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DISPERSAL AND SURVIVAL IN THE BANK SWALLOW *(Riparia riparia)* IN SOUTHEASTERN WISCONSIN

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Introduction

Most adult birds tend to return to the same, or nearly the same, breeding locality year after year (Lack, 1954; Mayr, 1963; Nice 1941). Stoner (1941) found loyalty to nesting sites among Bank Swallows *(Riparia riparia)* that he recaptured in his studies in Iowa and New York. However, he had a low return rate, which he speculated was due to high mortality. Sargent (1962), performing homing experiments with incubating Bank Swallows, found that the birds were able to return to their nest holes within a short time after being displaced and released from a variety of distances and directions.

The senior author had banded Bank Swallows in limited numbers in Minnesota, Wisconsin and Michigan during the 1950's, and was impressed during annual banding visits to the various colonies that the vast majority of birds captured were "new" rather than returns from previous years. Also, some movement of individuals from one sand bank to another distant one during subsequent breeding seasons was detected. This provoked questions about this species' annual return behavior as compared with other passerines. Stoner (1941) felt that "mortality factors incident to migration and the other activities would appear to hold the possible and probable number of banded individuals so in check that in any one season the inhabitants of a colony would comprise very few banded birds." He added, however, that "essentially similar and possible equally attractive nesting places are available in contiguous territory as well as throughout a large part of the breeding range of this species." Thus, "many of the Swallows banded by us might well find homes beyond the geographical range of our activities."

Berndt and Sternberg (1968) define spacing as "a movement forced upon a bird by external circumstances" and dispersal of adult birds as a "movement [that] occurs as a result of an innate mechanism." The present study was devised to investigate spacing, dispersal, and survival in Bank Swallows. Colonies were studied over a 13-year period in an area covering roughly 6480 km^2.

Methods

Portions of Dodge, Jefferson, Milwaukee, Ozaukee, Racine, Washington and Waukesha counties were selected for study. These counties are contiguously located in southeastern Wisconsin, in a glacial moraine area dotted with commercial sand and gravel pits. Banding sites were chosen as nesting colonies of Bank Swallows became known, either by inquiry or exploration. To determine the coverage of possible nesting sites, two 15-minute U.S. Geological Survey topographic maps covering a portion (1160 km^2) of the study area were examined. Of the 153 pits determined to be available in that area, 18% were eventually located and checked for swallows. Each was surveyed to estimate the population, and an attempt was made to recheck as many pits as possible from year to year even where no birds were recorded initially, or when in subsequent years they failed to return. From 1959-1972, 28 of the available pits over the whole study area were surveyed more or less regularly, and were used in this research (Fig. 1). Of these, seventeen were selected for the capture and recapture studies.

Japanese mist nets were placed in front of nest cavities in order to capture the birds. The contour of the bank used by a nesting colony as well as the height of the colony above the talus slope often presented problems in net placement. Winds and bank configurations which made the nets readily visible also limited sample size at times. Inclement days were avoided.

From 1959 through 1972, 6781 Bank Swallows were banded with Fish and Wildlife Service bands and released. Age (immature versus adult), location and date were recorded. From 1967 sex and other data were taken in addition. Sexes were distinguished during the breeding season by the presence of incubating patches in females and cloacal protruberances in males. Of the total banded there were 1495 adult males, 1575 adult females, 2730 unsexed adults, and 981 unsexed juveniles. Eight of the juveniles were sexed as males and six as females when later captured as adults.

To avoid undue disturbance at a colony, sampling usually was confined to a period of two to five hours. Two to 12 of the 28 colonies were sampled in any one year, with the usual number of visits to a specific colony during a season ranging from one to four. Some colonies received more concentrated banding effort than others and therefore had better continuity of data. For example, the colony at WK-1 was visited at every breeding season from the start of the project in 1959 except 1963 and 1965, resulting in the banding of 2277 individuals.

Two other banders, Edward Peartree and David Stoner, cooperated in this study. Stoner made a concerted effort to capture all individuals at WK-1 in 1967 by banding on 16 days during the breeding season. At colony WK-4, 743 birds were banded on visits during seven out of the ten breeding seasons between 1959

and 1968. Other colonies were not used consistently for a variety of reasons and had only insignificant numbers banded. Some of these, however, provided interesting captures of birds banded elsewhere.

