November 2003

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Abstract: Red-winged blackbirds (*Agelaius phoeniceus*) have a polygynous breeding system that results in a group of nonbreeding males (floaters) who are unable to obtain territories. Floaters are often unaccounted for in population estimates during the breeding season because they are difficult to locate. We used a series of removals to estimate the population of non-breeding after-second-year male red-winged blackbirds in two townships in the northern Great Plains. The number of floaters determines the level of competition for vacant territories. In our study population, we estimated there were more floaters than territorial males, indicating that competition for vacant territories was strong. Finally, we failed to detect any evidence that our removal efforts reduced the number of floaters in the subsequent year.

Key words: North Dakota, population size, red-winged blackbird, removal estimation, territory acquisition.

Red-winged blackbirds have a polygynous breeding system that results in a group of males who are physiologically capable of reproduction but are unable to obtain territories. After arriving on their breeding grounds in the spring, after-second-year [ASY]) male red-winged blackbirds compete for territories that they vigorously defend in an attempt to attract mates (Orians 1961). This creates a surplus population of floater males who travel an area searching for an opportunity to claim a territory. Included in this group of floaters are a portion of the ASY males, who are comparable in size and plumage to territory owners, and virtually all second-year (SY) males, who are smaller and have a distinctly duller plumage (Yasukawa and Searcy 1995).

Based on an annual mortality rate near 50%, the floater pool should be larger than the population of territorial males. However, the size of the floater population is difficult to estimate. Floaters can be hard to locate during the breeding season, making traditional sight or sound surveys difficult. Capture-recapture methods might be useful, but red-winged blackbirds can become trap-happy, and it might be difficult to separate floaters from territorial males when captured in traps. Finally, an estimate of floater population size may be derived from average harem size. Assuming an approximately 50:50 sex ratio (Fiala 1981), and assuming that all female red-winged blackbirds breed (Holcomb 1974), it is possible to derive an estimate of the size of the floater population indirectly. However, accurate empirically derived estimates of harem size are difficult and time-consuming to obtain (Searcy and Yasukawa 1995).

While the size of the floater population is difficult to estimate, the number of floaters has important consequences for wildlife managers. Population estimates of red-winged blackbirds typically count territorial males and assume a 1:1 ratio of males to females (Igl and Johnson 1997, Nelms et al. 1999). In reality, this method almost certainly underestimates population size. A census of territorial males is probably a better indication of the number of available territories than the population of red-winged blackbirds. For example,

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a population of 400 male red-winged blackbirds might appear similar to a population of 200 birds if only 85 territories are available. The number of territorial males would only change when the amount of breeding habitat changes, or when the number of potential territory owners drops below the number of available territories. Most researchers understand this problem, but they lack the information needed to make more realistic assumptions (Igl and Johnson 1997, Nelms et al. 1999).

In addition to making estimates of population size difficult, the number of floaters is also important for red-winged blackbirds seeking to obtain territories. The acquisition of a territory is a prerequisite to attracting a female. There is an additional incentive to acquire a territory quickly because lifetime reproductive success among males depends primarily on the number of years they spend as territory owners (Orians and Beletsky 1989, Beletsky and Orians 1993). While a few males gain territories by replacing existing males or by inserting between existing territories, the majority of territorial males gain their territories from owners who have disappeared (Picman 1987). The level of competition for vacant territories depends on the population of floaters, and floater population size may have important implications for the strategies floaters use to acquire territories.

Removal methods, which estimate population size based on the number of birds removed from the population during consecutive removal periods, might be one way to estimate the number of floaters available to replace territory owners. Additionally, wildlife managers have considered local and regional population reduction as a strategy for reducing blackbird damage to agricultural fields (USDA 2001). If enough replacement territory owners are not available, or if replacement owners realize less reproductive success than original owners, removals could decrease red-winged blackbird population growth. A series of removal periods, in addition to providing an estimate of the number of replacement territory owners, would provide insights into the efficacy of localized removals for management purposes.

A valid concern associated with removals is that immigration from other areas will counteract the effects of removals (Van Vuren and Smallwood 1996). Red-winged blackbirds can show strong breeding site fidelity; territorial males might occupy the same territory for many consecutive years (Yasukawa and Searcy 1995). In Washington a population of red-winged blackbirds, Beletsky and Orians (1993) found support for the hypothesis that eventual breeders travel a short distance from natal site to breeding territory (1,420 ± 1,350 m). On the other hand, dispersal is difficult to estimate (Wasser et al. 1994), and there is considerable debate over the strength of natal philopatry. There is evidence to suggest that dispersal rates vary widely, even between different populations of the same species (Weatherhead and Forbes 1992).

