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FLEDGING SUCCESS AS AN INDEX OF RECRUITMENT IN RED-WINGED BLACKBIRDS

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ABSTRACT.—We used data from an 11-year study of Red-winged Blackbirds (*Agelaius phoeniceus*) to test the hypothesis that fledging success is a reliable index of recruitment at the population and the individual level. Natal philopatry was only 2.37% overall (3.51% for males and 1.49% for females) in our study population. However, the number of fledglings that returned as breeding adults from an annual fledgling cohort was significantly correlated with the size of the cohort. The correlation was also significant when males and females were analyzed separately, despite sex differences in natal philopatry, age of first breeding, and probable differences in mortality factors. Recruitment increased disproportionately with the size of the fledgling cohort. Thus, years of high production produced proportionately more breeding adults. At the individual level, the number of fledglings sired by a male in his lifetime was significantly correlated with the number of his descendants that eventually returned to breed in the study population. These results support the widely held assumption in avian field studies that fledging success is a reliable index of fitness. *Received 9 February 1999, accepted 26 October 1999.*

REPRODUCTIVE SUCCESS is one of the most commonly measured variables in ornithological research. The true variable of interest is the number of young that ultimately survive to become breeding adults (i.e. fitness), but what is measured is the number of young that leave the nest (i.e. fledging success). We must then rely on the assumption that the number of young that fledge is a good index of the number of young that are recruited into the population as breeding adults. The reason we use fledging success in place of true reproductive success is very simple. Measuring the latter often is exceptionally difficult because of the time involved (one must wait until fledglings become adults) and because many fledglings disperse before they mature. Our goal in this study was to determine whether the number of nestlings that were recruited as breeding adults in our study population of Red-winged Blackbirds (*Agelaius phoeniceus*) was reliably indexed by fledging success at the level of the population and of the individual.

It might be argued that it is unnecessary to test the hypothesis that fledging success predicts recruitment, because the hypothesis must be true. Across entire populations and long periods of time that almost certainly must be the case. However, at the small scales of population size and time employed by ornithologists, stochastic or other factors could easily weaken the link between fledgling production and recruitment sufficient to invalidate the assumption that fledging success is a reliable index of fitness. Thus, given how important and widespread this assumption is in ornithological research, we considered that testing the assumption was warranted.

Despite the difficulties in assessing the relationship between fledging success and recruitment, some studies have successfully demonstrated that the relationship is positive. In addition to meeting the obvious prerequisite of being of sufficient duration and scope to allow recruitment to be determined, these studies generally have other features in common. The study species often are nonmigratory (Blue Tit [*Parus caeruleus*], Dhondt 1989; Florida Scrub-Jay [*Aphelocoma caerulescens*], Fitzpatrick and Woolfenden 1989; Splendid Fairy-Wren [*Malurus splendens*], Rowley and Russell 1989; Eurasian Sparrowhawk [*Accipiter nisus*], Newton 1989b), nest on islands (Collared Flycatcher [*Ficedula albicollis*], Gustafsson 1989), or both (Song Sparrow [*Melospiza melodia*], Smith 1988).

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When neither of these criteria apply, the study species tend to have fairly high levels of natal philopatry (Meadow Pipit [*Anthus pratensis*], Hotker 1988; Pied Flycatcher [*Ficedula hypoleuca*], Sternberg 1989; Osprey [*Pandion haliaetus*], Postupalsky 1989). However, natal philopatry is very low in most migratory passerines, particularly those that do not breed on islands (Weatherhead and Forbes 1994), so even long-term studies are unlikely to encounter many breeding adults that were banded as nestlings. Red-winged Blackbirds are typical of such species and thus are poorly suited to the goals of our study. However, the species that are most in need of confirmation that fledging success reliably predicts recruitment are those that are poorly suited to studying that relationship; i.e. those with low natal philopatry. In another way, Red-winged Blackbirds are particularly well suited to our goals because there is probably no other species for which reproductive success has been documented so extensively (Searcy and Yasukawa 1995, Beletsky and Orians 1996).

