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SOURCES OF VARIATION IN LOSS RATES OF COLOR BANDS APPLIED TO ADULT ROSEATE TERNS (*STERNA DOUGALLII*) IN THE WESTERN NORTH ATLANTIC

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ABSTRACT.—A model-based analysis was done to test several hypotheses concerning the rates of loss of butt-ended color bands placed on adult Roseate Terns (*Sterna dougallii*) in the western North Atlantic. These birds were captured and color banded from 1987-1991 at four colony sites, and recaptured from 1989-1992 as part of a study of the population dynamics of this species. Two types of color bands, Darvic and celluloid, were used, but only one band type was used for each individual bird. Each bird was given three color bands. The estimated probability that a bird with all color bands present during one breeding season still had all color bands during the next breeding season was 0.87. The analysis provided no evidence that colony site, cohort, calendar year of banding, age of color band, or whether or not the bands were heat-sealed closed, were important sources of variation in band-retention probabilities. *Received 16 April 1993, accepted 17 August 1993.*

WE HAVE BEEN studying Roseate Tern (*Sterna dougallii*) populations at four breeding colonies in the western North Atlantic since 1987. Part of this cooperative work has involved a coordinated effort to trap and color band adults that later can be resighted and/or recaptured so the resulting data can be used to estimate colony-specific rates of survival and movement. This study requires the use of both recapture and resighting data. Recapture data are required because the nesting habitat at some sites makes it difficult to resight and identify individuals; resighting data are needed because of low recapture rates at other sites.

As in many other studies of banded birds (Ludwig 1967, 1981, Kadlec 1975, Anderson 1980, Reese 1980, Bailey et al. 1987, Lensink 1988, Nisbet 1991), some individuals were observed to have lost one or more color bands during our study, and such losses affected our ability to identify these birds by resighting them (a recaptured bird that lost color bands was still identifiable by its uniquely numbered metal band). It became necessary, therefore, to investigate the effects of loss of color bands on the estimated rates of survival and movement, and to incorporate these rates of loss into our analyses whenever appropriate. To avoid the problem of potential misidentifications of resighted birds, we investigated the rates of loss using data only from birds that were recaptured.

The manner in which information on band loss is used in the estimation of survival and movement rates depends on the sources of variation in the rates of loss. If the annual rate of band loss can be regarded as a constant and can be estimated, then the *a posteriori* "correction" of capture-recapture/resighting estimates of survival rate is relatively simple (Arnason and Mills 1981, Pollock 1981). However, if rates of loss vary as a function of time since initial banding, then incorporation of band-loss information into survival-rate-estimation analyses is more complicated (Kremers 1987, Nichols et al. 1992, Nichols and Hines 1993). Similarly, if different types of bands or application methods were used that produced different retention rates, this variation would require more complicated analyses for survival estimation. Our purpose was to investigate sources of variation in loss rates of color bands placed on Roseate Terns at four colony sites from 1987–1991 for our future demographic analyses, but the general approach we developed for our specific study can be applied to other studies that make use of a combination of retrapping and resighting data.

METHODS

Study sites.—Our cooperative fieldwork, including trapping and color banding adult terns, was directed by: Nisbet at Bird Island, Marion, Massachusetts (41°40'N, 70°43'W); Hays and Cormons at Great Gull Island, New York (41°12'N, 72°07'W); Spendelow at Falkner Island, Guilford, Connecticut (41°13'N, 72°39'W); and Burger and Gochfeld at Cedar Beach, Islip, Long Island, New York (40°37'N, 73°21'W). These four sites contained more than 90% of the entire western North Atlantic breeding population of Roseate Terns, and more than 95% of the breeding population west of Cape Cod in the late 1980s (U.S. Fish and Wildlife Service 1989) and early 1990s. Detailed descriptions of the colony sites and the nesting habitats used by Roseate Terns at them are given for: Bird Island by Nisbet et al. (1990); Great Gull Island by Cooper et al. (1970), Hays (1970, 1975), and DiCostanzo (1980); Falkner Island by Spendelow (1982) and Spendelow and Nichols (1989); and Cedar Beach by Gochfeld (1976), Burger and Gochfeld (1988), Gochfeld and Burger (1988), and Nisbet et al. (1990).

