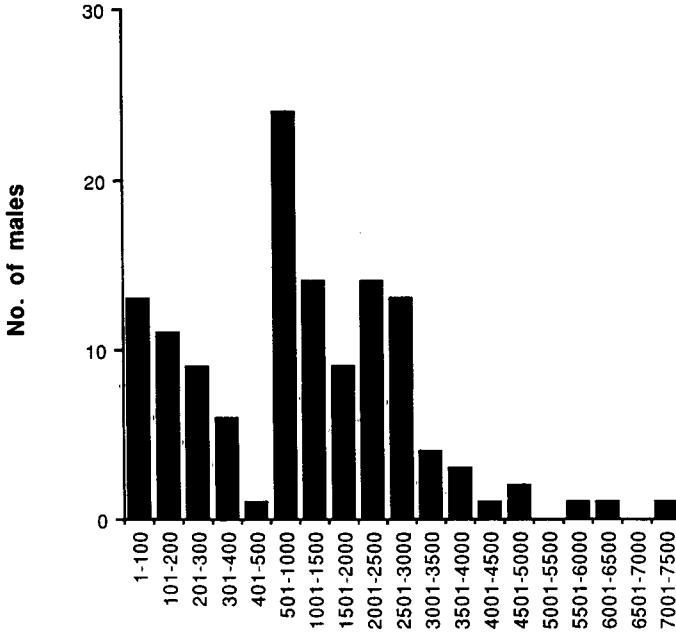


FIGURE 1. Distances (m) between natal and breeding territories of male Red-winged Blackbirds ($n = 127$). Note that X-axis units between 1-500 m and 501-7,500 m are of different magnitudes.

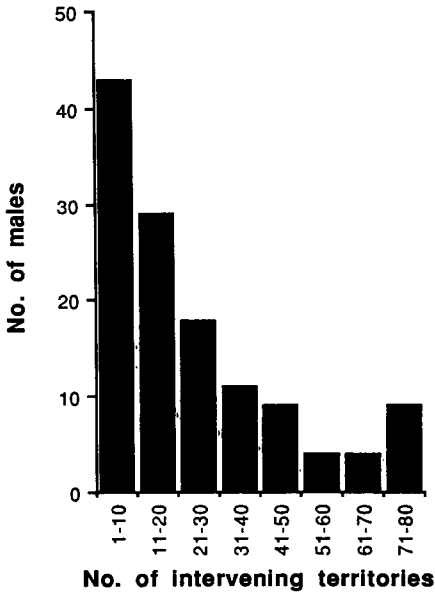


FIGURE 2. Number of intervening territories between natal and breeding territories of male Red-winged Blackbirds ($n = 127$).

timeters of volcanic ash. Although many broods fledged prior to the eruption and others fledged from nests initiated afterwards, the very low number of territory owners born in 1980 suggests that the survival of fledglings was poor.

A distribution of the first egg dates of the clutches from which territorial males came shows that the birth dates of these males were not weighted toward the early part of the breeding season (Fig. 4). In fact, the mid-point of the breeding period produced the highest proportion of clutches that resulted in successful males. Furthermore, males that were born during the first half of breeding seasons (first egg dates before 10 May, the approximate midpoint of seasonal laying), did not tend to obtain territories on the study area at a younger age than males born during the latter half of breeding seasons (first egg dates on or after 10 May). The mean number of adult years spent as floaters for the former group was 0.72 ± 1.1 ($n = 53$) and for the latter, 0.76 ± 1.1 ($n = 82$; Mann-Whitney test, $z = -0.33$, 1-tailed $P = 0.38$). The prediction that males which fledged during early portions of breeding seasons were more likely to obtain territories was therefore not supported. Similarly, the predic-

