Demographic parameter estimates and their biological implications

for a seabird metapopulation

By

André R. Breton

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Supervisor: A. W. Diamond, D. Phil., Biology & Forestry and

                              Environmental Management

Examining Board: Stephen B. Heard, D. Phil., Biology

                              Tillmann J. Benfey, D. Phil., Biology

                              Tom A. Al, D. Phil., Geology

External Examiner: Paul F. Doherty, Jr., D. Phil., Department of Fishery and

                              Wildlife Biology, Colorado State University

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In memory of my friend,

Bradford James Kennedy

August 23, 1972 - December 20, 1999

Abstract

Opportunities to study population processes at the metapopulation scale are rare. Within the Gulf of Maine and Bay of Fundy eight active Atlantic Puffin (*Fratercula arctica*) colonies are known, five are managed. For over two decades, island managers have monitored puffins through capture-mark-resight/recapture (CMR). These data were used to investigate detection, survival and movement processes. Two analyses of surface wear on darvic and incoloy bands and its effect on our ability to resight marked birds were also conducted. In addition, the overlap assumption is introduced to make explicit a source of bias that may be prevalent in studies of migratory animals. I close with significance and implications of results and with suggestions for local managers.

CMR data were analyzed with program MARK. Model support was judged using Information-Theoretic criteria and estimated effect sizes. Survival varied as a function of age, colony, and colony size; pre-breeding movement (PBM) declined with age to essentially zero at age seven; PBM and natal dispersal probabilities were colony dependent. Resighting effort was a strong predictor of detection probabilities. Results include support for the conspecific attraction hypothesis and movement as a key parameter driving local population dynamics.

Wear and loss of marks is a source of bias in CMR studies. In long-lived seabird studies, band degradation is particularly problematic. After five years, 25% and 87% of darvic bands applied to chicks and adults respectively were 'worn' - one or more characters difficult to read or illegible. Wear was reduced

by over 70% annually on incoloy compared to darvic bands. Given these results, I recommend that incoloy replace darvic in studies of seabirds that use coarse nesting substrates.

I expand a common assumption to 'all randomly selected individuals from the population experienced the effect fitted to the data' and refer to this as the overlap assumption. The assumption makes explicit ("all…experienced the effect") a source of bias that may be common in migratory animal studies; this is substantiated by hypothetical and published examples. I suggest discussing overlap with other results and reviewing previous work to determine if results might have been biased by overlap failure.

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[1] Known up to just recently as Petit Manan National Wildlife Refuge.

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Chapter 1

I<small>NTRODUCTION</small>

This dissertation reports on an investigation into the demography of a long-lived seabird, the Atlantic Puffin (*Fratercula arctica*); data come from five colonies in the Gulf of Maine and Bay of Fundy, USA and Canada. It also provides a critique of analysis, marking, and sampling methods commonly used in studies of birds. The objectives of this dissertation were 'to provide accurate estimates of critical demographic parameters for a seabird metapopulation and investigate the biological implications of those estimates'. Parameters of interest were adult and immature survival, pre-breeding movement, and natal dispersal.

Many results of this thesis are applicable to long-lived seabirds in general. In order to make this and other aspects of the thesis available to a non-specialist audience, it will be necessary to expand here on several topics. A review of these topics will be followed by a brief species account and review, current and historical, of Atlantic Puffin nesting in the Gulf of Maine and Bay of Fundy. I conclude with an overview of thesis chapters. To reduce repetition, the in-depth literature review necessary to demonstrate the relevance of results in Chapters 2-5 are maintained in the introduction and discussion of those chapters and not repeated here.

1.1 Seabirds, their Life-History and Demography

In its most strict usage, 'seabird' refers to any member of the orders Charadriiformes, Pelecaniformes, Procellariiformes, and Sphenisciformes that feed at sea and come to land only to reproduce. Species outside of these orders that live at sea in the non-breeding period, such as Spectacled Eider (*Somateria fischeri*), and species within these orders that feed along seacoasts such as many

gulls, terns, and cormorants, are not 'seabirds' under this strict definition. Alternatively, Weimerskirch (2002) defines a seabird as "species breeding along the seashore and relying on marine resources during the breeding period".

Small clutch size, delayed maturation, and long adult life are common seabird life-history characteristics. Seabirds often lay only a single egg annually (Weimerskirch 2002) and sometimes biennially (or less) such as the Amsterdam (*Diomedea amsterdamensis*; Jouventin *et al.* 1989) and wandering albatross (*D. exulans*; Croxall *et al.* 1990). Young seabirds typically delay breeding for 2-5 years (Weimerskirch 2002). However, storm petrels and albatross, both procellarids, may not breed for the first time until eight and nine years respectively after fledging (Weimerskirch 2002); fledging refers to the transition from land to sea that all young seabirds make a few weeks to months after hatching. Adult life expectancies in seabirds are, in general, above five years and below about twenty (Weimerskirch 2002). Albatross are the longest-lived of all the seabirds; the wandering albatross may live for well over 40 years after breeding for the first time (Weimerskirch 2002).

Stability of any population is a function of survival, dispersal, and fecundity; these are often referred to collectively as population 'vital rates' or demographic parameters. By dispersal I refer to permanent movement by adults (breeding dispersal) or chicks (natal dispersal) between local populations (Greenwood and Harvey 1982; Hanski and Gilpin 1991). Any change in a demographic parameter translates into a change in population abundance. Due to life-history characteristics including a small clutch and deferred reproduction,

fecundity in seabirds is at a minimum. To compensate, seabirds rely heavily on the long-life of adults to maintain or increase population numbers (Perrins 1991, Croxall and Rothery 1991).

A related and key characteristic of seabird populations is that small changes in adult survival translate into surprisingly large changes in life expectancy (LE). Using the estimator LE = -1/ln(s) where s = annual survival (Lack 1954), an adult with a survival probability of 0.97 would be expected to live 33 years while an adult with a survival probability of 0.95 would be expected to live just 20 years. This demonstrates how a drop of only two percent can reduce an adult's life by thirteen years, which translates into a lifetime reduction of thirteen nesting attempts (for annually nesting species). Of course, low reproductive success, adult survival, or both might be compensated for by increased dispersal into the affected population (Pulliam 1988).

The majority (95%) of seabirds aggregate annually into discrete breeding groups called colonies (Coulson 2002). Colonies are often distributed on near shore or oceanic islands, composed of multiple seabird species, and may consist of only a few individuals or well over 100,000 (Coulson 2002). Seabirds breed typically, but not exclusively, in summer. Since seabirds exist in both hemispheres, this means that seabirds, as a whole, are breeding year-round.

A group of conspecifics breeding in a discrete colony is equivalent to a local population (Hanski and Gilpin 1991). As a local population, it is not necessarily cut-off from neighboring groups, but it is subject to its own fluctuations in numbers due to changes in survival, dispersal, and fecundity.

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During the non-breeding portion of the year, individuals disperse widely over the sea. Outside of the breeding period, aggregations comparable to colonies are uncommon (Coulson 2002).

Networks of discrete colonies that are connected by infrequent dispersal are not uncommon; and many of these are distributed on islands. These local population groups function on a metapopulation, rather than a local, scale (Hanski and Gilpin 1991). On the local scale, individuals move frequently between 'clumps' within a single local population. This scenario, often confused with a metapopulation, is best described as a spatially structured local population (Hanski and Gilpin 1991). The metapopulation scale embodies a system of discrete local populations that are connected through infrequent dispersal and that are subject to extinction and reoccupation (Hanski and Gilpin 1991).

1.2   The Method of Capture-Mark-Reencounter

1.2.1   CMR Data and Models

Changes in local population size, survival, and dispersal are commonly measured using the method of capture-mark-reencounter (CMR; White *et al.* 1982, Lebreton *et al.* 1992, Lebreton and Pradel 2002); reencounter, or simply, encounter or detection methods include resight, recapture, and recovery. CMR involves marking, releasing, and reencountering individuals from one or more groups on two or more sampling occasions; data are, in part (see Chapter 6), the encounters on these occasions with unmarked and previously marked individuals (Lebreton *et al.* 1992). Studies can continue in this way, e.g., for days, weeks, or years. Short studies are typically directed at estimating only population size.

Longer studies may be interested in estimating parameters such as population size and survival. Studies of short duration generally apply closed population CMR models to estimate population size from their CMR data (White *et al.* 1982); data analyzed using closed models must meet the following assumptions: no deaths, births, emigration or immigration while the study is being conducted (White *et al.* 1982). Studies of longer duration, e.g., months or years, require open population CMR models to estimate parameters (Pollock *et al.* 1990, Lebreton *et al.* 1992). These are not required to meet the closed model assumptions. Alternatively, a combined open-closed 'robust design' is also available (Pollock 1982).

Early uses of data from marked animals to estimate demographic parameters date back to the 1930s (Lebreton *et al.* 1992). However, significant improvements were made to these early attempts independently by Cormack (1964), Jolly (1965) and Seber (1965). Their work was eventually combined into the Cormack-Jolly-Seber (CJS) open population model. The CJS model allows estimation of time-dependent survival and encounter probabilities. Since the advent of the CJS design, advances in CMR models and theory have been rapid (Lebreton *et al.* 1992, Williams *et al.* 2002) resulting in a family of CMR models with different strengths and weaknesses. For example, models have been developed to take advantage of combined live and dead encounter data, radio-telemetry or 'known-fate' data and data from multiple sites (White and Burnham 1999, Williams *et al.* 2002). Multi-strata or state models estimate transition probabilities among sites (or states) including dispersal among local populations (Hestbeck *et al.* 1991, Brownie *et al.* 1993).

Three assumptions are shared by most (open or closed) CMR models: (1) individuals within each group must have the same probability of surviving and (2) being detected (e.g., resighted or recaptured) on each sampling occasion, and (3) marks do not fall off or become illegible (Nichols and Pollock 1983). When data fail to meet these assumptions, important biases can result (Nichols and Pollock 1983, Anderson *et al*. 1994). For example, if marks become illegible or fall off, affected individuals will appear dead and this will cause survival estimates to be negatively biased.

Alternative estimators (formulae) were popular before the introduction and improvement of CMR models (Nichols and Pollock 1983). Many of these do not account for detection (or encounter) probabilities, i.e., they assumed that either all animals that were alive on each occasion were observed or the proportion alive and observed did not vary among occasions. These unrealistic assumptions are rarely met in CMR studies and as a result, these estimators often give biased results (Pollock *et al*. 1990). The estimator (notation varies) $\phi_i = r_{i+1} / R_i$ where R_i is the number of marked animals released at time i and r_{i+1} is the number reencountered in year $i+1$ was once a popular way to estimate 'return rates' (ϕ_i) in the bird literature (Pollock *et al*. 1990). It is an example of an estimator that does not account for detection probabilities.

1.2.2 Marks in Studies of Birds

The principal method for marking birds has been to apply one or more bands to the tarsi (Marion and Shamis 1977, Calvo and Furness 1992). For studies interested only in long distance movements, an engraved metal band,

generally with eight or nine characters, provides a sufficient mark. In North America, these are distributed by the United States Geological Survey and are often referred to simply as federal bands. Although aluminum bands are still popular in terrestrial bird banding, this metal has been replaced by monel, stainless steel, incoloy, and others in studies of seabirds. These alternative metals are substantially more resistant to corrosion and abrasion due to contact with salt water and coarse substrates respectively. Seabird bands are often exposed to abrasive substrates during the breeding period.

For studies requiring several detections of an individual throughout its life, a federal band is often combined with a unique set of colored coils or a field-readable band. Special features of field-readable bands allow them to be read from a distance using spotting scopes, binoculars, or in some cases, the unaided eye. Field-readable bands are engraved with only a few characters and these may be twice repeated on the band, e.g., 510 – 510. In addition, these are often made of two-layered plastic, such as rigid polyvinylchloride (trade name 'darvic'). Engraving is done through the first layer, often a dark color, exposing the inner layer, often a light color. Due to the problem of band wear, wear-resistant metals are now being used to form field-readable bands. These retain the field-readable characteristic of 'a few characters that are (or may be) twice repeated', but they lose the desirable quality of strong contrast provided by bi-laminate plastic bands. As a result, metal field-readable bands will generally be more difficult to resight using spotting scopes and binoculars. However, when applied to long-lived seabirds, fewer detections are outweighed by gains in band longevity.

1.3   Atlantic Puffin Species Account

The Atlantic Puffin is a medium-sized alcid (Family Alcidae, Order Charadriiformes; Gaston and Jones 1998). The species shows the typical dark above light below pattern of many marine birds. Males are often heavier and larger than females but otherwise the sexes are identical (Harris 1984). Unique to this species and congeners in the North Pacific, the horned (*Fratercula corniculata*) and tufted puffin (*F. cirrhata*), is its massive (relative to the body), colorful, and laterally compressed bill (Harris 1984). The bill grows larger and more colorful as puffins approach breeding age at or near four years post-fledging (Harris 1984). The winter or basic plumage and beak is dull compared to the summer or alternate plumage and beak (Gaston and Jones 1998). Several colored plates fall off the beak as part of the pre-basic molt, reducing its size and flair (Gaston and Jones 1998).

Atlantic Puffins are endemic to the North Atlantic. They form colonies in summer and are pelagic in winter (Brown 1985). Breeding and wintering ranges typically overlap (Harris 1984). Exceptions include birds that over winter in the Mediterranean (Gaston and Jones 1998); the nearest puffin colony to this area is on the Atlantic coast of France (Lowther *et al.* 2002). The most recent Atlantic Puffin population estimates give a range of 3.8 - 8.2 million individuals (Lowther *et al.* 2002). The largest breeding concentrations are located around Britain and Ireland, Norway and the Faeroes, Iceland, and Newfoundland (Gaston and Jones 1998, Lowther *et al.* 2002). Three races of the Atlantic Puffin are recognized (Bédard 1985).

Puffins breed during the Northern Hemisphere summer. Nesting is initiated

latest in northern areas due to ice in burrows (Harris 1984). Mate and nest site

fidelity in puffins are strong (Ashcroft 1979, Hudson 1985). Puffins lay their

single egg clutch in crevices within piles of boulders, rock slabs, talus[2] or nest

cavities dug into soft peat. Incubation and chick rearing occurs over about 80

days; each stage requires about 40 days (Lowther *et al.* 2002). Chicks are

semiprecocial[3] and nidiculous[4] (Lowther *et al.* 2002). Puffins typically breed for

the first time at age 4 or 5 years (Harris 1984). Young puffins are known to

disperse among breeding colonies (Harris 1984), but adults do not change

breeding colonies (Harris and Wanless 1991). The longevity record for a puffin is

31 years 11 months (Klimkiewicz 2002). Many more puffin life-history details

are available in Harris (1984), Nettleship and Birkhead (1985), Gaston and Jones

(1998) and Lowther *et al. (*2002).

1.4   Current and Historical Account of Atlantic Puffin Nesting in the Gulf

  of Maine and Bay of Fundy, USA and Canada

Currently, there are five managed and at least three non-managed[5] colonies

of Atlantic Puffin that are active in the Gulf of Maine and Bay of Fundy (Chapter

3, Figure 3.1). Managed sites in the Gulf of Maine are Eastern Egg Rock

(43°52′N, 69°23′W), Matinicus Rock (43°47′N, 68°51′W), Seal Island National

Wildlife Refuge (NWR) (43° 50′N, 68° 40′W), and Petit Manan Island NWR (44

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[2] Rock fragments that accumulate as slopes below exposed rock cliffs.
[3] Able to stand-up and thermoregulate shortly after hatching.
[4] Confined to the nest and/or area immediately around the nest.
[5] Managed colonies are monitored by resident observers throughout the majority of the breeding period. Non-managed sites are infrequently or rarely visited.

$^{\circ}$ 22´N, 67 $^{\circ}$ 52´W)[6]. Machias Seal Island Migratory Bird Sanctuary (44°30´N, 67°06´W) is located at the mouth of the Bay of Fundy[2]. Non-managed sites are White Horse Island, in the Bay of Fundy, and Green, and Noddy Islands, off the southern shore of Nova Scotia in the Gulf of Maine (Lowther *et al.* 2002).

In 2004, close to 98% of the ca. 3,600 breeding pairs in the region nested at managed sites. The most recent estimates of breeding pairs for each site are (estimate; year): Machias Seal (2,800, 1999); Matinicus Rock (280; 2003); Egg Rock (70; 2004), Seal Island (290; 2004), and Petit Manan (35; 2004) (Diamond and Devlin 2003, Fall 2004 GOMSWG Minutes). No estimates are available for non-managed sites. However, observations made by fishermen working in the area of the Mud and Tusket Island Groups (includes Noddy and Green respectively), Nova Scotia suggest fewer than 20 pairs have nested in recent years on Noddy and Green Islands (Appendix 2). Observations made by T. D'Eon in 2002 suggest the colony on Green may be growing or more substantial than reports from fishermen suggest (Appendix 2): "August 1, 2002: approximately 90 puffins were counted on [and around] Green Rock" (T. D'Eon, 2002 Puffin Report, http://pages.ca.inter.net/~deonted/puffin02.html). Observations by T. D'Eon and fishermen also suggest nesting activity on Round Island (part of the Mud Island Group); but J. Nocera visited the small island in May 2001 with six other observers and found no sign of nesting puffins (Appendix 2). Evidence of breeding on White Horse Island, New Brunswick (Lowther *et al.* 2002) is based on a single observation of a puffin flying with fish in 2001 (A. W. Diamond pers.