The simple hypothesis we test here is that the number of offspring that eventually return as breeding adults is positively correlated with the number of banded nestlings that fledged. At the population level, we test whether the number of fledglings produced in a given year is correlated with the number of individuals from that cohort that are observed breeding in the study area. We test this hypothesis separately for males and females for several reasons. Females first breed in their second calendar year, whereas males seldom breed until after their second calendar year, and rates of natal philopatry differ for males and females (Weatherhead and Montgomerie 1995). Also, mortality patterns outside the breeding season are likely to differ for males and females because patterns of mortality relative to body size differ between the sexes (Weatherhead and Clark 1994). At the individual level, we test whether the number of offspring produced by an individual in its lifetime is correlated with the number of those offspring that return as breeding adults. We had sufficient data to test this hypothesis only for males because lower site fidelity by females made it more difficult to estimate their lifetime reproductive success (Weatherhead and Boag 1997). Because approximately 25% of the nestlings in our study population are sired by extrapair males (Gibbs et al. 1990, Weatherhead and Boag 1997), we assessed the relationship between fledging and recruitment success over a male's lifetime using both apparent and true (i.e. genetic) measures of paternity.

METHODS

We conducted our study from early April to late July, 1985 to 1995, at the Queen's University Biological Station in eastern Ontario, Canada (45°37′N, 76°13′W). All study areas were marshes located in beaver ponds or along the shore of Lake Opinicon, within a maximum distance of approximately 10 km of each other. Males were captured and banded as they began defending territories in April, and females were captured and banded as they began nesting in May. Adult males and females received a unique combination of color bands including an individually numbered U.S. Fish and Wildlife Service metal band. Nestlings were banded at approximately six days of age and received a numbered metal band only. Beginning in 1986, we collected a blood sample from all adults and nestlings that we banded, although the eventual parentage analysis with these samples was limited to data from three of the marshes. More detailed information on the study area, general field methods, and parentage analysis are available elsewhere (Gibbs et al. 1990, Weatherhead 1995, Weatherhead and Boag 1997).

We assigned nestling sex based on analysis of growth from measurements of body mass taken at two-day intervals from hatching until the young left the nest (9 to 12 days posthatching). Nestling Red-winged Blackbirds are sexually dimorphic, and the sex of most individuals can be determined by the time they are seven days old (Holcomb and Twiest 1970, Fiala 1981, Weatherhead and Teather 1991, Westneat et al. 1995). Using criteria similar to those used in the studies cited above, we determined the sex of approximately 90% of all nestlings that fledged. For sex-specific analyses of recruitment, we compared the number of individuals of a given sex that recruited with the number of individuals of that sex known to have fledged. We encountered no case of a returning individual being the opposite sex from that assigned based on its pattern of growth (P. Weatherhead and K. Dufour unpubl. data).

We used several criteria to designate a nestling as having fledged. The most straightforward criterion was direct observation of the nestling leaving the nest or near the nest. If we found the nest empty after the nestlings would have been at least nine days old (the earliest age at which fledging was observed), and the nest was undisturbed, we considered the nestlings to have fledged. When hatching asynchrony occurred, we still applied these criteria at the level

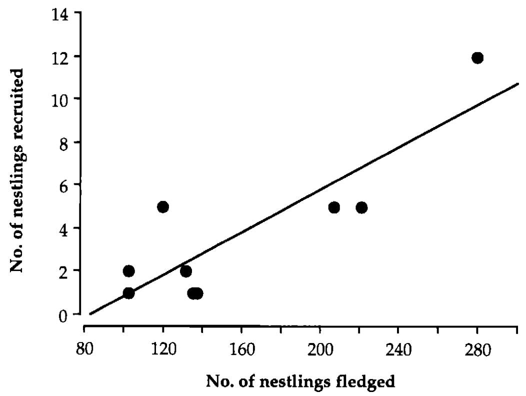

FIG. 1. Total number of breeding adult Red-winged Blackbirds recruited into the study population in eastern Ontario relative to the total number of young fledged in the annual cohort from 1985 to 1993. Each point represents one year. Line of best fit determined by linear regression ($y = -4.105 + 0.05x$).