Trapping and color-banding techniques.—Most breeding adults were caught at their nests using one of several differently shaped Potter-style treadle traps (for basic design, see Canadian Wildlife Service and U.S. Fish and Wildlife Service 1977:fig. 2.10); a few birds at several sites were caught by hand. Adult Roseate Terns were color banded with celluloid bands at Great Gull Island for many years before our cooperative research study began; birds color banded in 1987 at this site, but not those color banded in earlier years, are included in our study. Color banding was not done at the other three sites until 1988. From 1988–1991, unbanded adult Roseate Terns and those banded previously with less durable (Hatch and Nisbet 1983) aluminum U.S. Fish and Wildlife Service (FWS) bands were banded or rebanded with three color bands and a uniquely-numbered "size 2" FWS incoloy (4.3 mm internal diameter; see Hatch and Nisbet 1983, Nisbet and Hatch 1983) or a stainless-steel band. With only a few exceptions, birds previously banded with incoloy bands were released with the same band, but in some cases the band was shifted to the bird's other leg as part of our band-combination scheme. Adults were given two bands on each leg in unique combinations so that by using binoculars or spotting scopes we could recognize individuals at a distance. All bands were placed on the tarsometatarsus below the joint with the tibiotarsus. Except for several individuals retrapped at Great Gull Island, previously color-banded adults were not given new color-band combinations when retrapped.

At Bird Island, Falkner Island, and Cedar Beach, only Darvic color bands (supplied by A. C. Hughes, Ltd., Hampton Hill, Middlesex, United Kingdom) were used. These butt-ended bands have an internal diameter of about 4.0 mm when fully closed (Nisbet 1991). Darvic color bands were chosen because they are more colorfast and wear resistant than celluloid bands (Anderson 1980). At Great Gull Island, a mixture of both Darvic and similarly-sized celluloid bands from the same supplier was used. Some celluloid bands were bicolored or striped, but all Darvic color bands had only one color. The colors used were black, brown, dark blue, dark green, light green, orange, purple, red, white, and yellow. All color bands were placed on a bird's leg by sliding them up a tapered opening tool supplied by Hughes, placing the leg into the gap between the ends, and then sliding the bands off the tool and around the leg. To correct for any stretching of the band that may have occurred during opening, we closed the bands by squeezing them shut twice with finger and thumb, first with one side, and then the other, overlapping. All bands were fully closed when the birds were released. After noticing birds with missing bands, Nisbet began experimenting with methods for sealing the Darvic bands in 1989 (Nisbet 1991). Based upon his recommendations, we all used battery-powered cordless soldering irons (ISOTIP, Wahl Clipper Corporation, Sterling, Illinois) to heat seal almost all the Darvic color bands used at our study sites from 1990 onwards.

Recapture techniques.—Resightings of incomplete band combinations do not provide unambiguous identifications. Therefore, to ensure the proper identification of the birds involved, we have excluded our data on resighted birds and used only recaptured birds from 1989–1992 in the analyses reported here. Also, because the status of old color bands was not recorded for all individuals at Great Gull Island, we have used only data on birds recaptured at the other three sites. Our sample sizes for birds banded with celluloid color bands at Great Gull Island that were recaptured elsewhere, therefore, are small.

Statistical modeling and estimation.—The data relevant to the estimation of band loss were the number of terns recaptured one or more years after banding, and the number of these that had retained all their color bands. In our models, we conditioned on the numbers of recaptures and considered the number of these retaining all color bands as binomial random variables (Nichols et al. 1992, Nichols and Hines 1993). Losses of metal FWS bands are not relevant to this analysis (because we condition on birds recaptured with FWS bands and assume independence of loss of metal FWS bands and plastic color bands), but such losses were rare (only four color-banded birds recaptured had lost FWS bands).