The techniques that floaters use to locate territories are still being studied, but 2 of the 3 popular theories (Resource Holding Potential hypothesis and Value Asymmetry hypothesis) predict that floaters travel small search areas while looking for territories (Searcy and Yasukawa 1995). However, the Lottery Hypothesis predicts wide search areas and has also found support (Eckert and Weatherhead 1987, Shulter and Weatherhead 1992). Studies of genetic variability (Gavin et al. 1991) and band recovery records (Dolbeer 1978, Besser et al. 1983, Gammell et al. 1986) have found greater dispersal and suggested that dispersal varies between populations. Our objectives were to (1) evaluate consecutive removals as a method to estimate the population of ASY nonbreeding red-winged blackbirds (floaters) in central North Dakota, and (2) evaluate the carry-over effects of the removals in the subsequent breeding season.

METHODS

During the 2000 breeding season, we estimated the population of ASY male floaters in Manns (T137N R62W) and Severn (T137N R64W) townships (9324 ha) in eastern Stutsman County, North Dakota. These 2 townships were selected from 5 townships in the southern Drift Plains of eastern Stutsman County (Bryce et al. 1998) because we had historical data from 1996 to 1999 on the number of territorial male red-winged blackbirds (Linz et al. 2000). It is primarily an agricultural area containing a mix of row crops and CRP grasslands interspersed with numerous temporary and seasonal wetlands. The southern Drift Plains ecoregion hosts a large population of red-winged blackbirds (Nelms et al. 1999).

The population of nonbreeding ASY male red-winged blackbirds available to occupy vacant territories was estimated from a series of removal efforts (Otis et al. 1978, Lancia et al. 1996). First, 2 large blocks of unclaimed territories were created by using shotguns to remove all of the territorial males from accessible wetlands in Manns and Severn townships during the first half of the breeding season. This created a block of vacant territories, which were filled by nonbreeding floaters that probably could not have claimed territories in the absence of artificial removals. After allowing a day for nonbreeding floaters to locate and occupy vacant territories, the replacement birds were removed so additional floaters could claim the territories. In this way, the block of vacant territories acted as a sink, which was used to remove birds from the nonbreeding (source) population. Beletsky and Orians (1996) report that within years, they regularly caught the same floaters in traps located 2.0 to 2.5 km apart, a distance

that corresponds with what we observed from recapturing a small number of banded birds in North Dakota. Township roads are laid out at 1.6 km intervals, thus most floaters search areas large enough to allow them to encounter an artificially vacant territory created in this experiment.

Removals in each township took place every other day until 6 removal periods were completed. During each removal period, 2 teams of 2 investigators recorded the number and age (SY or ASY) of territorial male red-winged blackbirds accessible for removal and the total number of birds removed from each marsh. Removals were conducted during 4 hours in the morning and 4 hours in the evening when the birds were most active. Removers revisited the same areas during each removal period with approximately equal amounts of effort. This intensity of effort was enough to remove a large proportion of the population, a requirement if good estimates of population size are to be obtained via removal methods (Lancia et al. 1996).

The ASY floater population was calculated using the removal estimator described by Otis et al. (1978) for removal experiments. This method is based on theory developed for estimating animal abundance in closed populations, and it allows for different removal probabilities during different removal periods (a different removal probability can be estimated for each removal period except the last one). A computer program, CAPTURE, was used to assist with the calculations (Otis et al. 1978, White et al. 1982). The estimates included both the original territory owners as well as the replacements for the territories where removals take place. Accordingly, we recorded the number of original territory owners (prior to removals) and used these data to adjust the estimates.

We followed the removals in 2000 with a study to compare the floater populations in Manns and Severn townships with floater populations in 2 reference townships from LaMoure (Adrian T136N R63W) and Stutsman (Corwin T138N R63W) counties. Floaters are attracted to social instability, because instability can indicate boundary disputes and an opportunity to obtain a territory by claiming a vacancy or inserting between 2 established territories (Beletsky 1992). Therefore, we measured an index to floater populations by artificially creating social instability and observing the age and number of floaters attracted to the dispute. If the floater population in the 2 removal townships was depressed in 2001, we expected to observe fewer floaters and a higher proportion of SY floaters in removal townships.