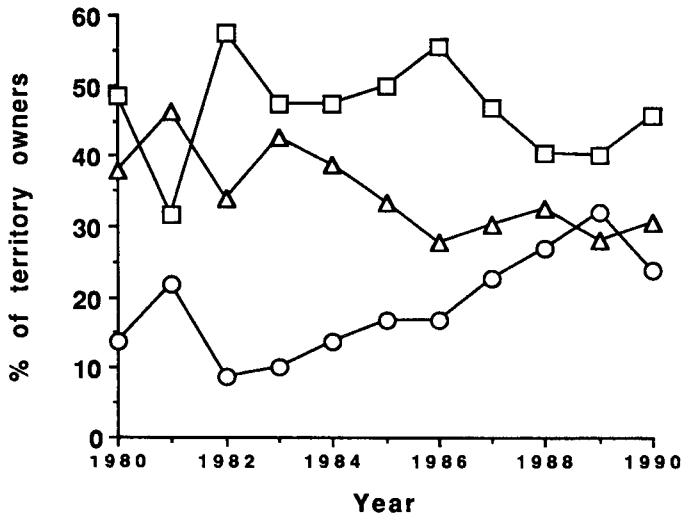


FIGURE 3. Proportions of male Red-winged Blackbirds initially banded as nestlings ("locals"; circles), subadults ("second-year males"; triangles), and adults ("after-second-year males"; squares) holding territories on core marshes each year (annual n given in Table 3).

tion that early-born males would obtain territories faster than those later-born was also rejected.

The majority of new breeders each year (except 1990) obtained territories during their first adult year (Table 3). However, 35% of new owners spent at least one nonterritorial adult year prior to joining the breeding population, and about 10% floated for at least two years.

The proportions of two-year-old males and three- and four-year-old males that obtained ter-

ritories on the more-productive pocket marshes were not statistically distinguishable (38.5% [102/265] and 46.3% [69/149], respectively, $\chi^2 = 2.09$, $P = 0.15$). Thus, two-year-old males did not obtain territories more often on pocket marshes than males that gained territories at later ages. Moreover, males that acquired territories at age two did not hold their territories longer than other males (average territory tenure for males that first obtained territories at two, three and four years of age = 2.6 ± 1.9 years, 2.2 ± 1.7 years,

TABLE 2. Natal years of all known-age^a male Red-winged Blackbirds which obtained territories on core-area marshes.

First year on territory	Number of males with natal year															Total
	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	
1977	5	7														12
1978	1	1	8													10
1979			1	4												5
1980			4	3	13	2										22
1981				3	9	20										32
1982					1	4	1	2								8
1983					1	4	1	13	1							20
1984					1			7	4	5						17
1985						1		1	4	11						17
1986										3	5	1				9
1987										3	7	11	1			22
1988											2	3	13	2		20
1989													6	10	1	17
1990														5	1	6
Total	6	8	13	10	25	31	2	23	9	22	14	15	20	17	2	217

^a Includes males banded as nestlings or subadults.

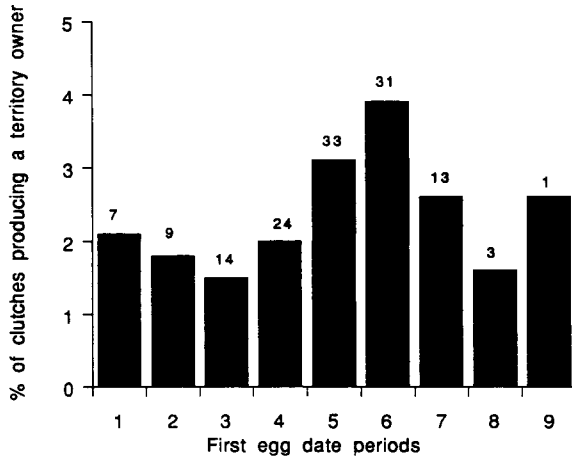


FIGURE 4. Percentages of Red-winged Blackbird clutches, 1977-1988 (total $n = 5,536$), by 10-day period, that produced territorial males. First egg date periods: 1 = 1-10 April, 2 = 11-20 April, 3 = 21-30 April, 4 = 1-10 May, 5 = 11-20 May, 6 = 21-30 May, 7 = 31 May-9 June, 8 = 10-19 June, 9 = 20-29 June. Values above bars are numbers of territorial males produced.

