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INTRODUCTION

Eastern Bluebirds (*Sialia sialis*) commonly nest in boxes provided by humans (e.g., Bauldry et al. 1995), and, as a result, they are among the easiest species of North American passerines to study. Over the last several decades, Eastern Bluebirds in the Midwest have experienced dramatic swings in population size, reaching very low levels in the late 1970s and recovering more recently (Zeleny 1976, Sauer and Droege 1990, Bauldry et al. 1995). For these reasons, Eastern Bluebirds offer amateur and professional ornithologists exceptional opportunities to investigate the factors that limit populations. Understanding how populations of birds are limited is one of the long standing goals of ornithological research (Lack 1954, Fretwell 1972, Sherry and Holmes 1995); such understanding is also the first step in diagnosing the causes of population decline, and in managing for the increase and persistence of a species (Caughley 1994, Sherry and Holmes 1995).

One reason we do not yet understand how Eastern Bluebird populations are limited is that few comprehensive population studies of this species have been conducted. Moreover, despite the many bluebirds banded each year, few banders report more than a handful of recaptured birds (but see Pinkowski 1971, Plissner and Gowaty 1996). As a result, few data exist to relate annual variation in return rates of bluebirds to observed changes in local and regional population size.

In this paper, we provide results of a long-term study of Eastern Bluebirds banded and recaptured as adults from 1968 to 1995 near Green Bay, WI. Specifically, we report the return rate of adult bluebirds for the five years following banding. We test if males and females return in similar proportions each year. We also compare our results with those reported for migratory and non-migratory populations of Eastern Bluebirds elsewhere. Lastly, we test if annual variation in adult return rates was related to observed changes in population size from 1968 to 1995, as would be expected if adult survival over-winter has been a key factor affecting population fluctuations in the upper Midwest. Overall, our main goal in this paper is to suggest that by increasing efforts to re-trap banded birds, and to band and re-trap breeding adults, banders could help to improve dramatically our understanding of bluebird population dynamics. Gaining such an understanding is essential if we intend to conserve bluebird populations into the future.

METHODS

Study Area and Procedure -- Our study was conducted in Brown and Oconto counties, near Green Bay, WI, in cooperation with several bluebird trail monitors operating under the supervision of VMB. General details of the study area and methods used to follow over 2,000 nesting attempts from 1968 to 1995 are given in Bauldry et al. (1995) and Radunzel et al. (1997). Overall, we monitored ca. 500-700 boxes annually. The total number of breeding pairs never exceeded 250, and it fell as low as 14 in 1979.

In this paper we report the return rates of 2527 AHY bluebirds banded during the breeding season. Each year, all boxes in the study area were monitored more or less continuously for signs of occupation. Occupied boxes were visited regularly to check for eggs or nestlings, and young were banded with a single USFWS band at about 10 days of age. At the time of banding, a Bauldry Bluebird Trap (Anonymous 1989) was attached to the entrance on the inside of the nest box. Adult bluebirds were trapped in the box as they returned to feed nestlings, usually within 10 minutes of setting the trap. The first adult trapped was held until the second adult was captured. In no case did adult bluebirds abandon their nest as a result of being trapped and having their young banded. Adults without bands were banded and released. Banded adults were recorded and released. All adults were sexed by their coloration and behavior at the nest box (Zeleny 1976, Pinkowski 1977). A total of 1345 females and 1182 males are considered here.

Statistical Analyses -- We used standard statistical techniques including t-tests, Pearson's r (correlation), and chi-squared tests (Sokal and Rohlf 1982), using the SYSTAT and SYGRAPH software packages (Wilkinson 1988). In most cases we report our results as simple fractions; i.e. the number of birds in a cohort that returned in year 2, divided by the total number banded in year 1, equals the 'return rate' of a cohort in the first year after banding. Number of cohorts varied from 27 to 23, because at the time of analysis, birds banded in cohorts of 1990 to 1994 had not yet had an opportunity to return for a second, third, fourth or fifth year.

A few birds banded as adults were not recovered in one or more years between their initial and subsequent captures. These birds amounted to only 1.0% of males (SE = 0.3%, N = 27 cohorts) and 1.4% females (SE = 0.5%, N=27 cohorts) on average. We therefore assume that these birds 'skipping' a year in our records either bred outside the study area or went undetected in the years between captures, and we include them in the fraction of birds counted as returning for all years in which they were known to be alive.