We conducted 14 (Severn, Manns, Adrian) or 15 (Corwin) trials at randomly selected wetlands within the 4 townships between 30 May 2001 and 11 June 2001. To provide a buffer area to absorb immigration from surrounding areas, trial wetlands were at least 2.4 km from the township border. Trials were conducted during the first 2 hours of daylight, when territorial males are typically at or near their territories (Beletsky 1992). Trials were conducted simultaneously in removal and reference townships, and observers alternated between removal and reference areas.

For each trial, social instability was generated by placing a caged male red-winged blackbird within the boundaries of an established territory. The presence of an intruder male would typically elicit repeated song-spread displays, an indication to floaters of a boundary dispute. After generating a response from the territory owners, we observed the number and age (SY or ASY) of floaters attracted to the territory. We conducted 3 trials each in removal and reference townships each morning.

RESULTS

From 31 May to 11 June 2000, we removed 2,581 ASY and SY male red-winged blackbirds from Manns and Severn townships (Table 1). We estimated that 1715 (95%CI = 1553-1992) and 1102 (95%CI = 1070-1156) ASY male redwings were available for removal in Manns and Severn townships, respectively. The statistical model used for both estimates assumed a unique removal probability for the first 3 removal periods followed by a constant removal probability for the remaining 3 intervals (Table 2). These numbers include both the original owners of the territories where removals took place and

Table 1. From 31 May to 11 June 2000, male red-winged blackbirds were removed from Manns and Severn townships in Stutsman County, North Dakota to estimate the size of the floater population.

Removal period	Township			
	Manns		Severn	
	ASY[a]	SY[b]	ASY	SY
1	291	4	280	17
2	240	18	203	19
3	236	27	183	20
4	243	22	193	26
5	177	23	109	19
6	137	16	60	18
Totals	1324	110	1028	119

[a]After-second-year (ASY) males removed.
[b]Second-year (SY) males removed.

Table 2. Estimated removal probabilities (p_i's) for nonbreeding after-second-year male red-winged blackbirds during 6 removals periods from 31 May to 11 June 2000 in Manns and Severn townships in Stutsman County, North Dakota.

Township	Removal probabilities					
	p^1	p^2	p^3	p^4	p^5	p^6
Manns	0.170	0.169	0.199	0.255	0.255	0.255
Severn	0.254	0.247	0.296	0.446	0.446	0.446

Table 3. The number of floater red-winged blackbirds observed in response to simulated social instability at wetlands in removal and reference townships in LaMoure and Stutsman counties, North Dakota.

Township	Total ASY	% ASY	Total SY	% SY	Floaters per trial, (95% CI)
Manns[a]	16	40.0%	24	60.0%	2.85 (1.20 – 4.48)
Severn[a]	17	65.4%	9	34.6%	1.86 (0.54 – 3.18)
Adrian[b]	18	52.9%	16	47.1%	2.54 (1.25 – 3.82)
Corwin[b]	18	51.4%	17	48.6%	2.33 (1.02 – 3.65)

[a]Removals took place in Manns and Severn townships from 31 May to 11 June 2000.
[b]Reference townships.

the ASY floaters who attempted to obtain territories in the township. We counted 573 and 557 original territory owners from removal territories in Manns and Severn townships, respectively. If we subtract these numbers from each of the estimates, then we removed between 40% and 76% of the ASY male floaters in Manns Township and between 79% and 92% of the ASY male floaters in Severn Township.

If the removals in 2000 resulted in depressed floater populations in 2001, then we expected 2 patterns to emerge. First, we expected to observe fewer floaters attracted to artificially generated social instability. Second, we expected that a decreased population of ASY floaters would lead us to observe a larger proportion of SY floaters in removal townships than in reference areas.

Floaters responded to 15 of the 24 trials in removal townships and 19 of 25 trials in reference townships. Owners typically responded to the artificial intrusion during the first 5 min of each 30 min trial, and owners spent the remaining time performing territorial displays (Removal 95%CI = 23.7-26.8min, Reference 95%CI = 24.5-26.6min). When floaters approached, they usually landed briefly on the territory where the trial was taking place and were quickly chased away by the territorial male. Sometimes floaters would leave the area, but they often landed outside the territory and tried to approach again. Occasionally males from neighboring territories would approach the decoy cage, but they were chased away as well.

