

Surface wear of incoloy and darvic bands on Atlantic Puffin adults and chicks

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ABSTRACT. Bands are a common marking method in bird studies and capture-mark-reencounter (CMR) models are often used to analyze banding data. Common to this family of models are two assumptions: marks do not fall off or become unreadable and individuals within groups remain equally detectable. When data fail to meet these assumptions, results of CMR analyses may be biased. In studies of long-lived seabirds exposed to coarse nesting substrates, band wear is especially problematic. We compared surface wear from abrasion against rocks on incoloy and darvic bands applied to a long-lived seabird, the Atlantic Puffin (*Fratercula arctica*). In 2003 and 2004, surface wear on bands applied to chicks and adults was scored at five colonies in the Gulf of Maine. We used logistic regression to analyze two subsets of these data by fitting the probability of being worn (one or more characters difficult to read or obliterated) to band age, bird age, and band type. In both analyses, an evidence ratio provided exclusive support for the model that included all factors. Immature puffins largely avoid colonies and remain at sea until their second or third summer after hatching. Consequently, probabilities of being worn were delayed on both band types by 4 yr on bands applied to chicks compared to adults. Based on our estimates, 25% and 87% of darvic bands applied to chicks and adults, respectively, were worn after 5 yr. Wear was reduced by 71% and 87% annually on incoloy compared to darvic bands applied to adults and chicks, respectively. To uphold assumptions of CMR models, we recommend incoloy bands over darvic in studies spanning more than about 5 yr of long-lived seabirds exposed to coarse substrates.

SINOPSIS. Desgaste de anillas de metal y plásticas colocadas en adultos y juveniles de *Fratercula arctica*

Las anillas colocadas en las patas son un método común de marcar aves y se han establecido modelos (recuento de aves marcadas – siglas en inglés CMR) para analizar los datos obtenidos de esta forma. Hay dos postulados que deben aceptarse en estos modelos: que las anillas no se pierden o que se puedan leer y que los individuos marcados y no-marcados tienen la misma probabilidad de ser contados. Cuando los datos no cumplen con las dos condiciones previamente mencionadas el análisis de CMR puede contener sesgo. En estudios de aves marinas que viven por mucho tiempo, el desgaste de las anillas crea problemas. Comparamos el desgaste y daño de anillas de metal (níquel-cromo y acero) y anillas de plástico (policloruro de vinilo) colocadas en individuos de *Fratercula arctica*. Durante el 2003 y 2004, estudiamos el desgaste y daño de anillas colocadas a pichones y adultos del ave en cinco colonias de estas en el Golfo de Maine. Utilizamos una regresión logística para analizar dos conjuntos de datos sobre la probabilidad de desgaste (uno o más caracteres en la anilla difíciles de leer) a la edad de la anilla (tiempo en la pata del ave), edad del ave y tipo de anilla. Las aves inmaduras, evitan los grupos en las colonias y permanecen en el mar hasta el segundo o tercer verano. Como resultado, la probabilidad de que ambos tipos de anillas hubieran estado desgastadas o dañadas en los juveniles se dilato por unos cuatro años, al ser este grupo comparado con los adultos. El 25% y el 87% de las anillas plásticas colocadas en pichones y adultos, respectivamente, estaban desgastadas a los cinco años. El desgaste en las anillas de metal se redujo en un 71% y 87% anual al compararse con las plásticas colocadas en adultos y pichones, respectivamente. Para cumplir con los postulados de los modelos CMR, recomendamos el uso de anillas de metal en aquellos estudios pautados para más de cinco años particularmente en aves marinas que utilizan o se exponen a sustratos duros.

Key words: Atlantic Puffin, Bay of Fundy, capture mark recapture, CMR, *Fratercula arctica*, seabird

Capture-Mark-Reencounter (CMR) is a commonly used method to gain insights about unobservable demographic processes including sur-

vival and dispersal (Pollock et al. 1990, Lebreton and Pradel 2002). Data consist of new captures and subsequent encounters (e.g., by resight or recapture) of marked individuals. Analysis of these data is often done using CMR models, a diverse suite of model types (White et al. 1982, Lebreton et al. 1992, Lebreton and

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Pradel 2002). Common to this family of models are two assumptions: marks do not fall off or become unreadable and detectability does not vary among individuals within groups. These assumptions make explicit processes that, if present and undetected in the data, can lead to biased CMR model estimates. In the case of open CMR models (Pollock et al. 1990, Lebreton et al. 1992), individuals that lose their marks or whose marks become unreadable will confound estimates of survival. If marks degrade and this results in heterogeneous encounter probabilities, data become overdispersed (Anderson et al. 1994). Overdispersion can cause sampling variances to be underestimated leading to false confidence in demographic parameter estimates. In the case of closed CMR models (White et al. 1982, Pollock et al. 1992), heterogeneity can also lead to severe bias in abundance estimates.

