2014

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Western North American Naturalist 74(1), © 2014, pp. 123–129

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ABSTRACT.—The Red-winged Blackbird (*Agelaius phoeniceus*) is a polygynous species, and females are typically responsible for the majority of parental care. Despite their limited involvement, males can contribute to reproduction through nest defense and the feeding of nestlings. Some aspects of nest defense may be learned, and older males are more likely to feed young, suggesting that males with previous breeding experience may enjoy higher nest success than their naïve counterparts. We manipulated territory ownership on 10 wetlands in central North Dakota in order to examine the influence of breeding experience on reproductive success. We found no evidence that breeding experience increased nest survival ($\bar{x}$ = 23.0%) or increased the number of fledglings per nest ($\bar{x}$ = 2.2). In this population, territory quality may contribute more to nesting success than male parental contributions.

RESUMEN.—El mirlo de alas rojas (*Agelaius phoeniceus*) es una especie polígama, por lo general, las hembras se encargan de la mayor parte del cuidado parental. A pesar de que los machos no participan mucho en el cuidado parental, contribuyen defendiendo el nido y alimentando a las crías. Algunos aspectos relacionados con la defensa del nido se aprenden, y los machos más viejos tienen mayores posibilidades de alimentar a los jóvenes, lo cual sugiere que los machos con experiencia previa en la crianza tienen mayor éxito en el nido que los más inexpertos. Manipulamos la propiedad del territorio en 10 pantanos en la parte central de Dakota del Norte con el fin de examinar qué influencia tiene la experiencia en la crianza para el éxito reproductivo. No encontramos pruebas de que la experiencia en la crianza haya incrementado la supervivencia de las crías en el nido ($\bar{x}$ = 23.0%) ni de una mayor cantidad de crías por nido ($\bar{x}$ = 2.2). En esta población, es posible que la calidad del territorio contribuya más que la experiencia parental del macho para el éxito del nido.

The Red-winged Blackbird (*Agelaius phoeniceus*) is a polygynous species, breeding in marsh and upland habitats throughout North America. Their ubiquity and polygynous breeding system have made them a common subject for behavioral and ecological studies. There are over 1000 scholarly reports on Red-winged Blackbirds, and many of these studies have focused on various aspects of the species' breeding ecology (Yasukawa and Searcy 1995). Some aspects of Red-winged Blackbird biology have been studied in more than one population, and these studies have highlighted some important differences between breeding Red-winged Blackbirds in different geographic regions (e.g., Yasukawa et al. 1990, Shulter and Weatherhead 1992, Weatherhead 1995).

The amount and quality of parental investment provided by males and females are important because parental investment can contribute directly to the survival and development of offspring. Female Red-winged Blackbirds provide the majority of parental investment; their responsibilities include nest-building, incubation, nest defense, and provisioning of nestlings and fledglings. In comparison, males limit their direct involvement to nest defense and limited provisioning (Beletsky 1996).

Despite their limited involvement, male Red-winged Blackbirds may make contributions that increase their reproductive success. Additionally, the value of these contributions may increase with experience, making breeding experience an important factor in determining reproductive success. Some aspects of nest defense might be learned, such that experienced breeders can better defend against potential predators (Knight and Temple 1986). Most studies have demonstrated that experienced male Red-winged Blackbirds are more likely to feed nestlings than are males breeding for the first time (Yasukawa et al. 1990, Patterson 1991; but see Westneat 1995). Studies examining the effects of increased male contributions have provided mixed results. Beletsky and Orians (1989) suggested that nesting

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adjacent to familiar neighbors (from previous breeding seasons) increases the effectiveness of antipredator behavior. However, Westneat (1995) found that nesting adjacent to familiar neighbors had no advantages. Similarly, Yasukawa et al. (1987) found that intensive nest defense did not result in higher nest success. On the other hand, Knight and Temple (1988) and Weatherhead (1990) found that nests defended aggressively were more likely to be successful than nests defended with less vigor. A consistent finding has been that increased male provisioning contributes to increased reproductive success (Yasukawa et al. 1990, Patterson 1991).

