

SURVIVAL ESTIMATES OF INDIGO BUNTINGS: COMPARISON OF BANDING RECOVERIES AND LOCAL OBSERVATIONS¹

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Abstract. We compared estimates of adult survival of Indigo Buntings (*Passerina cyanea*) from Bird Banding Laboratory banding recoveries and from field observations of color-banded birds in breeding areas in southern Michigan. Color-banded males in two breeding populations in Michigan had similar survival ($S_0 = 2.41$ years, $P_s = 0.586 \pm 0.018$ SE; $S_0 = 2.08$ years, $P_s = 0.519 \pm 0.021$ SE). Survival estimates in females were lower ($P_s = 0.465$ and 0.335). Banding recovery data indicated a mean adult survival S_0 in males of 2.34 years and a probability of survival to the next year P_s of 0.57 ± 0.037 SE. Survival estimates from local observations and banding recoveries did not differ significantly in either sex. The agreement of survival estimates in banding recoveries with an area-free sampling distribution and in local observations indicates that local observations are not biased against dispersal when the study areas and populations are sufficiently large.

Key words: *Indigo Bunting; Passerina cyanea; banding recoveries; demography; dispersal; finite area sampling; population biology; adult survival.*

INTRODUCTION

Local observations of individual birds and analysis of banding recoveries provide more information on demography and population structure than does either technique alone. Recent discussions of estimating survival from regional banding programs emphasize statistical methods for describing variance and the implications of age-dependent survival (Anderson et al. 1985, Brownie et al. 1985, Morgan and North 1985, North 1987). Regional banding recovery data are area-free, that is, the chances of recovery are independent of the bounded area that comprises a local study population. However, the North American Bird Banding Laboratory (BBL) recovery retrieval file currently does not include returns when a bander finds a bird in the original banding site, so the recoveries are limited to birds found in a second area or reported dead by the bander.

In addition to regional banding and recoveries, local observations and recaptures of marked birds are useful in determining survival and are especially useful when variation in survival can be related to the behavior and observed histories of the individuals (Clutton-Brock 1988, Newton 1989). Survival estimates in local observations

are open to some uncertainty, however, as the disappearance of a bird may be due to either dispersal or mortality. Nevertheless, where banding recoveries have been compared with observations of marked local populations, the estimates of survival have been similar (Dobson 1990).

It is desirable to check the validity of local survival estimates by comparing them with estimates from banding recoveries. If local estimates of survival are lower than estimates from banding recoveries, we may suspect a problem in observing surviving birds due to their dispersal. Here we compare estimates of survival of color-marked individual Indigo Buntings, *Passerina cyanea*, in two breeding populations with estimates of survival from BBL banding recoveries.

METHODS

LOCAL OBSERVATIONS

The study areas were on and around the E. S. George Reserve in Livingston County, an area of 10 km², and 3 km NE of Niles, in Cass County, an area of 4 km², both in southern Michigan. Nearly all territorial males and about half of the breeding female Indigo Buntings were color-banded in the two areas from 1978 through 1985. Each bunting was marked with an USFWS metal band and three color bands. The color bands

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were plastic coils wrapped twice around the tarsus and sealed with acetone.

Males were aged at capture by the greater primary coverts, which are brown in yearlings and blue in older adults. The greater primary coverts have long been used to age male Indigo Buntings based on a study of museum specimens (Dwight 1900). The coverts were reliable indicators of age in males that we banded as nestlings in the previous year and recaptured on their natal area, and in banded males whose minimal age was known when they were recaptured from year to year (Payne et al. 1988, Payne and Payne 1989). They also were reliable indicators of age in birds reared and observed through molts in 1 and 2 years in captivity (Payne 1982). Age was unknown in females unless they had been banded in an earlier year. The greater primary coverts of females of known age showed no consistent tendency for older birds to have blue coverts, or for females to be more bluish in later years. Females banded as nestlings in the previous year and returning to breed in their natal area (Payne et al. 1987, Payne and Payne 1989) usually had brown greater primary coverts, but so did older females that were examined from year to year. First-year females did not have darker outer primaries and lighter inner primaries in spring, as Rohwer (1986) suggested from a study of specimens collected in autumn.