Population estimates were frequently derived from visual observation of birds flying in the vicinity of the colony. However, the numbers in many colonies were estimated by counting the number of visible excavations and applying the formula

$$N_{ve} \times .80 \times 2 = EAP$$

where N_{ve} is the number of visible excavations, .80 is the porportion of these excavations in active use (this percentage being based on sample counts of active versus inactive cavities in several colonies), and 2 is the number of adults that were assumed to be occupying each active nest cavity. EAP, therefore, is the estimated adult population. Population estimates were further checked at some locations by applying the Schnabel method to capture/recapture data (Smith, 1966). Most estimates were made in June, the peak nesting time prior to fledging.

When a pit could not be surveyed every year to check for the existence of a colony, the owners often supplied the missing information. In the absence of confirmation it was assumed that birds were using a pit during a non-survey year if a colony existed both in the year prior and the year after. The combination of visits and owner information were used to ascertain the longevity of pit use by breeding Bank Swallows. Bank Swallow survival and longevity estimates were made according to Robbins (1969; see Table 1).

Results

Colonies were generally active for up to four years. However, the surveys showed that three colonies were active for at least five years and one each for six, eight, nine, eleven, and thirteen years. Population estimates with the Schnabel method were in general agreement with the other methods described, and the latter were used for calculations. Populations of active colonies ranged from less than 10 to 2,000 in number.

Three hundred and twelve of the 6781 banded birds were recaptured in the study area in years subsequent to banding, a return rate of 4.6%. Data on sex ratios of swallows at original banding and at time of recapture were examined with a chi-square test. No differences were found. Survival rates for adult swallows in three of the most well-studied colonies ranged from 36.0% to 46.3%, with a rate of 34.9% for all sites combined (Table 2). Maximum ages calculated from these survival rates were 5-7 years (combined data, 6 years). The maximum age observed was eight years.

Of the 309 recaptures made at nesting sites, 213 (68.9%) were at the site of banding (Table 3). Only 33 birds (10.6%) were found at sites more than 6.6 km away. Two hundred and eighty-nine of the total recaptures at pits were of birds banded as adults. Seventy percent (203) of these recaptures were made at the site of banding. Of the 86 adults that were found at different pits, 55 had moved "voluntarily," i.e., their original colonies were still active. One of the two 14.6-40 km movements (Table 3) was voluntary, as was the longest movement in the study (134.4 km). In 28 cases of adult movement, the original site had been destroyed ("forced" movements). The status of three moves could not be determined. Juveniles demonstrated a lesser degree of banding site loyalty; 40% of the juvenile returns were voluntary moves compared to 19% of the adult returns.

Return success was examined for two of the most thoroughly studied colonies, using the calculated survival and site loyalty rates (Table 4). Only a small proportion of the expected recaptures (from 12-38%) was made in any year, leaving a large number of birds "unaccounted for."

Discussion

Extensive work on the Bank Swallow's breeding cycle is detailed in Petersen (1955). He found that these birds arrived near Madison, Wisconsin, during the latter part of April and began hole excavation or rehabilitation shortly thereafter, usually early in May. The greatest degree of activity at the nest holes took place in June, with a limited number of Swallows at the sand banks as late as mid-August. Bank Swallows usually leave the Madison area by early September (the latest record is 11 September).

Four points seem to be apparent from our population data on Wisconsin Bank Swallows; (1) few banded adults are recaptured in subsequent years regardless of "home site," (2) in those adult Bank Swallows that are recaptured there appears to be general fidelity to the original breeding site, (3) some adult birds are forced to move, while others apparently move voluntarily, and (4) a few adults move considerable distances. Although statistical significance was not achieved, probably due to small sample size, juvenile Bank Swallows exhibited a greater tendency to disperse from the home site, as expected. Some difficulties with adult returns, however, are evident in the data.

In previously published studies (Mason, 1953; Anderson and Maxfield, 1967; Robbins, 1969; Davis, 1971; Roberts, 1971), return rates for migratory summer resident passerine species from five families ranged from 9.1 to 44.1%. Rates of return in Bank Swallow studies (Stoner, 1941; W. Nickell, *pers. comm.*; E. Neeb, *pers. comm.*) have ranged from 3.0 to 12.5%. The latter figures are more comparable to the return rate of this study, although

4.6% still seems somewhat low. The results of the recapture success analysis (Table 4) add to this suspicion. In the two colonies analyzed, only 12-38% of the expected recaptures were made. The proportion of unaccounted-for birds becomes even more interesting in light of the fact that any factor lowering recapture success also would have lowered the calculated survival rate below the "real" value. Using a larger survival value in calculations for Table 4 would result in an even larger residue of missing birds.