Bands are by far the most common marking technique used in bird research (Marion and Shamis 1977, Calvo and Furness 1992). For demographic studies of long-lived seabirds, including several members of the orders Procellariiformes, Pelecaniformes, and Charadriiformes, band wear is particularly problematic because adult life expectancies often exceed 10 yr and nesting substrates often consist of coarse material including sand, talus, and bedrock. Several studies of gulls and terns (Family Laridae, Order Charadriiformes) have revealed loss rates (Kadlec and Drury 1969, Kadlec 1975, Spindelov et al. 1994) and rates of wear, including comparisons between band types (Ludwig 1967, Ludwig 1981, Hatch and Nisbet 1983, Nisbet and Hatch 1983, Nisbet and Hatch 1985, Bailey et al. 1987, Nisbet and Hatch 1988). However, due to differences in habitat preference and behavior, we and others (e.g., Bailey et al. 1987, Ludwig et al. 1995) suspect that band wear is a function of at least the family level and perhaps even species. Excluding those on gulls and terns, papers reporting band wear or loss rates in long-lived seabirds are uncommon (Anderson 1980, Wooller et al. 1985, Ludwig et al. 1995).

Atlantic Puffins (*Fratercula arctica*) are long-lived seabirds with an average life expectancy for adults of about 20 yr (Harris 1984). At five colonies in the Gulf of Maine, two types of field-readable bands, incoloy (nickel-chromium steel alloy) and polychloride vinyl (trade name, "darvic"), have been applied to puffin adults and chicks for five or more years, respectively.

These field-readable bands are twice engraved with 1–4 large characters that are easily read from a distance. Darvic bands worn by puffins on these islands wear rapidly due to abrasion against island rock (Breton et al. 2005) and incoloy was introduced in 1999 as a potential solution. However, after only 2 yr, a few incoloy bands showed noticeable surface wear. In response, surface wear scores for both band types on all islands were collected in the summers of 2003 and 2004.

From these data, we were particularly interested in isolating wear that affected our ability to resight bands and that could lead to band loss. Consequently, four wear scores were summarized as either not worn (not worn or all characters easily read) or worn (one or more characters difficult to read or obliterated). Here we report results from two logistic regression analyses of these data. Our aims were to measure the importance of band age, bird age (chick or adult), and band type on the process of a band becoming worn and to determine whether incoloy bands were a sufficient replacement (i.e., would uphold mark-related assumptions of CMR models) for darvic bands in demographic studies of this and other long-lived seabirds exposed to abrasive substrates.

METHODS

Study sites. Bands were applied and scored at five seabird colonies in the Gulf of Maine, USA and Canada: Eastern Egg Rock (43°51'N, 69°22'W), Matinicus Rock, National Wildlife Refuge (NWR; 43°47'N, 68°51'W), Seal Island (44°14'N, 68°44'W), Petit Manan NWR (44°22'N, 67°52'W), and Machias Seal Island Migratory Bird Sanctuary (44°30'N, 67°06'W). The landscape of these treeless islands is granite bedrock and boulder berms along the shore and herbaceous meadow covering the interior. Crevices within boulder piles are the primary nesting sites for puffins in the region (see also Breton et al. 2005).

Bird age: chick or adult. About 6 weeks posthatch, Atlantic Puffin chicks abandon colonies for the ocean (Harris 1984) and most do not return to colonies until their second or third summer (Kress and Nettleship 1988, SWK and AWD, unpubl. data). By remaining at sea, these young puffins also avoid wear on their bands. For this reason, we grouped data by

bird age, adult or chick, prior to analysis. Adults are birds identified as second-year or older on initial capture and were immediately susceptible to band wear.

Trapping and marking. Chicks were captured by hand, and adults with noose mats, box traps, or by hand in nest cavities. Adults were trapped from May–August, and chicks from mid July–late August. Darvic bands were applied between 1979 and 2004 and incoloy bands between 1999 and 2004. All birds received a United States Geological Survey (hereafter “federal”) band engraved with eight or nine digits on the tarsus opposite the field-readable band. Although engraving design varied on darvic bands, all those analyzed here were engraved horizontally and twice repeated, for example, 1108–1108. Incoloy bands were engraved with two characters above and two below, for example, AZ above 01, and twice repeated.