Field observations were made from early May through August. Beginning in 1978, in each study area we observed all 100–150 resident breeding pairs of buntings for survival and breeding through 1985 (Payne 1982, 1989; Payne et al. 1987, 1988; Payne and Westneat 1988; Payne and Payne 1989), and we determined survival through 1990. Observations on survival of resident and breeding birds on the study area are thought to be complete.

RECOVERIES FROM THE BIRD BANDING LABORATORY

The banding retrieval file of Indigo Buntings was read from 96,474 birds banded from 1955 through 1987, including 66,360 from 1965 through 1984. Nearly all buntings (more than 95%) were banded as independent birds, either adults in spring or autumn or birds of the year in autumn, and few were banded as nestlings. Most were banded in migration during May, September, and October.

In BBL terminology, a recovery is a bird banded

and found later, and from 1965 the file excludes birds that returned to their banding site. In the present study of survival, a recovery is restricted to an encounter in a calendar year after a bird was banded and at a site other than the banding site. A return is an encounter by a bander with a bird at its banding site or in the same 10' block.

The records were examined for time elapsed from banding to recovery, and the records including the local returns prior to 1965 involved 295 recoveries. An HY is a bird banded in the calendar year of hatching (not including birds banded as nestlings), an SY is a bird banded in the calendar year after hatching, an ASY is a bird banded in the second calendar year or later after hatching, and an AHY is a bird banded at least one calendar year after hatching. In male Indigo Buntings, both SYs and ASYs are sexually mature and breed, though SY success is lower (Payne 1982, 1989; Payne et al. 1988). An adult male was banded as an SY or an ASY in the same year or in an earlier year. An older adult is a bird 2 years or older.

Cases were selected from the BBL recovery retrieval file for estimating adult survival if they met the following criteria: (1) the bird was recovered at least one calendar year after banding, (2) the bird was banded in Canada or the United States, (3) when the bird returned to the same 10' block and was recorded by a bander, survival estimates were restricted to birds recovered in 1965 or later, and (4) the bird was banded no later than 1983, so survival estimates would not be biased towards short-lived birds. Recoveries with missing data on date and locality were excluded. The data include birds found dead, birds recaptured and released, and birds of unknown condition at recovery.

ESTIMATION OF SURVIVAL

Survival was estimated from the same expression for the banding recoveries and for local observations. The selection of cases for the sample estimates differed between the two sets of data. For estimating survival from the banding recoveries, we included all birds recovered in a year after they were banded. For the local observations we included all resident birds in their year of banding, and observations in later years were used to determine the terminal year, or the year of banding for birds that were not seen in a later year. Lifetime survival in each set of data was

calculated combining all years into a composite cohort (Seber 1973).

We estimated survival from the proportion of birds surviving to the next year from the number alive in the beginning of the year (Lack 1951). Beginning in year 1, s_1 = the proportion of birds that survive only the year of banding, and n_1 = the number alive at the beginning of the year. Survival S_0 was estimated as the sum of bird-years through the oldest survivor, divided by the number alive in the beginning of the year, or

$$S_0 = \frac{s_1n_1 + s_2n_2 + s_3n_3 \dots + s_in_i}{n_1 + n_2 + n_3 \dots + n_i}$$

The value S_0 indicates the mean expected number of years of survival and was used to estimate the probability of surviving from one year to the next, P_s , where

$$P_s = [1 - (1/S_0)].$$

The standard error (SE) of the survival estimate (P_s) was estimated (Haldane 1955, Møller 1983, Dobson 1990), where N = total bird-years, as

$$SE = (1 - P_s) \times [P_s / (N - n_1 - n_2 \dots - n_i)]^{exp 1/2}$$

The estimate of variance allows inference of whether the estimates of P_s are statistically equivalent (Conroy and Williams 1984, Pyke and Thompson 1987, Dobson 1990). Two-tailed Student's t -tests and chi-square tests were carried out to determine whether the P_s values differed using a significance level of 0.05. Estimates of survival based on banding recoveries were compared with estimates based on direct observation of color-banded birds returning to the breeding populations.