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[6] Throughout the text, Seal Island NWR is generally referenced as 'Seal Island', Petit Manan Island NWR as 'Petit Manan', and Machias Seal Migratory Bird Sanctuary as Machias Seal.

comm.); the White Horse Island puffin colony probably comprises fewer than 10 pairs.

One managed site, Petit Manan, was colonized (not previously occupied by puffins) and two others, Eastern Egg Rock and Seal Island, were recolonized in the last 22 years (Kress 1978 – 2004, Kress 1997). The distinction between colonization and recolonization is based on historical records (see below). Timing of colonization at non-managed sites is not known but probably occurred in the last 30-40 years (Bryant 1857, Tufts 1986, Squires 1976, Erskine 1992, Appendix 2). Prior to these colonizations, and since the last documented extinction of a puffin colony in the region (early 20th Century), all breeding puffins were confined to Matinicus Rock and Machias Seal Island (Drury 1973, Tufts 1986).

Historical records from several sources strongly suggest that most colonizations in the Gulf of Maine and Bay of Fundy in the last 30 or 40 years represent reoccupations of previously held nesting sites: Erskine (1992) reported unconfirmed historical nesting accounts in the Tusket (includes Green Island) and Mud Island Groups (includes Noddy Island) off Southwest NS. Tufts (1986) reported, "Puffins formerly bred on several islands off Yarmouth [NS]". Yarmouth is located on the mainland adjacent to the Tusket and Mud Island Groups. Bryant (1857) reports one puffin egg and several nest cavities "probably made by the puffin" on Green Island in the summer of 1856. Drury (1973) reports that puffins once nested on Eastern Egg Rock and Seal Island; Drury (1973) refers to Seal Island by a previous name, Matinicus Seal. No mention of

White Horse Island or Petit Manan could be located to determine historical

nesting status (Bryant 1857, Tufts 1986, Squires 1976, Erskine 1992).

1.5   Overview of Chapters

Chapters 2-5 were submitted for publication prior to final submission of this

dissertation to the School of Graduate Studies. And prior to the writing of the

complete dissertation, Chapter 2 had been accepted for publication by The Auk.

To maintain continuity of style, an organization similar to The Auk is applied

throughout. Because the dissertation is written in articles format, each manuscript

chapter (2-5) can stand alone, e.g., species names are given even when available

in previous chapters and each chapter includes its own set of acknowledgements.

A primary goal of this dissertation was to provide estimates of age-specific

survival using a sample of known-age birds from the five managed colonies in the

Gulf of Maine and Bay of Fundy. However, before the first analysis was

initiated, it became clear that severe wear experienced by darvic leg bands might

confound adult survival probabilities from this dataset. In an attempt to avoid

biases and produce accurate estimates of adult survival, I conducted a survival

analysis using CMR data from known breeders ($n = 148$) on islands where

resighting effort was extremely high. I also performed an analysis of band wear

using a band readability index to determine how quickly darvic bands were

wearing out. These analyses are reported together in Chapter 2, **adult survival**

estimates from two Atlantic Puffin (Fratercula arctica) colonies in the Gulf of

Maine.

Chapter 3, **encounter, survival, and movement probabilities from an Atlantic Puffin (*Fratercula arctica*) metapopulation**, satisfies all of the objectives of my dissertation. This is a complex CMR analysis involving over twenty years of data collected simultaneously at four managed colonies; CMR data are from 2,050 puffins marked as chicks. As expected, it appears that adult survival probabilities may have been negatively biased from band wear in this analysis. While completing early drafts of this dissertation, Chapter 3 was submitted to Ecological Monographs and subsequently invited for resubmission following revisions.

Surface wear on incoloy and darvic bands applied to Atlantic Puffin (*Fratercula arctica*) adults and chicks, Chapter 4, reports specifically on band wear using band wear scores collected on all islands in 2003 and 2004. Wear on darvic and incoloy field-readable bands accumulated over five years on bands applied to chicks and adults are compared to determine if incoloy is a sufficient replacement for darvic. An analysis and results of data from ten years for darvic bands applied to chicks is also presented. This chapter was submitted to the Journal of Field Ornithology on 4 February 2005.

Chapter 5, **the overlap assumption: an important source of bias in studies of migratory animals**, does not involve any analyses of data. Instead, it introduces an idea, the overlap assumption, and then provides both hypothetical and published examples of how incomplete overlap between a sample and an effect might bias data in studies of migratory animals. My earliest notions of this idea surfaced three years ago when I was trying to imagine how an effect of the

North Atlantic Oscillation, such as increased winter storm frequency, could be expected to covary in a predictable way with survival of puffins. The problems I found most difficult to reconcile were that (1) I did not know, very well, where puffins marked in the region over-wintered and consequently, (2) I could not say if and how much winter storms might have overlapped with these birds. This chapter was submitted to the Journal of Wildlife Management on 7 February 2005.

In Chapter 6 (general discussion), I identify the significance and implications of results from Chapters 2-5 for the species and other long-lived seabirds in the region and elsewhere. These are followed by suggestions for managers monitoring puffins in the Gulf of Maine and Bay of Fundy to improve the CMR dataset for future analyses.

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Chapter 2

ADULT SURVIVAL ESTIMATES FROM TWO ATLANTIC PUFFIN (*FRATERCULA ARCTICA*)

COLONIES IN THE GULF OF MAINE

Authorship: André R. Breton,[1,2] Antony W. Diamond,[1] and Stephen W. Kress [2]

[1]Atlantic Cooperative Wildlife Ecology Research Network (ACWERN),

University of New Brunswick, P.O. Box 45111, Fredericton, N.B. E3B 6E1,

Canada

[2] Seabird Restoration Program, National Audubon Society, 159 Sapsucker Woods

Road, Ithaca, NY, 14850 USA

Contribution of Authors: A. R. Breton performed analyses, wrote the majority of

the manuscript, collected data on Eastern Egg Rock 1996-1997 and Seal Island

1995, 1998-2001; A. W. Diamond primary editor, very little writing, contributed

some data; S. W. Kress editing, contributed the majority of the dataset.

2.1   Abstract

We report survival probabilities from 148 breeding adult Atlantic Puffins (*Fratercula arctica*) monitored through capture-mark-resight at two colonies over 11 years (1992 – 2003). The colonies - Eastern Egg Rock and Seal Island - are ca. 42 km apart in the Gulf of Maine, USA. Support for competing models in program MARK suggests constant survival of $0.95 \pm 0.01 \; \hat{SE}$ that is independent of colony. Our high survival probability is consistent with published estimates for puffins and other long-lived seabirds. No time-variance contrasts with many long-term seabird studies, which often report high survival in most years broken occasionally by low survival events. However, a *post hoc* observation of survival estimates from the time dependent model suggests there may have been at least two low survival events in our time-series; sparse data may have precluded detection by our models. In this study, each bird received an individually engraved plastic field-readable leg band as well as the standard metal band. Using an index of band readability, we show that plastic bands wore rapidly resulting in accumulating losses of engraved characters through time. Degradation and loss of marks is a common source of overdispersion in capture-mark-reencounter data and results in underestimated sampling variances. In the presence of a 70% reduction in band readability over eight years, an estimate of $\hat{c}$ (1.14) identified very little overdispersion in our data. Overdispersion was avoided by double banding and intensively resighting metal bands.

2.2   Introduction

Most species occur as several "local populations, each one intercommunicating and intergrading with the others" (Mayr 1970). While the truth of this premise remains generally accepted, studies aimed at measuring communication and intergradations between or among local populations remain relatively rare. Instead, sampling at a single local population remains the norm in population research. This represents a bias that may have deep implications for established population theory, and consequently for management decision-making.

Breeding colonies of Atlantic Puffin (*Fratercula arctica*) are distributed across eight islands in the Gulf of Maine (Lowther *et al.* 2002, J. Nocera pers. comm.). At five of these colonies and for several years, both adult and juvenile puffins have been monitored through capture-mark-resight/recapture (CMR). These data provide a rare opportunity to measure demographic processes simultaneously across two or more local populations.

We had two aims in the paper; the first was to report survival probabilities from two Gulf of Maine colonies: Eastern Egg Rock (EER) and Seal Island (SI). Given the high risk of finding spurious results with few birds marked ($n = 148$) relative to the number of predictor variables in our models (Freedman 1983, Flack and Chang 1987, Anderson *et al.* 2001), we limited our CMR analysis to a series of exploratory tests (using models) that looked for differences in survival and resighting probabilities among years and between colonies. In our discussion, we (1) explore two implications of our results concerning differences in survival

between two neighboring local breeding populations, (2) compare survival

probabilities from this study to other studies of long-lived seabirds, and (3) draw

attention to the regional importance of our survival estimates. Another aim was to

provide quantitative evidence that in the presence of rapidly degrading leg bands,

individual heterogeneity (differences in detection probabilities among individuals)

and problems that this can cause, may have been avoided.

2.3   Study Area and Methods

2.3.1   Study Sites

Data were collected at two colonies, SI (44° $14'$N, 68° $44'$W; 40.5

hectares) and EER (43° $51'$N, 69° $22'$W; 2.9 hectares), Maine (Fig. 2.1; Kress and

Nettleship 1988); SI is ca. 42 km east of EER. Restoration efforts, including

transplanting chicks from Newfoundland and social attraction (Kress 1997),

preceded recent puffin recolonization of both EER (Kress and Nettleship 1988)

and SI (Kress 1997) in 1981 and 1992 respectively. Since recolonization, the

number of puffins breeding increased to 70 pairs on EER and 290 pairs on SI in

2004 (Kress 1978-2004). Both islands consist of granite bedrock with numerous

boulder and rock slab berms; rock crevices within these features are the primary

nest site for puffins in the Gulf of Maine. The non-forested interior of the islands

consists mainly of dense raspberry thickets and herbaceous meadow (Kress and

Nettleship 1988).

2.3.2   Sampling Scheme

Breeding adults were captured by hand in nesting burrows, with noose

mats tied to rocks, or with wooden drop or swivel-lid boxes. Native chicks were

captured in burrows by hand or while fledging (Diamond and Devlin 2003). Each

puffin received an individually engraved plastic or metal (incoloy) field-readable

band on one tarsus and a metal United States Geological Survey (hereafter

"federal") band on the other. Eight birds included in the CMR analysis received

the metal type field-readable band. However, these were applied in 1999 ($n = 5$)

and 2000 ($n = 3$), i.e., near the end of the study. Worn plastic bands were

replaced on a small proportion of birds; these few recaptures were excluded due

to an abundance of resightings. Federal bands, made of monel or incoloy, were

rarely replaced and all remained readable throughout the study.

Bands, preferably field-readable type, were resighted using binoculars and

spotting scopes by observers concealed in blinds. Banding and resighting

occurred every year from mid-late May to early-middle August. This period

overlaps with the breeding period for Atlantic Puffin at both colonies (mid-April

through late August).

2.3.3 Band Wear

Our plastic field-readable leg bands consist of two layers of darvic (rigid

polyvinylchloride) plastic with repeated characters (e.g., U12 – U12) engraved

through the surface layer. In our region, surface wear, from abrasion against

colony rock sources, appears to accumulate over time resulting in gradual losses

of engraved characters and a concurrent decrease in plastic band readability.

Band degradation is a source of failure of the 'individual heterogeneity'

assumption common to all CMR data types (White *et al.* 1982, Burnham *et al.*

1987, Pollock *et al.* 1990, Lebreton *et al.* 1992). When violated, data become

'overdispersed' (see below) resulting in underestimated sampling variances and inflated confidence in survival estimates (Anderson *et al.* 1994).

Given the generality of the problem of overdispersion, we felt that (1) validation of rapid wear and (2) confirmation of our assumption that detectability was unaffected, would provide valuable contributions to the CMR literature. To quantify band wear through time we developed a band readability curve. To determine if CMR data were overdispersed, we estimated ĉ (see below).

2.3.4   Band Readability Curve and Dataset

We fit a quadratic regression line (readability curve) to the mean resighting frequency in each year divided by the mean frequency in the first year after banding against age of band in years. Date of banding varies so we exclude application year, i.e., year zero. Age-specific sighting counts from 38 plastic bands applied to known breeders on EER (14), SI (3), and Matinicus Rock (21) (island substrates do not differ) were used to calculate means. All individuals sampled were detected for at least 8 years post-banding and were fitted with a plastic band as a breeder on islands where resighting effort is not time varying. Criteria were developed in order to maximize sample size, minimize confounding factors, and cover the typical readability life span of a plastic band. By applying these sampling criteria, our readability curve should isolate the effect of wear on our ability to read aging bands.

2.3.5   CMR Dataset

Data from adults breeding on Matinicus Rock, Petit Manan, and Machias Seal Island (Fig. 2.1), islands where resighting effort has been low relative to EER

and SI, were excluded from the CMR analysis in an attempt to avoid problems associated with individual heterogeneity from degrading plastic bands. Based on counts of hours spent resighting bands, we felt that resighting effort on EER and SI would be high enough to compensate for failing bands (SWK unpublished data). Nevertheless, we tested this assumption by estimating $\hat{c}$ (see below).

Birds were marked as either breeding adults ($n = 70$) or chicks ($n = 78$); 46 of the chicks had been transplanted from Newfoundland and raised on EER or SI in artificial burrows (Kress and Nettleship 1988, Kress 1997). All adults were initially captured and marked on EER and SI. The majority of native Gulf of Maine chicks were captured and banded on Matinicus Rock; those remaining were marked on EER, SI, Petit Manan, or Machias Seal Island (Fig. 2.1). Although almost half our sample was initially marked as chicks, including those transplanted from Newfoundland, we analyze survival only in their adult years in this paper (see below); immature survival and natal dispersal probabilities (Greenwood and Harvey 1982) are analyzed elsewhere.

Birds entered and remained in the sample only after their first observed breeding attempt, i.e., as breeding adults; earlier failed nesting attempts may have gone unnoticed. Breeding was confirmed either by watching marked birds deliver fish (puffins carry fish exposed in their beak back to an awaiting chick; Harris 1984) to a concealed nest, or by observation of an egg and later confirmation of adults moving in and out of that nest site. We found no evidence of breeding dispersal, i.e., adults changing islands between breeding attempts (Greenwood

and Harvey 1982); breeding dispersal has not been detected in this species (Harris and Wanless 1991).

2.3.6 CMR Analysis

We tested for differences in annual survival and resighting probabilities between colonies and among years by comparing models built in program MARK (White and Burnham 1999). We based support for individual models on Δ $QAIC_c$ values and 95% confidence intervals around model effect sizes; $QAIC_c \equiv$ Akaike's Information Criterion (AIC) corrected for overdispersion (Q; using $\hat{c}$) and small sample size (c) (Burnham and Anderson 2002). Δ $QAIC_c$ is the $QAIC_c$ difference between the top ranked model, i.e., the model with the smallest $QAIC_c$ value (*min*), and a competing model (*i*), $\equiv QAIC_{c,min} - QAIC_{c,i}$. Rules of thumb were adopted from Burnham and Anderson (2002): Δ $QAIC_c$ 0-3 indicates "substantial support" for both models, 4-7 "considerable" support in favor of the top model, > 10 "essentially" no support for the competing model.

Survival and resighting probabilities are maximum likelihood estimates generated from our best model. The logit link function was maintained in all models following construction in the design matrix of program MARK (White and Burnham 1999). Consistent with Lebreton *et al.* (1992), we began our analysis by assessing goodness-of-fit of our global model: survival and resighting probabilities are time and colony dependent but the effect of time on colony is not colony specific, i.e., the model does not include time*colony interaction terms. Exclusion of interaction terms was required due to sparse data. Following GOF

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testing, we tested for colony and time dependence in resighting and then survival

probabilities by comparing support for the global model versus nested designs.

Due to sparse data, assessment of model fit with program Release was

limited to only the combined chi-square results for Tests 2 and 3 from Burnham *et*

al. 1987. We also assessed fit using the parametric bootstrap approach: divide the

deviance of the global model by the average model deviance from 100 bootstraps

to produce an adjusted overdispersion factor, ĉ. ĉ provides an omnibus measure of

problematic structure in the data including individual heterogeneity (Anderson *et*

al. 1994). When data fit the model perfectly, ĉ equals 1.0; this is also referred to

as unadjusted ĉ. Burnham and Anderson (2002) suggest that both AIC_c and

estimated sampling variances should be adjusted using $\hat{c}$ only if some 'distinct

lack of fit has been found'. Given our limited ability to assess fit with program

Release, we took a modest approach, and applied ĉ if it was > 1.0. This is

'modest' because by applying ĉ to both AIC_c and sampling variances, support for

models with fewer parameters and uncertainty in parameter estimates, increases

respectively; in effect, our ability to draw inference about subtle to moderate

features of the data declines.

2.4   Results

2.4.1   Readability Curve

Fit of a quadratic regression line (readability curve) to our data

demonstrates a strong relationship between our readability index and age ($R^2 >$

0.96, $y = -0.0123(x^2) + 0.0068(x) + 1.0254$) including a period of high

detectability followed by a rapid decline; between years 3 and 8, readability declined steeply by 70% (Fig. 2.2).