Because the number of adults banded each year varied from 16 to 230, we employed a statistical transformation to take into consideration the fact that estimates of return rate based on small samples of birds are less reliable than those based on larger samples. Following Gilbert's (1973) suggestion for analysis of samples based on counts, we weighted the fraction of birds returning by square-root of cohort size, after standardizing for mean and standard deviation of the distribution. We did this because it is inappropriate to make direct comparisons of the fraction of birds returning without taking into account the higher expected random errors in small versus large samples. To convey visually the reliability of estimates of return rate, we scaled symbol size by square-root of cohort size in our graphs. Thus, larger symbols represent more reliable estimates of return rate, and small symbols represent estimates that should be given less attention because they are based on fewer birds.

RESULTS

Fraction of Adults Returning One or More Years — Of 2527 bluebirds banded as adults, a mean of 16.0% (SE = 1.40) returned in the first year after banding. By contrast, 3.7% (SE = 0.60) of birds returned for a second year, 1.4% (SE = 0.40) for a third year, and only two females and three males returned after four years (0.4%, SE = 0.20). No adult returned in the fifth year after being banded. Because few birds returned more than one year after banding, we focus our following analyses primarily on the return rates of adults in the first year after banding.

Return Rates by Sex — Male and female bluebirds returned in the first year after banding at about the same rate (males = 15.5%, SE = 1.5, N = 27 cohorts; females = 16.4%, SE = 2.3, N = 27 cohorts); return rates by sex remained similar for succeeding years (Fig.1). Within cohorts, return rates for males and females were also significantly positively correlated (Fig. 2). However, we found no marked correlation between the return rate of males and females in their second ($r = -0.09$, N = 26 cohorts, $P > 0.50$) or third years of return ($r = 0.26$, N = 25 cohorts, $P > 0.20$). Lack of a correlation in these latter comparisons may result simply because of the larger amount of random variation in estimates based on small numbers of birds (see statistical analyses above).

Fig. 1. Fraction of male (open diamonds) and female (solid diamonds) bluebirds in cohorts of adults that returned to breed from one to five years after being banded. Diamonds represent the mean rate of return for each successive year following banding, vertical bars indicate ± Standard Error. Sample sizes are 27, 26, 25, 24, and 23 cohorts for 1, 2, 3, 4, and 5 years after banding, because the cohorts banded most recently have had only one or two years in which to return.

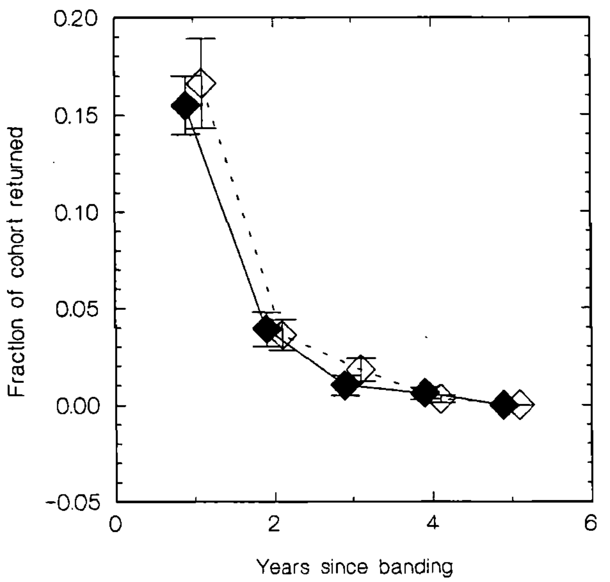
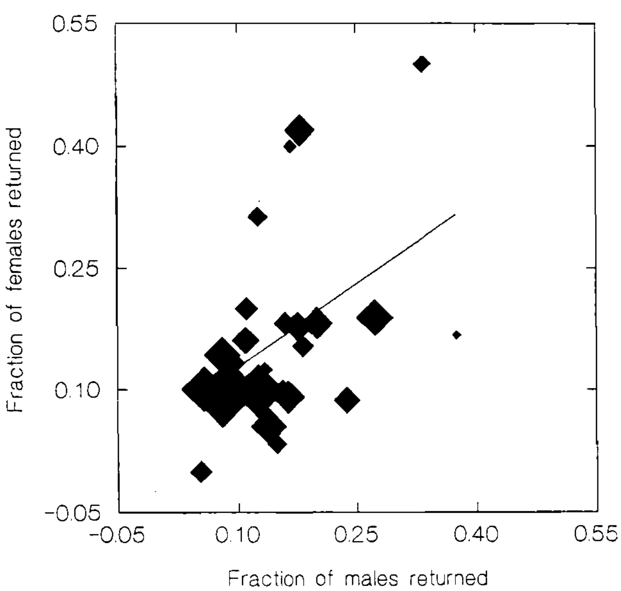


Fig. 2. Fraction of male and female bluebirds in 27 cohorts returning one year after banding. The size of the diamonds is adjusted to reflect the accuracy of each estimate, with larger diamonds being based on larger numbers of birds per cohort (see statistical analyses). The solid lines represent the best linear fit to the data and the 95% confidence intervals on the estimate slope ($r = 0.51$, $P < 0.01$).