RESULTS

SURVIVAL OBSERVATIONS OF LOCAL RETURNS

In the breeding populations in Michigan, we observed the color-banded Indigo Buntings from one season to the next. A total of 260 banded males at the George Reserve and 215 banded males at Niles were used for estimation of survival. This sample includes all SY males that were banded during the breeding season in 1979 through 1984 and that remained on the study area 28 days or longer, and all SY males that remained a shorter time but returned the next year. The first time criterion is necessary because

(1) SY males often move from one territory to another during their first breeding season, (2) 28 days is the minimal time to nest and rear the young to fledging (Payne 1989), and (3) birds present for a shorter period may have dispersed and settled elsewhere. The second criterion provides an allowance for birds being overlooked for a short time when they first arrived and for local dispersal between the study area and the nearby area within the male's first year. Survival was observed by repeated field census through 1990. Within each study area no demographic differences were found among the six cohorts, using an analysis of variance (mean survival for females at Niles varied significantly among years, but the variances also differed significantly, so an inference of significant mean differences among year cohorts is unwarranted). The six cohorts were combined within each area and sex to be analyzed as a composite cohort. Survival estimates were similar to those assessed through 1987 (Payne 1989). The data in Table 1 include corrections, an additional cohort, three additional years of observation of survival, and estimates of confidence limits. Over all ages, male P_s was not significantly different between the George Reserve and Niles ($t = 1.33, P > 0.05$).

At the George Reserve, males were not significantly less likely to return after their SY year than after years 2 to 6 (SYs, 125 returned, 135 did not; older males, 153 returned, 120 did not, counting each male-year as a separate case, $\chi^2 = 3.46, P > 0.05$). Similarly at Niles, SY males were as likely to return as older males (SYs, 112 returned, 81 did not; older males, 137 returned, 89 did not, $\chi^2 = 1.85, P > 0.1$). No decrease in survival was observed in the later years of life.

Females were netted at the nest site and most were of unknown age when banded. Table 2 includes the minimum survival for females on territories in the part of the study area where nearly all breeding females had been banded in the previous year. Although some may have dispersed from a breeding area in an earlier season, most females were probably in their first year when they were first banded. About 10% had been banded on the area as nestlings. Minimum survival to the next season did not differ in females known to be in their first year and in females banded when their age was unknown (Payne 1989). Female survival, P_s , was significantly lower at the George Reserve than at Niles ($t = 2.09, P < 0.05$).

TABLE 1. Survival of male Indigo Buntings banded as SYs from 1979 through 1984 in southern Michigan and observed through 1990.¹

Area	n	Years observed on study area									Survival		
		1	2	3	4	5	6	7	8	9	S ₀ ²	P _s ³	SE
George Reserve	260	135	52	34	16	10	8	3	0	2	2.08	0.519	0.021
Niles	215	81	63	27	18	8	12	3	1	2	2.41	0.586	0.018

¹ In 1990, one male (9 years of age) was still alive at the reserve, and four males (two of 7 years, two of 9 years) were still alive at Niles; these birds are included.

² S₀ = mean expected number of years of survival.

³ P_s = probability of surviving from one year to the next.