2.4.2   CMR Analysis

From 1992 – 2003, 148 adults, 59 from EER and 89 from SI, were released. These birds were later resighted a total of 18,376 times. The combined result for Test 2 and 3 in program Release was not significant ($\chi^2 = 24.72$, DF = 28, p > 0.64). Our adjusted ĉ, global model deviance (188.13) divided by average deviance from 100 bootstraps (164.99), was 1.14. Although these results suggest appropriate fit and little or no heterogeneity, we applied our adjusted ĉ to sampling variances and AIC_c prior to running additional models.

Models D-G (Table 2.1) were compared to determine importance of colony and time in predicting resighting probabilities. In these models, colony and time dependence were maintained in survival probabilities. Models D (resighting probabilities a function of colony), E (resighting probabilities constant), and F (global model; resighting probabilities a function of colony and time) acquired near equal Δ $QAIC_c$ support. However, with only one exception, estimated time effect sizes in Model F widely bound zero (e.g., slope coefficient for time effect in 1996, 0.55 ± 1.04 $\hat{SE}$, and its 95% $\hat{CI}$ -1.48, 2.58). Wide CIs demonstrate high uncertainty regarding the importance of time effects on resighting probabilities, precluding confident inference. The colony effect in Model D, in contrast, was positive and did not bound zero (1.06 ± 0.48 $\hat{SE}$, 95% $\hat{CI}$ 0.13, 1.99); under certain assumptions, this suggests that the difference in resighting probabilities is a true feature of the sampled colonies. Based on Δ

$QAIC_c$ and confidence intervals around model effects, we maintained the colony

effect in resighting probabilities and proceeded to test for colony and time

dependence in survival (Models A-D; Table 2.1).

Models D and C (survival a function of time) acquired essentially no

support compared to the highly Δ $QAIC_c$ favored Models A (survival

probabilities constant) and B (survival a function of colony). Models A and B

acquired equal support. However, the CIs around the colony effect in Model B

bound zero substantially (0.31 ± 0.33 $\hat{SE}$, 95% CI -0.35, 0.96); consequently,

there is high uncertainty regarding a colony effect and so the estimated effect size

should not be used as a basis for inference. Δ $QAIC_c$ and model effects suggest

Model A as an overall best model given the data. Estimates from Model A are

provided in Table 2.2.

2.5 Discussion

2.5.1 Band Wear and Overdispersion

Calvo and Furness (1992) reviewed 786 papers on birds and found that

39.6% used engraved or non-engraved plastic color bands. Given this wide use of

plastic bands it seems likely that band wear, as in our study, is common.

Therefore, analyses aimed at gaining insights into the process and severity of

wear and ensuing biases should be valuable. Plastic bands in our study wore

rapidly but did not result in overdispersion; this was accomplished by applying a

wear-resistant federal band in combination with a plastic band and intensively

resighting birds. Detection of marked animals was maintained, as plastic bands

wore out, by switching focus to the less readable federal band.

It is unlikely that our high resighting probabilities can be accomplished in most studies. Whether or not this is the case, we recommend double banding and careful selection of band types especially if substrates in the study area may cause wear. Planners should keep in mind that resistance qualities of plastics vary and other non-metal alternatives exist. Studies experiencing band wear should estimate $\hat{c}$ for the data they have to determine if overdispersion is present. In most cases, it may not be possible to preclude overdispersion by increasing effort; switching to a more durable band may be the only solution.

2.5.2   Survival Effects and Inference

Exclusive support for Model A suggests that probabilities of resighting and survival were, respectively, a function of colony and constant over the period studied (1992 – 2003). Consistency in survival between EER and SI (ca. 42 km between islands) over 11 years suggests that mortality factors affecting breeding adults were independent of local breeding population (colony). Shared survival combined with very little evidence of mortality in the breeding period (AWD and SWK unpublished data) provides evidence that adults from EER and SI may exist sympatrically in the non-breeding period (fall, winter, spring). This inference, if true, makes an important contribution to our limited knowledge of the winter distribution of Western Atlantic Puffins (Lowther *et al.* 2002).

It is generally accepted and implemented by managers that by protecting several spatially discrete local populations, the chance for species persistence improves. However, this belief hinges on the critical assumption that adult survival is a local population phenomenon, i.e., independent of neighboring

conspecific groups. Obviously, if this assumption fails, several 'discrete' local breeding populations could go extinct simultaneously, due to shared high adult mortality. Suggestions to avoid this scenario go beyond the scope of this paper, but clearly our results suggest that in order to make confident management decisions, we need to know more about shared characteristics of local populations. Results also demonstrate that our understanding of population dynamics, based mainly on knowledge from single local population research, may in some cases be deficient and misleading.

2.5.3   Survival Pattern and Comparisons

Our estimate of adult survival is consistent with published estimates for many long-lived seabirds experiencing conditions conducive to low mortality (see summaries in Spendelow and Nichols 1989, Jouventin and Weimerskirch 1991, and Harris *et al.* 2000). Survival estimates from Atlantic Puffin colonies in the Eastern and Western Atlantic (Table 2.3), again for adults experiencing favorable conditions (estimates ≥95%), are also consistent with our own. With our small dataset, we did not detect biologically important changes in survival over the period studied. High survival in most years broken only occasionally by low survival is a common finding in long-term studies of k-selected seabirds including, e.g., the Shag (*Phalacrocorax aristotelis*), Common Murre (*Uria aalge*), and Razorbill (*Alca torda*) in the Northern Hemisphere (Harris *et al.* 2000), and Light-Mantled Sooty Albatross (*Phoebetria palpebrata*) and Sooty Albatross (*P. fusca*) in the Southern Hemisphere (Weimerskirch *et al.* 1987). Although results from these studies contrast with our own, a *post hoc* observation

of estimates from Model C (survival and resighting a function of time and colony respectively) suggests two low survival events in our data may have eluded detection: 1999/2000 (0.91 ± 0.03 $\hat{SE}$) and 2001/02 (0.92 ± 0.03 $\hat{SE}$). Interestingly, these events precede two of three low estimates of fledging success for the period studied (SWK and AWD unpublished data). It is not surprising, given our small sample size, that we were unable to detect these potentially important events. Subsequently, the time-independent or 'average' survival probability reported here (0.95 ± 0.01 $\hat{SE}$) might be too low for most years.

An unusual survival pattern was documented by Harris *et al.* (1997) in CMR data from adult Atlantic Puffins monitored at the Isle of May, Scotland. Harris *et al.* (1997) report a stepped pattern in survival over the period studied, 1973 - 1990 (Table 2.3). We speculate that such a stepped pattern might be detectable only in datasets approaching 20 years or more.

2.5.4 <u>Regional Contribution</u>

Survival probabilities from this paper are the first for Atlantic Puffin in the Western Atlantic to be estimated from competing models using the maximum likelihood method, and update the last published estimates for the region from 1987 (Kress 1978 – 2004; Table 2.3). As shown in Table 2.3, previously published estimates in the Western Atlantic estimated survival from year *i* to *i*+1 as return rates given by the estimator (notation varies) $\phi_i = r_{i+1} / R_i$ where R_i is the number of marked animals released at time *i* and r_{i+1} is the number subsequently encountered in year *i*+1 (Pollock *et al.* 1990). Using this estimator, return rates underestimate survival unless the encounter (e.g., resight, recapture or both)

probability at year i+1 is equal to 1.0. Considering major factors that complicate our ability to relocate marked animals, including landscape heterogeneity and observer experience, it seems reasonable to assume that return rates are confounded by encounter probabilities and to use CMR models to estimate survival.

2.6   Acknowledgements

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Table 2.1. Competing models ranked ascending by $QAIC_c$ including model

selection criteria, $QAIC_c$, Δ $QAIC_c$, Akaike Weight, model likelihood, model

deviance, and number of model parameters (K). A-G used to reference models in

text.

Model	$QAIC_c$	Δ $QAIC_c$	Akaike Weight	Model Likelihood	K	Model Deviance
A $\{\phi$ (.) p (c)$\}$	496.28	0.00	0.650	1.000	3	189.61
B $\{\phi$ (c) p (c)$\}$	497.54	1.26	0.346	0.533	4	188.85
C $\{\phi$ (t) p (c)$\}$	507.58	11.30	0.002	0.004	13	180.49
D $\{\phi$ (c+t) p (c)$\}$	509.07	12.79	0.001	0.002	14	179.92
E $\{\phi$ (c+t) p (.)$\}$	511.95	15.67	0.000	0.000	13	184.87
F $\{\phi$ (c+t) p (c+t)$\}$	515.16	18.88	0.000	0.000	24	165.03
G $\{\phi$ (c+t) p (t)$\}$	523.25	26.97	0.000	0.000	23	175.23

ϕ = survival parameter, p = resighting parameter, (.) parameter constant, (c)

parameter a function of colony, (t) parameter a function of time, (c+t) parameter a

function of colony and time (with no interaction).

Table 2.2. Survival and resighting probabilities as maximum likelihood estimates

(MLE) generated in program MARK (White and Burnham 1999) from our top

model, Model A: ϕ (.) p (c), survival probabilities constant, resighting

probabilities a function of colony.

Colony	Parameter	MLE	$\hat{S}E$	95% $\hat{C}I$ Lower	Upper
Both	ϕ: All Years	0.950	0.008	0.931	0.964
EER	p: All Years	0.982	0.009	0.958	0.992
SI	p: All Years	0.946	0.013	0.915	0.968

Note: ϕ = survival parameter, p = resighting parameter, EER = Eastern Egg

Rock, SI = Seal Island

Table 2.3. Annual survival estimates from breeding adult Atlantic Puffins

(*Fratercula arctica*) including study location and methods from the Eastern and

Western Atlantic.

Eastern Atlantic	Method	Survival Estimate (%)	Author(s)
British Isles	Ring Recoveries	95.5	Mead (1974)
Skomer I., Wales	Resight (color bands) [a, c]	95.0	Ashcroft (1979)
Skomer I., Wales	Resight (color bands) [a, d]	89.0	Hudson (1979)
Isle of May, Scotland	Resight (color bands) [a, c]	96.3	Harris (1983); Harris and Wanless (1991); Harris and Bailey (1992)
Isle of May, Scotland	Resight (color bands) [b, c]	97.5 (1973-1980) 92.4 (1981-1994) 80.6 (1990)	Harris *et al.* (1997)
Rost, Norway	Resight (color bands) [b, c]	92.7	Erikstad *et al.* (1998)
Hornoya, Norway	Resight (color bands) [b, c]	86.0	Erikstad *et al.* (1998)
Skomer Wales	Resight (color bands) [b, c]	91.3	Poole *et al.* (1998)
Isle of May, Scotland	Resight (color bands) [b, c]	91.6	Harris *et al.* (2000)
Western Atlantic			
Great Island, NF	Resight (color bands) [a, c]	95.0	Nettleship (1972) and pers. comm. from Hudson (1985)
Eastern Egg Rock, Gulf of Maine	Resight (color bands) [a, c]	> 95.0	Kress (1987)
Gulf of Maine	Resight (color bands) [b, c]	95.0	This Study

a = Survival rate estimated using return rates, i.e., by dividing the number of

marked animals encountered in year i+1 by the number marked in year i.

b = Maximum likelihood method used to estimate survival probabilities following

a CMR analysis.

c = Sample consists of known breeders captured at burrows.

d = Breeding status of birds not always known (Gaston and Jones 1998).
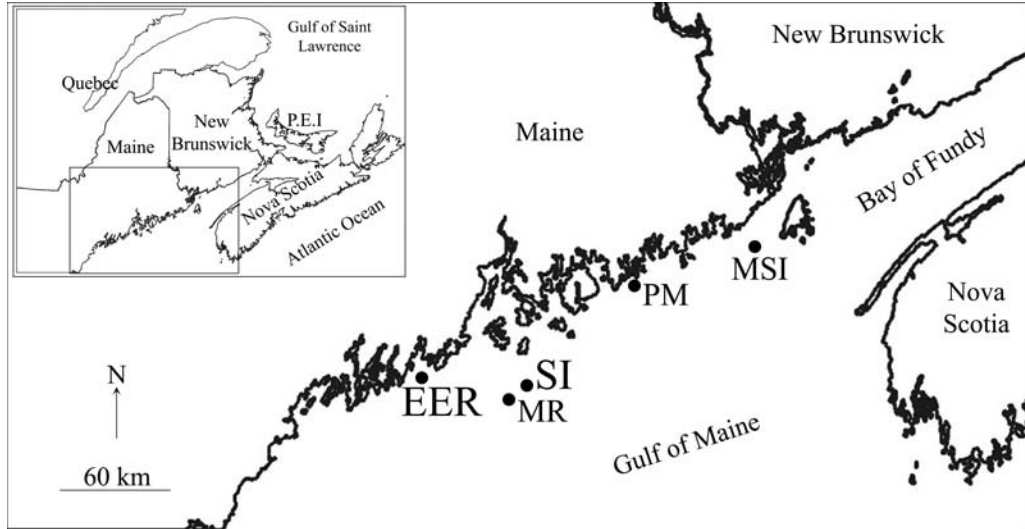
Fig. 2.1. Locations of managed Atlantic Puffin (*Fratercula arctica*) colonies in the Gulf of Maine and Bay of Fundy: EER (Eastern Egg Rock), MR (Matinicus Rock), SI (Seal Island), PM (Petit Manan), MSI (Machias Seal Island).
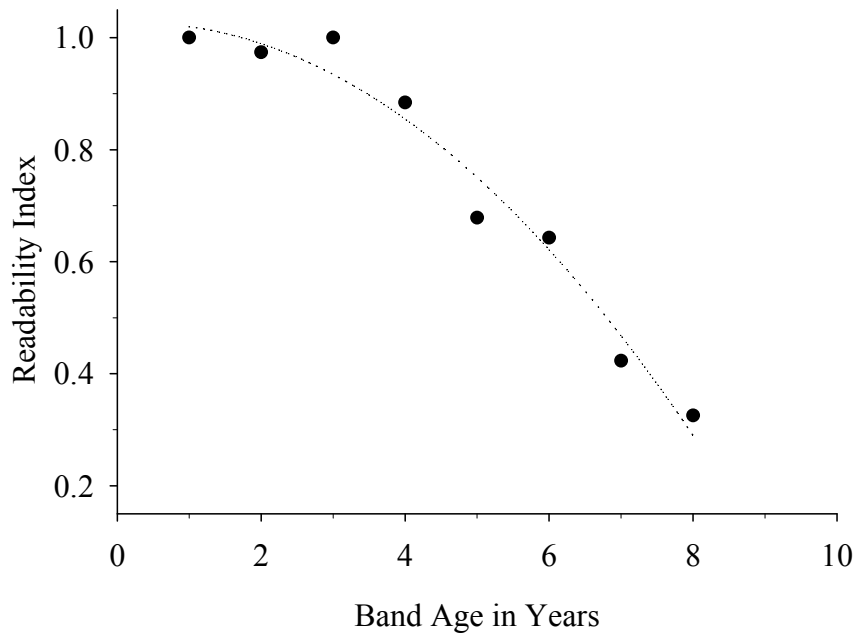
Fig. 2.2. An index of band readability, mean number of resightings/year divided by the mean in year one, against age of band in years ($n = 38$ plastic bands). Data were fitted to a line using a quadratic equation resulting in our readability curve ($R^2 > 0.96$).

Chapter 3

Encounter, survival, and movement probabilities from an Atlantic

puffin (*Fratercula arctica*) metapopulation

Authorship: André R. Breton,[1,2] Antony W. Diamond,[1] and Stephen W. Kress [2]

[1]Atlantic Cooperative Wildlife Ecology Research Network (ACWERN),

University of New Brunswick, P.O. Box 45111, Fredericton, N.B. E3B 6E1,

Canada

[2] Seabird Restoration Program, National Audubon Society, 159 Sapsucker Woods

Road, Ithaca, NY, 14850 USA

Contribution of Authors: A. R. Breton analysis and majority of writing, data

collection on Eastern Egg Rock 1996-1997, Matinicus Rock 1995, Seal Island

1995, 1998-2001, Machias Seal Island 2002; A. W. Diamond primary editor, very

little writing, contributed all of the data from Machias Seal Island; S. W. Kress

editing, contributed all of the data from the remaining islands (excluding Petit

Manan).

3.1 Abstract

Several weaknesses in our understanding of long-lived animal populations have persisted due mainly to a prevalence of single local population research at the expense of multi-site studies. We performed a multi-site capture-mark-resight analysis using 2,050 Atlantic Puffins (*Fratercula arctica*) banded as chicks on four islands (colonies) over 24 years in the Gulf of Maine, USA and Canada. Within program MARK, encounter, apparent survival, pre-breeding movement (PBM; annual movements between colonies prior to breeding), and natal dispersal (ND) probabilities were modeled as functions of age, colony and several covariates. Information-theoretic model selection criteria and estimated model effect sizes were used to (1) identify important effects and (2) select models to estimate parameters. Encounter probabilities were extremely variable (0.10-0.95) and declined annually starting six years after bands were applied, due to changes in resighting effort, and band wear respectively. Colony-dependent survival probabilities increased to a peak at age six years; arithmetic means from all colonies: age 0-3 (0.70); 4 (0.78); 5 (0.81); 6, 7, 8 (0.84). Low adult survival (age ≥ 5 years) may reflect inclusion of breeding and non-breeding adults in our sample or a bias due to band loss and illegibility. Consistent with a density-dependent prediction, the effect of colony size on survival was negative and acquired strong AIC_c support; however, this effect was inconsistent with strata effects in competing top models; the latter suggest survival was lowest on the smallest island. The effects of origin and destination colony, and origin colony size in PBM and ND probabilities resulted in important variation in these parameters. As

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few as 8% and as many as 57% of the puffins we marked may have bred away

from their natal colony, a signal of highly variable philopatry. Consistent with the

conspecific attraction hypothesis, ND and PBM probabilities declined as the size

of the origin colony increased. PBM probabilities were highest in the age 0-3

period and these declined quickly with age thereafter. Strong colony and age

effects in ND and PMB probabilities identify movement as a critical contributor

to local population dynamics at our four study sites.