Our incoloy (nickel-chromium steel alloy, type 825) bands were 9 mm tall, 30 mm long, and 0.85 mm thick, and characters were stamped into these bands. Darvic bands were formed from 11 mm tall \times 30 mm long sections cut from two-layered 1.5 mm \times 1 m² darvic sheets. Engraving was made through the top layer exposing the inner layer. Different color schemes were used for each island.

Wear scores. Observers scored bands on all five islands using spotting scopes from blinds from late May–early August 2003 and 2004. Four scores were used: (1) no wear, (2) all characters easily read, (3) one or more characters difficult to read, or (4) one or more characters illegible (Fig. 1). Twice repeated engravings required the following scoring rules: Score 1–3, must observe both sides of the band, score most worn side and ignore the other; Score 4, if the visible side of the band is consistent with score four then the opposite side of the band does not have to be observed.

Bands that acquire severe wear are highly susceptible to cracking and falling off where the band has become thin from wear. For this reason, we did not use a more complex scoring scheme, for example, one that included “both sides severely worn.” We expect that counts of bands with severe wear on both sides would be negatively biased due to band loss.

Several bands were scored multiple times during a summer ($N = 135$) or in both 2003 and 2004 ($N = 175$). To avoid autocorrelation and



Fig. 1. Worn darvic and incoloy bands representing band wear scores 1–4: no wear, (1); all characters easily read, (2); one or more characters difficult to read, (3); one or more characters illegible, (4). The arrow identifies a character on an incoloy band that may fit the criterion of “difficult to read” in the field. Score 2 and 4 on incoloy bands were not available and not observed, respectively.

because band scores became less common with age, we used only the most recent score for each band.

Analysis. Prior to analysis, wear scores were reduced to “not worn” (score 1–2) or “worn” (score 3–4) and analyzed using logistic regression. Although we had data for darvic bands applied to chicks and adults beyond 5 yr postapplication, data for incoloy bands were limited to 5 yr (see above) and scores for adult bands older than 5 yr were sparse. To compare both band types and bird ages, we excluded, in one analysis, data beyond 5 yr. Separately, we analyzed a 10-yr data set from darvic bands applied to chicks.

The global or starting model for the 5- and 10-yr analyses contained all the factors that we thought might be important and were available: band age in weeks (since application) in both analyses, and bird age (chick, adult) and band type (incoloy, darvic) in the 5-yr analysis only. In a preliminary analysis of the 5-yr data set, we assessed the performance of a model that included interactions among the main effects; precision around estimates in this highly parameterized model was poor. Based on these results, we excluded interactions and nonlinear effects from our models.

Goodness-of-fit (GOF) testing using a Hosmer and Lemeshow χ^2 test (Hosmer and Lemeshow 1989, Stokes et al. 2000) and model

fitting were carried out using the Statistical Analysis System (SAS Institute 2004). The null hypothesis is that observed and predicted values are equal. Thus, fit is judged as adequate when the χ^2 test is not significant. In addition, we visually estimated GOF in the 5- and 10-yr data sets by plotting observed annual proportions \pm SE on top of model-predicted probabilities.

Following GOF testing, we constructed all possible models from our three main effects. We used evidence ratios calculated from small sample Akaike's Information Criterion weights to determine support for competing models (Franklin 2001, Burnham and Anderson 2002). An evidence ratio of about 50:1 provides essentially zero support for the competing model (Franklin 2001, Burnham and Anderson 2002).

Improvement in annual wear resistance by incoloy bands over darvic is quantified as a percent difference % \hat{D} using the estimator $\frac{\hat{p}_{1i} - \hat{p}_{2i}}{\hat{p}_{1i}} \times 100$, where \hat{p}_{1i} and \hat{p}_{2i} are darvic and incoloy wear probabilities in the i th year, respectively, from our top 5-yr model. Ninety-five percent confidence intervals are estimated as

$$\% \hat{D} \pm (1.96 \times \text{SE}_{(\hat{p}_{1i} - \hat{p}_{2i})}) \times 100,$$

where

$$\text{SE}_{(\hat{p}_{1i} - \hat{p}_{2i})} = \sqrt{\frac{\hat{p}_{1i}(1 - \hat{p}_{1i})}{n_{1i}} + \frac{\hat{p}_{2i}(1 - \hat{p}_{2i})}{n_{2i}}}.$$

RESULTS

Data. Scores from 386 bands were available for the 5-yr analysis (Table 1). Our 10-yr analysis included scores from 275 darvic bands.