There could be a number of explanations for this discrepancy between expected and actual recaptures. In this study the mist nets were placed in nearly the same position during each visit, even during subsequent years, if the colony site had not been altered. It is probable that the birds became wary of nets following repeated visits during the same breeding season, resulting in a low recapture success within years. Indeed, although the number of adult birds captured in consecutive visits within a season was relatively constant (during early summer when populations were stable), each catch was made up largely of individuals not previously captured.

Visual observations also support the idea of net "smartness." Many birds were seen to avoid the nets while in flight. Some roost sites required net placements so visible that birds occasionally perched on the top shelf-string. It seems unlikely, however, that Bank Swallows would remain cautious enough, following a year or more of the absence of mist netting between breeding season visits, to contribute more than a small proportion of the missing recaptures. It would appear, then, that a much larger proportion of adult birds must have been "disloyal" to the site of banding in subsequent breeding seasons than the calculations indicate.

In the glaciated areas of the breeding range of this species there is a plethora of suitable nesting sites. It was impossible to locate every Bank Swallow nesting site within the selected study area. Certainly any sites not at commercial sand and gravel pits were missed. Even if all sites could have been located, it would have been impossible to adequately sample them all with the time and personnel resources available. Over the 13 years an average of 5.4 of all the sites used to acquire banding data were visited each year. This factor undoubtedly masked much of the possible movement of birds among pits.

Long-distance movements (out of the study area) were even less likely to be discovered than short ones. Despite this, however, some long movements were observed (Table 3). Further evidence that they occur was the capture, during this study, of a Bank Swallow banded the previous year (1968) in Farmington, Michigan. This bird was an adult at banding, and was nesting 402.6 km from the nesting site of banding when recaptured.

Considering the mobility of the species, the large number of potential nesting sites, and the sampling limitations, it becomes

apparent that the adult breeding fidelity mentioned previously (also see Table 3) may have been more indicative of researcher location than species behavior. Any comparison of adult versus juvenile tendencies toward movement would still be valid, since both age classes would be affected equally by the sampling bias. In fact, if juveniles are more likely to disperse widely, they could be even less likely to be found at their new pits than adults. Lower survival, of course, also makes their recapture more difficult.

It is possible that sampling errors contributed to the number of adult birds counted as having switched colonies. For example, three adults turned up at two different pits in the same nesting season. In all three cases, the initial banding occurred relatively early in the season (June 6, 7, 15), and the birds were recaptured relatively late (July 1, 2, 9). Perhaps these and other "disloyal" individuals which were not caught twice in a year had terminated their nesting responsibilities and were wandering about preparatory to fall migration. The recapture in a subsequent year of one of those same-year movement birds, not at the original site, but at the second site, argues against the importance of this bias, however. The 55 voluntary movements and low overall return rate remain strong evidence that there is a wide dispersal of adult individuals from year to year, although adults probably are more loyal than juveniles.

If it is assumed, then, that adult Bank Swallows exhibit a pattern of relatively frequent changes in choice of breeding site, it is appropriate to hypothesize on the mechanisms and results of this behavior. It does not seem likely that, following migration, the birds are unable to find their original pit. Downhower and Windsor (1971) concluded that most Bank Swallows are familiar with local landmarks within 5 km of their breeding colony, and that cues other than landmarks are used at greater distances. Sargent (1962) found that 87% of the Bank Swallows he released 40-80 km away were able to return to their home site.

Destruction or disturbance of pits undoubtedly caused some of the movements observed (the "forced" movements discussed earlier). Most pit operators avoid disturbing Bank Swallow colonies during the nesting period, but other operators dig into a colony as the necessity occurs. Swallows disturbed by digging frequently do not abandon the site, excavating new holes either at the same position or in an adjacent position within the pit.