3.2   Introduction

Three persistent weaknesses in our understanding of demography of long-

lived seabirds have been identified: (1) very few data on movement patterns and

processes (Greenwood and Harvey 1982, Clobert and Lebreton 1991, Coulson

1991, Wooller *et al.* 1992, Brownie *et al.* 1993, Walters 2000, Weimerskirch

2002, Lebreton *et al.* 2003); (2) few rigorous estimates of sub-adult survival

probabilities (Weimerskirch 2002, Lebreton et al. 2003); and (3) sparse evidence

for density-dependent population regulation (Croxall and Rothery 1991, Wooller

et al. 1992, Weimerskirch 2002) in these so-called K-selected species (MacArthur

and Wilson 1967). Estimates of movement between sites require overcoming the

challenge of monitoring two or more local populations simultaneously. Because

long-lived seabirds often delay maturation by three or more years, estimates of

sub-adult survival require a long-term commitment to collect data. Additionally,

since dispersal of pre-breeding birds (natal dispersal) is much more common than

dispersal of established breeders (Greenwood and Harvey 1982, Lebreton *et al.*

2003), investigators interested in estimating sub-adult survival probabilities must

monitor several local populations simultaneously or risk reporting negatively biased estimates.

Researchers often monitor a single local population for a few years, often fewer than the life span of the focal species. In contrast, multi-site and long-term studies are extremely rare; however, considerable challenges often preclude initiation or completion of these studies (Wooller *et al.* 1992). In addition, necessary statistical theory (Arnason 1972, 1973, Schwarz *et al.* 1993, Lebreton *et al.* 2003) and relatively easy-to-use computer software for running required multi-site, or strata, models have been developed only recently (see review in Lebreton and Pradel 2002). Importantly, these multi-site models, and other mark-encounter type models, include encounter probabilities; the lack of these is a crippling source of bias in earlier methods for estimating demographic parameters (Pollock *et al.* 1990, Lebreton *et al.* 1992). Studies that have overcome these challenges and produced rigorous estimates of sub-adult survival and/or movement are rare (Hestbeck *et al.* 1991, Spendelow *et al.* 1995, Lindberg *et al.* 1998, Grosbois and Tavecchia 2003, Lebreton *et al.* 2003, Cam *et al.* 2004, Doherty *et al.* 2004, Oro *et al.* 2004, Schreiber *et al.* 2004). Consequently, knowledge of factors driving local population dynamics within metapopulations (Hanski and Gilpin 1991) remains limited (Walters 2000, Weimerskirch 2002, Lebreton *et al.* 2003).

In the Gulf of Maine (GOM; Fig. 3.1), including the Bay of Fundy, eight currently active Atlantic Puffin (*Fratercula arctica* Linnaeus; Charadriiformes: Alcidae) breeding colonies are known (Lowther *et al.* 2002, J. Nocera pers. comm.). Three non-managed colonies represent less than 5% of the regional

breeding population (Fig. 3.1; Lowther *et al.* 2002, J. Nocera pers. comm.). The

remaining 95% nest at five managed colonies: Eastern Egg Rock (EER),

Matinicus Rock (MR), Seal Island (SI), Petit Manan (PM), and Machias Seal

Island (MSI; Fig. 3.1). At these five colonies, resident summer observers have

monitored puffins through capture-mark-resight/recapture since the 1980s. In

2000, through a cooperative agreement among the three managing agencies,

mark-resight/recapture data from all five colonies were made available for multi-

site analyses.

We report here on a multi-site capture-mark-resight (CMR) analysis using

Atlantic Puffins banded as chicks at four colonies in the GOM. Breton *et al.*

(2005) report adult survival estimates from breeders nesting on EER and SI over

11 years. Here we expand coverage to 24 years of data (1980 – 2003), to sub-

adult as well as adult survival, and from two islands to four (MR, SI, PM, and

MSI); EER contributed too few chicks ($n = 12$) to justify inclusion in the analysis.

Using CMR models, we performed several exploratory and hypothesis-driven

tests to (1) identify important structure in the data and (2) produce estimates of

three demographic parameters and encounter probabilities. Demographic

parameters measured here were: apparent survival (White and Burnham 1999);

pre-breeding movement (annual inter-island movements prior to first breeding);

and natal dispersal (a single transition from colony of birth to nesting colony at

age five years; Greenwood and Harvey 1982). We distinguish between non-

explanatory, or structural, factors (such as age and colony); and explanatory

factors, such as resighting effort and distance between colonies, which involve a

specific cause-effect relationship. Our exploratory tests involve non-explanatory factors, while explanatory factors are reserved for hypothesis-driven tests. Tests and hypotheses were prepared prior to analysis of data and were guided mainly by the weaknesses described above. In addition, by simultaneously measuring two sources of movement between colonies, and survival, our analysis provided a rare opportunity to determine the relative influence of these parameters in local population dynamics.

3.3   Study Area and Methods

3.3.1   Study Sites and Data Collection

3.3.1.1   Study Sites

Island descriptions are available in: Kress and Nettleship (1988), Matinicus Rock (MR) and Eastern Egg Rock (EER); Breton *et al.* (2005), Seal Island (SI); Anderson and Devlin (1999), Petit Manan (PM); Diamond and Devlin (2003), Machias Seal Island (MSI). MSI (44°30´N, 67°06´W) is owned by the Canadian Coastguard, managed by the Canadian Wildlife Service (CWS) and monitored cooperatively by CWS and the Atlantic Cooperative Wildlife Ecology Research Network (ACWERN) (Fig. 3.1). Petit Manan (PM; 44°22´N, 67°52´W), SI (44°14´N, 68°44´W) and Matinicus Rock (MR; 43°47´N, 68°51´W) are National Wildlife Refuges owned by the United States Fish and Wildlife Service (USFWS) and managed by them and cooperatively by the National Audubon Society's Seabird Restoration Program (Fig. 3.1). PM (6.5 ha) is located ca. three kilometers south of Petit Manan Point. MR (7 ha) and SI (40.5

ha) are ca. 45 km south of Rockland, Maine. MSI (9.5 ha) lies 18.9 km west of
Grand Manan Island, New Brunswick, Canada (Fig. 3.1).

3.3.1.2   Data Collection

All puffins were marked as chicks with two individually engraved leg
bands. Each bird received a monel or incoloy United States Geological Survey
(hereafter "federal") band and colored field-readable band on opposite tarsi.
Plastic bands were bi-laminar polyvinylchloride (PVC or darvic; darvic rarely
substituted) with one to four characters engraved through the top layer;
engravings were repeated on the band (e.g., 101 – 101). Each island used a
unique color scheme (MR used two).

Banding occurred annually from mid July to late August. Chicks were
captured in burrows (by hand) or (on MSI only) while fledging. Atlantic Puffins
'fledge' when they leave their burrows for the ocean at ca. six weeks post-hatch
(Harris 1984, Lowther *et al.* 2002). Marked animals were resighted annually,
with few exceptions, from mid May to late August; colored leg bands were read
preferentially over the less readable but more durable federal bands using spotting
scopes (power 25 – 70x) and occasionally binoculars or naked eye. Observers
varied seasonally; each made one observation stint daily to resight puffin leg
bands; stint duration varied between islands and years.

3.3.2   <u>Analysis</u>

3.3.2.1   Encounter Histories and Parameter Estimates

CMR data were summarized and then imported into program MARK as
individual multi-strata or site encounter histories (White and Burnham 1999).

Encounter histories (EH) used to model encounter, apparent survival and pre-breeding movement (PBM) were 24 occasions long (1980 – 2003).

The EH set used to model natal dispersal (ND) probabilities was imported and analyzed in MARK independent of the EH set used to model encounter, apparent survival, and PBM probabilities. These EHs were set-up 'as if' birds were banded at age four years at their colony of birth resulting in 20 occasions rather than 24 (as above). With EHs modified in this way, we estimated ND as the probability of transitioning from colony of birth to location at age five years, i.e., as the first diagonal in the ND parameter index matrices (White and Burnham 1999); justification for the age five cut-off is given below.

Because a few birds did not breed until their 6th, 7th or 8th year after fledging, PBMs continued, and were therefore potentially estimable, beyond our age five cut-off used to measure ND. In the analysis of encounter, apparent survival, and PBM, we retained the 'pre-breeding' description for these age-specific transition probabilities (ages 5-6, 6-7, 7-8) because dispersal by adults has never been observed in Atlantic Puffin (Harris and Wanless 1991).

Several ($n = 411$) individuals were seen on more than one island within a summer. In order to set up EHs, which require only one character per occasion (White and Burnham 1999), and measure between summer (annual) movement probabilities and ND, we had to reduce multi-site sightings within a summer to a single record. We chose the location at last sighting from each summer.

Parameters reported here are maximum likelihood estimates (Lebreton *et al.* 1992, White and Burnham 1999); the logit-link and 2nd partial options in

program MARK were used to calculate probabilities from model intercepts and offsets (betas) and the variance-covariance matrix respectively (White and Burnham 1999). Apparent survival (ϕ) and PBM (ψ) are the probabilities of surviving or moving between colonies, respectively, from occasion i (origin colony) to $i+1$ (destination colony), while encounter probabilities (p) estimate the probability of being resighted on occasion i. Natal dispersal is the probability of a permanent movement from first release location (origin colony) to location at age five years (destination colony). In order to separate the probability of surviving (ϕ) and moving (ψ) from occasion i to $i+1$, multistrata models used in this study condition survival only on location at occasion i, ϕ_i^r, and condition PBM and ND probabilities on surviving from period i to $i+1$, ψ_i^{rs}, where r is location at time i (origin colony) and s is location at $i+1$ (destination colony; Spendelow *et al.* 1995). In addition, movement probabilities for strata- and age-specific cohorts are constrained to sum 1.0.

3.3.2.2 *Modeling Strategy and Global Model Structure*

We used multi-strata models developed by Arnason (1972, 1973) and Schwarz *et al.* (1993; Arnason-Schwarz model). Parameters were modeled in the following order: encounter, apparent survival, PBM, ND. Our global model was:

$p_{age3\_8+effort+effort^2}^s \; \phi_{age3\_5,\geq6}^r \; \psi_{age3\_8}^{rs}$ where superscripts represent strata, origin (r) and destination (s) colonies, and subscripts refer to all other model effects. Age 3_8 describes a unique effect for each age 0-3, 4, 5, 6, 7, 8 and age 3_5, $\geq$6 for each age 0-3, 4, 5, 6-8; effort is a resighting effort covariate (see below). To

perform various tests, reduced designs of the global model and several models constrained by covariates were built.

We assumed a constant adult survival probability between ages 6-8 in order to reduce the number of parameters thereby increasing the precision in those that remained. To avoid bias and loss of precision due to a decreasing sample size from mortality and accumulating effects of band surface wear (see below), encounter, survival, and transition probabilities for ages above eight years were fixed to zero; consistent with this approach, we also replaced encounters with birds after their eighth year with zeros (not seen) in EHs. Transition probabilities between ages 7-8 were too close to zero to be estimable; these were fixed to zero in all PBM models. Transition parameters beyond age five years (5-6, 6-7, 7-8) in ND models were all fixed to zero.

Atlantic Puffins are rarely seen at colonies in their first summer after fledging; many are seen for the first time as two year olds, and virtually all survivors return by year three (Harris 1984, Gaston and Jones 1998, Lowther *et al.* 2002, SWK unpubl. data, AWD unpubl. data). These life-history traits conflict with an important assumption of CMR models: all animals surviving from occasion *i* to *i*+1 are available for encounter on occasion *i*+1, i.e., no temporary emigration (see below; Lebreton *et al.* 1992). To satisfy this assumption, we modeled the age period 0-3 as a single effect, giving a single survival estimate, by fixing age one and two encounter and movement probabilities to zero (not observable) and survival probabilities to one (zero mortality); we also replaced encounters with one and two year-old birds with zeros (not seen) in EHs.

Atlantic Puffins recolonized SI and colonized PM in 1992 and 1987

respectively (Drury 1973, Kress 1997, Anderson and Devlin 1999); MSI and MR

were occupied throughout the study period. All islands had resident summer

observers by 1984 (SI) or much earlier (all others). Prior to recolonization, with

the exception of seven native MR chicks seen on SI in 1990 and 1991, native

GOM puffins banded as chicks were not seen on either SI or PM. Pre-

colonization encounter parameters for SI and PM, 1980-1989 and 1980-1985

respectively, were fixed to zero in all models.

An important limitation was our inability to include time as a factor in our global

model due to too few birds released in most colony-year cohorts (Table 3.1);

model interaction terms were also excluded, with one exception, due to sparse

data.

3.3.2.3   *Goodness-of-Fit of our Global Model*

We were aware of two statistical tests for assessing the fit of multi-strata

models: median $\hat{c}$ in program MARK (White and Burnham 1999); and the

multiple test approach proposed by Pradel *et al.* (2003). An important limitation

of the multi-strata GOF tests proposed by Pradel *et al.* (2003) and implemented in

program U-CARE (Utilities Capture-Recapture; Choquet *et al.* 2003) was that we

could test the fit of our data to only the time-dependent Arnason-Schwarz and

JMV (see below) models. U-CARE implements several contingency table tests to

assess GOF of the Arnason-Schwarz and JMV models; our data produced too

many low values (≤ 2) in the expected cells to successfully perform these tests.

We considered the option of extensive pooling to increase expected values (Pradel

et al. 2003) but decided that a test of these extensively pooled data would not give

a reliable measure of GOF for our unmanipulated data and global model, a model

fitted to an important source of time structure (resighting effort; see below) in

encounter probabilities but not survival or movement. We suspect that limitations

of our data were also responsible for complications we encountered while trying

to estimate median $\hat{c}$, the overdispersion parameter, in program MARK (White

and Burnham 1999). These complications left us without a formal way to test for

the presence of overdispersion in our data or structural inadequacies in our global

model.

Our response was to devise an *ad-hoc* test involving $\hat{c}$ and combine this

with (1) and (2) to provide an overall assessment of GOF: (1) we carefully

assessed each multi-strata model assumption and the potential of our data to

uphold them, which led to the addition of four non-biological factors into our

analysis; and (2) the biological tenability of our top model estimates was

determined by comparing these to published estimates for the species. For the $\hat{c}$

component, we started by assuming that overdispersion (several sources are

provided in our discussion) was not present in our data ($\hat{c} = 1.0$) and went

through the process of model building, selection, and inference described above

and below. Following these steps, we applied $\hat{c}$ values of 2.0 and 4.0 to all

model sets in order to simulate inference following adjustments for overdispersed

data (Burnham and Anderson 2002); an important consequence of adjusting $\hat{c}$ is

that sampling variances are inflated which leads to a lower risk of falsely

identifying a model factor as important, i.e., of making a Type 1 Error (Lebreton

et al. 2003). After applying each level of $\hat{c}$, we noted important changes in model support; we report these with other results.

Multi-strata model assumptions that were a concern with our data were: no heterogeneity in encounter and demographic parameters within strata- or age-specific cohorts; marks remain readable throughout the study; sampling instantaneous; no temporary emigration away from study colonies (Hestbeck *et al.* 1991). And specific to the Arnason-Schwarz multi-strata model, is the 'memoryless' assumption (Brownie *et al.* 1993). Failure to meet these assumptions can lead to biased estimates and underestimated sampling variances (Arnason 1972, 1973, Schwarz *et al.* 1993, Anderson *et al.* 1994).

To address the heterogeneity assumption, we included age and colony terms in our models, acknowledging any among group heterogeneity in the data that we could identify. In place of time effects on encounter probabilities, we tested a time-varying effort covariate (number of observation stints/colony/year) to account for an important source of time-dependence in our data. To assess the additivity and linearity assumptions of the effort effect, we tested interaction (site*effort) and quadratic (effort^2) terms respectively.

The assumption of marks remaining readable was an issue for our study. Breton *et al.* (2005) showed a reduction in band readability of 70% between the third and fifth year post-application on adult breeding puffins; in the first three years, readability remained high. In our sample of puffins marked as chicks, we predicted that band readability would not decline until age six years, i.e., following two summers at sea (see above) and three at colonies accumulating

wear. Therefore, we tested a delayed, declining, trend effect, which, if present, would account for a decline in encounter probabilities due to band wear; trends in our analysis were fitted using index values and a single beta in the design matrix of program MARK (White and Burnham 1999, Franklin 2001). Lastly, in an attempt to 'shave-off' data most affected by band wear, encounter, survival and transition probabilities above age eight were fixed to zero in our models; this effectively removes each bird from our analysis at the end of their eighth year.

Sampling all individuals simultaneously cannot be expected in studies requiring resampling of marked animals. However, the concern of this assumption, that mortality occurs only between sampling periods, should be approximately met with our data. In our study, losses of marked or unmarked birds within the summer sampling period have rarely been suspected or documented.