BANDING RECOVERIES

Of the 295 recoveries of Indigo Buntings in the BBL recovery retrieval file, 105 met the criteria for estimation of survival. An additional 103 birds returned to their banding area before 1965 and were analyzed separately (Table 3). For the 105 recent recoveries, S₀ = 2.19 years, and P_s = 0.54, combining males and females, and combining adults and birds captured as HY where sex was not determined. For males, S₀ = 2.34 years, and P_s = 0.57. For females, survival is lower but the sample size is small and the variance is large. The survival estimates for local returns before 1965 were lower than for the more recent and nonlocal recoveries, even though only the latest return was used for returning birds that were reported more than once. In the recent recoveries, 21 buntings were reported to be alive when recovered, with S₀ = 1.95, P_s = 0.488, and SE = 0.113, suggesting a lower survival than in the total sample of 105 birds.

COMPARISON OF SURVIVAL IN LOCAL POPULATIONS AND BANDING RECOVERIES

The survival estimates from the marked breeding populations at the George Reserve and at Niles were similar to survival estimates from the BBL banding recoveries. The estimates of P_s for males did not significantly differ between the 60 recent BBL recoveries and survival observed in

Michigan (BBL and George Reserve, $t = 0.66$, $P > 0.5$; BBL and Niles, $t = 0.21$, $P > 0.5$). The estimates of female survival P_s also did not differ (BBL and George Reserve, $t = 0.34$, $P > 0.5$; BBL and Niles, $t = 0.06$, $P > 0.5$), although the sample size of BBL recoveries is low and statistical inference is problematic. The estimate from the banding recoveries was intermediate between the estimates from observations in the two breeding populations both for male and for female buntings.

DISCUSSION

LOCAL OBSERVATIONS, SURVIVAL, AND THE PROBLEM OF DISPERSAL

Local population studies allow direct observation of minimum lifetime survival, rather than an indirect reconstruction from an inferred age structure in a regional banding recoveries program. The major limitation of local observations is that birds may leave the area and settle elsewhere within a season or between seasons. The question of the degree of philopatry is perhaps the greatest uncertainty in extracting demographic statistics from observation of a marked population of mobile animals such as birds (Seber 1973, Mewaldt and King 1985). Uncertainty is greatest if the population area is small, and if point sampling (for example, fixed net sites) rather than observational censusing of an area is used

TABLE 2. Survival of female Indigo Buntings banded from 1979 through 1984 in southern Michigan and observed through 1990.

Area	n	Years observed on study area							Survival		
		1	2	3	4	5	6	7	S ₀ ¹	P _s ²	SE
George Reserve	226	159	42	13	6	2	4	0	1.50	0.335	0.036
Niles	243	127	63	30	11	7	3	2	1.87	0.465	0.023

¹ S₀ = mean expected number of years of survival.

² P_s = probability of surviving from one year to the next.

TABLE 3. Number of years elapsed between banding and recovery of Indigo Buntings in the BBL recovery retrieval file from 1926 through January 1988, for birds banded by 1983 and recovered in a later year. Row 1 includes all recoveries of birds banded in 1965 or later, and birds in earlier years except for live returns. Row 4 includes the local returns to the banding site before 1965.

Recoveries	n	Years elapsed from banding to recapture								Survival		
		1	2	3	4	5	6	7	8	S ₀ ¹	P _t ²	SE
Recent, all	105	48	24	15	12	4	1	1	0	2.19	0.54	0.030
Recent males	60	22	11	12	9	4	0	0	0	2.34	0.57	0.037
Recent females	21	10	9	0	2	0	0	0	0	1.71	0.42	0.288
Returns	103	65	15	15	6	1	0	0	1	1.72	0.42	0.044

¹ S₀ = mean expected number of years of survival.

² P_t = probability of surviving from one year to the next.

to determine the presence or absence of individual birds.

Several criteria can be used to test the assumptions and accuracy of observations of survival and the degree to which survival estimates may be biased downward by dispersal outside the area of observation. Criteria to determine the effectiveness of observational population sampling include the degree of (1) natal philopatry to an area, (2) breeding philopatry to an area, (3) completeness of sampling, with all individuals that are still alive and present being observed in each season, (4) agreement of survival estimates from breeding populations in different areas, and (5) agreement of survival estimates in breeding and wintering areas. In evaluating criteria (4) and (5), discrepancies might be interpreted as demographic or dispersal differences among populations, and additional sampling would be required. All five criteria involve philopatry relative to a finite area. Since the larger the area, the greater the philopatry, on a scale of a single territory to an entire continent, it is important to sample an area that is large enough to include most surviving birds that may disperse on a local scale.