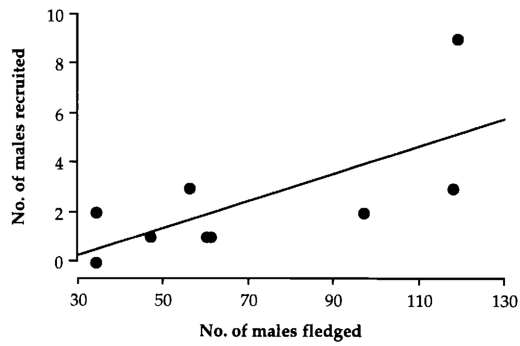

FIG. 2. Total number of breeding male Red-winged Blackbirds recruited into the study population in eastern Ontario relative to the total number of male fledglings in the annual cohort from 1985 to 1993. Each point represents one year. Line of best fit determined by linear regression ($y = -1.394 + 0.055x$).

of the brood. Thus, if most nestlings were at least nine days old but the last-hatched nestling was a day younger, we assumed that all nestlings had fledged if they had disappeared synchronously and the nest was undisturbed. Although some of these criteria are arbitrary, they best fit what we know about the age of fledging. Equally important is the fact that we applied these criteria uniformly across all the data, so any bias inherent in our assumptions should not influence our conclusions with respect to the hypothesis we are testing.

We considered a bird we had banded as a nestling to have recruited into the population if we observed it breeding in any of our study marshes, regardless of the marsh from which it had fledged. This meant that males had to be seen holding a territory at least once, and females must have initiated at least one nest. Because we used territorial and nesting behavior to capture (and thus identify) males and females, respectively, these criteria were applied uniformly across all years. For population-level analyses, we used data from 1985 through 1993 as our values for fledgling production and breeding data from 1986 through 1995 for quantifying recruits. Throughout, "year" refers to the year of fledgling production, in part because birds that fledged in the same year could recruit into the population in different years.

For the analysis of lifetime reproductive success of individual males, we use the 36 individuals analyzed by Weatherhead and Boag (1997). These males came from a subset of the marshes and years because paternity was determined genetically only for that subset. Paternity analyses involved a combination of single-locus and multiple-locus DNA techniques (Gibbs et al. 1990). Because the analysis of individual success involved such small samples, we broadened the criteria for recruitment to include birds banded as nestlings that we captured as adults on the study area, even if we did not observe them breeding.

RESULTS

Population recruitment.—In the nine years that we include for fledgling production, we banded 1,433 fledglings, 626 of which we identified as males and 670 as females (sex not determined for remainder). Annual fledgling totals ranged from 102 to 279; only 34 (2.37%) individuals returned to breed. Males returned at approximately twice the rate of females (3.51% vs. 1.49%).

The number of fledglings that returned as breeders from an annual cohort was significantly correlated with the total size of that cohort ($r = 0.86$, $P = 0.003$; Fig. 1). Recruitment of males by year was significantly correlated with the total size (i.e. both sexes) of the annual cohort of fledglings ($r = 0.82$, $P = 0.006$) and with the total number of male fledglings ($r = 0.70$, $P = 0.037$; Fig. 2). Similarly, recruitment of females by year was significantly correlated with total fledgling production ($r = 0.81$, $P = 0.008$) and female fledgling production ($r = 0.79$, $P = 0.012$; Fig. 3).