Logistic regression. Fit of our 5-yr data to the global model was not significant ($\chi^2_8 = 14.29$, $P = 0.08$). An evidence ratio exclusively supported the global model over the next best

model by 299,000:1. Global model effect sizes ($\hat{\beta}$) and their precision (SE) were:

$$\begin{aligned} \hat{\beta}_{\text{band age in weeks}} &= 0.0137 \pm 0.0027 \\ \hat{\beta}_{\text{bird age}} &= -1.4638 \pm 0.02383 \\ \hat{\beta}_{\text{band type}} &= -1.0641 \pm 0.02278 \\ \hat{\beta}_{\text{intercept}} &= -4.2354 \pm 0.5418. \end{aligned}$$

Predicted estimates from this model are plotted in Figure 2 with annual proportions (\pm SE) of worn bands. Overlap between predictions and annual proportions suggest wear in darvic bands applied to adults may have been underestimated and adult incoloy type overestimated by our top model. Chicks required 5 yr to accumulate the same amount of band wear as adults accumulated in one (Table 2). Twenty-five percent (0.17, 0.37[95% CIs]) of darvic and <5% (0.02, 0.09) of incoloy bands applied to chicks were worn after 5 yr (Table 2). When applied to adults, 87% (0.69, 0.95) and 43% (0.26, 0.64) of darvic and incoloy bands, respectively, were worn after 5 yr (Table 2). On average, wear probabilities were reduced on incoloy bands by about 87% and 71% annually relative to darvic bands worn by chicks and adults, respectively (Table 2).

Fit of the 10-yr data set was not significant ($\chi^2_8 = 8.56$, $P = 0.38$). An evidence ratio supported the global model over the no effects model by $>10^9$:1. Estimated effect sizes ($\hat{\beta}$) and their SEs from the global model were: $\hat{\beta}_{\text{band age in weeks}} = 0.0143 \pm 0.0017$; $\hat{\beta}_{\text{intercept}} = -4.75 \pm 0.5386$. Predicted estimates are plotted in Figure 3 along with proportions of worn bands (\pm SEs). Overlap between observed proportions and predicted probabilities provide strong evidence that our data fit the model well. Within 7 yr, more than 50% (0.52,

Table 1. Number of bands scored for wear ($N = 386$) and used in the 5-yr logistic regression analysis summarized by location (island) and year collected.

Island	2003		2004		Total
	Incoloy	Darvic	Incoloy	Darvic	
Eastern Egg Rock	8	8	14	21	51
Matinicus Rock	10	40	38	61	149
Seal Island NWR	51	30	27	27	135
Petit Manan NWR	1	21	0	5	27
Machias Seal Island	24	0	0	0	24
Total	94	99	79	114	386

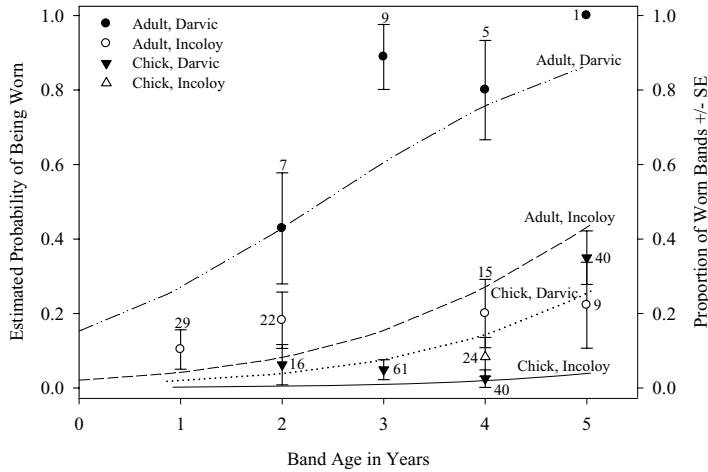


Fig. 2. Model predicted (lines; left y-axis) probabilities and annual proportions (\hat{SE} ; sample sizes provided above \hat{SE} bars) of worn bands for both ages and band types against band age in years. Annual proportions that were zero are not shown.

0.70) of darvic bands applied to chicks were worn.