(1) Few Indigo Buntings returned to their natal areas. Within the natal area as defined by the 4 and 10 km² of our study areas in Michigan, 147 of 2,544 nestlings banded were seen to return through 1988, and most surviving young were not recovered in a later year (Payne et al. 1987, Payne 1989, Payne and Payne 1989). Nolan et al. (1975) found three of 185 banded nestlings returning to an area of 75 ha in Indiana in the 1970s, and none of 21 young banded by W. L. Thompson in 600 ha at the George Reserve in the 1960s were seen again (Emlen et al. 1975). Two recoveries at 52 and 350 km from the George Reserve in Michigan in the following breeding

season (Payne et al. 1987) suggest some long-distance natal dispersal, though these are the only recoveries in the BBL recovery retrieval file for buntings banded as nestlings. The natal returns and recoveries are too few to estimate survival in the first 12 months of life.

(2) In local observations, individuals may disperse within or out of the study area. When mortality and emigration cannot be distinguished, dispersal out of a study area would lead to underestimation of survival. We have observations of hundreds of Indigo Buntings that indicate a high degree of local site fidelity and area fidelity. In Michigan most birds returned to the same territory in successive years and most relocations were within 200 m of the previous site, even though the population size and the study area were large enough to detect movement over greater distances. Several moved within a season and nested in territories as far as 1 km apart, and some males and females were found nesting in their second year as far as 2 km from their yearling territory. In male Indigo Buntings nearly all cases of breeding dispersal involved SYs. Similarly, nearly all dispersal observations between years were of males banded in the previous year as SYs. Nevertheless, in parts of the study area where buntings had been banded for the previous 4 years, 31–34% of the breeding adults older than a year had immigrated into the study area in the first instance as adults rather than as SYs (Payne 1989). All buntings that had been banded as nestlings and first returned to the study area as older adults were observed on the area in their second year after hatching (Payne et al. 1988). The observations suggest that after the first year, Indigo Buntings generally return to the area of the previous year.

Ecological changes may occur that affect the age structure of a local population from year to

year through survival and dispersal. The lower survival of females at George Reserve than at Niles might be due to breeding dispersal though higher predation at the nest may have occurred there as well. The natural succession of vegetation and the invasion of fields by introduced shrubs, especially autumn-olive (*Elaeagnus umbellata*), which overgrow the native vegetation and destroy the habitat of buntings, may have forced dispersal or emigration of buntings from George Reserve. During our 12 years of observation on the reserve, buntings decreased to less than 50% of their numbers in 1978, and the decrease was associated with the change in habitat.

The BBL banding recoveries file was examined for cases of buntings that were recovered in different areas either within or between breeding seasons. In 10 cases, the dates of banding and recovery suggest possible breeding dispersal. The dates of all but one involved May, and since many buntings are in migration in May, these may not have been residents. The dates for a male AHY 660-33373, banded by K. Petts near Alpena, Michigan, on 17 June 1962 and recovered 65 km west on 19 June 1964, suggest breeding dispersal. Both dates are too late for spring migration. The bird may have moved within a season or between seasons.

(3) Observations appeared to be reasonably complete, as nearly all birds that were seen in three or more seasons were observed in all successive seasons. One male was not observed in his third year but reappeared in the following year. Another was rediscovered 2 km from his banding site 6 years after banding; he was present only during his SY year at the banding site. The proportion of cases where a male may have been overlooked or spent a season off the area, and was not seen in every year until the final year of observation, was less than 0.2%. Several color-banded females were seen after a year when they were not observed, so some females may have avoided observation in their last year as well. These unaccounted absences involved about 6% of the cases, where a case is a female in a season (Payne 1989).