Studies of male breeding experience must separate the contribution of the male from the influence of his territory (Yasukawa 1981). A good territory can contribute to reproductive success by providing protection from predators and resources to feed young (Searcy 1979). Territory acquisition may be based on a meritocracy, so we might expect some correlation between male quality and territory quality. On the other hand, if territory acquisition occurs at random, then male quality and territory quality may not be related. Male Red-winged Blackbirds typically show strong between-year territory fidelity (Beletsky and Orians 1987, Picman 1987). In some populations, males that do move between years typically claim territories within 200 m of their previous territories and increase their reproductive success (Beletsky and Orians 1987). However, studies in other areas have noted few between-year movements (Picman 1987).

We report the results of an experimental study on the relationship between male breeding experience and reproductive success. We broke the possible link between male breeding experience and territory quality by manipulating territory ownership on 10 experimental wetlands. To facilitate comparison of our results with previous observational studies where ownership was not manipulated, we also observed reproductive success in wetlands where territory ownership was not manipulated. If there is an advantage to breeding on the territories of experienced males, then we expected to observe higher nest survival rates in unmanipulated areas (i.e., a higher proportion of successful nests) than in manipulated areas. Similarly, we expected more Red-winged Blackbird chicks to fledge from nests on the territories of males with previous breeding experience than on the territories of inexperienced males.

METHODS

Study Area

We manipulated territory ownership and monitored reproductive success at 10 wetlands in east central North Dakota. The study took place in Barnes County, which is in the central portion of the Drift Plains ecoregion (Bryce et al. 1998). All of the wetlands used in this study were located within a 22-km radius of Sanborn, North Dakota (46.93° N, 98.24° W).

The Drift Plains is primarily an agricultural area that contains a mix of row crops and CRP grasslands interspersed with numerous temporary and seasonal wetlands. The Drift Plains ecoregion hosts a large population of Red-winged Blackbirds that breed in both wetland and upland habitats (Nelms et al. 1999). Our 10 study marshes (7 in 2000 and 3 in 2001) contained a variety of wetland habitats, including wetlands covered by emergent vegetation, open water ringed by cattails (*Typha* spp.), and roadside ditches.

Manipulation of Territory Owners

We manipulated territory ownership on 10 study wetlands to examine the effects of breeding experience on nest success. Being polygynous, male Red-winged Blackbirds establish exclusive territories and attempt to attract multiple females. Because the overall sex ratio for Red-winged Blackbirds approaches 1:1, this arrangement leaves a pool of floater males who regularly monitor territory ownership and look for a chance to establish a territory in a vacant area (Moulton et al. 2013). One difficulty with territory manipulations involving Red-winged Blackbirds is that neighboring territory owners often annex the territories of removed males, thereby preventing floaters from filling vacancies (Beletsky and Orians 1996). This behavior complicates any effort to manipulate ownership of individual territories.

To circumvent this problem while still controlling for variation among wetlands, we used a box trap with a live decoy bird and shooting (permit #MB019065-5) to permanently remove territory owners on a randomly selected half of each study wetland. Prior to removal, we captured all territorial males and fitted

them with a USGS aluminum band (permit #21672) and a unique combination of plastic color bands. These enabled us to track male movements into vacated territories. The original territory owners remained in place on the other half of the wetland. We also captured and banded the replacement males on the manipulated portion of the wetland. The result of the manipulations was that half of the territory owners resembled the overall population (reference), with a mix of experienced and new breeders. The other half (treatment) contained largely after-second-year floaters (presumed inexperienced) that moved into the vacated territories (Sawin et al. 2003a). Most of these floater males probably never maintained a territory and are presumed to have no breeding experience (Beletsky and Orians 1996). Removals occurred before most females had started to build nests.

Nest Searches

We searched for nests from 20 May to 30 July 2000 and from 18 May to 28 June 2001, these dates coincided with the majority of nesting activity. Throughout the experiment, we tracked active nests by searching for new nests every 6 days and checking on the status of known nests every 3 days. This search schedule duplicated other studies of Red-winged Blackbird nesting and resulted in a reasonable compromise between knowledge and disturbance (Beletsky and Orians 1996). Though it is impossible to avoid all disturbance, searches were conducted quickly and efficiently in order to minimize observer influence. We used the same search techniques in treatment and reference areas.

