SITE FIDELITY AND SURVIVAL DIFFERENCES BETWEEN TWO GROUPS OF NEW WORLD RED KNOTS (CALIDRIS CANUTUS)

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ABSTRACT.—During the boreal winter, New World Red Knots (*Calidris canutus rufa*) principally occupy two areas widely separated in latitude. The larger group of approximately 100,000 birds is distributed along the Patagonian Atlantic coast, the smaller group of about 10,000 along Florida's Gulf coast. Resightings of banded individuals showed no interchange between these groups. The annual survival rate of knots marked in Florida is twice that of marked knots that winter in Patagonia. During northward migration Florida knots were sighted significantly less often at a major New Jersey stopover site than knots marked in Argentina. Whether this segregation is maintained during the breeding season is unknown. Wing and culmen lengths did not differ between the groups. The higher survival of individuals from the smaller Florida group, which presumably migrates a much shorter distance than the Argentina birds, runs counter to current evolutionary theories on the benefits of migration. *Received 1 May 1987, accepted 31 January 1988.*

MIGRATION is defined as any deliberate movement from one place to another that is driven by the benefits of moving vs. the costs of staying (Baker 1978). Cost is measured as either mortality or loss of reproductive output. Many specific costs or benefits that might lead to migratory behavior have been proposed. Ketterson and Nolan (1982) suggested that smaller birds are less capable of surviving winter food shortages and climatic extremes at higher latitudes; thus, selection favors their annual movement south to more moderate climes. In his dominance hypothesis, Gauthreaux (1978, 1982) hypothesized that inferior competitive skills result in longer movements to areas where competition is reduced.

Contemporary hypotheses propose that migrating individuals accrue greater fitness than do nonmigrants. Greenberg (1980) proposed that a critical difference between resident and migrant birds was the mutually exclusive allocation of time to reproductive activities vs. allocation to strictly survival-oriented activities. Year-round residents face reduced survival because of harsher wintering environments, but gain reproductive benefits by having an extended breeding season. In contrast, migrants may have higher survival by avoiding harsh winters, but sacrifice time spent on the breeding grounds. Bull et al. (1987) argued that migratory phenotypes without direct fitness benefits can exist when genetic exchange between population demes is skewed.

Except for Bull et al.'s (1987), these hypotheses recognize that selection for a migratory phenotype should be driven by increased fitness (survival × fecundity) (Lack 1968). The practical problems of studying reproductive success as a function of migration distance and annual survival have impeded direct tests of the hypothesis. In fact, simply demonstrating migration-related differences in survival is difficult because specific wintering areas of breeding populations rarely are known. Analysis of intraspecific survival rates and migration distance will help develop an understanding of the evolution of migration. Greenberg (1980) hypothesized that individuals that migrate farther invest more in their own survival by exploiting a more benign nonbreeding habitat. Until a relationship between migration distance and survival is demonstrated, it will be difficult to evaluate these models.

The Red Knot (*Calidris canutus*) migration is one of the longest in the New World. The southeastern breeding limit of the North American race (*C. c. rufa*) is Southampton Island in northern Hudson's Bay (Abraham and Ankney 1986). The range extends northwest to Victoria Island (Parmelee et al. 1967), but the northeastern limit is not known. A disjunct group breeds on the Alaskan North Slope (Conover 1943). *Rufa* has two centers of distribution during the boreal winter (Morrison 1984). The larger group winters on the Patagonian coast of southern Argentina and Chile (Morrison et al. 1985), while

TABLE 1. Numbers and locations of banded Red Knots.

Band class (state-year)	Number
Scituate, Massachusetts	
MA-80	133
MA-81	340
MA-82	172
MA-83	290
MA-84	389
Cape May Co., New Jersey	
NJ-80	130
NJ-81	307
NJ-83	309
NJ-85	245
NJ-86	456
Longboat Key, Florida	
FL-1/81	263
FL-10/81	101
Argentina, Peninsula Valdez, Chubut	
AR-81	181

the smaller group winters 9,200 km north on the Gulf coast of Florida (Harrington and Leddy 1982a). These two groups, which appear discrete (see below), offer an opportunity to compare intraspecific survival in relation to migration distance and thus to test some elements of current migration models.