Let M_x be the number of birds recaptured exactly x years after color banding, let C_x denote the number of these that have retained all their color bands, and let π_x be the binomial probability of having retained all color bands for the entire period. We can estimate π_x as:

$$\hat{\pi}_x = C_x / M_x, \tag{1}$$

and then write the π_x of these conditional binomials as:

$$\pi_x = \prod_{y=1}^{x} \theta_y, \tag{2}$$

where θ_y is the annual band-retention probability or the probability that a bird alive with color bands at the beginning of the yth year after banding retains all of them until the end of the yth year.

Potential sources of variation in band-retention probabilities can be incorporated in the parameters θ_j and tested by contrasting general and constrained models. Our modeling philosophy was similar to that expressed generally by Lebreton et al. (1992) and Burnham and Anderson (1992), and for band-loss problems by Nichols et al. (1992). We began with a general model incorporating several potential sources of variation in band-retention probabilities. Likelihood-ratio tests of models omitting one or more of these sources of variation (null-hypothesis model) versus the general model (alternative-hypothesis model) tested the significance of the omitted source(s) of variation. Akaike's information criterion (AIC) was computed as a means of testing between non-nested models (where one model cannot be obtained by constraining parameters of the other model) and of selecting a parsimonious model that described the data (Akaike 1973, Burnham and Anderson 1992, Lebreton et al. 1992). These models were implemented using the program SURVIV (White 1983), primarily because of our familiarity with this software. Other software packages implementing generalized linear models (e.g. GLIM with a log link or SAS) could have been used as well. Goodness-of-fit tests (cells with small expected values pooled) were conducted to assess the fit of the models to the recapture data.

Specifically, we began our modeling efforts by considering five possible sources of variation in annual band-retention probabilities: (1) calendar year (j = 1987, . . . , 1991; where θ_j denotes probability that bands are retained during interval between sampling in year j and year $j + 1$); (2) year of banding (i = 1987, . . . , 1991); (3) age of bands ($j - i$); (4) colony where banded (k = 1 [Bird Island], 2 [Cedar Beach], 3 [Falkner Island], 4 [Great Gull Island]); and (5) color-band type (l = 1 [Darvic, not sealed], 2 [Darvic, sealed], 3 [celluloid]).

Because recapture data at Bird Island and color-band-loss data at Great Gull Island were limited, we restricted our initial modeling efforts to recapture data from only Falkner Island and Cedar Beach. The most general model for data from these two locations included all five sources of variation listed above. Following the general notation of Lebreton et al. (1992), we can denote this general model as $\theta_{\text{yr}\cdot\text{cohort}\cdot\text{colony}\cdot\text{band type}}$. The subscripts specify the sources of variation in band-retention probability, and the dots indicate that these sources may vary independently of each other. We did not include age of band as a separate subscript because specification of both cohort (year of banding) and calendar year automatically specifies age. Note that even more general models can be considered by including all possible interactions among the five main effects. Because of data limitations, however, we could not fit even a model including all first-order interactions, so our model with main effects was the most general model actually used. Results of the modeling and testing based on data from Falkner Island and Cedar Beach were used to decide which sources of variation to model and test using data from all four colony sites.

For one analysis we were interested in approximating the power of a particular likelihood-ratio test (see Results). For these approximations, we followed the approach of Burnham et al. (1987:214–217; see also Lebreton et al. 1992:82–83) of first computing the expected number of birds with one or more missing color bands, conditional on the observed number of recaptures ($E[C_x \mid M_x]$) under the alternative-hypothesis model (the model that includes the source of variation in band-retention probability of interest). We then analyzed these expected values (expressed as integers) using program SURVIV as though they were actual data. The chi-square test statistic computed by SURVIV for the likelihood-ratio test of the null-hypothesis versus alternative-hypothesis models approximates the noncentrality parameter, λ, of the distribution of the test statistic under the alternative hypothesis. Power is obtained directly from this distribution.