However, one instance was observed in 1971 where a colony abandoned its pit following disturbance. On June 8 approximately 280 adult birds were nesting at site WK-6A. The site was revisited on June 17 and July 2, and the population was estimated to have fallen to less than a dozen birds. This pit was not being worked by the owners, but the pit manager said that an unauthorized group had been there one weekend and had "shot up the

place." No carcasses were found, so it is not known if any of the birds were killed. One of the swallows banded on June 8 at this location was recovered (as a road kill) in early July about 84 km away.

Such forced movements, then, are examples of spacing as defined by Berndt and Sternberg (1968). Other pressures resulting in spacing could include intraspecific competition for food or mates. These would be interesting areas for future investigation. The recaptures made in the present study, however, indicate that voluntary movement, or dispersal, is at least an equally important factor in nest site switching. There were several instances of birds that were faithful to one site for several years and then deserted it in favor of another, despite the continued existence of the first. Competitive forces would seem to be unlikely factors in the movements of such established individuals.

The tendency of migratory birds to return each year to the same locality to breed has been investigated for several species. Howard (1960), referring to vertebrates in general, states that "for the most part, the major dispersal movements are made by virgins about the time they attain puberty." He further feels that many species have innate dispersal mechanisms or motivations which have important survival values. According to Howard, such mechanisms "(1) increase the spread of new genes, (2) create wide outbreeding, (3) enable a species to spread its range rapidly as favorable habitats are created, (4) permit the species to have a discontinuous distribution, and (5) help the species quickly reinvade areas that may have been depopulated by catastrophes, such as floods, fires, or man's activities."

The Bank Swallow is nearly a cosmopolitan species. It breeds in suitable sites of the Holarctic areas of the world, and annually migrates south to non-breeding ranges in the Neotropical or Ethiopian regions. In Mayr's (1963) opinion, "all species are composed of local populations, and, since in sexual species no two populations are identical, all species show geographic variation, much of it not expressed in the visible phenotype." Ehrlich and Raven (1969) suspect that "in some species, gene flow is an important factor in keeping populations of the species relatively undifferentiated," although they feel that in most species it is of little or no importance. They also state that "for sexual organisms it is the local interbreeding population and not the species that is clearly the evolutionary unit of importance."

It appears to the authors that it is improbable that Bank Swallows are subject to greater mortality during migration than other passerines, as Stoner (1941) surmised, and that the low return rates for this species may be explained better by a lesser tendency for colonial organization within this species to exhibit continuity from year to year. Individual survival rates calculated for this species thus would be expected to be, at the most, minimum values, and if Howard (1960) is correct, this innate dispersal mechanism should have considerable survival value for the species.

If the dispersal hypothesis is true, there must be considerable gene flow among different colonies of Bank Swallows, and one would expect the phenotypic characteristics of the species to be fairly constant over its range. Berndt and Sternberg (1968) point out that "the greater the extent of dispersion . . . , the fewer the geographical races that have been formed, presumably because dispersion is related to gene flow." Accordingly, there is little phenotypically observable subspecific variation in the Bank Swallow throughout its world-wide range. The testing of this hypothesis, unfortunately, would require a study of tremendous scope.

Summary

Faithfulness of Bank Swallows *(Riparia riparia)* to colonial nesting sites was studied at 28 locations from 1959 through 1972. A low adult return rate of 4.6 was recorded, with an adult survival rate of 34.9. Calculations of survival and fidelity to "home" pit resulted in an unrecaptured residue of the swallow population which was not immediately explainable. Of the 289 adult recaptures obtained, a relatively large number (19%) moved voluntarily to pits other than the site of banding. A few birds moved during the same breeding season.

Results of this study suggest a relatively low tendency toward year to year colonial continuity in this species. The increased gene flow resulting from this dispersion may help maintain geographical variability at the low level observed in the species.

Acknowledgments

A survey of this magnitude covering such a wide area and encompassing 13 years required the help of many persons. The cooperation of the many operators of the commercial sand and gravel pits was essential. Edward Peartree and David Stoner, who were netting swallows within the boundaries of this study, gave many hours of their time banding and recording and subsequently reporting their data to the senior author.

Barbara Robertson and Joan Jass acted as recorders and assisted with mist netting on many field excursions. The junior author refined the statistical treatment and contributed to the discussion portion of the paper.

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Literature Cited

Anderson. K. S. and H. K. Maxfield. 1967. Warbler returns from southeastern Massachusetts. Bird-Banding, 38:218-233.