METHODS

Red Knots were captured, banded, and released in Massachusetts, New Jersey, Florida, and Argentina between 1980 and 1986 (Table 1). Birds from each area were marked with distinctive colored leg bands, plastic tape, or solid plastic flags according to year and location of banding, thus becoming members of specific "band classes."

In Florida Red Knots were captured and banded at Longboat Key (27°21′N, 82°36′W) near Sarasota. All banding in Florida occurred during January or October 1981. Banding in Massachusetts occurred between July and September at Third Cliff Beach in Scituate (42°00′N, 70°40′W) or, for 6 birds, at Plymouth Beach (41°50′N, 70°30′W). Catches in New Jersey were during May at Reeds Beach (39°00′N, 74°50′W) or, for 14 birds, at Moores Beach (39°10′N, 74°50′W). In Argentina birds were banded between 11 and 20 April 1981 at Peninsula Valdez (42°20′S, 64°15′W).

With the exception of 6 Red Knots in Massachusetts caught with mist nets, all birds were captured with a 12.2 × 21.3 m rocket net of 2.5-cm, knotless nylon mesh, propelled by 5 rockets (Winn-Star, Marion, Illinois). Captured knots were banded and measured at capture locations and were released within 6 h.

Measurements included wing length (natural chord) and exposed culmen length.

We returned to banding sites for up to 60 months after banding each class. On each visit Red Knot flocks were searched systematically for color-banded birds marked up to 60 months earlier. We used 20× scopes to count the total number of knots and the number found from each band class. After each visit a resighting rate for each band class was calculated by dividing the number of class members found by the original band-class size, and dividing this quotient by the total number of birds that had been checked. Survival rates of knots from different locations were calculated by linear regression of the log of the resighting rate vs. time since banding. Survival rates among locations were then compared by testing for heterogeneity of slopes (SAS GLM procedure; SAS 1985, 1986).

RESULTS

Between 1980 and 1986 we banded 3,316 Red Knots at the 4 study sites (Table 1) and resighted 1,730 (Table 2). The mean size of the Florida wintering group was 6,300 ± 3,400 (1 SD) birds, based on 4 aerial surveys between October and January 1980–1982. In 9 yr of censusing, an average of 1,661 ± 724 birds used the Massachusetts stopover site at peak migration. The average peak number at Delaware Bay during northward migration was 60,000 ± 40,000 (1 SD) birds for 3 yr (Dunne et al. 1982, Wander and Dunne 1982, Kochenberger 1983). The Patagonian group consisted of at least 67,500 knots in 1985 (Morrison and Ross in press). Thus, Delaware Bay is a major staging area in spring migration, and the Massachusetts site is a minor one during fall migration. Patagonia is the major known wintering area, and Florida is a minor wintering area.

To establish relationships between these groups (Florida, New Jersey, Massachusetts, Patagonia), we examined the interchange of marked individuals among them. We also compared the frequency of Florida-banded knots with Argentina-banded knots that appeared at the New Jersey and Massachusetts stopover sites. Loss of color markers in the Argentina cohort prevented the use of resightings more than 18 months after banding. Thus, we used the comparable Florida cohort from the same time span for the analysis.

Relative to their band-class sizes, Argentina knots were found 4.5 times more often at New Jersey and Massachusetts than Florida-banded birds (Table 3; χ^2 = 16.7, 1 df, $P < 0.01$). Birds

TABLE 2. Red Knots color-banded in North America and resighted 3 or more months later at original banding area.

Band class	Months elapsed	No. sighted	No. checked
Scituate, Massachusetts			
MA-80	12	20	2,529
MA-80	24	14	2,220
MA-80	48	1	1,506
MA-80	60	2	11,499
MA-81	12	53	2,220
MA-81	36	2	1,506
MA-81	48	7	11,499
MA-81	60	2	2,071
MA-82	24	15	1,506
MA-82	36	11	11,499
MA-82	48	2	2,071
MA-83	12	52	1,506
MA-83	24	217	11,499
MA-83	36	32	2,071
MA-84	12	442	11,499
MA-84	24	57	2,071
Cape May Co., New Jersey			
NJ-80	12	12	19,997
NJ-80	24	24	59,403
NJ-81	12	12	59,403
NJ-81	24	3	8,069
NJ-81	48	1	33,684
NJ-83	24	54	33,684
NJ-83	36	94	153,684
NJ-85	12	233	153,684
Longboat Key, Florida			
FL-1/81	9	57	2,825
FL-1/81	11	63	2,904
FL-1/81	22	84	4,001
FL-1/81	46	42	4,621
FL-10/81	3	42	2,904
FL-10/81	14	46	4,001
FL-10/81	38	34	4,621

TABLE 3. Sightings of Red Knots marked during January–April 1981 in Florida and Argentina and found during spring and autumn migration in New Jersey and Massachusetts, 1981–1982.