DISCUSSION

In 1961 and 1962, Coulson (1963) applied darvic bands to Black-legged Kittiwakes (*Rissa tridactyla*) and Shags (*Phalacrocorax aristotelis*)

as an alternative nonmetal bird band. Since then, the use of darvic bands in bird studies has increased dramatically (Marion and Shamis 1977, Calvo and Furness 1992), but few investigators have reported on the performance of these bands in the field. Most have reported rates of band loss (Reese 1980, Nisbet 1991, Spendelow

Table 2. Estimated probabilities with 95% CIs of acquiring moderate to severe wear for darvic and incoloy bands aged 1–5 yr applied to chicks and adults.¹ Also shown are percent differences (% \hat{D}) between darvic and incoloy wear probabilities with 95% CIs.

	Age of band (yr)					Mean
	1	2	3	4	5	
Chicks						
Darvic	0.0194	0.0388	0.0760	0.1436	0.2548	—
95% CIs ²	0.01, 0.05	0.02, 0.08	0.05, 0.12	0.10, 0.21	0.17, 0.37	—
Incoloy	0.0024	0.0048	0.0097	0.0196	0.0391	—
95% CIs	0.00, 0.01	0.00, 0.02	0.00, 0.03	0.01, 0.05	0.02, 0.10	—
% \hat{D}	87.89	87.67	87.24	86.37	84.65	86.76
95% CIs	85.52, 90.26	84.35, 90.99	82.66, 91.82	80.23, 92.51	76.81, 92.49	—
Adults						
Darvic	0.2699	0.4298	0.6058	0.7581	0.8647	—
95% CIs	0.14, 0.44	0.27, 0.61	0.43, 0.76	0.57, 0.88	0.69, 0.95	—
Incoloy	0.0422	0.0823	0.1547	0.2717	0.4320	—
95% CIs	0.02, 0.10	0.04, 0.15	0.09, 0.25	0.16, 0.42	0.26, 0.64	—
% \hat{D}	84.38	80.84	74.47	64.16	50.04	70.78
95% CIs	69.15, 99.61	63.57, 98.11	56.78, 92.16	47.48, 80.84	35.09, 64.99	—

¹Wear probabilities and their 95% CIs are from the top model in the 5-yr analysis.

²Confidence intervals were rounded-up to two significant digits. Those reported here as 0.00 were between 0.0001 and 0.0044 prior to rounding.

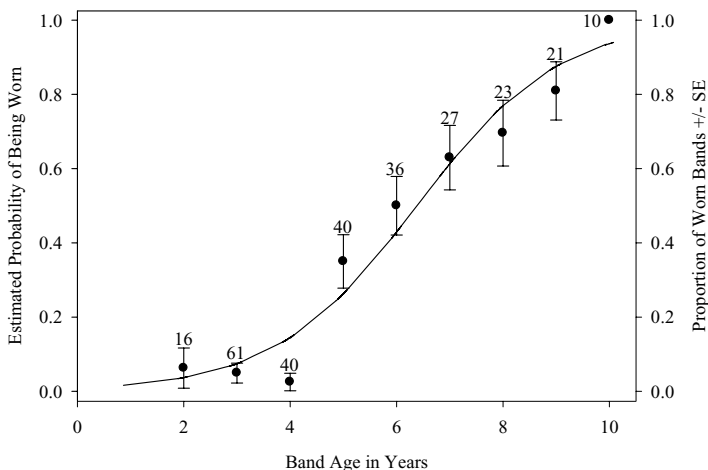


Fig. 3. Model predicted (line; left y -axis) probabilities and annual proportions ($\hat{S}\hat{E}$; sample sizes provided above $\hat{S}\hat{E}$ bars) of worn darvic bands applied to chicks against band age in years. Application year (0) and year 1 annual proportions were zero and are not shown.

et al. 1994) or wear (Regehr and Rodway 2003), but have had limited success at identifying important contributing factors. Nichols et al. (1992) and Regehr and Rodway (2003) demonstrated that darvic markers break down over time when applied to Tundra Swans (*Cygnus columbianus*) and Harlequin Ducks (*Histrionicus histrionicus*), respectively. Reese (1980) tested age of bird at initial banding and sex, but found no effect on band loss. Nichols et al. (1992) found an effect of age of bird and sex in the retention rates of darvic neck collars on Tundra Swans.