After accounting for the delayed return of young puffins to the colonies (see above), the requirement of no temporary emigration should be approximately met in our data. Exceptions would include birds visiting EER or another island(s) in or outside the GOM exclusively and then returning to our study sites on a subsequent occasion. Although rare, this has likely occurred with EER and other GOM puffin islands. There have been no reports of a native GOM chick visiting or emigrating out of the GOM. The two nearest puffin colonies to those in the GOM, Pearl Island and Bird Islands, NS, are ca. 220 and 680 km over water respectively from the Tusket and Mud Island Groups (Fig. 3.1).

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A simple scan of our encounter histories demonstrates that puffins in our study tend to return at occasion i to their location at i-1. However, our data were too sparse to apply the Jolly-movement (JMV) or memory multi-strata model from Brownie *et al.* (1993) in place of the Arnason-Schwarz model; the latter assumes that "transition probabilities for period i [do not] depend on the stratum occupied at i-1" (Brownie *et al.* 1993). With our data, the memory model would require 64 transition probabilities to be estimated per period, or 1472 for all periods (Brownie *et al.* 1993). This number of parameters is close to the number of animals in our sample.

3.3.2.4 Model Selection

Information-Theoretic model selection criteria (Burnham and Anderson 2002), model effect sizes and their 95% CIs (on the logit scale) were used to determine support for competing models so that we could (1) perform tests (see below) and (2) select one or more best models to estimate parameters. Selection criteria we used were: Akaike's information criterion (AIC) adjusted for small sample size (AIC_c ; Anderson *et al.* 1994); delta (Δ_i) AIC_c where (i) is a particular model in the set; AIC_c weights (w_i) for each model (i); and evidence or odds ratios (w_i / w_j) where (i) and (j) are competing models. A Δ AIC_c difference of about two is equivalent to an evidence ratio of ~3:1; a difference of four, ~7:1; eight, ~55:1; ten, ~150:1. Strong support is therefore inferred for all models within 0-3 AIC_c units from the top model, considerably less for those between 4-7, and essentially none for models achieving a Δ AIC_c ≥ 10 (Burnham and Anderson 2002).

3.4   Tests and Hypotheses

3.4.1   Encounter Models

The process of detecting a marked animal, unlike survival or movement, is partially a function of the behavior of the investigators. Certain bird 'states', such as sex or age, and degradation or loss of marks may also influence the detection process. *A priori*, differences among colonies (including distribution of breeding pairs) and resighting effort were identified as features that would likely contribute to our detection probabilities; age of bird and a delayed decline in band readability from surface wear (see above) were also identified as potential contributors. We assessed the assumption of additivity and linearity of the effort effect by testing an interaction (site*effort) and quadratic term (effort^2) respectively.

Estimation problems occurred when the s*effort interaction term was included in the global model. In order to test the s*effort term, we fitted the s*effort interaction term with the declining trend effect in place of the age effects in our global model ($p^s_{trend+effort+effort^2+s*effort}$). Support for this model was then compared to the global model and the trend model without the interaction term ($p^s_{trend+effort+effort^2}$). We then tested all possible combinations of factors from the best model from this small set.

3.4.2   Apparent Survival Models

Acquiring empirical evidence of shared characteristics between discrete local populations, such as seabirds breeding on islands, requires a multi-site design and therefore has rarely been provided (see introduction). However, a

common assumption made by investigators monitoring migratory species is that the 'isolation' of local groups, e.g., on islands or among forest patches, translates into an independent risk of mortality. Although sample size was small, Breton *et al.* (2005) failed to detect a biologically important difference in adult survival between two colonies (separated by ca. 42 km); here, we test for a difference in age-specific survival among four colonies (greatest distance between colonies 167 km). No evidence for a biologically important difference in survival would suggest that birds from four discrete colonies share the same risk of mortality. This test was performed in an exploratory way by comparing the global model for this set ($\phi^r_{age3\_5,\geq6}$) to a model without colony ($\phi_{age3\_5,\geq6}$); we also considered colony effect sizes from the global model and support for the colony only design (ϕ^r).

For long-lived species, differences in survival probabilities between sub-adult (pre-breeding) and adult (potential breeders) stages are widely recognized (Ricklefs 1973, Hudson 1985, Dobson 1990, Sibley *et al.* 1997, Gaillard *et al.* 1998, Loison *et al.* 1999). However, much of the supporting empirical evidence does not account for encounter probabilities and rarely accounts for dispersal out of a single mark-encounter site (Pollock *et al.* 1990, Hestbeck *et al.* 1991, Lebreton *et al.* 1992, Lebreton *et al.* 2003). We tested for age differences in survival by comparing the global and three reduced age-structured models, $\phi_{age3\_5,\geq6}$, $\phi_{age3,\geq4}$, $\phi_{age3\_4,\geq5}$ and $\phi_{(.)}$ respectively, while accounting for movement between sites and site-specific encounter probabilities; age 3, ≥4 provides a

unique effect in the model for each age 3, 4-8 and age 3_4, ≥5 for each age 3, 4, 5-8.

We monitored four colonies: three small, one relatively large. Although many factors other than density might explain a survival difference between these colonies, we recognized in our data a rare opportunity to test for a density-dependent response in both survival and movement (pre-breeding and natal dispersal). To set up these tests, we adopted the convention of using abundance (colony size), rather than individuals per unit area, to test for a density-dependent response (Lack 1954). With the exception of SI, we used colony size estimates from 2003: PM (25), SI (231), MR (280) and MSI (2800). Numbers on SI have been increasing rapidly in the last ten years, while the others have remained relatively constant. To better reflect the majority of the years of the study when numbers of breeding pairs on SI was much lower than 2003, we used the average number of pairs from 1992-2003 for this island: $\hat{\mu}_{SI\,Colony\,Size} = 86$. We constrained the top survival model from above with the rescaled colony size covariate; rescaling (0.0001*colony size) was necessary to avoid estimation problems in MARK (White and Burnham 1999). Strong support for this model along with a negative colony size effect would support a negative density-dependent relationship between source-colony size and survival.

3.4.3 Determining Dispersal Status

Before we could perform any tests of ND, we first had to identify the ND status (disperser or non-disperser) of every individual in our sample. The norm in seabird studies is to determine dispersal status based on knowledge of individual

breeding histories (e.g., see Spendelow *et al.* 1995). Using this approach, marked

birds that breed away from their natal colony are dispersers and the remainder are

non-dispersers. For most of the birds in our study, breeding histories were not

known. In place of this information, we determined ND status based on estimates

from a PBM model fitted only to a declining age trend (ψ_{trend}). We looked for an

age at which most individuals had stopped moving between colonies; this age was

then used as an end point to estimate a single transition or ND probability from

initial release location.

3.4.4   Movement Models

Opportunities to identify factors controlling the processes of movement

among local populations, and consequently, philopatry, have been rare; here we

measure movement in two forms: as short-term PBMs and ND. In contrast,

several hypotheses have been proposed to explain directional biases in movement;

these include ideal-free distribution (Fretwell and Lucas 1970) and conspecific

attraction (Stamps 1988, Serrano and Tella 2003).

Our initial sets (PBM and ND) of tests were purely exploratory: all

possible designs of the global PBM ($\psi_{age3\_8}^{rs}$) and ND (ψ^{rs}) models were

compared. From these models, we hoped to identify the biological importance of

the non-explanatory predictors origin and destination colony, and age. Kress and

Nettleship (1988) reported a decline in PBM probabilities with age starting from a

peak at age 3 years. However, their estimates, based on percentages of birds

moving, do not account for birds that were present but not seen. As part of our

analysis, we wanted to confirm this important result; this was done by constraining the top PBM model from preceding tests with a declining age trend.

As distance between colonies increases, movement between them is thought to decline as the exploration boundary of the species is reached (MacArthur and Wilson 1967). In both PBM and ND, we tested this hypothesis by comparing support for a model constrained by distance (km) between colonies to the top model from preceding tests.

Conspecific attraction (Stamps 1988) and ideal-free distribution hypotheses (Fretwell and Lucas 1970) predict two contrasting relationships between destination colony size and movement probability. Conspecific attraction suggests movers are attracted to conspecifics (Stamps 1988) and possibly in greater numbers as abundance of established conspecifics increases (Serrano and Tella 2003). Here we test the hypothesis discussed by Serrano and Tella (2003), which predicts a positive relationship between destination colony size and movement probability. Ideal-free distribution predicts animals are 'free' to disperse to an 'ideal' habitat where competition is relatively low (Fretwell and Lucas 1970). If we assume that, excluding density, all factors that affect suitability of breeding habitat among the islands are equal, an inverse relationship between destination colony size and movement would be expected under the ideal-free distribution hypothesis (Fretwell and Lucas 1970). Although no formal study has been conducted to assess habitat suitability among islands, the assumption that these are equal should be approximately met in this study (see island descriptions and references above, *Study Sites*).

Conspecific attraction and ideal-free distribution predict different relationships between origin or source colony and movement probability: respectively, the probability of movement away from colonies declines as a function of colony size (Serrano and Tella 2003) or movement away increases as a function of colony size (Fretwell and Lucas 1970). We tested the relationship between origin and destination colony size and movement to assess these hypotheses.

3.5   Results

3.5.1   Data set

From 1980 to 2003, 2,050 chicks were marked and released from all islands (Table 3.1); these animals were subsequently resighted 17,311 times.

3.5.2   Encounter Models

Three models acquired all of the AIC_c support in this set: $p^s_{trend+effort+s*effort}$,

$p^s_{trend+effort+effort^2+s*effort}$, $p^s_{trend+effort+effort^2}$ (A_{en}, B_{en}, C_{en} respectively; Table 3.2). In model B_{en} and C_{en} the effort^2 quadratic effect was weak and strong respectively; and 95% $\hat{C}$Is around the effort^2 effect in model B_{en} widely bounded zero (Table 3.3). None of the interaction effects in model A_{en} bounded zero; however, the PM*Effort interaction effect was highly imprecise (Table 3.3). The MSI*Effort and SI*Effort interaction effects in model B_{en} bounded zero; all interaction effects were highly imprecise in this model. Ninety-five percent $\hat{C}$I around strata effects in these top models (A_{en}, B_{en}, C_{en}) bounded zero about half the time (Table 3.3). The effort and declining age trend effects were strongly and weakly positive in models A_{en} (Table 3.3), B_{en}, C_{en}; the effort effect in model B_{en} bounded zero

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(Table 3.3). Based on AIC_c support for the interaction and strata effects in

models A_{en} and B_{en} (Table 3.2) and strong positive trend and effort effect sizes,

model $p^s_{trend+effort+s*effort}$ (A_{en}; Table 3.2) was maintained in all subsequent survival

and movement models.

3.5.3   Apparent Survival Models

The colony size and strata models $\phi_{origin\,colony\,size+age3\_5,\geq6}$ and $\phi^r_{age3\_5,\geq6}$

acquired all of the AIC_c support in this set (models B_s, A_s respectively, Table

3.4). Although the fit of the colony size model was slightly poorer than the strata

effects model A_s ($\Delta\,AIC_c = 1.74$), this fit was achieved with two fewer

parameters. In model B_s, the colony size effect was strongly negative and its 95%

$\hat{CI}$ did not bound zero (Table 3.3). Strata effects in model A_s were all negative

relative to the reference site, MR; the SI effect widely bounded zero (Table 3.3).

Inconsistent with the colony size effect, strata effects in model A_s suggest that

survival was lowest on PM ($\hat{B}_{PM} = -0.60 \pm 0.25\,SE$, $\hat{B}_{MSI} = -0.33 \pm 0.10$,

$\hat{B}_{SI} = -0.12 \pm 0.18$; Table 3.3). Age effects in models A_s and B_s were all strongly

positive suggesting survival probabilities were age-dependent and that these

increased rapidly from the reference age 0-3 to adult ages 6-8 (Table 3.3).

Given the inconsistency between the colony size and strata effects and to

avoid problems associated with under-fitting (Burnham and Anderson 2002),

model A_s ($\phi^r_{age3\_5,\geq6}$) is used as a starting survival structure in PBM models. The

colony size covariate is introduced into the top PBM model following all other

tests.

3.5.4 Pre-breeding Movement Models

AIC$_c$ exclusively favored the global model in this set (B$_{pbm}$) over all of its reduced forms (Table 3.5). Improvement over the global model (B$_{pbm}$) when age effects were substituted by a declining age trend (A$_{pbm}$) was marginal (Δ AIC$_c$ = 1.09); however, the trend model achieved this better fit with three fewer parameters (Table 3.5). All of the age effects in model B$_{pbm}$ were negative and these increased with age (Table 3.3); apparently, as with the trend fitted to encounter probabilities, the trend effect (Table 3.3) in model A$_{pbm}$ adequately captured the age structure in PBM probabilities. With the exception of the SI destination colony effect, none of the strata effects in model A$_{pbm}$ bounded zero (Table 3.3).

PBM models fitted to destination colony size (F$_{pbm}$) and distance (E$_{pbm}$) effects acquired no AIC$_c$ support (Table 3.5). Consistent with the conspecific attraction hypothesis (Serrano and Tella 2003), the origin colony size effect fitted to PBM was negative and its $\hat{C}I$ did not bound zero (D$_{pbm}$; Table 3.5). Model C$_{pbm}$, which included the colony size constraint on survival in place of strata effects in model A$_{pbm}$, acquired support equal to other top models in this set. The colony size effect fitted to survival was strongly negative. Strata effects fitted to survival in model A$_{pbm}$ were also negative; but as in the survival model set, these suggested PM survival, rather than MSI, was lowest.

Given the uncertainty as to which model was best (A$_{pbm}$, B$_{pbm}$, C$_{pbm}$, D$_{pbm}$; Table 3.5), we used a form of multimodel inference known as model averaging (Burnham and Anderson 2004) to produce estimates of parameters from all of the

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models in the PBM set (Figures 3.2-3.3, Tables 3.6-3.8). The contribution that each model makes to a model-averaged estimate of a parameter is determined by its AIC_c weight; additional details are available in Burnham and Anderson 2004.

3.5.5 Natal Dispersal Models

PBM estimates from model K_{pbm} (ψ_{trend}; Table 3.5) remain high from age three to five years and then decline from age five to six suggesting location at age five is generally maintained (Table 3.9). Based on these estimates, location at age five was selected as a cut-off to estimate ND probabilities as a single transition from initial release location.

The origin colony size model (B_{nd}) and global model (A_{nd}) acquired exclusive AIC_c support in the ND model set (Table 10). The colony size effect in model B_{nd} was strongly negative and its 95% $\hat{\text{CI}}$ did not bound zero (Table 3.3). Consistent with the colony size effect, the MSI origin colony effect was negative and PM effect was positive compared to the reference MR site (A_{nd}; Table 3.3). All destination colony effects in model A_{nd} were negative, suggesting movement to SI, the reference effect, was preferred over the other three sites (Table 3.3). None of the strata effects in model A_{nd} bounded zero (95% $\hat{\text{CI}}\text{s}$; Table 3.3). In order to account for model selection uncertainty in this set, we estimated ND probabilities by model averaging (Table 3.11) across the full ND model set.

3.5.6 Goodness-of-fit

Harris (1983) monitored the movements of color-ringed Atlantic Puffins among several colonies in northeast Scotland from 1972 to the early 80's. From these data, Harris (1983) estimated survival up to age five years as 39% and natal

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dispersal as 23%; the method used to estimate immature survival incorporated

encounter probabilities and their estimate of natal dispersal. Based on arithmetic

means of age 0-3, 3-4, and 4-5 survival from our top survival model (Table 3.7),

survival to age five years is 44%. Based on estimates from our top ND model, the

probability of dispersing from each site was 0.25 (MR), 0.57 (PM), and 0.08

(MSI); and the arithmetic mean of these estimates, 0.30.

An increase in $\hat{c}$ from unadjusted 1.0 to 2.0 in the encounter, PBM, and

ND model sets had no effect on our inference. An adjustment to 2.0 in the

survival model set resulted in five top models (A_s-E_s; Table 3.4); the colony size

and age model (B_s) was best. With $\hat{c}$ set at 4.0, support for effects in model A_{en}

remained strong; and the effort[2] effect acquired unambiguous support. With $\hat{c}$

adjusted to 4.0 in the survival model set all models were within 5 AIC_c units

from the top model, $\phi_{age3,\geq4}$ (E_s; Table 3.4). Model effect sizes and their 95% CIs

favored inference from model E_s. Support for effects in top models did not

change when $\hat{c}$ was increased to 4.0 in the PBM set. ND models including

distance (D_{nd}) and destination colony size effects (C_{nd}) acquired moderate support

when $\hat{c}$ was increased to 4.0; however, the origin colony size (B_{nd}) and strata

models (A_{nd}) remained the AIC_c favored models in this set (Table 3.10). In

summary, with $\hat{c}$ set at 2.0 and 4.0, inference from the encounter, PBM, and ND

model sets remained essentially unchanged. Support for colony and age effects in

survival remained essentially unchanged in the presence of moderate ($\hat{c} = 2.0$)

overdispersion; inference in the presence of severe ($\hat{c} = 4.0$) overdispersion would

have favored a reduced age model without strata or colony size effects.