Berndt, R. and H. Sternberg. 1968. Terms, studies, and experiments on the problem of bird dispersion. Ibis, 110:256-269.

Davis, R. S. 1971. Survival rates of barn swallows at Glenhaven Farm. IBB News, 43:13-15.

Downhower, J. F. and D. Windsor. 1971. Use of landmarks in orientation by Bank Swallows. Bio Science, 21:570-572.

Ehrlich, P. R. and P. H. Raven. 1969. Differentiation of populations. Science, 165:1228-1232.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Amer. Midl. Nat., 63:152-161.

Lack, David. 1954. Natural Regulation of Animal Numbers. Oxford Univ. Press (Clarendon), London, 343 pp.

Mason, E. A. 1953. Barn Swallow life history data based on banding records. Bird-Banding, 24:91-100.

Mayr, E. 1963. Animal Species and Evolution. Belknap Press of Harvard Univ. Press, Cambridge, 797 pp.

Nice, M. M. 1941. The role of territory in bird life. Amer. Midl. Nat., 26:441-487.

Petersen, A. J. 1955. The breeding cycle in the Bank Swallow. Wilson Bull., 67:235-286.

Robbins, C. S. 1969. Suggestions on gathering and summarizing return data. Bur. Sport Fish. Wildlife, Migratory Bird Pop. Station, Laurel, Md. (unpublished report).

Roberts, J. O. L. 1971. Survival among some North American Wood Warblers. Bird-Banding, 42:165-184.

Sargent, T. D. 1962. A study of homing in the Bank Swallow *(Riparia riparia).* Auk, 79:234-246.

Smith, R. L. 1966. Ecology and Field Biology. Harper and Row, New York, 686 pp.

Stoner, D. 1941. Homing instinct of the Bank Swallow. Bird-Banding, 12:104-109.

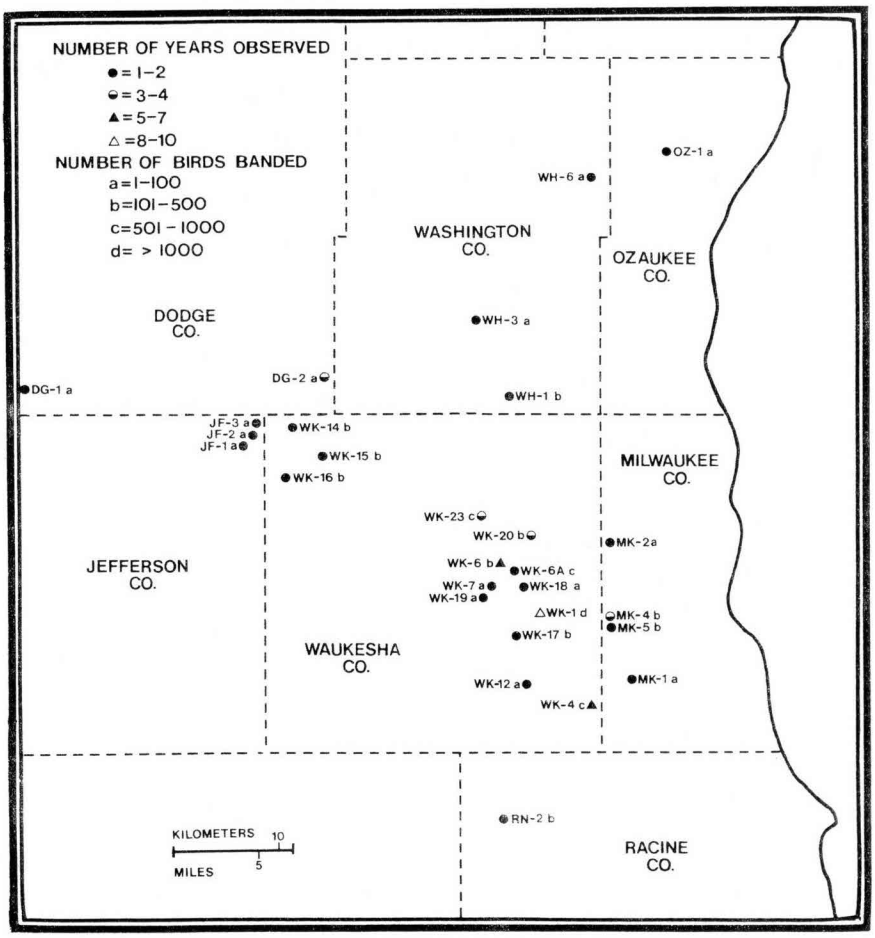

FIGURE 1 — Site locations, number of years studied, and number of Bank Swallows banded.