2.6 ± 1.5 years, respectively; Kruskal-Wallis test, $\chi^2 = 3.60$, $P = 0.17$).

DISCUSSION

DISPERSAL

Close monitoring over a 14-year period of a banded population of Red-winged Blackbirds allows us to characterize territorial males as to their birth places, natal dispersal distances, and pre-territorial histories (i.e., number of years floating). Our data indicate that territory owners on the core study marshes were born either on those marshes or on others probably no more than 5 km (or 4 to 5 marsh units) away. We conclude this because (1) the average measured natal dispersal distance was 1,400 m, (2) an average of about 20% of males owning territories each year in the core area were born there (i.e., they were banded as nestlings), and (3) there is more than enough breeding habitat surrounding our core marshes (approximately 200 territories within a 2-km radius [Beletsky and Orians 1987] and at least 400 territories within a 5-km radius) to supply the remainder of our breeding males (on average, the other 80%), if males from these peripheral marshes disperse in all directions at the same rates and distances as the ones we monitored. In other words, although many adult males that gain territories on our core marshes are initially unbanded, given the known dispersal distances of marked nestlings and the large pool of

males born on nearby surrounding marshes, we have no reason to believe that more than a small fraction of our territory-owners were born >5 km distant.

Two additional sources of evidence support this belief: our annual surveys of the identities of territorial males on all breeding marshes within 4-5 km of the core study area center, and

TABLE 3. The number of years male Red-winged Blackbirds which eventually owned territories spent as adult floaters.

Year	No. of territory owners on core marshes	No. of new owners	No. of adult years prior to territory ownership			
			0 ^a	1 ^b	2	3 or more
1980	66	29	17	4	6	2
1981	82	37	23	11	3	0
1982	68	37	27	9	1	0
1983	80	36	23	7	5	1
1984	80	26	15	7	3	1
1985	84	36	26	8	1	1
1986	83	28	23	4	1	0
1987	79	31	18	9	4	0
1988	89	26	19	4	3	0
1989	75	22	15	6	0	1
1990	59	12	2	6	1	3
Total		320	208	75	28	9
%			65.0	23.4	8.8	2.8

^a Includes known-age males which obtained territories at one or two years of age and estimated-age males that were assumed to be two years old the first year that they owned territories (see text).
^b Includes males that initially owned territories as known-age three-year-olds and estimated-age males that were at least three.

USFWS recoveries of our banded males. Almost all territory-owners at 4–5 km from our core marshes are unbanded, whereas males we banded as nestlings are often found breeding on nearer marshes. This pattern indicates that locally-born males rarely disperse farther than the most distant marshes we monitored.

Despite the large numbers of nestlings we banded, very few USFWS recoveries were reported from outside the study area and its immediate surroundings. The most distant are one locally-born male found dead at 6 km from his natal marsh and one at about 10 km. Moreover, these few long-distance dispersers were not necessarily breeding where recovered. Given that the great majority of males breeding on our core marshes were born there or nearby, it is probable that the same is true in other areas. Thus, some males that move long distances after birth, say 10 km or more, may not be breeders, but “losers,” i.e., males unable to obtain breeding territories anywhere (Moore and Dolbeer, 1989).

It is also plausible that some males born on our core marshes disperse long distances, out of our range of detection. The corresponding cohort born in distant areas that might immigrate to our core marshes to breed would therefore comprise a set of territory owners that are *not* locally-born. However, even though our data suggest that long-distance natal dispersal is rare, even small numbers of long-distance movers can be significant from the point of view of population genetics (Moore and Dolbeer 1989, Gavin et al. 1991).