3.5.7   Dispersal to Other Colonies in the Gulf of Maine

The following counts of puffins from this study have been confirmed breeding on EER: MR (10), SI (3), PM (1), and MSI (3). On 1 August 2002, two puffins banded on MSI (green plastic leg bands) were observed loafing on Green Island, Nova Scotia (Fig. 3.1; T. C. D'Eon pers. comm.). However, neither identity nor breeding status could be determined.

3.6   Discussion

3.6.1   Goodness-of-fit

In order to compare our estimates to those from Harris (1983), it is important that we can demonstrate that the environmental conditions experienced by puffins in our study and those monitored by Harris (1983) were similar. Percentages calculated from our resighting data provide three-year return rates post-fledge of 75%, 67%, 64%, and 47% for cohorts released from 1980-2000 at MR, SI, PM, and MSI respectively; the anomalous percentage from MSI is due to low resighting effort relative to colony size. Without accounting for encounter probabilities and other structure in our data, these percentages already demonstrate a high immature survival rate. Similarly, counts of puffins at colonies and breeding pairs have increased in recent years at all colonies (SWK and AWD unpublished). These data, which are free from biases due to poor model fit, suggest that environmental conditions experienced by puffins in our study were similar to those reported by Harris (1983), i.e., conducive to high survival and colony expansion.

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Also important, is assurance that estimates from Harris (1983) are biologically tenable. During the study by Harris (1983), the number of puffins at the Isle of May "quadrupled". At another study site, the Farne Islands, the population "doubled in seven years": 6,800 (1969) - 13,600 breeding pairs (1975). Although high survival rates alone cannot account for the growth at these colonies, high immature survival must have been at least partially responsible for the observed growth (Harris 1983). Based on these observations and given the complementary estimates of immature survival and natal dispersal from our study and Harris (1983), it seems reasonable to assume that models we fitted to encounter, survival, and movement probabilities were appropriate for assessing variation in these parameters.

Heterogeneity among individual probabilities (such as survival or encounter) and dependence among individuals (such as flocks, or mated pairs with strong pair bonds) are scenarios that can lead to underestimated sampling variances due to a condition in the data known as overdispersion (Anderson *et al.* 1994). Given what is known about the biology of Atlantic Puffin (Harris 1984, Lowther *et al.* 2002) and other members of the Family Alcidae (Nettleship and Birkhead 1985, Gaston and Jones 1998), we did not expect 'dependence' to be an issue with our data. However, heterogeneity in detection and movement probabilities due to aspects of our study design (e.g., varying band colors among islands), not accounting for 'memory' in our data, and other sources (e.g., unaccounted heterogeneity from band wear) could produce overdispersion.

In the absence of an estimate of $\hat{c}$, we applied $\hat{c}$ values of 2.0 and 4.0 in order to determine how much, if any, our inference would have changed if an overdispersion adjustment had been made. Important differences were: weakened support for the colony size covariate, strata effects and the full age structure (3_5, >=6) in survival probabilities; and increased support for the effort^2 effect fitted to encounter probabilities. Below we incorporate the uncertainty detected here into our inference concerning the importance of effects fitted to our survival probabilities. Although some uncertainty was detected in the ND set, inference below concerning encounter, PBM, and ND should be robust to even severe ($\hat{c}$ = 4.0) amounts of overdispersion in our data.

3.6.2 Encounter Effects and Probabilities

Accounting for major factors that contribute to the encounter process (e.g., time, age, effort) has been a primary focus in the development of CMR models (White *et al.* 1982, Lebreton *et al.* 1992). However, as demonstrated by recent publications (e.g., Holl *et al.* 2004, Lin and Batzli 2004), some wildlife biologists remain unconvinced that the process of detecting an animal contributes critical structure to their data. Validity of these studies often hinges on the assumption that detection probabilities are constant across space and time. With data available from twenty-four years and four islands, our study provided a rare opportunity to test for spatio-temporal variability in encounter probabilities: results identified strong temporal, 0.10-0.95, and spatial, MR (0.73), SI (0.94), PM (0.55), MSI (0.40), variation; the latter are arithmetic means before bands begin to wear. These results emphasize why it is wrong to assume spatio-

temporal variation in encounter probabilities is negligible when estimating demographic parameters.

Strong support for the effect of resighting effort on detection probabilities demonstrates the importance of carefully budgeting banding and reencounter components of CMR studies. Further, our data were too sparse to support a high-dimensional time-dependent encounter model; without the effort covariate, a CMR analysis with our data would likely not have been possible.

Tag loss and wear is a recurring problem in mark-encounter studies causing heterogeneity and is a major source of bias in estimates (Arnason and Mills 1981, Pollock *et al.* 1990); therefore, knowledge of the presence and process of wear and ways to avoid potential biases will be valuable for future CMR studies. Breton *et al.* (2005) show that plastic field-readable bands applied to adult (breeding) puffins in our region wore rapidly from abrasion against island bedrock and rock piles. To avoid heterogeneity due to band wear, Breton *et al.* (2005) used double-banded adults monitored intensively at two small puffin colonies; as plastic bands wore out, bias was avoided by resighting the less readable but more durable federal band. In the present study, bias may or may not have been avoided (see below) by removing birds from the sample eight years after initial marking, prior to the onset of severe wear; and by fitting encounter probabilities to a declining age trend to account for a decline in band readability from surface wear.

Although these *ad hoc* solutions may have removed or reduced negative effects due to band wear and loss, researchers should keep in mind that rigorous

quantitative solutions are also available, such as modeling a band loss rate along with other parameters (Spendelow *et al.* 1995) or including individual states, such as presence or absence of a highly visible marker, in multi-state models (Conn *et al.* 2004). Application of these solutions often requires a large dataset and/or ancillary data, which were both unavailable in our study. We recommend that investigators become familiar with the requirements of these solutions prior to initiating CMR studies.

3.6.3   Apparent Survival Effects and Probabilities

As K-selected species (MacArthur and Wilson 1967), puffins and many other marine birds are expected to maintain their populations near carrying capacity through density-dependent mechanisms; but evidence to support this view is sparse (Wooller *et al.* 1992). Under the assumption of no ($\hat{c} = 1.0$) and moderate ($\hat{c} = 2.0$) heterogeneity in our data, and using colony size as an index of density, we detected a biologically important, negative, density-dependent response in survival probabilities. Although under the assumption of severe heterogeneity ($\hat{c} = 4.0$) support for this result declined, we suspect that this assumption was unrealistic for our data; and instead favor the assumption of moderate heterogeneity. Similarly, colony effects suggest individuals from the smallest, rather than the largest, colony experienced the highest mortality. However, our index of density, colony size, did not account for the amount of available breeding habitat. This resource is extremely limited on Petit Manan (Anderson and Devlin 1999) relative to the other three sites (Breton *et al.* 2005 and references therein). Given this, if a true measure of density had been

available, PM may have ranked close to the crowded MSI colony (Diamond and Devlin 2003).

Given the strong support for both the colony size covariate and colony effects, we feel confident that a biologically important colony effect in survival, from density or some other factor(s), contributed to the survival process measured by our data. However, considering complicating factors, including those described above and the important limitation imposed by measuring survival at three small and one relatively large colony (MSI), we recommend that the inverse association between density and survival be regarded as only an exploratory result; and that inference beyond this be reserved for a meta-analysis.

It is often assumed by managers that the fates of discrete breeding colonies are independent; this view, however, may be biased from an abundance of single local population research and few multi-site studies. Breton *et al.* (2005) did not detect a biologically important difference in adult survival between two colonies. However, their sample included only 148 individuals, and support for the colony effect on survival in their models was equivocal. In the present study, which included a larger sample and 24 years of data from four islands, support for a colony effect was again equivocal, but this time the evidence favored a biologically important difference.

Considering that important mortality in alcids has often been shown to be a winter phenomenon (Harris 1984, Hudson 1985, Gaston and Jones 1998), knowledge of shared demographic characteristics derived from simultaneously monitoring multiple sites may be critical for making reliable management

decisions; further, reliable decision-making for other long-lived migratory species may require the same insights. For these reasons, we have emphasized in our research the need to identify shared characteristics, if any, among local populations. However, combined results from this study and Breton *et al.* (2005) demonstrate how difficult it will be to achieve this important insight.

It is generally thought that in long-lived organisms, survival is age-dependent, especially between sub-adults and potential breeders (Lack 1954, Ricklefs 1973, Hudson 1985, Dobson 1990, Sibley *et al.* 1997, Gaillard *et al.* 1998, Loison *et al.* 1999). After accounting for nearly all dispersers, using multiple sites within a metapopulation, and site-specific encounter probabilities, we found strong evidence for an age effect on survival. The largest mortality occurred in the first few years and likely, as shown by many seabird studies (Hudson 1985, Gaston and Jones 1998), in the first fall-winter-spring period of life. Thereafter, survival increased steadily to age 6 years, but fell far short of the range of estimates typical for adult Atlantic Puffins and other long-lived seabirds, ca. 0.92-0.98 (Breton *et al.* 2005 and references therein). Failure to reach a high survival rate near age of first breeding (typically age 4-5; Harris 1984) contrasts with many mammal (Sibley *et al.* 1997, Loison *et al.* 1999) and bird (Ricklefs 1973, Wooller *et al.* 1992, Harris *et al.* 1997, Harris *et al.* 2000) studies across diverse taxa which report high survival of breeding adults maintained over several years.

Low adult survival probabilities could be due to band loss or illegibility from band wear; an analysis of surface wear accumulated on our plastic bands

suggests that severe band wear may have been prevalent enough in adult cohorts to produce these problems (Breton *et al.* in review). Alternatively, high adult survival observed in many studies of long-lived seabirds may, due to sampling design, be consistent with only the breeding segment of the population; typically, it is the latter that is sampled to measure adult survival (see summaries in Spendelow and Nichols 1989, Croxall and Rothery 1991, Jouventin and Weimerskirch 1991, Harris *et al.* 2000, and Breton *et al.* 2005). In contrast, and consistent with our results, the non-breeder segment of the adult population, which is typically excluded from such studies, may be experiencing much lower survival. Consequently, (1) adult survival estimates would be misleading (too low for some, too high for others) and (2) a small number of adults would be responsible for producing the majority of the next generation. The latter point is consistent with many bird studies including long-lived seabirds (Newton 1995). In summary, we do not know whether high adult mortality was a function of failing bands or actual losses of birds in our study.

3.6.4   Movement Effects and Probabilities.

Coulson (1991) identified studies of dispersal as the "most neglected aspect of avian demography"; and these comments certainly apply to studies of PBM as well. Since then, few studies have contributed real-life insights into these demographic processes (Brownie *et al.* 1993, Walters 2000, Lebreton *et al.* 2003). Our results move towards a better understanding of ND and PBM and provide rare estimates of these parameters. As in previous studies (Harris 1983, Kress and Nettleship 1988), we found that the prevalence of non-movers increased with

increasing age. In addition, we were able to demonstrate that the proportion of non-movers increased simultaneously at four sites and exceeded 92% between ages 6-7.

Whether or not philopatry is strong or varies much represents an old and unresolved issue in ornithology (Greenwood and Harvey 1982; Wooller *et al.* 1992, Weimerskirch 2002). Origin and destination colony achieved strong AIC_c support suggesting characteristics of both factors are important predictors of movement, and hence philopatry. Similarly, age 0-3 estimates for movers varied from about 10-52% (MSI, PM); and as few as 8% (MSI) and as many as 57% (PM) of the puffins we marked bred away from their natal colony. Strong variation in ND and age 0-3 PBM summarized here show without doubt that philopatry varied considerably across the local populations we sampled.

As predicted by the conspecific attraction hypothesis discussed by Serrano and Tella (2003), birds marked on (age 0-3) or arriving to (all other ages) the two smallest islands were more likely to shift colonies than those marked on or arriving to MR and MSI. And with the exception of the rapidly expanding SI colony (Kress 1997, SWK unpubl. data), natal recruitment (1-ND) probabilities increased as a function of colony size. These results suggest that birds arriving or being born at large colonies (MR, MSI) were more likely to remain there relative to those arriving or being born at small colonies (SI, PM). However, as Cam *et al.* (2004) point out, the source-sink hypothesis proposed by Pulliam (1988) may also result in a negative relationship between movement and colony size. Future

investigators will need to plan carefully in order to isolate evidence for these competing hypotheses.

3.6.5 Consequence of Natal Dispersal Probabilities for Genetic Mixing

It is important to recognize, especially for genetic mixing, that ND probabilities reported here do not reflect numbers of dispersing individuals; the number dispersing is a function of both the probability of moving from a particular island and the number of individuals that survive to age five years. Consequently, a low probability of ND away from MSI, by far the largest colony and producer of young in our study, sends out more young than the small SI and PM colonies and possibly MR even though the latter all demonstrated much higher dispersal probabilities. In summary, movement probabilities and factors tell us something about processes of ND and PBM; colony size together with probabilities provide an estimate of the contribution of young among islands, which has considerable genetic as well as purely demographic consequences.

3.6.6 Local Population Dynamics

Traditionally, the contributions of dispersal and short-term exploratory movements, here measured as PBM, to population dynamics were generally thought to be unimportant (Lidicker 1975). The predominance of single local population research in the last twenty years suggests the traditional view is still generally held or is maintained due to the difficulties of measuring movement between local populations. In our study, strong colony-dependent variation in movement probabilities identifies ND and PBM as key parameters affecting numbers of individuals at each colony. This important result has been replicated

in all other multi-site studies of birds known to us (Hestbeck *et al.* 1991,

Spendelow *et al.* 1995, Lindberg *et al.* 1998, Grosbois and Tavecchia 2003,

Lebreton *et al.* 2003, Cam *et al.* 2004, Oro *et al.* 2004). Many years ago a

minority of authors, including Andrewartha and Birch (1954) and Lidicker (1975)

challenged the traditional view by predicting that dispersal would be elevated to

vital status in future studies. Recent multi-site CMR studies are providing strong

support for these predictions; consequently, the validity of studies monitoring a

single local population to estimate demographic parameters is surely suspect.

3.6.7   <u>Additional Suggestions for Improving on our Multi-strata Study Design</u>

Our use of different band color schemes on islands could cause bias in our

encounter and survival probabilities by introducing differences in observability

and wear rates respectively. To avoid these potential problems, we suggest a

generic metal-type field readable band for all islands or groups in multi-site mark-

encounter studies; generic features of these bands should include non-group-

specific characters. We do not recommend plastic bands due to their high

susceptibility to wear (Breton *et al.* in review).

Our use of location at last sighting results in a loss of information about

movement and survival processes for animals that visited more than one site

within a summer (see also Spendelow *et al.* 1995). Also, multiple transitions

between occasions violate an implicit assumption of multi-strata models: all

transitions take place at the end of the survival interval. We know of no solution

to account adequately for these problems but expect an extension of current multi-

strata models will be required.

Given the duration of our study and high rate of observer turnover, we were reluctant to remove suspicious sightings, including birds seen one time after an absence of five or more years. However, the cost was likely inclusion of a small percentage of sightings that were not in fact 'data', i.e., information that is consistent with the process under study (Romesburg 1981, Anderson 2001); in this case, misread bands. Studies like ours that require observers to read engraved marks from a distance should consider a screening method to reduce numbers of erroneous sightings. Solutions include requiring two or three sightings of each animal or alternatively, including only sightings made by more than one observer.

Sparse data on SI and PM and for early cohorts on MSI and MR required that we treat all colony-year cohorts as one age-specific cohort per colony. The obvious solution is to mark an adequate number of chicks on each occasion. However, for small local populations, like EER and PM, with ca. 50 and 25 breeding pairs in 2003 respectively, a large sample is not possible (Pollock *et al.* 1990). Researchers interested in investigating processes occurring across multiple sites should carefully consider the sample potential of prospective study species and their local populations.

Our approach to estimating ND probabilities required removal of all parameters between release and age five years and loss of information about dispersers that were not seen at age five. Ideally, we would have used an alternative modeling strategy, proposed by Lebreton *et al.* (2003), which allows state as well as strata transitions to be modeled (see also Conn *et al.* 2004). However, the small numbers of releases described above could not support the

high dimensional models this solution requires. Investigators planning dispersal studies should attempt to meet the minimum data requirements of this rigorous method (Lebreton *et al.* 2003).

Few approaches are available for assessing the goodness-of-fit of many types of capture-mark-recapture models, including the multistrata models used in this study (Lebreton *et al.* 2003). And the few options that exist are often limited in their ability to assess fit to a few pre-defined models, rather than the global model for a particular study. Until significant progress can be made in these areas, investigators will have to rely, as we've done here, on careful *a priori* selection of candidate predictor variables and models (see excellent discussion in Burnham and Anderson 2002: pages 15-19) in place of formal GOF testing. A comparison of estimates from other studies, such as our use of estimates from Harris (1983), might also contribute valuable evidence for assessing fit. If these alternatives can be carefully applied, and confirmatory inference is reserved for meta-analyses rather than individual studies, we suspect that the importance of formal GOF testing may decline or even become unnecessary.