On the 7 wetlands where territory ownership was manipulated in 2000, a portion of the territory owners from 2000 returned to breed in 2001 with at least one year of breeding experience. This treatment resulted in 7 wetlands where returning breeders (banded) were interspersed with new breeders. Compared to our experimental manipulations, where experienced breeders were limited to half of each wetland, the birds returning from the 2000 breeding season were located across the entire wetland and interspersed with first-year breeders. We tracked territory boundaries and analyzed reproductive success on the territories of newly breeding and returning Red-winged Blackbirds.

Analysis

We estimated daily survival rates and 95% confidence intervals for nests by using the maximum likelihood estimator derived by Bart and Robson (1982). This estimator is a generalized version of the traditional Mayfield estimator and does not require the midpoint assumption. We calculated separate estimates for nests in treatment and reference areas in 2000 and 2001 (4 groups) and for nests on the territories of new and returning breeders in 2001 (2 groups). Additionally, for each of the 6 groups, we calculated the average number of Red-winged Blackbirds fledged per successful nest. If male breeding experience plays a role in reproductive success, we would expect to see higher reproduction on the territories of birds with breeding experience.

RESULTS

Territory manipulations were performed at 7 wetlands from 15 to 21 May 2000 and at 3 wetlands from 14 to 19 May 2001 (Table 1). At each wetland, the number of floating males was large (Sawin et al. 2003a). Thus, to ensure that all original territory owners were removed, we took out at least 2.5 times the number of eventual territory owners on the treatment half of each wetland. The removed birds likely consisted of original territory owners and floaters that were attracted to the area by an opportunity to obtain a territory (Beletsky 1992). The number of males exhibiting territorial behavior while territories were being established was higher than the number of eventual territory owners in both treatment and reference areas. Territorial males removed from the lowest-quality habitats sometimes were not replaced by floaters. We speculate that these males held that particular territory in previous years but that the habitat was not sufficient to attract a new owner. Territory owners on the reference side of the treatment-control interface often expanded their territories slightly, and the number of final territory owners in treatment areas was slightly lower than the number of territory owners in reference areas in 2000. None of the banded males from the reference side of the experimental wetlands abandoned their territories and moved to the treatment side.

In 2000, we monitored 310 active nests for 1123 three-day intervals at 7 wetlands (Table 2). Of these nests, we found 101 nests before the

TABLE 1. Number of original and final Red-winged Blackbird territory owners at 10 wetlands where territory ownership was manipulated.

Wetland	Number of males removed from territorial area[a]	Final number of replacement territory owners	Number of unmanipulated territory owners
Brock	36	8	10
Campbell	28	4	6
Gravel Pit	20	4	6
Highway	19	4	7
Meadow Lake	29	5	7
Pipeline	21	5	7
Powerline	25	6	7
Nelson	21	6	6
Railroad	32	8	7
Trucker	24	9	9

[a]Some of these birds were probably not territory owners. Instead, they could have been floaters attracted to the area by social instability.

TABLE 2. Number of Red-winged Blackbird nests monitored, number of 3-d exposure intervals survived, and number of exposure intervals failed for nests in treatment and reference areas at 10 wetlands where territory ownership was experimentally manipulated.

	Treatment			Reference		
Wetland	Nests monitored	Intervals survived	Intervals failed	Nests monitored	Intervals survived	Intervals failed
Brock[a]	51	151	39	35	89	25
Campbell[a]	11	30	7	16	44	14
Gravel Pit[a]	11	13	10	26	68	20
Highway[a]	6	22	3	23	66	18
Meadow Lake[a]	23	78	18	31	107	25
Pipeline[a]	12	34	9	28	71	26
Powerline[a]	14	35	9	23	75	17
Nelson[b]	10	15	8	36	50	34
Railroad[b]	31	128	19	45	179	30
Trucker[b]	42	124	37	37	129	27
TOTAL	211	630	159	300	878	236

[a]Manipulated and observed in 2000
[b]Manipulated and observed in 2001

TABLE 3. Estimated daily nest survival rates and number of Red-winged Blackbirds fledged per successful nest for treatment and reference groups at 7 wetlands where territory ownership was manipulated in 2000.