The data in Figure 1 suggest that in years of high fledgling production, breeding adults are disproportionately successful in producing recruits. To evaluate this possibility statistically, we employed the power law model:

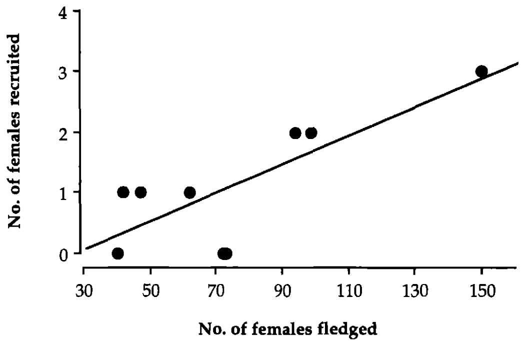

FIG. 3. Total number of breeding female Red-winged Blackbirds recruited into the study population in eastern Ontario relative to the total number of female fledglings in the annual cohort from 1985 to 1993. Each point represents one year. Line of best fit determined by linear regression ($y = -0.648 + 0.024x$).

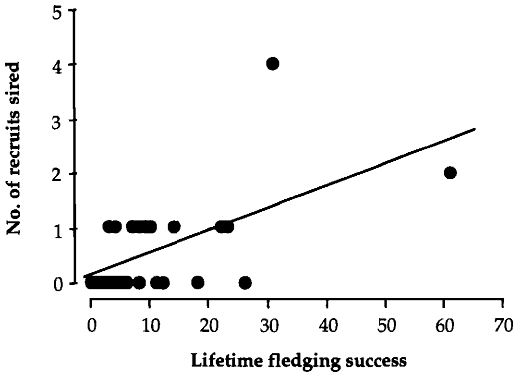

FIG. 4. The number of descendants of individual male Red-winged Blackbirds recruited into the study population in eastern Ontario relative to the number of fledglings sired by those males in their lifetimes. Line of best fit determined by linear regression ($y = 0.101 + 0.041x$).

$$Y = aX^b, \quad (1)$$

where Y is the total number of recruits produced in a given year, X is the corresponding total number of fledglings produced, and a and b are constants (Sokal and Rohlf 1981, Ricker 1984). If the percentage rate of change in Y is proportional to that in X, then b should equal 1. Using geometric mean regression (Ricker 1984), we applied the linear form of the model:

$$\log(Y) = \log(a) + b[\log(X)] \quad (2)$$

and tested for departure of the slope from 1. Results confirmed that years of high fledgling production were indeed characterized by disproportionately high levels of recruitment ($b = 2.51 \pm$ SE of 0.62, $t = 2.44$, df = 8, $P = 0.041$).

Individual recruitment.—A total of 356 banded nestlings fledged from the territories of the 36 males included in the analysis of lifetime reproductive success. These fledglings constitute apparent reproductive success for these males because prior to the advent of DNA-based analyses of parentage, these offspring would have been assumed to have been sired by the male on whose territory they were produced. In total, 354 fledglings were sired by these 36 males (i.e. true reproductive success). For individual males these include fledglings sired on their own territories and fledglings sired on territories of other males. The total numbers of fledglings that were recruited into the study population were 17 (4.8%) for apparent offspring and 18 (5.1%) for true offspring. These recruitment rates were slightly higher than we reported in the population-level analysis because in this analysis we considered fledglings seen as adults but not necessarily seen breeding as having been recruited.

The production of recruits over an individual's lifetime was significantly correlated with both their apparent lifetime fledging success ($r = 0.62$, $P < 0.001$) and their true lifetime fledging success ($r = 0.57$, $P = 0.0002$; Fig. 4). The distribution of lifetime fledging success across males was highly skewed, with many individuals producing few or no fledglings (either apparent or true), and with two males having extremely high success. To ensure that this distribution did not unduly bias the regression analyses, we reanalyzed the data using binary logistic regression (SAS 1994). In both instances, the probability of producing at least one recruit over an individual's lifetime was significantly related to the number of fledglings produced in their lifetime (apparent success, $G = 10.28$, df = 1, $P = 0.001$; true success, $G = 5.52$, df = 1, $P = 0.019$).