Return Rates by Year of the Study— Return rate in the first year after banding varied from a low of 2.6% of 40 birds in 1977, to a high of 37.5% of 16 birds in 1979. Some random variation in return rate is expected because of the small size of some cohorts (see Statistical Analyses above). However, over all years, return rate varied more than would be expected by chance alone ($X^2 = 88.06$, df $= 26$, $P > 0.001$). This variation suggests that one or more factors that affect the return rate of Eastern Bluebirds have changed during the last 27 years.

Two possible explanations for why birds returned at different rates over the course of the study include (a) that survival rates of bluebirds may have declined during periods of cold winter weather (e.g., Pinkowski 1979, Sauer and Droege 1990), and (b) more birds may have dispersed to breed outside the study area in years of high population density (e.g., Arcese et al. 1995). We offer two preliminary analyses to test these ideas in the following sections.

Winter Severity and Return Rate— An unusually severe string of cold winters occurred in the continental US in 1975-6, 1976-7 and 1977-8 (Kerr 1985, Karl et al. 1984). For example, Karl et al. (1984) showed that in the 89-year period from 1895 to 1983, the three winters noted above were among the worst 11 in terms of average temperature in December through February. Moreover, 1977-8 was the single coldest winter over the entire 89-year period.

Several authors have suggested that Eastern Bluebirds suffered high mortality during these three cold winters (Pitts 1978, Graber and Graber 1979, Pinkowski 1979, Sauer and Droege 1990), and also that bluebirds suffered high winter mortality during several earlier cold winters (Wallace 1959, James 1962). We, therefore, tested if variation in average winter temperature was related to variation in the return rates of adult males and females in our study area.

To do this, we compare return rates of all adults known to have bred in the springs of 1975, 1976 and 1977 (just prior to severe winters), with the return rates of all adults breeding just prior to three mild winters (Table 1). These mild winters — e.g.,

1974-5, 1979-80, 1981-2 — are three of the seven mildest winters between 1895 and 1984 (Karl et al. 1984). If winter temperature was a key factor affecting the return rates of bluebirds in our study area, we expected to observe significantly lower return rates following cold as opposed to warm winters.

Table 1. The number and percentgage of adult male and female Eastern Bluebirds returning to breed following the three coldest and warmest winters from 1968 to 1983 (winter severity based on Karl et al. 1984; see text).

		Sex of Birds		
Winter Weather	**Number of Adults**	**Male**	**Female**	**Pooled**
Cold:				
1977-78	retuned	2	0	2
	not returned	20	24	44
	percent	9.1	0.0	4.4
1976-77	returned	3	4	7
	not returned	18	20	38
	percent	14.3	16.7	15.6
1975-76	returned	5	4	9
	not returned	26	27	53
	percent	16.1	12.9	14.5
Pooled Cold	returned	10	8	18
	not returned	64	71	135
	percent	13.5	10.3	11.8
Warm:				
1981-82	returned	2	4	6
	not returned	15	17	32
	percent	11.8	19.1	15.8
1979-80	returned	2	4	6
	not returned	6	6	12
	percent	25.0	40.0	33.3
1974-75	returned	10	9	19
	not returned	34	46	80
	percent	22.7	16.4	19.2
Pooled Warm	returned	14	17	31
	not returned	55	69	124
	percent	20.3	19.8	20.0

In support of this hypothesis that cold winters cause high adult mortality, we found that only 10.1% of 79 females returned following the three cold winters, as compared to 19.8% of 86 females returning after three warm winters (Table 1). This trend was similar in males, but was less pronounced (13.5% of 74 versus 20.3% of 69 males in cold versus warm winters, respectively). These differences in return rate were statistically significant when the data for males and females were pooled ($X^2 = 3.90$, df = 1, $P < 0.05$), but not when males ($X^2 = 1.17$, df = 1, $P > 0.25$) or females ($X^2 = 2.98$, df = 1, $P > 0.05$) were considered separately.