(4) Indigo Buntings return to their breeding areas with a high area fidelity from year to year in all breeding populations where they have been observed (Emlen et al. 1975, Nolan et al. 1975, Carey and Nolan 1979, Carey 1982, Payne et al. 1988, Payne 1989). Field studies in other areas suggest similar philopatry and survival to that

in Michigan. Nolan et al. (1975) found 60% survival in breeding males and 50% survival in females in Indiana. No significant change in survival with age was observed in breeding buntings in Indiana. Using Haldane's (1955) technique for estimating survival where birds were missed in a year of observation, Blake (1969) calculated a survival of 58.5% in North Carolina; age, sex, and breeding status were not noted.

In addition to survival estimates, the maximum survival observed in banded buntings is similar in other populations. The oldest known buntings, neither of which were in the BBL recovery retrieval file, were two females banded at Powdermill Nature Reserve in Pennsylvania, where numbers comparable to the Michigan population have been banded (Leberman and Wood 1983). One was banded in 1974 as an AHY and was recaptured for a minimum age of 10 years (Mulvihill and Leberman 1984, Leberman et al. 1985). The other was banded as an AHY in 1972 and recaptured in 1980 with a brood patch, indicating breeding at 9 years (Leberman 1982).

(5) Banding returns show philopatry of Indigo Buntings to their wintering areas in the tropics (Van Tyne 1932; Nickell 1968; Downer 1972; Fisk 1978, 1979; Rappole and Warner 1980). Fisk (1978) observed 80 winter returns of buntings banded from 1968 to 1976 in southern Florida. Two returned 8 years after banding. Sex and age at banding were not indicated; most of her buntings were banded as HYs (Fisk 1979). From the data we estimate $S_0 = 2.16$ years, $P_s = 0.54$, and $SE = 0.035$. The survival estimate from southern Florida is close to that observed in the breeding population, and suggests a similar degree of philopatry in wintering and breeding buntings. The only recovery in different areas in two winter seasons was a male ASY banded on the Gulf coast of Florida on 9 January 1984 and repeating on five occasions through 14 March. It was captured again in the Bahama Islands on 29 December 1984 and did not repeat during that season at its banding site on the Gulf coast, although it was still alive and was recovered in Nova Scotia on 26 May 1986 (Stedman and Stedman 1988; A. B. Stedman, pers. comm.).

SURVIVAL ESTIMATES FROM BANDING RECOVERIES

Methods of estimating survival from banding recovery data and its statistical interpretation have

received considerable attention, especially on age-specific differences in survival, which are most difficult to determine from birds banded as young of the year (Lakhani and Newton 1983, Anderson et al. 1985, North 1987). Adult survival can be estimated with greater confidence (Dobson 1990).

Recovery data of birds banded as adults are subject to several sampling biases and uncertainties. Some assumptions in estimating a single value of adult survival from capture-recapture data are that (1) probability of death is independent of age after a certain date, (2) survival is similar in different subsets of data (sample homogeneity), (3) loss of bands through age is negligible, and (4) the sample is representative of the population (Seber 1973, Lakhani and Newton 1983, Anderson et al. 1985, Brownie et al. 1985, Morgan and North 1985, North 1987, Dobson 1990).

(1) Survival can be estimated directly when it does not vary with age, and age-specific estimates are possible only in birds of known age at banding. In the BBL recovery retrieval file, most buntings were of unknown age. A few males were aged as SYs when banded, and a few buntings were banded as HYs but most HYs were not sexed; so the data are of limited value for comparison of age-specific survival of adult males and females. By using the criterion that birds were recovered in the year after banding or in a later year, the survival estimates in the present study are from birds that survived through the period of juvenile dependence and the first long-distance migration, i.e., times of highest mortality in birds (Lack 1954). Indigo Buntings do not show a senescent increase in mortality, at least through 95% of their lifetimes.