DISCUSSION

The return rate of banded nestlings that we found (2.4%) is comparable to that of many migratory passerines (Weatherhead and Forbes 1994). This value is higher than previously reported for this population of Red-winged Blackbirds (Weatherhead and Forbes 1994, Weatherhead and Montgomerie 1995) for several reasons. Here, we analyzed data collected over a longer period, and we also restricted the analysis to nestlings known to have fledged, whereas in previous analyses, we included all banded nestlings. Natal philopatry in our study population was approximately 50% lower than in a population of Red-winged Blackbirds in Washington that was partially migratory (Beletsky 1996). Despite the substantial differences in overall natal philopatry between populations, males returned at approximately twice the rate of females in both studies (see also Orians and Beletsky 1989).

Given that so few of the young we banded returned to breed in their natal area, it is impressive that the size of the annual cohort of fledglings was such a good predictor of the number of fledglings that returned. The positive relationship between fledglings and recruits was true not only for total fledglings, but also separately for males and females, where sample sizes were divided in half, return rates were unequal, and the factors affecting survival were probably different. These results, in conjunction with those from species with higher rates of natal philopatry (Newton 1989a), should reassure those of us who measure reproductive success in birds and must rely on the assumption that fledging success is a reliable index of recruitment. In reaching this conclusion, we are making the new assumption that the number of returning young is a reliable index of the number of surviving young. However, we can see no reasonable way that this assumption could be false and still yield the results that we obtained.

An unexpected result was that recruitment success increased disproportionately with the size of the fledgling cohort. One reason that fledglings might survive better in years with more fledglings could be that fledgling mortality is negatively density dependent, as might occur if animals that prey on fledglings were swamped by large numbers of fledglings. Alternatively, the same factor(s) that promote higher fledgling production (e.g. lower nest predation) also could promote higher fledgling survival (e.g. lower fledgling predation). Because fledglings are so difficult to observe after they leave the nest, assessing these or other alternatives will be very difficult. Nonetheless, the potential importance of this result to topics as diverse as population dynamics and female choice of where to nest suggests that this problem is worth exploring.

For most studies that measure reproductive success, the primary interest is in comparing how individuals perform, because the hypotheses being tested are evolutionarily based. Again, our results should be reassuring to researchers, because consistent with previous long-term studies (Newton 1989a), we found that the lifetime fledging success of an individual male reliably predicted how many of his descendants returned to breed in the study population. We further showed this to be true when the paternity of all offspring was confirmed using DNA-based methods.

Ultimately, one would like to refine these analyses when testing hypotheses about individual performance. For example, in this population of Red-winged Blackbirds, older males are more successful at obtaining extra-pair matings (Weatherhead and Boag 1995). Thus, it would be instructive to know whether the progeny of older males are more likely to survive, as one might predict if females prefer older males because their longevity is heritable. Unfortunately, our data have little to say on this point. Distinguishing between random survival of fledglings and differential survival as a function of paternal reproductive success would require substantially larger samples. In particular, one would like to have higher rates of natal philopatry overall, making Red-winged Blackbirds and most other passerines poor study species for such tests.

Although our results support the assumption that fledging success is a reliable index of recruitment, it is appropriate to add two notes of caution. First, finding a significant correlation between fledgling production and recruitment in one situation (e.g. lifetime success of males) does not necessarily mean that the same will be true for situations we did not examine (e.g. lifetime success of females). Second, we were pleasantly surprised to find support for the hypothesis that fledging success is a reliable index of recruitment in a population with such low natal philopatry. However, had our analyses not supported the hypothesis, we would have been uncertain whether that lack of support was a failure of the hypothesis, or simply a problem of too few returning offspring to provide adequate resolution. Our uncertainty would have reduced our inclination (or opportunity) to report our results. Given that low natal philopatry is the norm, at least in migratory passerines (Weatherhead and Forbes 1994), a reporting bias among analyses of the relationship between fledging and recruitment seems a real possibility. Although this possibility does not invalidate our results and those of the other studies we have cited here, it does warrant circumspection when generalizing from these results.

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