	Treatment		Reference	
	Estimate	95% CI	Estimate	95% CI
Daily survival rate	0.9243	0.9087–0.9381	0.9214	0.9084–0.9331
Fledged	2.161	1.876–2.446	2.000	1.576–2.423

last egg was laid; 193 were located with eggs, and 16 were discovered with chicks. We found that 105 Red-winged Blackbirds (67 reference and 38 treatment) and 10 Brown-headed Cowbirds (4 reference and 6 treatment) fledged from 50 nests (31 control, 19 treatment). We found that nest survival (23.0%) and number of fledglings per nest (2.1) did not differ between reference and treated areas (Table 3).

In 2001, we manipulated 3 additional wetlands and monitored 201 active nests for 780 three-day intervals (Table 1). On these 3 wetlands, 131 nests were discovered before the clutch was complete, and 70 nests were discovered with eggs. We found that 94 Red-winged Blackbirds (62 reference, 32 treatment) and 3 Brown-headed Cowbirds (3 reference, 0 treatment) fledged from 36 nests (22 reference, 14 treatment). We found that nest survival (23%) and number of fledglings per nest (2.6) were not significantly different between reference and treated areas (Table 4).

Across both study years, daily nest survival rates and the number of Red-winged Blackbirds

TABLE 4. Estimated daily nest survival rates and number of Red-winged Blackbirds fledged per successful nest for treatment and reference groups at 3 wetlands where territory ownership was manipulated in 2001.

	Treatment		Reference	
	Estimate	95% CI	Estimate	95% CI
Daily survival rate	0.9302	0.9126–0.9455	0.9264	0.9110–0.9401
Fledged	2.286	1.716–2.856	2.818	2.333–3.032

TABLE 5. The number of new and returning Red-winged Blackbird territory owners in 2001 at 7 wetlands where territory ownership was manipulated in 2000.

Wetland	New territory owners in 2001	Returning owners from 2000
Brock[a]	3	3
Campbell	9	1
Gravel Pit	3	4
Highway	8	2
Meadow Lake	4	7
Pipeline	11	6
Powerline	7	4

[a]These data include only the reference side of Brock from 2000. The vegetation on the treatment side from 2000 was removed between the 2000 and 2001 breeding seasons.

fledged were similar in treatment and reference areas. However, nesting activity tended to end sooner in treatment areas, and we typically located more active nests per male in reference areas. The exception was at the Brock wetland, where we located more active nests overall and more active nests per territorial male on the treatment side.

In 2001, we also monitored the 7 original study wetlands and found that 33% of the breeding males had been banded in 2000 (Table 5). Return rates varied from wetland to wetland, but the number of territorial males in 2001 was similar to the number of territorial males in 2000 at 5 of the 7 wetlands. The overall return rate was low because the emergent vegetation at Brock was greatly reduced. The water level had declined due to drought, and half of the wetland vegetation was burned. Furthermore, raised water level at the Pipeline marsh increased the amount of emergent vegetation, providing opportunity for the nesting birds to move to different locations.

In 2001, we found and monitored 222 active nests for 901 three-day intervals at the 7 original study wetlands (Table 6). We located 163 nests before the clutch was complete, 57 nests with eggs, and 2 nests containing chicks. We discovered 106 Red-winged Blackbirds (71 new breeders and 35 return breeders) fledged from 51 nests (35 new breeders and 16 return breeders). We found that nest survival (29.9%) and number of fledglings per nest (2.1) did not differ between new breeders and return breeders (Table 7).

DISCUSSION

We found that daily nest survival rates and the number of fledglings per successful nest in the territories of original males (both experienced and inexperienced breeding birds) are similar to those on the territories of replacement males (presumed inexperienced breeders). Consequently, our prediction of greater reproductive success at nests on the territories of males with previous breeding experience was not supported. One possible explanation is that the characteristics of the territories outweighed any contributions made by experienced males. That is, territory quality may be independent of male quality, and the quality of the territory may have the dominant effect. Another possibility is that males with breeding experience are no better at nest defense against diurnal avian scavengers or parental provisioning than are inexperienced males. Finally, regardless of experience, Red-winged Blackbirds have no defense against nocturnal scavenging mammals, especially raccoons (*Procyon lotor*), that are known to efficiently find and destroy bird nests in shallow water (Sawin et al. 2003b, Slowik et al. 2010). The latter factor could negate any advantage experienced males have over inexperienced males.