One reason for the apparently weak effect of winter severity on return rate is that the three cold winters included in our analysis did not affect return rates equally. For example, in 1977-8, the coldest winter, only 4.6% of 44 adults known to have been alive in 1977 returned to breed in 1978, and none of the returning birds were females. By contrast, the return rate for birds alive following the severe winter of 1976 (15.6%, Table 1) is about equal to that observed in the winter of 1981-2 (15.8%, Table 1), which was the second warmest year included in our analysis. We note also that the very low return rate of birds in 1978 (4.4%, Table 1) is much lower than in either of the two prior 'cold' winters. Overall, therefore, our results suggest that cold weather was probably sufficient to reduce the return rates of adult Eastern Bluebirds, but some warm years were also associated with low return rates.

Population Density and Adult Dispersal — A second possible explanation for annual variation in return rate could be that, at high population density, more birds bred outside the local study area, perhaps because competition for nest boxes was more intense. To test this idea we examined the rate at which adult birds went undetected for a year or more after being banded, prior to a subsequent recapture. We did so because this might identify birds that temporarily dispersed to nest sites outside the study area before returning to breed locally. We also tested if return rates declined as population density increased.

In support of our hypothesis above, a higher than expected percentage of birds went undetected when the local population was equal to or larger than the median size of 59 pairs (1.6%, SE = 0.30, N=13 cohorts) than when it was smaller (0.8%, SE = 0.40, N = 13 cohorts; t = 2.55, df = 23.2, $P < 0.02$). However, the rate at which birds went undetected in relation to population size was not equal among the sexes. Males went undetected more often at high density (r = 0.58, N = 25 cohorts, $P < 0.01$), but there was no relationship between the fraction of undetected females and density (r = 0.006, N = 25 cohorts, $P < 0.95$).

We also found that return rate declined for males (r = -0.56, N = 27 cohorts, P = 0.003) and females (r = -0.55, N = 27 cohorts, P = 0.003) as the number of breeding pairs in the year following banding increased (Fig. 3a). This shows that as population density increased, return rate of adults declined. However, we also found that return rates of males and females tended to decline over the course of the study, irrespective of large fluctuations in number of breeding pairs (Fig. 3b).

Because there was an overall increase in the number of breeding pairs of bluebirds from 1968 to 1995, we cannot rule out the possibility that return rate declined because of real reductions in the survival of adults on the winter range. This left us with at least two potential explanations for this apparent decline: (a) change on the winter range (e.g. habitat alteration; Temple 1995) leading to reduced survival over-winter, and (b) change on the breeding range (e.g. increased density; analysis above) causing more dispersal out of the study area. Although we attempted to disentangle these effects statistically using partial correlation analyses, we were not successful because of the high degree of co-linearity between return rate, year of the study, and the number of breeding pairs.

DISCUSSION

Our results on the return rate of adult Eastern Bluebirds are comparable with those of Pinkowski (1971), who reported the return rate of a much smaller number of bluebirds at Stoney Creek, MI, banded in 1968 and 1969. Pinkowski (1971) found that 28.0% of 18 banded adults returned in a following year. Our results show that, for these same two cohorts, 16 of 104 (15.4%) birds returned.

Although our value appears to be lower than Pinkowski's, there is no statistically significant difference in these return rates ($X^2 = 1.65$. df = 1, P > 0.25). Overall, therefore, we conclude that adult Eastern Bluebirds in northeastern Wisconsin return at rates similar to those in at least one other migratory population in the upper Midwest. Unfortunately, the only other published return rates for Eastern Bluebirds based on a substantial number of birds are those for birds banded as nestlings, and both of these studies concern non-migrants. Lasky (1943) found that 5.4% of 1564 fledglings returned to breed locally in Tennessee (assuming a 1:1 ratio of males to females among fledglings). Plissner and Gowaty (1996), who recorded the sex of nestlings, found that 15.8% of 1898 males and 13% of 1900 females returned to breed locally in South Carolina.

These results could be interpreted as suggesting that return rates vary substantially between areas. However, in the absence of evidence to the contrary, and given our comparison of Pinkowski's (1971) and our own results above, we suggest that at least three other explanations are possible: (a) differences result by chance, (b) differences result because the studies were conducted in different time periods (1930-40s versus 1970-90s), when different conditions for bluebirds prevailed, or (c) differences result because the studies employed different methods of searching for and recapturing adults. We doubt the first explanation because the large number of nestlings banded in each study makes the chance of random errors very small. However, we cannot rule out either of the last two explanations.