TABLE 1: Example of Survival Calculation Method, All Sites Combined

Banding Year	Recaptures, Adult Birds, by Years After Banding[1] 1	2	3	4	5	6	7	
1959	2	3	1	0	0	0	0	
1960	1	0	0	1	0	0	0	
1961	12	4	1	0	1	0	1	
1962	16	5	0	1	1	0	0	
1963	2	2	0	1	0	0	0	
1964	2	0	6	0	0	0	0	
1965	2	0	0	0	0	0	0	
1966	12	2	0	0	2	0	—	
1967	39	23	4	1	0	—	—	
1968	30	4	1	0	—	—	—	
1969	51	26	2	—	—	—	—	
1970	16	3	—	—	—	—	—	
1971	7	—	—	—	—	—	—	
Totals	192	72	15	4	4	0	1	= 288
	- 7[2]	- 3	- 2	-0	-0	- 0	- 0	
	185	69	13	4	4	0	1	

Survival Rates by Age Groups

Yr. 1 to Yr. 2 = 72 ÷ 185 = 38.9%
Yr. 2 to Yr. 3 = 15 ÷ 69 = 21.7%
Yr. 3 to Yr. 4 = 4 ÷ 13 = 30.8%
Yr. 4 to Yr. 5 = 4 ÷ 4 = 100.0%
Yr. 5 to Yr. 6 = 0 ÷ 4 = 0.0%
Yr. 6 to Yr. 7 = 1 ÷ 0 = —

Mean survival rate = 96 ÷ 275 = 34.9%

[1]Excluding one road kill and 3 same year movements.

[2]The last year's returns are subtracted since it would have been impossible to recapture them again.

TABLE 2: Survival Rates and Longevity of Adult Bank Swallows in Selected Colonies.

(Data are for all years combined, excluding 1972 bandings since recapture efforts ended that year.)

	Selected Colonies			
	WK-1	WK-4	WK-6/6A	All Sites Combined
Adults Banded	1813	725	785	5705
Adults Recaptured	121	26	67	288
Percent Recaptured	6.6	3.6	8.4	5.1
Calculated Mean Survival Rate	.361	.360	.463	.349
Maximum Age (Computed with mean survival rate)	5	6	7	6
Maximum Age (Observed)	6	5	8	8

TABLE 3: Nest Site Loyalty and Movement to Different Sites.

	Total Recaptures	Returned to Original Pit	Moved to Different Pit	Distance of Movement			
				6.5 km or less away	6.6—14.5 km away	14.6—40 km away	Greater than 40 km away
Adults (% of Total)	289*	203 (70.2)	86 (29.8)	59 (20.4)	24 (8.3)	2 (0.7)	1 (0.3)
Juveniles (% of Total)	20	10 (50.0)	10 (50.0)	4 (20.0)	6 (30.0)	0	0
	309	213 (68.9)	96 (31.1)	63 (20.4)	30 (9.7)	2 (0.6)	1 (0.3)

*Excluding one road kill and 2 recaptures not at a pit (all adults).

TABLE 4: Recapture Success Analysis For Adults

Year of Recapture:	WK-1 1968	WK-1 1969	WK-1 1970	WK-6/6A 1970	WK-6/6A 1971
A. Number of Banded Adults Present in Previous Year[1]	697	535	396	475	284
B. Theoretical Survivors (B = A x 36.1% and 46.3%, respectively)	252	193	144	220	132
C. Survivors Returning to Site of Banding (C = B x 70.2%)	177	136	101	154	92
Expected Recaptures (with Population Change Adjustment[2])	118	139	101	76	66
Actual Recaptures	34	33	12	29	16
Unaccountable (% of expected)	84 (71%)	106 (76%)	89 (88%)	47 (62%)	50 (76%)

[1] A = # banded previous year + accumulated total of survivals and returns.

[2] Population Change Adjustment = $\frac{\text{C x Estimated Population Year of Recapture}}{\text{Estimated Population Previous Year}}$