The earliest application of incoloy bands to seabirds that we are aware of was Lloyd and Perrins (1977) to Razorbills (*Alca torda*) in about 1971 (Mead 1974). Shortly after, Kadlec (1975) applied incoloy and titanium bands to Herring Gulls (*Larus argentatus*) in place of aluminum bands that had been shown to degrade rapidly and fall off (Kadlec and Drury 1968, 1969). Hatch and Nisbet (1983) and Nisbet and Hatch (1988) compared the performance of incoloy to aluminum bands applied to Common Terns (*Sterna hirundo*) and found that incoloy bands were "vastly superior." Both papers demonstrated that incoloy bands lose only a small fraction of their mass annually due to wear. We are not aware of any other study where an attempt has been made to identify factors that might modify the process of band wear experienced by incoloy bands.

In our analysis, bird age, band type, and band age contributed substantially to the probability of a band becoming worn. Band wear was delayed in both band types by 4 yr for chicks compared to adults. Wear probabilities for incoloy bands versus darvic were reduced on average by 87% and 71% annually on adults and chicks, respectively. Probabilities of wear for both band types and ages increased with band age. These results and those from other published studies (e.g., Nisbet and Hatch 1988, Regehr and Rodway 2003) demonstrate that band wear can represent a complex process involving multiple factors.

In CMR studies, band loss or, equivalently, band illegibility, confounds estimates of survival (Nichols et al. 1992). Assuming time spent searching for marked animals and other factors are held constant, as bands wear (prior to illegibility), detectability of individuals carrying the worn band will change. If unaccounted for, this leads to heterogeneity in detection probabilities that causes data to become overdispersed and sampling variances to be underestimated by CMR models (Anderson et al. 1994). In closed CMR models, heterogeneity can also lead to severely biased estimates of abundance (white et al. 1982, Pollock et al. 1990).

Intuitively, band wear will cause heterogeneity in detection probabilities before it confounds survival. However, the exact point at which band wear causes these biases is likely to remain elusive

for at least four reasons: (1) when bands are twice engraved, they may be readable even when one or more characters are obliterated, and (2) when individuals are banded with both a federal and field-readable band, observers will have the opportunity to read the federal band as the field-readable wears out. And, how easily a band, worn or not, is detected and read will be affected by (3) many landscape variables, and (4) effort spent resighting bands. Although these factors preclude us from identifying, in our or similar studies, the exact point at which wear causes confounding and heterogeneity, much can be gained from taking the conservative approach which we do here: when wear probabilities reach 0.50 (50% of the bands are worn), we assume that important biases, if unaccounted for, will be introduced into CMR estimates. Because we were interested in the sampled population as opposed to the sample, we identified the 50% cut-off using lower 95% CIs rather than the wear probabilities themselves.

The lower confidence interval that met this criterion for darvic bands applied to adults and chicks is acquired at four (0.57, 0.88) and 7 yr (0.52, 0.70), respectively. Incoloy bands worn by chicks are far from the 50% cut-off after 5 yr (0.02, 0.09), the extent of our results for this band type. The lower CI for incoloy bands worn by adults was 26% after 5 yr (0.26, 0.63).

Our conservative approach (50% cut-off) allows us to make a strong inference concerning biases from wear probabilities observed in our study. Within 4 yr for adults and 7 yr for chicks, degradation of darvic bands from surface wear will cause bias in CMR estimates unless either birds are double-banded and the second mark wears much slower or worn bands do not become completely illegible in this time. These scenarios also require that effort spent trying to relocate marked animals is enough to detect the second, typically nonfield readable, federal band. A combination of reading federal and worn field-readable bands was used successfully by Breton et al. (2005) to avoid biases from rapidly degrading darvic bands applied to adult Atlantic Puffins. In contrast, apparent survival estimates from puffins marked as chicks reported by Breton et al. (2006) appear to have been biased by band wear after only 5 yr, that is, earlier than our conservative 50% cut-off predicts.

Based on our 50% criterion, data from incoloy bands applied to chicks and adults experiencing

the same amount of wear as our study would not, within 5 yr, bias CMR estimates. Assuming that the 4-yr delay in wear between chicks and adults persists, and that wear probabilities for adult bands continue to double annually, then we would expect incoloy bands to reach the 50% cut-off at close to 6 and 10 yr for adults and chicks, respectively. These durations are much shorter than we would have predicted. However, these may be underestimates for at least two reasons (see others in Breton 2005). First, details on the surface of an incoloy band are more difficult to detect than those on two-layered/colored darvic bands. As the (often) dark-colored surface layer on a darvic band is removed, it exposes the (often) light-colored underlying layer. Even if an observer is color blind, the contrast between layers is easy to detect. In contrast, incoloy bands are a solid metallic color and not even severe wear will produce a contrast like that observed on darvic bands. We suspect that this lack of contrast on the surface of incoloy bands led to scores of 2 and 3 that should have been 1 and 2, respectively. If so, 6 and 10 yr may underestimate longevity of incoloy bands by several years.