Contrary to our expectations, similar numbers of floaters were observed in removal and reference townships (Table 3). Similarly, we did not observe a higher proportion of SY floaters in removal townships. Severn Township, where we observed the fewest floaters per trial, also contained fewer floaters than Manns Township in 2000. In comparison, we observed a higher proportion of SY floaters in Manns Township, even though the estimates from 2000 showed we removed a larger proportion of the ASY floaters in Severn Township. There was substantial variation in the number of floaters per trial with a range of 0-8 floaters per trial in both removal and reference townships.

DISCUSSION

We primarily removed ASY males because many SY males did not occupy territories even when given a chance. We admit that some additional SY males may have tried to obtain territories earlier in the season, but had stopped searching by the time our removal study began (Beletsky et al. 1989). Alternatively, competition between floaters might be such that SY floaters have little chance to obtain territories. The simulated social instability observations in 2001 indicate the SY floaters might have been attracted to vacant territories in 2000, but were unable to defend them from ASY males.

Surveys of territorial male red-winged blackbirds from 1996 to 2001 showed there were 1,500-1,700 territorial males per township in Stutsman County (Linz et al. 2000, G. M. Linz, National Wildlife Research Center and R. L. Wimberly, Wildlife Services, Bismarck, North Dakota, unpublished data). There probably were more floaters than territory owners in our study population. Therefore, population estimates based only on counts of territorial males probably underestimates the number of ASY males. The number of territorial male red-winged blackbirds in North Dakota varied by a factor of 2 over the last 35 years (Nelms et al. 1994, Linz et al. 2000). We assume that the population of floaters has varied substantially as well (Beletsky 1996).

Removal estimates might be better for estimating the amount of competition for vacant territories than for estimating the total number of ASY floaters. A major difficulty is that the removals draw from an area of unknown size. In addition to removing birds that search for territories within the target township, removals estimate a portion of the birds whose search areas overlap with the removal region. Beletsky and Orians (1996) showed that some floaters regularly travel 2.0 to 2.5 km; whereas, Shulter and Weatherhead (1994) found that distances traveled by floaters varies widely. The effects of floaters from other areas were reduced by increasing the area inside the township relative to the length of the border, and by limiting the time during which removals took place. Additionally, Shulter and Weatherhead (1994) found that an increased number of territory vacancies reduced dispersal of floaters. Vacancies created by the removal efforts might have reduced the size of floater search areas during the removal periods.

The number of potential territory owners in our study townships suggests that there may be substantial competition for available territories. Additionally, if red-winged blackbirds acquire territories from random vacancies (i.e., Lottery Hypothesis) then they might travel over large areas while searching for territories. Beletsky and Orians (1993) found that floaters in their study area commonly found territories within 1.5 km of their natal area. However, breeding habitat in their Washington study population is more limited than breeding habitat in the northern Great Plains. Several authors acknowledge that territory vacancies probably occur at random (Eckert and Weatherhead 1987, Shulter and Weatherhead 1992). As a result, chance probably plays a strong role in initial territory acquisition and birds may travel large areas over the course of a breeding season while searching for territories. The results from our follow-up study in 2001 support the idea that floaters in the northern Great Plains travel widely between seasons in their search for territories.

The number of replacement territory owners present in this study shows that local removal of male red-winged blackbirds will quickly be counteracted by immigration from other areas. Further, the results of substantial removals may not be visible in future years. Unless the quality of replacement males is lower than the quality of original territory owners, removing male red-winged blackbirds probably will not reduce population size beyond the actual number of birds removed.

ACKNOWLEDGEMENTS

This manuscript was a part of the senior author's dissertation submitted to the Graduate School at North Dakota State University (NDSU). M.E. Biondini and G.L. Nuechterlein provided comments on earlier drafts of this manuscript. This project was conducted with the approval of the NDSU Institutional Animal Care and Use Committee (IACUC), the National Wildlife Research Center IACUC and under conditions outlined by a scientific collecting permit (#MB 019065). Funding was provided jointly by the National Wildlife Research Center (Protocol QA-803) and North Dakota/South Dakota Wildlife Services, units within the United States Department of Agriculture, Animal and Plant Health Inspection Service, and by the Department of Biological Sciences at NDSU.

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