Although the Red-winged Blackbird is among the most studied of the songbirds, comparable dispersal data for other populations is scanty. Moore and Dolbeer (1989), estimating gene flow, used USFWS banding recovery data collected during breeding seasons and mathematical models to calculate Red-winged Blackbird dispersal distances. Their average estimates, using a root-mean-square method in which the distance dispersed is squared, ranged from 27 to 95 km. However, their analysis is not comparable to ours because (1) Moore and Dolbeer included all recoveries and not only territorial breeders; (2) Moore and Dolbeer deal with all dispersal, while our study is limited to natal dispersal; and (3) Moore and Dolbeer use gross dispersal distance categories of 20-km intervals. More than 80% of all recoveries of adult males fell into the smallest dispersal distance category, 0–20 km; and (4) our study is limited by our lack of knowledge of

whether some males dispersed long distances from the study area. However, the average natal dispersal distances of 1–2 km that we identified are congruent with the average dispersal distances found in similar studies of other songbirds (reviewed by Barrowclough 1980, Greenwood and Harvey 1982).

Males are year-round residents at our study area. In migratory populations of the same species, average natal dispersal distances may be greater, perhaps because the benefits of breeding near natal sites are canceled by the costs of leaving the natal area to migrate (Weatherhead and Boak 1986). A study of migratory Red-winged Blackbirds in Ontario supports this idea: banded male floaters tended to leave the study area and probably obtained territories elsewhere, i.e., there was apparently weak site fidelity among floaters (Shutler and Weatherhead 1992). Furthermore, Gavin et al. (1991) reported higher genetic distinctness in non-migratory Red-winged Blackbird populations than in migratory populations, suggesting lower dispersal among residents.

TESTING HYPOTHESES OF TERRITORY OWNERSHIP

If males that obtain territories when they are two years old are, on average, of higher RHP than males that obtain territories at later ages, and if RHP is a prime determinant of males' abilities to establish and hold territories, then they should obtain territories in better areas and hold them for longer periods. Instead, our data demonstrate that two-year-old males and older males establish territories in areas of equivalent quality and hold them for approximately the same number of years. One possible explanation for this pattern is that age contributes to RHP such that males who do not acquire territories at age two are more likely to do so at age three, and so on.

Each year-cohort of locally-born males contributed to the pool of males that eventually obtained breeding territories, but some cohorts contributed disproportionately. The most striking example, the dearth of 1980 natal year males recruited to breeding, is easily traceable to a volcanic eruption that nearly eliminated an entire year cohort. Thus, the fact that the natal year cohorts of 1978, 1979, and 1981 contributed disproportionately to the set of breeders is probably attributable not to their robustness and superior competitive qualities as groups, but rather to a lack of competition from a missing cohort.

Therefore, we found evidence that population structure rather than RHP appears to affect which males obtain territories. Similarly, we found no evidence that the timing of birth affects the relative abilities of males to establish territories. These results are consistent with other data. Recent studies of morphology, contest behavior, and territory acquisition methods among Red-winged Blackbirds all cast doubt on the validity of the RHP hypothesis as a likely explanation of territorial dominance in this species (Eckert and Weatherhead 1987a, 1987b; Beletsky and Orians 1989b; Shutler and Weatherhead 1991). Alternatively, there is empirical support for the role of value asymmetries (Beletsky and Orians 1989b) and VA has been advanced as a default option when RHP is rejected (e.g., Shutler and Weatherhead 1991).

The hypothesis that males able to establish territories are ones that are familiar with an area, e.g., have better information about food sources, shelter, and predators, is consistent with our results. However, because our data suggest that probably nearly all territory owners were born within a few km of their eventual settling sites, they all potentially had knowledge of the study site. We do not know if the individuals with which they were in direct competition for territories had less current knowledge of the area. Therefore, our data do not permit us to conduct a strong test of the familiarity hypothesis.

Relative knowledge possessed by males can be influenced by both a geographic dimension—where males were born and spend their early years, and a time dimension—how long males accumulate information prior to becoming territory owners. We found that the majority of males that obtained territories did so during their first adult year (at two years of age). These “fast track” males spent one year as subadult, nonterritorial floaters, and actually had between 18 and 22 months between fledging and territory acquisition to accumulate local knowledge. About a third of territory owners also spent at least one year as nonterritorial, adult floaters (“slow-track” males), some for 2–4 years. “Floating” may allow males to increase their store of knowledge of the area and its inhabitants, and/or await chance events, both of which may facilitate territory acquisition. Although being an adult floater may have these “advantages,” 30% to 40% (the average annual adult mortality [Orians and Beletsky 1989]) of these males will die before they

have another opportunity to acquire a territory. Also, territorial neighbors and not floaters contribute sperm during the extra-pair copulations of breeding Red-winged Blackbird females (Gibbs et al. 1990); floaters, therefore do not sire offspring.