Banding origin	No. marked	No. resighted in New Jersey or Massachusetts
Florida	263	8 (3.04%)
Argentina	181	25 (13.8%)

Massachusetts knots were sighted 10 times more often in New Jersey than were Florida birds.

Biometric comparisons between Red Knots can indicate genetically discrete breeding groups (Dick et al. 1987). Accordingly, we compared wing and bill lengths of knots caught in Florida with those caught in Argentina. We found no statistically significant differences between the means of either variable, nor were there differences between the Argentina/Florida groups and those caught in Massachusetts and New Jersey (Table 4) ($P > 0.05$, ANOVA; Sokal and Rohlf 1981). Likewise, a small sample of museum specimens from the disjunct Alaskan breeding group ($n = 9$) and from the larger contiguous breeding range in Canada ($n = 20$) were not different in these parameters ($P = 0.079$, Wilcoxon 2-sample test).

The lack of interchange between individuals in the wintering groups enables survival rates to be compared between these two differentially migrating populations. Although the Massachusetts and New Jersey knots apparently are from the same Argentina wintering group, we analyzed them separately. If they are from the same population, then their survival rates should be similar.

To evaluate survival rates of the three groups (Florida, New Jersey, Massachusetts), resighting rates at the original banding area vs. time elapsed since banding were plotted for each band class (Fig. 1). The slopes and intercepts of these regression lines were significantly different (ANOVA; intercept: $P \ll 0.01$, slope: $P = 0.014$). The difference between intercepts is a function of the number of birds surveyed at each site and has no bearing on comparison of survival rates (i.e. slopes). The slopes differed significantly among groups, and indicate that the sites differ in the probability of banded knots being resighted. In years subsequent to banding, Florida knots were resighted at higher rates than birds from Massachusetts and New Jersey.

banded in Massachusetts or New Jersey were resighted in Florida only 4 times (of 19,889 birds checked), and no Argentina birds were found in Florida or vice versa. Therefore, there seems to be no exchange of birds between the Florida and Argentina wintering groups and little overlap between them at spring and autumn migration staging areas.

To establish further that New Jersey and Massachusetts knots principally represent the Patagonian group, which is discrete from the Florida group, we compared the frequency of resightings of the Massachusetts and Florida 1981 banding classes. In New Jersey during spring 1982, 97 of 340 (29%) Massachusetts-banded knots were found the following spring vs. 7 of 263 (3%) Florida-banded knots. Thus,

TABLE 4. Wing and bill lengths of Red Knots captured at 4 locations.

Location	Wing length		Bill length	
	n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$
Massachusetts	751	162.2 ± 4.64	498	35.63 ± 1.94
New Jersey	439	162.6 ± 4.06	466	35.60 ± 1.78
Florida	211	162.3 ± 4.40	238	36.25 ± 1.94
Argentina	273	162.2 ± 4.78	279	36.19 ± 1.92

The slopes for the Massachusetts and New Jersey resightings were not statistically different ($P = 0.865$) from each other. Therefore, the differences among the three lines (Fig. 1) are due to greater resighting rates of the Florida birds.

Regression analysis was used to estimate annual survival for birds at each site by comparing the frequency of resightings at that location against time since initial capture, and calculating survival from the equation:

$$p = e^{12d},$$

where d = slope of the regression line and p = estimate of annual survival (Caughley 1977). The slope was multiplied by 12 in the exponent to convert monthly to annual survival estimates. Based on this analysis, the probability that knots wintering in Florida will live to the next year was more than twice that of knots
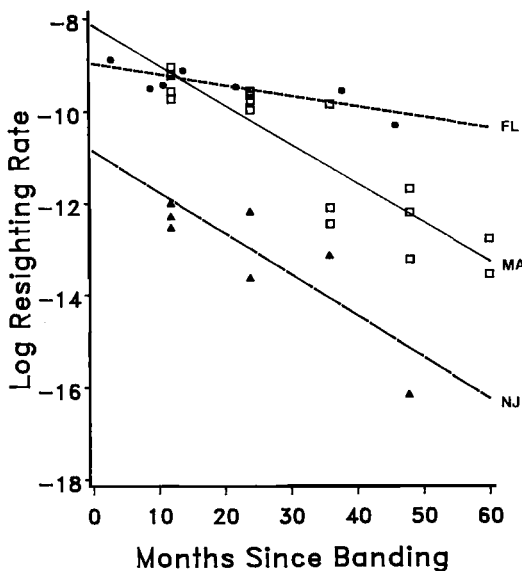

Fig. 1. Resighting rates of color-banded Red Knots at original banding areas according to capture date in Florida (FL), Massachusetts (MA), and New Jersey (NJ).

banded in Massachusetts and New Jersey (i.e. birds of the Argentina wintering group) (Table 5).

Different observed survival rates for the three sites do not prove that survival rates are different. The survival rates (Fig. 1) could be dictated by survival, "emigration" (failure to return to the banding site in subsequent years), or both. Thus, differences in slope could imply a difference in year-to-year site fidelity rather than a difference in survival. If New Jersey and Massachusetts birds were less faithful to their stopover sites than Florida birds were to their wintering site, the slope of the regression line would be steeper because of differences in site fidelity, lower survival, or both.

Survival rates of each band class at its original banding location compared with resighting rates of birds from the same band classes at other locations should reveal possible differences in site fidelity. This assumes that mortality contributes equally to decreased resighting rates at all locations, and that differences between survival rates will be caused only by differences in site fidelity. Only data from the Massachusetts cohorts were sufficient for this comparison. The slopes derived from resightings in Massachusetts (the banding site) and in New Jersey (Fig. 2) were not statistically different ($P = 0.764$). This suggests that the migrants traditionally use the same stopover sites every year, and that the results accurately measure survival rather than lack of between-year faithfulness to the banding site.

DISCUSSION

Red Knots travel routinely between North America and Argentina (Harrington and Leddy 1982b). Knots that visit Delaware Bay in spring come mostly from South America (Table 3). Red Knots that winter in Florida are underrepresented during migration in New Jersey and Massachusetts. With no evidence of exchange

TABLE 5. Slopes, R^2-values, and significance levels for individual linear regressions (see Figs. 1 and 2) fitted to the data from each site independently, and estimates of annual survival.

Location	Slope	R^2	P	Survival[a]
Massachusetts	−0.0855	0.8101	0.0001	0.358
Florida	−0.0231	0.6922	0.0203	0.758
New Jersey	−0.0899	0.6911	0.0105	0.340
Massachusetts in New Jersey	−0.0911	0.7510	0.0001	0.335

[a] $p = e^{12d}$, where d is the slope.

between Florida- and Argentina-marked birds, we propose that these wintering populations are discrete.

Because Red Knots that winter in South America have strong fidelity to migration stopover sites, the slopes derived from linear-regression analysis of annual resighting rates at stopovers are appropriate for determining annual survival. Even if differences in site fidelity were a factor, there is no reason to believe among-year attrition rates of marked birds from one area should differ from immigration rates of marked (or unmarked) birds from other areas. In addition, the resighting rate of Red Knots banded in Massachusetts and resighted in Massachusetts during subsequent autumns was the same as the rate for those same band-class members that were resighted in New Jersey during spring. These slopes also were the same as those for resightings of New Jersey–banded birds re-
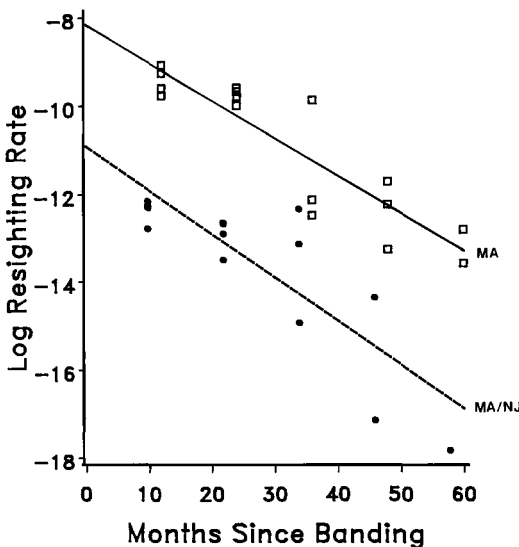

Fig. 2.   Resighting rates of Red Knots at their original autumn migration banding area (MA) and at a spring migration staging area on Delaware Bay (MA/NJ). Line MA is the same as in Fig. 1.

sighted in New Jersey. This conformity indicates that site-fidelity rates did not complicate the between-site comparison of annual survival.