3.6.8   Conclusion

Our study contributes to accumulating insights into local population dynamics within metapopulations and highlights ways of improving the inferential quality of future CMR multi-site studies. Twenty-four years of CMR data from four colonies revealed strong age variation in survival and uncertain support for a colony effect from density or some other factor. Consistent with colony growth and expansion during the study period, immature survival was

apparently extremely high. In contrast, our estimates of adult survival were anomalously low, suggesting a bias due to combining breeding and non-breeding adults in our sample or failure of plastic leg bands. Our estimates of movement show that philopatry varied considerably among islands; and that PBM declines as a function of increasing age. Support for the colony size constraint on movement probabilities provides evidence that PBM and ND varied inversely with colony size. By estimating survival and two sources of movement simultaneously, we were able to determine the relative contribution of these parameters to local population dynamics: our results suggest movement plays a much larger role in modifying numbers than established theory would predict. Based on our results and others (Hestbeck *et al.* 1991, Spendelow *et al.* 1995, Lindberg *et al.* 1998, Grosbois and Tavecchia 2003, Lebreton *et al.* 2003, Cam *et al.* 2004, Oro *et al.* 2004), we recommend long-term regional scale CMR studies involving simultaneous data collection at several local populations in place of the norm in population research (short-term and single site) to estimate parameters accurately and identify factors driving local population dynamics in long-lived animal species. Otherwise, inference is likely to be misled by many biases, especially unaccounted-for sources of movement among sites.

3.7   Acknowledgments

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Table 3.1. Colony- and time-specific numbers of Atlantic Puffin (*Fratercula arctica*) chicks banded with individually engraved plastic field-readable and federal leg bands (opposite tarsi) at all study sites from 1980 – 2003.

	Chicks Banded					Chicks Banded			
Year	MR	SI	PM	MSI	Year	MR	SI	PM	MSI
1980	0	NA	NA	56	1993	37	4	6	17
1981	0	NA	NA	18	1994	50	2	6	85
1982	0	NA	NA	0	1995	53	6	6	121
1983	0	NA	NA	68	1996	35	4	5	296
1984	0	NA	NA	69	1997	49	10	4	0
1985	0	NA	NA	0	1998	77	14	13	0
1986	13	NA	0	0	1999	56	0	0	0
1987	17	NA	2	0	2000	69	0	0	0
1988	14	NA	0	116	2001	NI	0	0	0
1989	10	NA	0	134	2002	NI	0	0	0
1990	30	NA	0	192	2003	NI	0	0	0
1991	24	NA	0	137	**Totals:**	**562**	**42**	**46**	**1400**
1992	28	2	4	91					

Notes: Because most birds do not return to colonies until age three years, chicks receiving plastic field-readable bands between 2001-2003 (if any) are not included (NI) in our analysis. SI and PM were recolonized and colonized in 1992 and 1986 respectively (NA = not active).

Table 3.2. Encounter (p) model set ($\hat{c} = 1.0$) including selection criterion and number of parameters (#Par) for each model A_{en}-Q_{en} referred to in the text.

Models		AIC_c	ΔAIC_c	Akaike Weight	#Par	Model Deviance
A_{en}	$p^s_{trend+effort+s*effort}$	13024.57	0.00	0.684	27	4794.28
B_{en}	$p^s_{trend+effort+effort^2+s*effort}$	13026.58	2.01	0.250	28	4794.26
C_{en}	$p^s_{trend+effort+effort^2}$	13029.52	4.95	0.057	25	4803.28
D_{en}	$p^s_{age3\_8+effort+effort^2}$	13033.35	8.78	0.008	29	4799.00
E_{en}	$p_{trend+effort+effort^2}$	13054.08	29.51	0.000	22	4833.91
F_{en}	$p^s_{effort+s*effort}$	13058.85	34.28	0.000	26	4830.59
G_{en}	$p^s_{effort+effort^2}$	13060.12	35.55	0.000	24	4835.90
H_{en}	$p^s_{effort+effort^2+s*effort}$	13060.69	36.10	0.000	27	4830.38
I_{en}	$p^s_{trend+effort}$	13063.18	38.61	0.000	24	4838.96
J_{en}	$p_{effort+effort^2}$	13084.77	60.20	0.000	21	4866.62
K_{en}	p^s_{effort}	13087.74	63.17	0.000	23	4865.54
L_{en}	$p_{trend+effort}$	13093.45	68.88	0.000	21	4875.29
M_{en}	p_{effort}	13118.41	93.84	0.000	20	4902.27
N_{en}	p^s_{trend}	13166.21	141.64	0.000	23	4944.02
O_{en}	p^s	13178.06	153.49	0.000	22	4957.88
P_{en}	$p_{(.)}$	13515.99	491.42	0.000	19	5301.87
Q_{en}	p_{trend}	13517.70	493.13	0.000	20	5301.56

Notes: Models are ordered ascending by AIC_c and model D_{en} is the global model for this set; pre-breeding movement and survival structure in all models: $\psi^{rs}_{age3\_8}$, $\phi^r_{age3\_5,\geq6}$.

Table 3.3. Estimates of model effect sizes ($\hat{\beta}_i$) with $\hat{S}Es$, 95% $\hat{C}Is$, and references, where appropriate, for effects referred to in the text; estimates are on the logit scale.

Model†	Par‡	Effect	Reference Island, Age	Effect Size ($\hat{\beta}_i$)	$\hat{S}E$	95% $\hat{C}I$ Lower	Upper
A_{en}	En	MSI	MR	-1.0660	0.2559	-0.5645	-1.5674
A_{en}	En	PM	MR	-0.3901	0.4665	-1.3045	0.5243
A_{en}	En	SI	MR	3.3968	1.2732	0.9013	5.8923
A_{en}	En	Declining Trend		0.4151	0.0631	0.2913	0.5388
A_{en}	En	Resighting Effort		1.5276	0.2563	1.0252	2.0299
A_{en}	En	MSI*Effort	MR	1.1530	0.3834	0.4015	1.9044
A_{en}	En	PM*Effort	MR	8.4469	3.1061	2.3589	14.5349
A_{en}	En	SI*Effort	MR	-1.6612	0.5179	-0.6462	-2.6763
B_{en}	En	Effort^2		-0.0972	0.8077	-1.6804	1.4859
B_{en}	En	Resighting Effort		1.7122	1.5562	-1.3379	4.7623
C_{en}	En	Effort^2		-0.6808	0.1150	-0.4553	-0.9062
A_s	S	MSI	MR	-0.3344	0.0974	-0.1435	-0.5252
A_s	S	PM	MR	-0.6020	0.2492	-0.1137	-1.0904
A_s	S	SI	MR	-0.1155	0.1756	-0.4597	0.2288
A_s	S	Age 4	0-3	0.3496	0.1679	0.0205	0.6788
A_s	S	Age 5	0-3	0.5345	0.1749	0.1916	0.8773
A_s	S	Age ≥6	0-3	0.7578	0.2204	0.3259	1.1898
B_s	S	Origin Colony Size		-1.0142	0.3420	-0.3439	-1.6846
A_{pbm}	PBM	Origin Colony, MSI	MR	-1.3262	0.1428	-1.0464	-1.6061
A_{pbm}	PBM	Origin Colony, PM	MR	0.5229	0.1986	0.1336	0.9121
A_{pbm}	PBM	Origin Colony, SI	MR	0.4395	0.1949	0.0575	0.8216
A_{pbm}	PBM	Destination Colony, PM	SI	-1.3089	0.2091	-0.8992	-1.7187
A_{pbm}	PBM	Destination Colony, MSI	SI	-1.1548	0.2045	-0.7539	-1.5557
A_{pbm}	PBM	Destination Colony, MR	SI	0.1451	0.1565	-0.1616	0.4518
A_{pbm}	PBM	Declining Trend		-0.4925	0.0527	-0.3891	-0.5958
B_{pbm}	PBM	Age 4	0-3	-0.2560	0.1234	-0.0142	-0.4978
B_{pbm}	PBM	Age 5	0-3	-0.8998	0.1767	-0.5535	-1.2460
B_{pbm}	PBM	Age 6	0-3	-1.5467	0.2752	-1.0073	-2.0861
B_{pbm}	PBM	Age 7	0-3	-2.3248	0.4816	-1.3808	-3.2688
C_{pbm}	S	Origin Colony Size		-1.0193	0.3425	-0.3481	-1.6906

D_{pbm}	PBM	Origin Colony Size		-5.9168	0.4683	-4.9989	-6.8347
A_{nd}	ND	Origin Colony, MSI	MR	-1.7352	0.2521	-1.2412	-2.2293
A_{nd}	ND	Origin Colony, PM	MR	0.8000	0.3646	0.0853	1.5147
A_{nd}	ND	Origin Colony, SI	MR	Fixed = 0			
A_{nd}	ND	Destination Colony, MR	SI	-0.2314	0.3156	-0.8500	0.3871
A_{nd}	ND	Destination Colony, PM	SI	-1.5430	0.3749	-0.8081	-2.2778
A_{nd}	ND	Destination Colony, MSI	SI	-3.7511	1.0211	-1.7499	-5.7524
B_{nd}	ND	Origin Colony Size		-7.5203	0.9428	-5.6724	-9.3682

† See Tables 3.2 (En), 3.4 (S), 3.5 (PBM), and 3.10 (ND)

‡ Identifies the parameter (par) where the constraint (effect) was applied: En = encounter, S = survival, PBM = pre-breeding movement, ND = natal dispersal

Table 3.4. Apparent survival (ϕ) model set ($\hat{c} = 1.0$) including selection criterion and number of parameters (#Par) for each model A$_s$-G$_s$ referred to in the text.

Models		AIC$_c$	Δ AIC$_c$	Akaike Weight	#Par	Model Deviance
A$_s$	$\phi^r_{age3\_5,\geq6}$	13024.57	0.00	0.684	27	4794.28
B$_s$	$\phi_{origin\ colony\ size+age3\_5,\geq6}$	13026.31	1.74	0.287	25	4800.06
C$_s$	$\phi_{age3\_4,\geq5}$	13032.52	7.95	0.013	23	4810.32
D$_s$	$\phi_{age3\_5,\geq6}$	13032.97	8.40	0.010	24	4808.75
E$_s$	$\phi_{age3,\geq4}$	13034.11	9.54	0.006	22	4813.94
F$_s$	ϕ^r	13038.72	14.15	0.001	24	4814.5
G$_s$	$\phi_{(.)}$	13053.74	29.17	0.000	21	4835.58

Notes: Models are ordered ascending by AIC$_c$ and model B$_s$ is the global model for this set; model B$_s$ is the same as model A$_{en}$ in Table 3.2; pre-breeding movement and encounter structure in all models: $\psi^{rs}_{age3\_8}$, $p^s_{trend+effort+s*effort}$.

Table 3.5. Pre-breeding movement (ψ) model set ($\hat{c} = 1.0$) including selection criterion and number of parameters (#Par) for each model A_{pbm}-N_{pbm} referred to in the text.

Model		AIC_c	Δ AIC_c	Akaike Weight	#Par	Model Deviance
A_{pbm}	ψ^{rs}_{trend}	13023.48	0.00	0.385	24	4799.26
B_{pbm}	$\psi^{rs}_{age3\_8}$	13024.57	1.09	0.224	27	4794.28
C_{pbm}	$\psi^{rs}_{trend} \phi_{origin\ colony\ size+age3\_5,\geq6}$	13024.69	1.20	0.211	22	4804.51
D_{pbm}	$\psi^{s}_{origin\ colony\ size+age3\_8}$	13025.00	1.51	0.181	25	4798.76
E_{pbm}	$\psi^{s}_{distance+age3\_8}$	13046.72	23.23	0.000	25	4820.47
F_{pbm}	$\psi^{r}_{destination\ colony\ size+age3\_8}$	13068.89	45.40	0.000	25	4842.64
G_{pbm}	$\psi^{r}_{age3\_8}$	13097.08	73.59	0.000	24	4872.86
H_{pbm}	ψ^{rs}	13130.57	107.09	0.000	23	4908.37
I_{pbm}	$\psi^{s}_{age3\_8}$	13181.04	157.55	0.000	24	4956.82
J_{pbm}	ψ^{r}	13189.32	165.83	0.000	20	4973.18
K_{pbm}	ψ_{trend}	13221.16	197.67	0.000	18	5009.06
L_{pbm}	ψ_{age3_8}	13222.00	198.52	0.000	21	5003.85
M_{pbm}	ψ^{s}	13273.16	249.68	0.000	20	5057.03
N_{pbm}	$\psi_{(.)}$	13304.02	280.54	0.000	17	5093.94

Notes: Models are ordered ascending by AIC_c and model B_{pbm} is the global model for this set; model B_{pbm} is the same as model A_s in Table 3.4; survival and encounter structure unless otherwise written: $\phi^{r}_{age3\_5,\geq6}$, $p^{s}_{trend+effort+s*effort}$.

Table 3.6. Model averaged year-, colony-, and age of band specific encounter

probabilities $\pm 1\ \hat{S}E$ from the full PBM model set (Table 3.5).

		Years Since Band Applied					Years Since Band Applied			
Col†	Year	3-5	6	7	8	Col†	3-5	6	7	8
MR	1983	0.93 (0.02)				PM	Fixed = 0.0			
MR	1984	0.89 (0.02)				PM	Fixed = 0.0			
MR	1985	0.85 (0.02)				PM	Fixed = 0.0			
MR	1986	0.75 (0.02)	0.67 (0.02)			PM	Fixed = 0.0			
MR	1987	0.65 (0.02)	0.55 (0.03)	0.44 (0.04)		PM	0.58 (0.08)	0.48 (0.08)	0.38 (0.08)	
MR	1988	0.59 (0.03)	0.48 (0.03)	0.38 (0.04)	0.29 (0.04)	PM	Fixed = 0.0			
MR	1989	0.64 (0.03)	0.54 (0.03)	0.43 (0.04)	0.33 (0.04)	PM	0.38 (0.08)	0.29 (0.07)	0.21 (0.06)	0.15 (0.05)
MR	1990	0.68 (0.02)	0.58 (0.02)	0.48 (0.03)	0.38 (0.04)	PM	0.92 (0.06)	0.88 (0.08)	0.83 (0.11)	0.77 (0.14)
MR	1991	0.65 (0.02)	0.56 (0.03)	0.45 (0.04)	0.35 (0.04)	PM	0.74 (0.08)	0.65 (0.10)	0.55 (0.11)	0.45 (0.12)
MR	1992	0.70 (0.02)	0.60 (0.02)	0.50 (0.03)	0.40 (0.05)	PM	0.79 (0.08)	0.71 (0.10)	0.62 (0.12)	0.52 (0.13)
MR	1993	0.67 (0.02)	0.57 (0.03)	0.47 (0.03)	0.37 (0.04)	PM	0.79 (0.08)	0.71 (0.10)	0.62 (0.12)	0.52 (0.13)
MR	1994	0.68 (0.02)	0.58 (0.02)	0.48 (0.03)	0.38 (0.04)	PM	0.34 (0.09)	0.25 (0.07)	0.18 (0.06)	0.13 (0.05)
MR	1995	0.81 (0.02)	0.74 (0.03)	0.65 (0.04)	0.55 (0.05)	PM	0.34 (0.09)	0.25 (0.07)	0.18 (0.06)	0.13 (0.05)
MR	1996	0.62 (0.03)	0.51 (0.03)	0.41 (0.04)	0.31 (0.04)	PM	0.38 (0.08)	0.29 (0.07)	0.21 (0.06)	0.15 (0.05)
MR	1997	0.80 (0.02)	0.72 (0.02)	0.63 (0.04)	0.53 (0.05)	PM	0.38 (0.08)	0.29 (0.07)	0.21 (0.06)	0.15 (0.05)
MR	1998	0.72 (0.02)	0.63 (0.02)	0.53 (0.03)	0.43 (0.05)	PM	0.43 (0.08)	0.34 (0.07)	0.25 (0.07)	0.18 (0.06)
MR	1999	0.74 (0.02)	0.65 (0.02)	0.56 (0.03)	0.45 (0.05)	PM	0.34 (0.09)	0.25 (0.07)	0.18 (0.06)	0.13 (0.05)
MR	2000	0.66 (0.02)	0.56 (0.03)	0.46 (0.04)	0.36 (0.04)	PM	0.61 (0.08)	0.50 (0.08)	0.40 (0.08)	0.31 (0.08)
MR	2001	0.89 (0.02)	0.84 (0.03)	0.77 (0.04)	0.69 (0.06)	PM	0.53 (0.08)	0.43 (0.08)	0.33 (0.07)	0.25 (0.07)
MR	2002	0.80 (0.02)	0.73 (0.02)	0.64 (0.04)	0.54 (0.05)	PM	0.91 (0.06)	0.87 (0.08)	0.82 (0.11)	0.75 (0.15)
MR	2003	0.65 (0.02)	0.56 (0.03)	0.45 (0.04)	0.35 (0.04)	PM	0.56 (0.08)	0.45 (0.08)	0.35 (0.08)	0.27 (0.07)
SI	1983	Fixed = 0.0				MSI	0.32 (0.02)			
SI	1984	Fixed = 0.0				MSI	0.31 (0.02)			
SI	1985	Fixed = 0.0				MSI	0.27 (0.02)			
SI	1986	Fixed = 0.0				MSI	0.24 (0.02)	0.17 (0.02)		
SI	1987	Fixed = 0.0				MSI	Fixed = 0.0			
SI	1988	Fixed = 0.0				MSI	0.36 (0.02)	0.27 (0.02)	0.20 (0.02)	0.14 (0.02)
SI	1989	Fixed = 0.0				MSI	0.39 (0.02)	0.30 (0.02)	0.22 (0.02)	0.16 (0.02)
SI	1990	Fixed = 0.0				MSI	0.37 (0.02)	0.28 (0.02)	0.20 (0.02)	0.15 (0.02)
SI	1991	Fixed = 0.0				MSI	0.40 (0.02)	0.30 (0.02)	0.22 (0.02)	0.16 (0.03)
SI	1992	0.95 (0.03)	0.92 (0.04)	0.88 (0.06)	0.83 (0.08)	MSI	0.38 (0.02)	0.29 (0.02)	0.21 (0.02)	0.15 (0.02)
SI	1993	0.95 (0.04)	0.93 (0.06)	0.90 (0.09)	0.85 (0.13)	MSI	0.31 (0.02)	0.23 (0.02)	0.16 (0.02)	0.11 (0.02)
SI	1994	0.94 (0.02)	0.91 (0.02)	0.87 (0.03)	0.82 (0.05)	MSI	0.48 (0.02)	0.37 (0.02)	0.28 (0.03)	0.21 (0.03)
SI	1995	0.94 (0.02)	0.91 (0.02)	0.87 (0.03)	0.82 (0.05)	MSI	0.44 (0.02)	0.34 (0.02)	0.25 (0.02)	0.18 (0.03)
SI	1996	0.94 (0.02)	0.92 (0.03)	0.88 (0.04)	0.82 (0.05)	MSI	0.37 (0.02)	0.28 (0.02)	0.20 (0.02)	0.14 (0.02)
SI	1997	0.94 (0.02)	0.91 (0.03)	0.88 (0.04)	0.82 (0.05)	MSI	Fixed = 0.0			
SI	1998	0.94 (0.02)	0.92 (0.03)	0.88 (0.04)	0.83 (0.06)	MSI	0.29 (0.02)	0.22 (0.02)	0.15 (0.02)	0.11 (0.02)
SI	1999	0.94 (0.02)	0.92 (0.03)	0.88 (0.05)	0.83 (0.06)	MSI	0.40 (0.02)	0.30 (0.02)	0.22 (0.02)	0.16 (0.03)
SI	2000	0.94 (0.02)	0.91 (0.03)	0.86 (0.04)	0.81 (0.06)	MSI	0.37 (0.02)	0.28 (0.02)	0.20 (0.02)	0.14 (0.02)
SI	2001	0.94 (0.02)	0.91 (0.02)	0.87 (0.03)	0.82 (0.05)	MSI	0.66 (0.03)	0.57 (0.03)	0.46 (0.04)	0.36 (0.05)