Various reports suggest that the typical life span of Eastern Bluebirds is between one and three years (e.g. Laskey 1943, Pinkowski 1978). For example, Laskey (1943) reports that of 42 females banded as fledglings and returning to breed, none did so for more than three years. Our results also suggest that few birds breed for more than three years, assuming that most of the birds banded as adults were first-year birds (Fig. 1). However, longer lived bluebirds have been reported. Pinkowski (1978) describes a male that bred in five consecutive seasons. In this study, two females and three males survived to breed in at least four seasons, and Farber (1973) reports one Eastern Bluebird reaching 6.5 years of age.

Our results for which there are the fewest comparisons available are those on long-term trends in return rate. This is unfortunate because our most puzzling results concern potential long-term changes in the rate at which adult Eastern Bluebirds have returned to the study area. Nevertheless, three patterns are clear in our analyses of these data and we will now discuss them in turn.

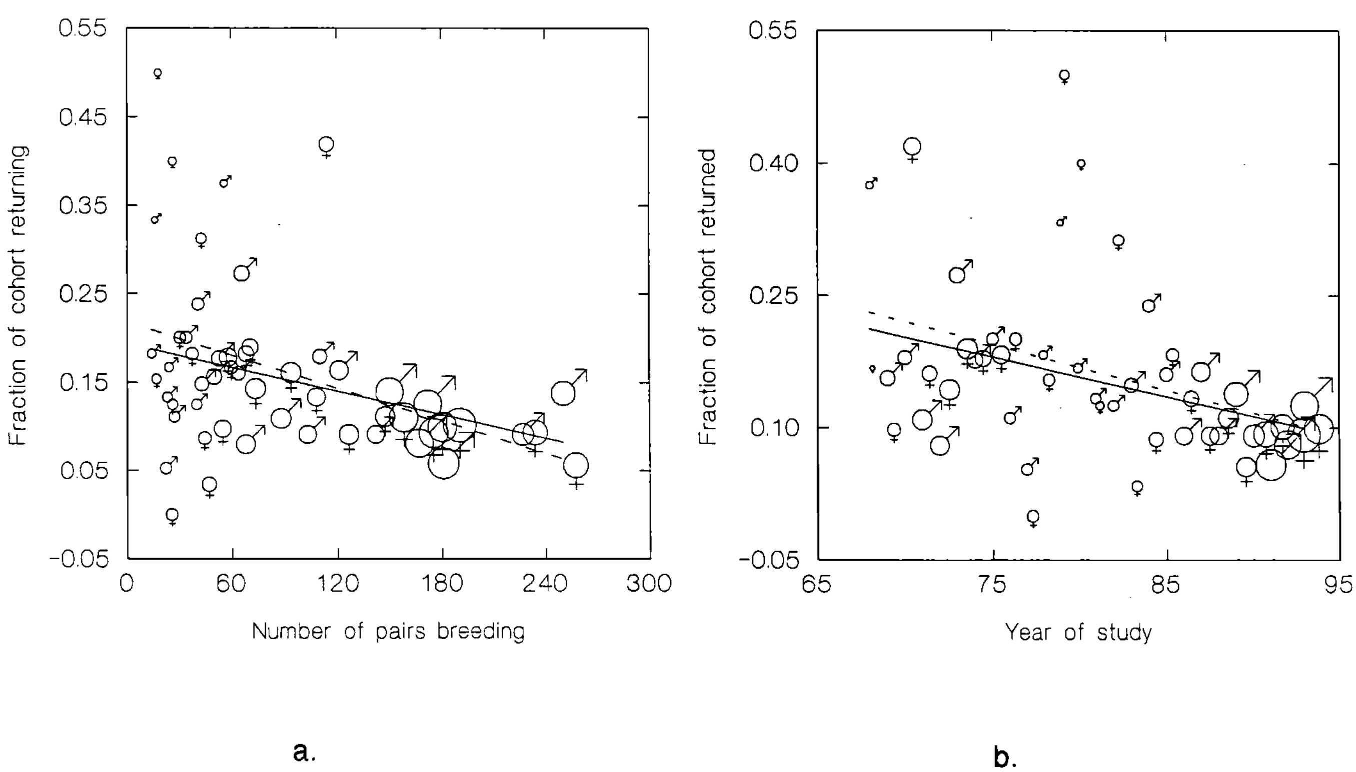
First, although severe cold during the winter of 1977-78 was associated with very few returning adults, returns in two other years with abnormally cold winters were not especially low (e.g. compare cold and warm years in Table 1). This is interesting because both Pinkowski (1979) and Pitts (1978) note declines in their study populations of 46.3% in Michigan and 44% in Tennessee, respectively, ostensibly as a consequence of the cold winter of 1976-5.