For example, assume that we were interested in the power of a test for differences in band-retention probabilities of sealed versus unsealed Darvic bands. We first hypothesize band-retention probabilities of the two types of bands that differed by some specified amount (e.g. 0.1), then look at the numbers of birds receiving these two band types that were recaptured in subsequent years, M_x. Using the two values for M_x, we compute expected numbers of recaptures of birds with these two types of bands that did and did not retain all bands until recapture. These expected values were entered into SURVIV as though they were actual data. The output of SURVIV includes a likelihood ratio, chi-square statistic for the test between

TABLE 1. Numbers of color-banded Roseate Terns recaptured at three colony sites (with number that lost at least one color band in parentheses), summarized by years of banding and last recapture, color-band material, color-band-sealing technique, and colony site where color banded.

			Colony			
Year banded	Color-band material	Sealed (S) or not (NS)	Bird Island	Cedar Beach	Falkner Island	Great Gull Island
			Last recaptured in 1989			
1987	Celluloid	NS	- (-)	- (-)	- (-)	2 (1)
1988	Darvic	NS	6 (1)	3 (0)	16 (2)	2 (0)
			Last recaptured in 1990			
1987	Celluloid	NS	- (-)	- (-)	- (-)	1 (1)
1988	Celluloid	NS	- (-)	- (-)	- (-)	3 (1)
1988	Darvic	NS	6 (2)	7 (0)	25 (5)	- (-)
1989	Celluloid	NS	- (-)	- (-)	- (-)	2 (0)
1989	Darvic	NS	1 (0)	2 (2)	33 (2)	- (-)
1989	Darvic	S	2 (0)	- (-)	- (-)	- (-)
			Last recaptured in 1991			
1988	Celluloid	NS	- (-)	- (-)	- (-)	4 (2)
1988	Darvic	NS	2 (0)	39 (12)	11 (4)	1 (1)
1989	Darvic	NS	1 (0)	9 (2)	16 (6)	- (-)
1989	Darvic	S	1 (1)	- (-)	- (-)	- (-)
1990	Celluloid	NS	- (-)	- (-)	- (-)	1 (0)
1990	Darvic	S	9 (1)	20 (2)	23 (5)	- (-)
			Last recaptured in 1992			
1988	Darvic	NS	5 (1)	15 (6)	5 (2)	- (-)
1989	Darvic	NS	1 (0)	12 (7)	8 (3)	- (-)
1989	Darvic	S	3 (2)	- (-)	- (-)	- (-)
1990	Celluloid	NS	- (-)	- (-)	- (-)	3 (1)
1990	Darvic	NS	1 (0)	- (-)	- (-)	- (-)
1990	Darvic	S	5 (0)	26 (5)	22 (6)	- (-)
1991	Celluloid	NS	- (-)	- (-)	- (-)	1 (0)
1991	Darvic	S	6 (0)	5 (0)	11 (4)	- (-)

the null-hypothesis model (parameterized using the same band-retention probabilities for sealed and unsealed bands), and the alternative-hypothesis model (using different band-retention parameters for sealed and unsealed bands). This chi-square statistic is then treated as a noncentrality parameter, and the power of the test is obtained from a noncentral chi-square distribution.

RESULTS

Recaptured terns from all sites had lost color bands. However, because of differences in colony sizes, the numbers of color-banded terns recaptured were larger at Falkner Island and Cedar Beach than at Bird Island (Table 1). In some instances color bands had not been lost, but some sealed color bands became unsealed, and some color bands were caught on the foot or toes of a few individuals; all of these individuals were considered to have retained their color-band combinations for the purpose of this analysis. Also, in four cases, celluloid color bands had not been lost, but the colors of the bands had changed so much that they had been consistently misidentified when the birds were resighted before being recaptured. Again, for the purposes of this analysis, these birds were considered to have retained their bands. Of all 355 color-banded adults that were retrapped, only four had lost their FWS band; these birds are not included in this analysis.