In comparison, Beletsky and Orians (1989) found an advantage to male experience in a Washington population, whereas Weatherhead (1995) found no advantage in an Ontario population. Weatherhead (1995) suggested that this difference between study areas was real and attributable to differences in predators and territory arrangement between the 2 areas. Original territory owners in some studies have been virtually indistinguishable from the floaters that replaced them following removals (Shulter and

TABLE 6. Number of Red-winged Blackbird nests monitored, number of 3-d exposure intervals survived, and number of exposure intervals failed for nests on the territories of new and returning birds at 7 wetlands in 2001.

	New breeders			Return breeders		
Wetland	Nests monitored	Intervals survived	Intervals failed	Nests monitored	Intervals survived	Intervals failed
Brock	14	61	9	10	32	8
Campbell	18	22	18	8	14	8
Gravel Pit	8	17	6	10	28	8
Highway	30	117	20	6	36	2
Meadow Lake	11	29	7	17	58	13
Pipeline	34	138	17	11	42	6
Powerline	33	108	26	12	44	7
TOTAL	148	492	103	74	254	52

TABLE 7. Estimated daily nest survival rates and number of Red-winged Blackbirds fledged per successful nest in 2001 for new and returning breeders at 7 wetlands where territory ownership was manipulated in 2000.

	New breeders		Return breeders	
	Estimate	95% CI	Estimate	95% CI
Daily survival rate	0.9382	0.9260–0.9491	0.9393	0.9221–0.9541
Fledged	2.028	1.681–2.377	2.188	1.668–2.707

Weatherhead 1991, Dufour and Weatherhead 1998), a pattern that could result when initial territory acquisition occurs at random.

It seems unlikely, given the patterns of parental provisioning, that experienced breeders do not contribute more than first-time breeders (Linz et al. 2011). However, the result of increased provisioning may not translate directly into any of the factors we measured. In previous studies where increased male provisioning increased the number of young fledged, starvation may have been more common than it was in our study area (Yasukawa et al. 1990). If starvation was less common in our population, then the outcome of increased male provisioning may not have resulted in more fledglings, but rather fledglings in better condition. Although we observed male provisioning of nestlings as young as 2 days old, the majority of male provisioning in this and other populations occurs late in the nesting cycle. This pattern would also serve to improve the physical condition, not the number, of birds fledged.

The return rate of territory owners observed in this population (33%) was lower than the rate of 50%–60% reported in previous studies of Red-winged Blackbirds (Beletsky and Orians 1987, Weatherhead 1995, Dufour and Weatherhead 1998). Additionally, the data on males from the 2000 breeding season returning in 2001 demonstrate that there is substantial variation in return rates among wetlands. If this pattern reflects the patterns of territory ownership in 2000 and 2001, then there may be high variability in the number of experienced breeders on the reference side of experimental wetlands. However, our study was conducted over 10 wetlands and the observational study at 7 wetlands in 2001 provided results similar to the experimental portion of this study. Even so, high nest failure across all study wetlands may have resulted in the movement of unsuccessful birds to more suitable habitat in the following year.

By breaking any potential link between territory quality and male breeding experience, our experimental design indicates that male breeding experience did not translate into increased nest survival or more Red-winged Blackbirds fledged. Territory quality and male quality can influence mate choice in Red-winged Blackbirds, although their relative roles may differ between populations (Yasukawa 1981). In this area, territory quality may be more important than male experience, particularly when nests are subjected to high predation rates (Searcy 1979). Male provisioning, which does occur regularly in this population, may contribute to reproductive success in ways not measured by this study.

ACKNOWLEDGMENTS

M.E. Biondini, W.J. Bleier and G.L. Nuechterlein provided comments on earlier drafts of

this manuscript. This study was conducted with the approval of the Institutional Animal Care and Use Committees of North Dakota State University (NDSU) and the U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center (WS–NWRC). Funding was provided jointly by the WS–NWRC (Protocol QA-803) and the Department of Biological Sciences, NDSU.

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Received 8 May 2013
Accepted 6 November 2013