Second, our top 5-yr model may have overestimated wear on incoloy bands applied to adults. Support for this observation is based on how well observed proportions overlap with model predictions. The former remain relatively stable between year 4 and 5 while the latter increase rapidly over the same period and substantially exceed the upper 95% CIs for the 5-yr observed value. It is unfortunate that we did not have more years of data for incoloy bands. In the absence of these data, we recommend that our estimates of 6 and 10 yr be regarded as minimum estimates when these bands are exposed to coarse substrates.

Our results and others demonstrate that the process of surface wear on darvic and incoloy bands can be complex and, if unaccounted for, may produce biases in CMR analyses well before the life expectancies of long-lived seabirds are reached. Although avoidance of these problems is the best solution, many options exist for accounting for these problems when CMR models are used (Arnason and Mills 1981, Nichols and Hines 1993, Spindelov et al. 1994, Breton et al. 2005, Breton et al. 2006). Exactly which options are applied will depend on what is known about structure in the data due to band wear. Ancillary data in CMR studies can be

useful for correcting biases, for example, data on band loss can be used to calculate a band retention rate (Spendlow et al. 1994). Multistate models can be used to model an unobservable state such as when bands become completely unreadable (Lebreton and Pradel 2002), and detection probabilities can be fitted to various covariates to account for variation in this parameter that is due to band wear including a time-dependent decline in band readability (Breton et al. 2006). Given these potential solutions and others (e.g., Pledger 2000), anyone experiencing or expecting problems should carefully review the literature to identify what data should be collected to correct for band wear.

Based on their poor performance over 5 (adults) yr and 10 (chicks) yr, we recommend that engraved darvic bands be abandoned as markers of long-lived seabirds that use coarse nesting substrates in studies spanning more than about 5 yr. Under these conditions, incoloy bands are preferable. In the absence of any corrections to account for wear that will be easy to apply in some cases, the usefulness of incoloy bands may be limited to species that delay return to colonies by two or more years and have a life expectancy of about 15 yr.

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LITERATURE CITED

- ANDERSON, A. 1980. The effects of age and wear on color bands. *Journal of Field Ornithology* 51: 213–219.
- ANDERSON, D. R., K. P. BURNHAM, AND G. C. WHITE. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75: 1780–1793.
- ARNASON, A. N., AND K. H. MILLS. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. *Canadian Journal of Fisheries and Aquatic Science* 38: 1077–1095.
- BAILEY, E. E., G. E. WOOLFENDEN, AND W. B. ROBERTSON, JR. 1987. Abrasion and loss of bands from Dry Tortugas Sooty Terns. *Journal of Field Ornithology* 58: 413–424.
- BRETON, A. R. 2005. Demographic Parameter Estimates and Their Biological Implications for a Seabird Metapopulation. Ph.D. dissertation, University of New Brunswick, Fredericton, NB, Canada.
- BRETON, A. R., A. W. DIAMOND, AND S. W. KRESS. 2005. Adult survival estimates from two Atlantic Puffin (*Fratercula arctica*) colonies in the Gulf of Maine. *Auk* 122: 773–782.
- , ———, AND ———. 2006. Encounter, survival, and movement probabilities from an Atlantic Puffin (*Fratercula arctica*) metapopulation. *Ecological Monographs*, 76:133–149.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd ed. Springer, New York, NY.
- CALVO, B., AND R. W. FURNESS. 1992. A review of the use and the effects of marks and devices on birds. *Ring and Migration* 13: 129–151.
- COULSON, J. C. 1963. Improved coloured-rings. *Bird Study* 10: 109–111.
- FRANKLIN, A. B. 2001. Exploring ecological relationships in survival and estimating rates of population change using program MARK. In: *Wildlife, land, and people: priorities for the 21st century* (R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, eds.), pp. 290–296. Proceedings of the Second International Wildlife Management Congress, The Wildlife Society, Bethesda, MD.
- HARRIS, M. P. 1984. *The puffin*. Poyser, Calton, UK.
- HATCH, J. J., AND I. C. T. NISBET. 1983. Band wear and band loss in Common Terns. *Journal of Field Ornithology* 54: 1–16.
- HOSMER, D. W., AND S. LEMESHOW. 1989. *Applied logistic regression*. John Wiley and Sons, Inc., New York, NY.
- KADLEC, J. A. 1975. Recovery rates and loss of aluminum, titanium and incoloy bands on Herring Gulls. *Bird-Banding* 46: 230–235.
- , AND W. H. DRURY, JR. 1968. Structure of the New England Herring Gull population. *Ecology* 49: 644–676.
- , AND ———. 1969. Loss of bands from adult Herring Gulls. *Bird-Banding* 40: 216–221.
- KRESS, S. W., AND D. N. NETTLESHIP. 1988. Re-establishment of Atlantic Puffins (*Fratercula arctica*) at a former breeding site in the Gulf of Maine. *Journal of Field Ornithology* 59: 161–170.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.
- LEBRETON, J. D., AND R. PRADEL. 2002. Multistate recapture models: modeling incomplete individual histories. *Journal of Applied Statistics* 29: 353–369.
- LLOYD, C. S., AND C. M. PERRINS. 1977. Survival and age of first breeding in the Razorbill (*Alca torda*). *Bird-Banding* 48: 239–252.