Models containing year, cohort, and age effects required large numbers of parameters and, hence, were applied only to the two larger recapture data sets (those for birds color banded at Falkner Island and Cedar Beach). Reduced-parameter models for the Falkner Island-Cedar Beach recapture data included $\theta_{yr \cdot colony \cdot band\ type}$ (no cohort or age effects), $\theta_{cohort \cdot colony \cdot band\ type}$ (no calendar year or age effects), $\theta_{age \cdot colony \cdot band\ type}$ (no calendar year or cohort effects other than via age), and θ (no effects; a single annual color-

TABLE 2. Band-retention-model statistics for data on recaptured color-banded Roseate Terns.

Model	Goodness of fit			Likelihood-ratio test				AIC
	X^2	df	P	X^2	df	P	Effect tested	
Terns color banded at Falkner Island and Cedar Beach[a]								
$\theta_{yr\cdot cohort\cdot colony\cdot band\ type}$[b]	—	—	—	—	—	—	—	91.3
$\theta_{yr\cdot colony\cdot band\ type}$	13.6	8	0.09	9.4	8	0.31	Cohort + age	84.7
$\theta_{cohort\cdot colony\cdot band\ type}$	13.7	12	0.32	10.1	12	0.61	Year + age	77.4
$\theta_{age\cdot colony\cdot band\ type}$	15.6	7	0.03	11.1	7	0.13	Year + cohort	88.4
θ	30.4	19	0.05	21.9	19	0.29	Year + age + cohort + colony + band type	75.1
Terns color banded at all four colony sites[c]								
θ_{colony}	46.7	40	0.22	3.1	3	0.38	Colony	115.8
$\theta_{band\ type}$	46.3	41	0.26	1.5	2	0.48	Band type	115.4
θ	47.8	43	0.28	—	—	—	—	112.9

[a] Likelihood-ratio tests were between model specified in far-left column and model $\theta_{yr\cdot cohort\cdot colony\cdot band\ type}$.

[b] General model was "saturated," so no goodness-of-fit test computed.

[c] Likelihood-ratio tests were between model specified in far-left column and model θ.

band-retention parameter). Likelihood-ratio tests provided no evidence that any of the reduced-parameter models differed significantly from the general model including all possible effects (Table 2). In fact, the Falkner Island and Cedar Beach data were adequately described (as indicated by goodness-of-fit test and lowest AIC value) by a model with a single annual color-band-retention parameter (Table 2). Therefore, we concluded that effects associated with year, cohort, and age could be omitted from subsequent models of color-band retention.

The entire data set of recaptures at Bird Island, Falkner Island, and Cedar Beach of birds color banded at all four colony sites was then used to address questions about potential effects of colony site and band type on band-retention probabilities. Models θ_{colony}, $\theta_{band\ type}$, and θ were fit to the combined data set from the four colony sites. Neither colony nor color-band type were significant sources of variation in band-retention probability (Table 2). Model θ, with a single annual band-retention parameter had the lowest AIC value and, hence, was judged as the most appropriate model for the recapture data (Table 2). The estimated retention probability from this model was $\theta = 0.87$ ($\widehat{SE}[\hat{\theta}] = 0.013$).

We were especially interested in the power of our test for detecting differences in band-retention probabilities associated with band type for making decisions about what band type to use in future work on this project. Thus, we approximated the power of the test of model θ versus model $\theta_{band\ type}$ with respect to two alternatives. First, we considered the question of whether to seal Darvic color bands. Point estimates for band-retention probabilities of unsealed and sealed bands, respectively, were 0.88 ($\widehat{SE} = 0.015$) and 0.86 ($\widehat{SE} = 0.026$) under model $\theta_{band\ type}$. Assuming that celluloid bands had a retention probability of 0.87 (estimate for all band types under model θ), and that sealed and unsealed bands had retention probabilities of 0.92 and 0.82, respectively (yielding a difference or $\Delta = 0.10$), the power of our likelihood-ratio test was about 0.86 for an α of 0.05. The power approached 1.0 when retention probabilities for sealed (0.97) and unsealed (0.77) bands differed by 0.20. Thus, we conclude that our inference of no difference between sealed and unsealed bands is a strong one.