Survival estimates of Florida Red Knots were based on a wintering population, whereas the values for the Massachusetts and New Jersey groups were derived from migrating groups. This condition should not bias survival estimates because resightings were made annually for each group. The age structure of the samples may be biased, however. Spaans (1984) found that Semipalmated Sandpipers (*Calidris pusilla*) remained in the nonbreeding range until 18 months old. Red Knots have been observed to be abundant in Florida (Below pers. comm.) and South America (Belton 1984) during the boreal summer. Thus, the annual survival estimate of Red Knots in Florida may include a subset of birds that did not migrate during the year subsequent to banding. In later years, however, these birds would be old enough to migrate. The resighting rates for these years should parallel the New Jersey and Massachusetts regressions if survival rates were similar. Even after the first return of the Florida cohort, the resighting probabilities remained higher than those for Massachusetts and New Jersey Red Knots (Fig. 1), so a potential difference in age structure does not explain the higher survival of the Florida knots.

One explanation for the disparity in survival rates of Patagonian and Floridan wintering knots is that they represent different breeding groups with little genetic exchange between them, and where different migration phenotypes are maintained. Nothing is known about the specific breeding distributions of either wintering group; they could range from complete overlap to complete disjunction. We know that the breeding range of *C. c. rufa* is disjunct, with separate breeding groups in the central Canadian Arctic and on the Alaskan North Slope. Whether this bears any relation to our obser-

vations of discrete wintering groups is unknown. Comparable distributional anomalies exist. For example, Red Knots that breed in Siberia migrate to Mauritania on the African west coast, and Red Knots that breed in Greenland and eastern arctic Canada winter on western European shores (Dick et al. 1976, 1987; Davidson et al. 1986). These groups have recently been described as separate subspecies (Roselaar 1983). Until more is known about the breeding distribution of New World Red Knots, the question of genetic separation between the Florida and Argentina wintering groups remains open. Based on two morphological measures, we found no distinctions between them.

If the Florida- and Argentina-wintering Red Knots come from different breeding areas and asymmetrical genetic exchange occurs, then survival differences may be maintained. Bull et al. (1987) challenged the claim that migration was favored whenever individuals realize increased fitness through migration. Because of the size disparity between the Red Knot groups that winter in Florida and Argentina, exchange of birds between the two could exist at substantially different rates. Moreover, the differential resighting rate of Red Knots marked in Florida and Argentina (Table 3) at stopover sites on the U.S. Atlantic coast could be construed as evidence of differential breeding-area exchange by birds from different wintering areas. Bull et al. (1987) showed that genetic migration is selected according to the geometric mean fitness of bidirectional dispersal between two groups, rather than unidirectional dispersal. Further, "no matter how large the short-term gain from genetic migration [breeding] site 1 to site 2," exchange of the migration phenotypes will *not* be favored if genetic exchange in the reverse direction is too small. Our results suggest the possibility of differential exchanges.

If the wintering and migrating groups of Red Knots we studied are from the same genetic group, then our results contradict Greenberg's (1980) time-allocation model. According to the model, migration distance correlates positively with the occupation of increasingly benign wintering habitats and, consequently, higher nonbreeding season survival. Birds that winter closer to the breeding range benefit from the reduced time and effort required to return to breeding areas and may gain breeding-season advantages (Myers 1981). Survival presumably is reduced by wintering in harsher, higher lat-

itudes. Yet knots that winter in Florida exhibit higher survival, despite being nearer the breeding range and, according to the model, occupying an inferior wintering habitat. That the Florida site represents inferior habitat remains to be documented. The question of what underlies the lower survival rate of the Patagonian knots is unanswered. If it is due to some unidentified environmental condition that prevailed during our 6 yr of study, then a serious conservation concern is indicated. Alternatively, if the differential survivorship is real over the long term, then an evolutionarily intriguing condition exists.

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