- LUDWIG, J. P. 1967. Band loss—its effect on banding data and apparent survivorship in the Ring-billed Gull population of the Great Lakes. *Bird-Banding* 38: 309–323.
- . 1981. Band wear and band loss in the Great Lakes Caspian Tern population and a generalized model for band loss. *Colonial Waterbirds* 4: 174–186.
- , C. L. SUMMER, H. J. AUMAN, T. L. COLBORN, F. E. LUDWIG, AND G. DIEFENDERFER. 1995. Band loss in North Pacific populations of Laysan Albatross (*Diomedea immutabilis*) and Black-footed Albatross (*D. nigripes*). *North American Bird Bander* 20: 157–164.
- MARION, W. R., AND J. D. SHAMIS. 1977. An annotated bibliography of bird marking techniques. *Bird-Banding* 48: 42–61.
- MEAD, C. J. 1974. The results of ringing auks in Britain and Ireland. *Bird Study* 21: 45–86.
- NICHOLS, J. D., J. BART, R. J. LIMPET, W. J. L. SLADEN, AND J. E. HINES. 1992. Annual survival rates of adult and immature eastern population Tundra Swans. *Journal of Wildlife Management* 56: 485–494.
- , AND J. E. HINES. 1993. Survival rate estimation in the presence of tag loss using joint analysis of capture-recapture and resighting data. In: *Marked individuals in the study of bird populations* (J.-D. Lebreton and P. M. North, eds.), pp. 229–243. Birkhauser Verlag, Basel, Switzerland.
- NISBET, I. C. T. 1991. Problems with darvic color-bands on Common Terns: band losses and foot injuries. *North American Bird Bander* 16: 61–63.
- , AND J. J. HATCH. 1983. Band wear and band loss in Roseate Terns. *Journal of Field Ornithology* 54: 90.
- , AND ———. 1985. Influence of band size on rates of band loss by Common Terns. *Journal of Field Ornithology* 56: 178–181.
- , AND ———. 1988. Durability of incoloy bands on Common Terns. *Colonial Waterbirds* 11: 113–114.
- PLEDGER, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics* 56: 434–442.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 1–97.
- REESE, K. P. 1980. The retention of colored plastic leg bands by Black-billed Magpies. *North American Bird Bander* 5: 136–137.
- REGHEHR, H. M., AND M. S. RODWAY. 2003. Evaluation of nasal discs and colored leg bands as markers for Harlequin Ducks. *Journal of Field Ornithology* 74: 129–135.
- SAS INSTITUTE. 2004. SAS software Version 8 of the SAS System for Windows. SAS Institute Inc., Cary, NC.
- SPENDELOW, J. A., J. BURGER, I. C. T. NISBET, J. D. NICHOLS, J. E. HINES, H. HAYS, G. D. CORMONS, AND M. GOCHFELD. 1994. Sources of variation in loss rates of color bands applied to adult Roseate Terns (*Sterna dougallii*) in the western North Atlantic. *Auk* 111: 881–887.
- STOKES, M. E., C. S. DAVIS, AND G. G. KOCH. 2000. *Categorical data analysis using the SAS system*, 2nd ed. SAS Institute Inc., Cary, NC.
- WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, AND D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory Report LA-8787-NERP, Los Alamos, NM.
- WOOLLER, R. D., I. J. SKIRA, AND D. L. SERVENTY. 1985. Band wear on Short-tailed Shearwaters *Puffinus tenuirostris*. *Corella* 9: 121–122.