The number of years vertebrate animals persist in an area before breeding and whether their local familiarity enhances their abilities to enter breeding populations is not generally known (Stamps 1987). Yasukawa (1979) found that Red-winged Blackbird floaters, adult and subadult, that lived in an area were more likely to acquire territories there in subsequent years than were new individuals. At least three studies have found high site fidelity for subadult male Red-winged Blackbirds, i.e., they tend to obtain territories as adults in places they resided in as one-year-olds (Laux 1970, Yasukawa 1979, Orians and Beletsky 1989). Here we show that pronounced site fidelity begins in our population at the natal stage.

Males that obtained territories at the earliest opportunities, two-year-olds, potentially with high RHP and/or great knowledge of or investment in the local area, did not then maintain their holdings longer than males acquiring territories at three or four years of age. This is the pattern expected if mortality is independent of adult age.

Our purpose here has been to bring to bear long-term demographic information to evaluate the contribution to territory acquisition of natal site, age and population structure. Thus, we define the pool of individuals from among which are drawn strong contenders for territory ownership. This study provided no support for Hypothesis 1, that RHP is a prime determinant of territory acquisition, and limited support for Hypothesis 2, that familiarity with particular areas contributes to territory ownership. We also showed that chance events (Hypothesis 4), in this case a volcanic eruption's influence on population structure, probably influence which males obtain territories (see also Eckert and Weatherhead 1987a, Beletsky and Orians 1989b).