In contrast, our study population declined only 20.6% between 1976 and 1977. While this may appear similar to declines reported by Pitts (1978) and Pinkowski (1978), it was less than the average annual rate of decline recorded over the eight-year period from 1971 to 1979 (Bauldry et al. 1995). During this period, bluebirds in our study area declined at an average rate of 22.1%, but only three of eight winters in this period were unusually cold (Karl et al. 1984). Moreover, the largest decline during this period was 36.4%, and it occurred from 1978 to 1979 in association with a winter that was slightly warmer than the 89-year average (Karl et al. 1984). Overall, therefore, our results suggest that while cold winters may negatively affect the return rate of adult Eastern Bluebirds, they are not a necessary cause of substantial declines in population size over-winter. Nor are cold winters a sufficient explanation for the general decline of our local study population from 1971 to 1979. We, therefore, plan to undertake more detailed analyses of the effects of weather on adult survival. For example, it is possible that winters following summer droughts result in poor over-winter survival because of reduced numbers of insect prey.

The second major pattern detected in our long-term analysis concerned an increase in the number of birds going undetected for a year or more at high density, and a reduction in adult return rate as population size increased (Fig. 3a). Both of these results are consistent with the idea that adult bluebirds disperse more during periods of high population density. For example, this might occur if at higher population size there is an increased chance of having an immigrant or returning juvenile usurp the nest box of an otherwise philopatric adult (cf. Pinkowski 1974). In other territorial passerines, dispersal frequently increases with population density (Arcese 1989, Arcese et al. 1995). To test this idea further, one might compare local bluebird density with distance moved between breeding attempts in adults, or distance moved between birthplace and the site of first breeding in juveniles. Our hypothesis predicts that dispersal distance would be greater at higher population density.

Finally, the third major pattern emerging from our analysis is that there has been a decline in the return rate of adult bluebirds to our study area from 1968 to 1995 (Fig. 3b). Understanding the cause of this trend is difficult, however, because it is confounded with the observed increase in population size and decline in return rate noted above. In essence, we are left with two possible interpretations, neither of which can be ruled out at present. These are: (a) that the decline in return rate is the result of an overall increase in population density (explanation above); or (b) the decline in return rate is the result of some undescribed change in the study area, wintering area, or structure of the Wisconsin bluebird population. The latter explanation is ambiguous, but some real changes over the last 27 years have doubtless taken place. For example, as more bluebird enthusiasts have erected nest boxes, a larger fraction of birds fledged in our study area

Fig. 3. The fraction of males and females in each of 27 cohorts that returned in the first year after banding in relation to: (a) the number of breeding pairs in the following year (females = 09.55, males = -0.56, both P's <0.005)); and (b) the year of the study (females = -0.58, males = -0.55, both P's <0.005). In each case, the size of bymbols to indicate the sexes are adjusted to reflect the accuracy of the estimates based on the number of birds per cohort (see Statistical analyses). The lines indicate the best linear fit to the data for males (solid) and females (broken).



may have dispersed to fill newly created vacancies elsewhere. Alternatively, with the introduction of exotic fire ants (*Solenopsis invicta*) to the southern US, arthropod densities may have declined to the extent that bluebirds are suffering reduced survival overwinter (cf. Allen et al. 1995, Temple 1995). We are now undertaking more detailed analyses of the dynamics of our study population to test some of these ideas.

CONCLUSIONS

Our results suggest that gaining an understanding of where and when bluebird populations are limited is a realistic, near-term goal. To achieve this goal requires that banders invest sufficient time and effort to monitor the return rates of young and adult bluebirds, and that they record data to estimate annual reproductive success (e.g. fraction of young banded or fledged from all nests; Bauldry et al. 1995). Towards this goal, our results show that cold winter weather is insufficient to have caused the overall changes in population size observed in the upper Midwest from 1968 to 1995, even though the cold winter of 1977-8 was associated with very low numbers of returning adults. Moreover, we have detected a long-term decline in the overall rate of return in our study area. We do not know the cause of this decline, but we suggest some hypotheses that other banders could test. We hope that our present analyses offer encouragement and direction to banders interested in continuing this effort, and in managing bluebird populations for persistence into the future.

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