Data on celluloid bands were much more limited because they were only applied at Great Gull Island, and only a few of these birds were retrapped elsewhere. The point estimate of the annual band-retention probability of celluloid bands under model $\theta_{band\ type}$ was 0.80 ($\widehat{SE} = 0.073$). Assuming that celluloid bands are being retained with probability 0.75 and Darvic bands with probability 0.85 ($\Delta = 0.10$), the power ($\alpha = 0.05$) of our model θ versus model $\theta_{band\ type}$ test was very poor (at only 0.23). For band-retention probabilities of 0.90 (Darvic) and 0.70 (celluloid; $\Delta = 0.20$), power ($\alpha = 0.05$) was approximately 0.72. Thus, the limited data on celluloid bands restricted us to weak inferences about possible differences in band-retention probabilities between Darvic and celluloid bands. The lower estimate of band-retention probability for celluloid bands may be indicative of lower retention rates, and the absence of a significant test statistic may have resulted from low power.

DISCUSSION

The average annual band-retention probability of 0.87 was much lower than we expected it would be when we began using Darvic color bands in 1988, and indicates the need to consider "band-loss parameters" in subsequent survival and movement analyses for this species. While the results of this specific study indicate that we can use a simple correction factor for our analyses, more complex correction factors may be called for in other similar survival analyses that rely heavily on resighting data.

We found no evidence of a change in the annual probability of band loss with age of the band. However, our oldest color bands were only four years old, and other studies (Ludwig 1967, Anderson 1980, Lensink 1988, Nichols et al. 1992) have noted an increase in the loss rates of older bands and neck collars. We will continue to test the hypothesis of age-specific variation in band loss as additional years of data become available.

We did not expect to find a "colony" effect due to differences in the way the color bands were applied by the investigators at the different colony sites, but we were surprised that sealing them closed did not reduce the loss rate of Darvic color bands as postulated by Anderson (1980) and Nisbet (1991). Nisbet (1991) thought that a major cause of color-band loss for Common Terns (*S. hirundo*) and Roseate Terns might be that the bands were being pulled over the foot when they became snagged on woody vegetation or other objects while the birds were at the breeding colonies. Although both types of color bands have a smaller internal diameter, they are lost at a much higher rate than the metal FWS bands. This, coupled with the apparent fact that sealing the color bands closed does not change their rate of loss, greatly decreases the chance that "passive loss" due to snagging or wear is a major cause of color-band loss, and suggests that a more biologically "active" force (such as the color bands being stripped off or pulled down over the foot during attacks by predatory fish) may be involved. Reese (1980) reported that Black-billed Magpies (*Pica pica*) removed plastic color bands by vigorously pecking at them; we have not observed this behavior by the terns, nor have we seen any terns with snagged color bands. Further work is needed both to determine the major cause(s) of loss and to find new methods of applying the color bands to reduce such losses.

For the purpose of this analysis, we restricted our definition of "loss" to physically lost bands. However, bands that had switched positions or that had changed color(s) also present problems in capture-recapture/resighting analyses. Although using bicolored or striped celluloid color bands, rather than only unicolored Darvic color bands, increases the number of different individuals that can be marked, this may result in a reduction in the percentage of marked individuals that can be correctly identified several years later if the celluloid bands are more likely to fade and change colors.

Our study has shown that a band-loss parameter can be estimated and used to allow researchers to use resighting data to estimate survival rates, but the annual rate of loss from our study was sufficiently high to produce non-negligible bias in uncorrected survival estimates. Thus, we strongly recommend that other studies using resighting data to estimate survival rates include double-banding and recapture efforts in the study design in order to provide the data needed to estimate and correct for tag loss.

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