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LITERATURE CITED

- BARROWCLOUGH, G. F. 1980. Gene flow, effective population sizes, and genetic variance components in birds. *Evolution* 34:789-798.
- BELETSKY, L. D., AND G. H. ORIANS. 1987. Territoriality among male Red-winged Blackbirds. I. Site fidelity and movement patterns. *Behav. Ecol. Sociobiol.* 20:21-34.
- BELETSKY, L. D., AND G. H. ORIANS. 1989a. Familiar neighbors enhance breeding success in birds. *Proc. Natl. Acad. Sci. USA* 86:7933-7936.
- BELETSKY, L. D., AND G. H. ORIANS. 1989b. Territoriality among male Red-winged Blackbirds. III. Testing hypotheses of territorial dominance. *Behav. Ecol. Sociobiol.* 24:333-339.
- BELETSKY, L. D., AND G. H. ORIANS. 1991. Effects of breeding experience and familiarity on site fidelity in female Red-winged Blackbirds. *Ecology* 72:787-796.
- BELETSKY, L. D., G. H. ORIANS, AND J. C. WINGFIELD. 1989. Relationships of steroid hormones and polygyny to territorial status, breeding experience, and reproductive success in male Red-winged Blackbirds. *Auk* 106:107-117.
- BELETSKY, L. D., G. H. ORIANS, AND J. C. WINGFIELD. 1990. Effects of exogenous androgen and antiandrogen on territorial and nonterritorial Red-winged Blackbirds (Aves: Icterinae). *Ethology* 85:58-72.
- ECKERT, C. G., AND P. J. WEATHERHEAD. 1987a. Ideal dominance distributions: a test using Red-winged Blackbirds (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.* 20:43-52.
- ECKERT, C. G., AND P. J. WEATHERHEAD. 1987b. Competition for territories in Red-winged Blackbirds: is resource holding potential realized? *Behav. Ecol. Sociobiol.* 20:369-375.
- FIALA, K. L. 1981. Reproductive costs and the sex ratio in Red-winged Blackbirds, p. 198-214. *In* R. D. Alexander and D. W. Tinkle [eds.], *Natural selection and social behavior*. Chiron Press, New York.
- GARNETT, M. C. 1981. Body size, its heritability and influence on juvenile survival among great tits, *Parus major*. *Ibis* 123:31-41.
- GAVIN, T. A., R. A. HOWARD, AND B. MAY. 1991. Allozyme variation among breeding populations of Red-winged Blackbirds: The California Conundrum. *Auk* 108:602-611.
- GIBBS, H. L., P. J. WEATHERHEAD, P. T. BOAG, B. N. WHITE, L. M. TABAK, AND D. HOYSAK. 1990. Realized reproductive success of polygynous Red-winged Blackbirds revealed by DNA markers. *Science* 250:1394-1397.
- GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* 13:1-21.
- GREENWOOD, P. J., P. H. HARVEY, AND C. M. PERRINS. 1979. The role of dispersal in the Great Tit (*Parus major*): the causes, consequences, and heritability of natal dispersal. *J. Anim. Ecol.* 48:123-142.
- HARRIS, M. P., D. J. HALLEY, AND S. WANLESS. 1992. The post-fledging survival of young Guillemots *Uria aalga* in relation to hatching date and growth. *Ibis* 134:335-339.
- LAUX, L. J. 1970. Nonbreeding surplus and population structure of the Red-winged Blackbird (*Agelaius phoeniceus*). Ph.D.diss. Univ. of Michigan, Ann Arbor, MI.
- MAYNARD SMITH J., AND G. A. PARKER. 1976. The logic of asymmetric contests. *Anim. Behav.* 24:159-175.
- MOORE, W. S., AND R. A. DOLBEER. 1989. The use of banding recovery data to estimate dispersal rates and gene flow in avian species: case studies in the Red-winged Blackbird and Common Grackle. *Condor* 91:242-253.
- NOLAN, V. 1978. Ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* 26:1-595.
- ORIANS, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton Univ. Press, Princeton, NJ.
- ORIANS, G. H., AND L. D. BELETSKY. 1989. Red-winged Blackbird, p. 183-197. *In* I. Newton [ed.], *Lifetime reproduction in birds*. Academic Press, New York.
- ORIANS, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Tricolored, and Yellow-headed Blackbirds. *Univ. Calif. Publ. Zool.* 84:1-81.
- PARKER, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* 47:223-243.
- SEARCY, W. A. 1979a. Female choice of mates: a general model for birds and its application to Red-winged Blackbirds. *Am. Nat.* 114:77-100.
- SEARCY, W. A. 1979b. Morphological correlates of dominance in captive male Red-winged Blackbirds. *Condor* 81:417-420.
- SEARCY, W. A. 1981. Sexual selection and aggressiveness in male Red-winged Blackbirds. *Anim. Behav.* 29:958-960.
- SEARCY, W. A., AND J. C. WINGFIELD. 1980. The effects of androgen and antiandrogen on dominance and aggressiveness in male Red-winged Blackbirds. *Horm. Behav.* 14:126-135.
- SHUTLER, D., AND P. J. WEATHERHEAD. 1991. Owner and floater Red-winged Blackbirds: determinants of status. *Behav. Ecol. Sociobiol.* 28:235-241.
- SHUTLER, D., AND P. J. WEATHERHEAD. 1992. Movement patterns and dynamics of territory acquisition by male Red-winged Blackbirds. Abstract, International Behavioral Ecology Congress, Princeton, NJ.
- STAMPS, J. A. 1987. The effect of familiarity with a neighborhood on territory acquisition. *Behav. Ecol. Sociobiol.* 21:273-277.
- WEATHERHEAD, P. J., AND K. A. BOAK. 1986. Site fidelity in Song Sparrows. *Anim. Behav.* 34:1299-1310.
- YASUKAWA, K. 1979. Territory establishment in Red-winged Blackbirds: importance of aggressive behavior and experience. *Condor* 81:258-264.
- YDENBERG, R.-C. 1989. Growth-mortality trade-off, and the evolution of juvenile life histories in the Alcidae. *Ecology* 70:1494-1506.