(2) Reasonable sample homogeneity is suggested by the lack of significant demographic differences among year cohorts in the local observations. The survival or return of SY males in the following year was lower than for older males in the George Reserve population, though not at Niles. Age was indicated for too few birds in the BBL data for comparison of survival of age groups. Combining years and cohorts for analysis in the BBL data is justified by the comparable netting effort over the years included, judging from the similar number of birds banded over a 40-year period.

Although male buntings may slightly outnumber females, nearly all of known sex were males.

Fewer females were recovered, probably as a result of their later migration and arrival on the breeding grounds (Johnston and Downer 1968, Taber and Johnston 1968, Blake 1969, Carey 1982, Quay 1987) after most banders have ceased netting, as well as their inconspicuous appearance and behavior. This sampling bias in seasonal activity would not lead to a false lower survival estimate for females, because the bias would be the same across years and the chance of recovery of females late in the season should not change with the number of years since banding. The lower survival in female buntings suggested in the few recoveries available is supported by the local observations, so is probably not an artifact of seasonal banding and recovery differences between the sexes.

(3) Recovery data may underestimate survival, as most recoveries of Indigo Buntings were of birds found dead, and the survivors may have lived longer. Few banded buntings (0.1%) were recovered, implying that the adult lifetimes of birds recovered may not be representative. Nevertheless, the survival estimates were consistent with survival observed in local breeding populations, so they appear to be adequate as a first approximation of survival in this species.

(4) Loss of bands and subsequent failure to recover data for the birds alive many years after banding was not a problem in Indigo Buntings. In the local observations, only one color-banded bunting was seen without a metal band in a later year. He lost that foot between his second and third year; he was recognizable by song, location, and the color bands on the other foot. Recaptures of birds in their sixth and seventh year showed the USFWS bands to be intact and legible. Annual loss of color bands was less than 1% and in each case the bird was recognizable by the remaining bands, by location within the study area, and in the male by song, which usually was unchanged from year to year (Payne et al. 1988).

COMPARATIVE SURVIVAL ESTIMATES

Survival estimates of Indigo Buntings were not statistically distinguishable in observations of color-banded birds and in the BBL recovery data. The BBL estimates of survival were intermediate between the estimates in the two color-banded populations. Few studies have compared survival estimates from local observations and regional banding recoveries. Perrins (1971) suggested that local studies might lead to higher estimates of

survival than regional recovery data due to sampling differences of the populations. In a comparative study of survival estimates based on local recaptures of breeding birds and on data from regional banding programs, Baillie and Green (1987) found estimates of adult survival in the Common Swift (*Apus apus*) to be nearly identical. The results were similar even though the sampling of breeding birds and the age-specific changes in breeding biology of Common Swifts differed from those in Indigo Buntings (Perrins 1971, Payne 1989). In four additional species where standard errors could be determined, survival estimates in long-term population studies and in regional banding recoveries in Britain also were statistically similar (Dobson 1990). The similar estimates of survival in these species suggest that the results of comparative studies in the Indigo Buntings may apply to other species as well, and we encourage comparative studies of survival in other species to test the generality of the results.

Regional banding recoveries may be more representative of survival over most or all of a species range. Also, the regional nature of the recovery data is independent of local dispersal that may lead to an underestimate of survival due to a finite area bias (Barrowclough 1978, Zeng and Brown 1987, Payne 1990). The size of a study area as well as effort of the observers determine whether a locally dispersing bird is likely to be seen again. When local observations involve complete samples of populations on large areas and comprise a large number of adjacent birds, most individuals are not near the margin of the study area, and local dispersal does not seriously bias the estimates of survival.

The agreement between survival estimates in the regional BBL banding recoveries and in observations of color-banded Indigo Buntings on their breeding grounds is encouraging for further use of recovery data and of long-term field observations of marked populations. An implication is that local estimates of survival may not be greatly distorted by dispersal, when birds are observed for many years in a large and continuous area.

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