| SI | 2002 | 0.94 (0.02) | 0.91 (0.03) | 0.87 (0.04) | 0.81 (0.05) | MSI | 0.62 (0.03) | 0.52 (0.03) | 0.42 (0.04) | 0.32 (0.04) |
| SI | 2003 | 0.95 (0.03) | 0.92 (0.05) | 0.89 (0.07) | 0.84 (0.09) | MSI | 0.54 (0.02) | 0.43 (0.02) | 0.33 (0.03) | 0.25 (0.04) |

Notes: Resighting effort in pre-colonization years 1980-1989 and 1980-1985 on

Seal Island and Petit Manan respectively were fixed to zero. Remaining years

labeled as 'fixed': data lost; not collected or zero.

† Col = colony: MR = Matinicus Rock, SI = Seal Island, PM = Petit Manan, and

MSI = Machias Seal Island.

Table 3.7. Model averaged age- and colony-specific apparent survival probabilities with $\hat{S}Es$ and 95% $\hat{C}Is$; arithmetic means for 'all' islands are also provided.

Age	Island	Estimate	±$\hat{S}E$	95% $\hat{C}I$ Lower	Upper
0-3	MR	0.7531	0.0200	0.7118	0.7903
4	MR	0.8129	0.0211	0.7679	0.8508
5	MR	0.8383	0.0226	0.7889	0.8779
6, 7, 8	MR	0.8665	0.0241	0.8120	0.9071
0-3	SI	0.7369	0.0329	0.6676	0.7962
4	SI	0.7995	0.0285	0.7380	0.8496
5	SI	0.8264	0.0283	0.7639	0.8751
6, 7, 8	SI	0.8564	0.0261	0.7974	0.9003
0-3	PM	0.6565	0.0683	0.5136	0.7757
4	PM	0.7307	0.0620	0.5941	0.8341
5	PM	0.7638	0.0600	0.6275	0.8613
6, 7, 8	PM	0.8018	0.0558	0.6701	0.8896
0-3	MSI	0.6895	0.0189	0.6514	0.7253
4	MSI	0.7597	0.0234	0.7110	0.8025
5	MSI	0.7906	0.0255	0.7363	0.8362
6, 7, 8	MSI	0.8254	0.0298	0.7591	0.8764
0-3	**All**	0.7090	-	-	-
4	**All**	0.7757	-	-	-
5	**All**	0.8048	-	-	-
6, 7, 8	**All**	0.8375	-	-	-

Table 3.8. Model averaged age- and transition-specific pre-breeding movement probabilities with ŜEs and 95% ĈIs from the full PBM model set (Table 3.5).

Age	Transition (km)	Estimate	±ŜE	95% ĈI Lower	95% ĈI Upper	Transition (km)	Estimate	±ŜE	95% ĈI Lower	95% ĈI Upper
0-3	B to B†	0.7671	0.0197	0.7286	0.8056	D to B (102)	0.2365	0.0363	0.1728	0.3147
3-4	B to B	0.8369	0.0185	0.8007	0.8731	D to B	0.1727	0.0287	0.1235	0.2363
4-5	B to B	0.9035	0.0127	0.8786	0.9284	D to B	0.1072	0.0207	0.0728	0.1551
5-6	B to B	0.9434	0.0111	0.9217	0.9651	D to B	0.0648	0.0165	0.0391	0.1058
6-7	B to B	0.9682	0.0103	0.9481	0.9883	D to B	0.0370	0.0142	0.0174	0.0773
0-3	B to C (15)	0.1411	0.0133	0.1170	0.1694	D to C (87)	0.2071	0.0360	0.1453	0.2864
3-4	B to C	0.1001	0.0136	0.0763	0.1302	D to C	0.1494	0.0261	0.1051	0.2080
4-5	B to C	0.0599	0.0083	0.0456	0.0784	D to C	0.0919	0.0190	0.0608	0.1365
5-6	B to C	0.0354	0.0070	0.0239	0.0521	D to C	0.0553	0.0148	0.0325	0.0927
6-7	B to C	0.0199	0.0066	0.0104	0.0377	D to C	0.0316	0.0125	0.0145	0.0675
0-3	B to D (102)	0.0425	0.0082	0.0290	0.0617	D to D	0.4802	0.0762	0.3309	0.6295
3-4	B to D	0.0291	0.0062	0.0191	0.0441	D to D	0.6254	0.0573	0.5131	0.7377
4-5	B to D	0.0169	0.0038	0.0109	0.0262	D to D	0.7700	0.0426	0.6866	0.8534
5-6	B to D	0.0098	0.0027	0.0045	0.0152	D to D	0.8618	0.0343	0.7945	0.9291
6-7	B to D	0.0055	0.0022	0.0012	0.0097	D to D	0.9212	0.0296	0.8633	0.9791
0-3	B to E (167)	0.0493	0.0088	0.0347	0.0695	D to E (64)	0.0762	0.0187	0.0467	0.1219
3-4	B to E	0.0339	0.0071	0.0225	0.0508	D to E	0.0525	0.0127	0.0325	0.0836
4-5	B to E	0.0197	0.0042	0.0129	0.0299	D to E	0.0309	0.0083	0.0182	0.0521
5-6	B to E	0.0114	0.0030	0.0068	0.0192	D to E	0.0181	0.0059	0.0096	0.0340
6-7	B to E	0.0064	0.0024	0.0016	0.0111	D to E	0.0102	0.0045	0.0043	0.0241
0-3	C to B (15)	0.2217	0.0309	0.1669	0.2881	E to B (167)	0.0480	0.0056	0.0381	0.0602
3-4	C to B	0.1610	0.0230	0.1208	0.2114	E to B	0.0330	0.0052	0.0242	0.0448
4-5	C to B	0.0994	0.0160	0.0722	0.1353	E to B	0.0192	0.0030	0.0141	0.0260
5-6	C to B	0.0599	0.0132	0.0387	0.0917	E to B	0.0111	0.0024	0.0073	0.0169
6-7	C to B	0.0342	0.0120	0.0170	0.0673	E to B	0.0062	0.0021	0.0020	0.0103
0-3	C to C	0.6470	0.0482	0.5525	0.7415	E to C (152)	0.0407	0.0054	0.0313	0.0527
3-4	C to C	0.7489	0.0332	0.6839	0.8139	E to C	0.0278	0.0041	0.0208	0.0370
4-5	C to C	0.8476	0.0235	0.8015	0.8937	E to C	0.0161	0.0025	0.0119	0.0219
5-6	C to C	0.9091	0.0197	0.8706	0.9476	E to C	0.0094	0.0021	0.0053	0.0134
6-7	C to C	0.9483	0.0177	0.9135	0.9831	E to C	0.0052	0.0018	0.0016	0.0088
0-3	C to D (87)	0.0609	0.0149	0.0374	0.0977	E to D (64)	0.0113	0.0024	0.0074	0.0172
3-4	C to D	0.0417	0.0094	0.0268	0.0644	E to D	0.0076	0.0016	0.0044	0.0109
4-5	C to D	0.0245	0.0061	0.0150	0.0397	E to D	0.0044	0.0010	0.0024	0.0064
5-6	C to D	0.0143	0.0044	0.0078	0.0260	E to D	0.0026	0.0007	0.0011	0.0040
6-7	C to D	0.0081	0.0034	0.0013	0.0148	E to D	0.0014	0.0006	0.0003	0.0026
0-3	C to E (152)	0.0704	0.0166	0.0440	0.1107	E to E	0.9000	0.0096	0.8811	0.9189
3-4	C to E	0.0484	0.0107	0.0312	0.0743	E to E	0.9316	0.0080	0.9159	0.9473
4-5	C to E	0.0285	0.0069	0.0176	0.0457	E to E	0.9603	0.0053	0.9499	0.9707
5-6	C to E	0.0167	0.0050	0.0093	0.0298	E to E	0.9769	0.0046	0.9679	0.9859
6-7	C to E	0.0094	0.0039	0.0017	0.0170	E to E	0.9872	0.0042	0.9789	0.9955

Notes: Distances (km) between islands are given in parentheses following transition descriptions; transition from age seven to eight (not shown) fixed to zero in all models.

† B = Matinicus Rock, C = Seal Island, D = Petit Manan, and E = Machias Seal Island; (A) was reserved for Eastern Egg Rock (islands are labeled ascending from west to east; Fig. 3.1) but this island was excluded from the CMR analysis due to small *n*.

Table 3.9. Age-specific pre-breeding movement probabilities with $\hat{S}Es$ and 95% $\hat{C}Is$ from model ψ_{trend} (K_{pbm}; Table 3.5).

Age	Transition	Estimate	$\pm\hat{S}E$	95% $\hat{C}I$ Lower	Upper
0-3	All	0.0634	0.0039	0.0561	0.0716
3-4	All	0.0427	0.0023	0.0384	0.0474
4-5	All	0.0285	0.0023	0.0244	0.0334
5-6	All	0.0190	0.0023	0.0149	0.0241
6-7	All	0.0126	0.0021	0.0090	0.0175
7-8	All	Fixed = 0.0			

Notes: Age seven to eight transition probability too small to be estimated.

Table 3.10. Natal dispersal (ψ) model set ($\hat{c} = 1.0$) including selection criterion

and number of parameters (#Par) for each model A_{nd}-G_{nd} referred to in the text.

Model	AIC$_c$	Δ AIC$_c$	Akaike Weight	#Par	Model Deviance
A_{nd} ψ^{rs}	18990.45	0.00	0.541	20	14526.85
B_{nd} $\psi^{s}_{origin\ colony\ size}$	18990.79	0.33	0.458	19	14529.22
C_{nd} $\psi^{r}_{destination\ colony\ size}$	19004.40	13.94	0.001	18	14544.85
D_{nd} $\psi^{r}_{distance}$	19006.54	16.09	0.000	18	14547.00
E_{nd} ψ^{r}	19039.87	49.41	0.000	17	14582.35
F_{nd} ψ^{s}	19059.43	68.98	0.000	18	14599.89
G_{nd} $\psi_{(.)}$	19090.30	99.85	0.000	15	14636.83

Notes: Models are ordered ascending by AIC$_c$ and model A_{nd} is the global model

for this set; survival and encounter structure in all models: $\phi^{r}_{age0\_5,\geq6}$,

$p^{s}_{trend+effort+s*effort}$.

Table 3.11. Model averaged natal dispersal probabilities with $\hat{S}Es$ and 95% $\hat{C}Is$ from the full ND set (Table 3.10).

Age	Transition (km)	Estimate	$\pm\hat{S}E$	95% $\hat{C}I$ Lower	Upper
0-5	B to B†	0.7462	0.0299	0.6956	0.8048
0-5	B to C (15)	0.1982	0.0251	0.1536	0.2519
0-5	B to D (102)	0.0499	0.0163	0.0261	0.0934
0-5	B to E (167)	0.0057	0.0057	0.0000	0.0169
0-5	C to B (15)	Fixed = 0.0			
0-5	C to C	Fixed = 1.0			
0-5	C to D (87)	Fixed = 0.0			
0-5	C to E (152)	Fixed = 0.0			
0-5	D to B (102)	0.2639	0.0741	0.1450	0.4310
0-5	D to C (87)	0.2968	0.0791	0.1672	0.4701
0-5	D to D	0.4294	0.1339	0.1669	0.6919
0-5	D to E (64)	0.0100	0.0105	0.0000	0.0306
0-5	E to B (167)	0.0335	0.0079	0.0210	0.0529
0-5	E to C (152)	0.0389	0.0082	0.0257	0.0585
0-5	E to D (64)	0.0086	0.0034	0.0019	0.0152
0-5	E to E	0.9190	0.0131	0.8933	0.9447

Notes: Distances (km) between islands are given in parentheses following transition descriptions; all Seal Island (SI) chicks were seen exclusively on SI (or EER, not in analysis) by age five years; for this reason, SI transitions are fixed to zero.

† B = Matinicus Rock, C = Seal Island, D = Petit Manan, and E = Machias Seal Island; (A) was reserved for Eastern Egg Rock (islands are labeled ascending from west to east; Fig. 3.1) but this island was excluded from the CMR analysis due to small *n.*.

† B = Matinicus Rock, C = Seal Island, D = Petit Manan, and E = Machias Seal Island; (A) was reserved for Eastern Egg Rock (islands are labeled ascending

from west to east; Fig. 3.1) but this island was excluded from the CMR analysis

due to small n.
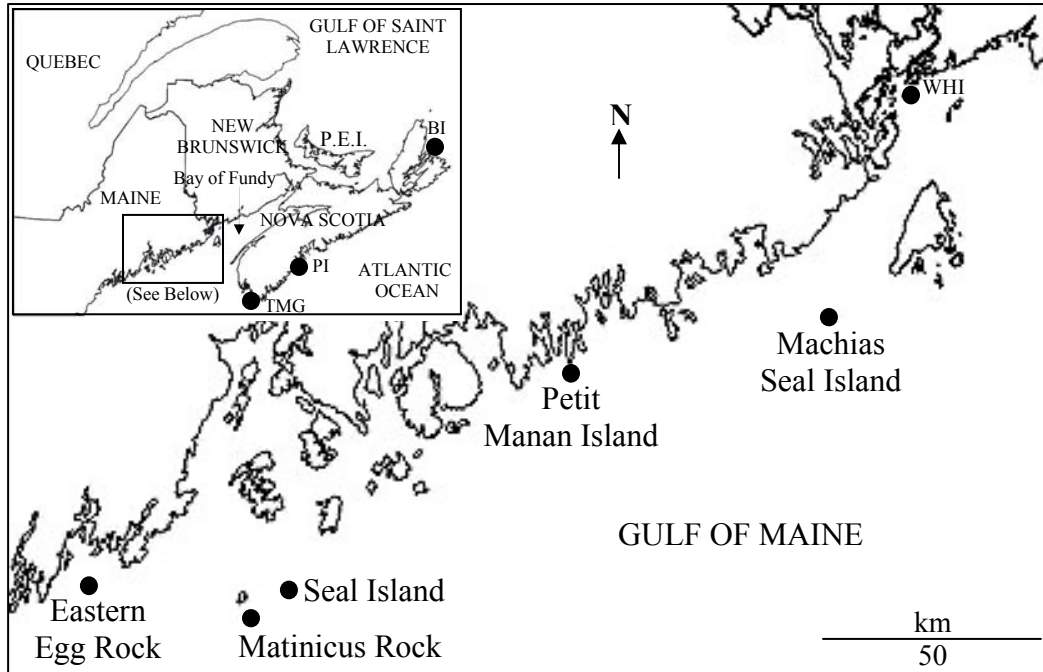
Fig. 3.1. Study sites in the Gulf of Maine and Bay of Fundy, USA and Canada.

Additional colonies mentioned in text are also shown: White Horse Island (WHI),

Tusket and Mud Island Groups (TMG; these include Green and Noddy Islands

respectively), Pearl Island (PI) and the Bird Islands (BI).
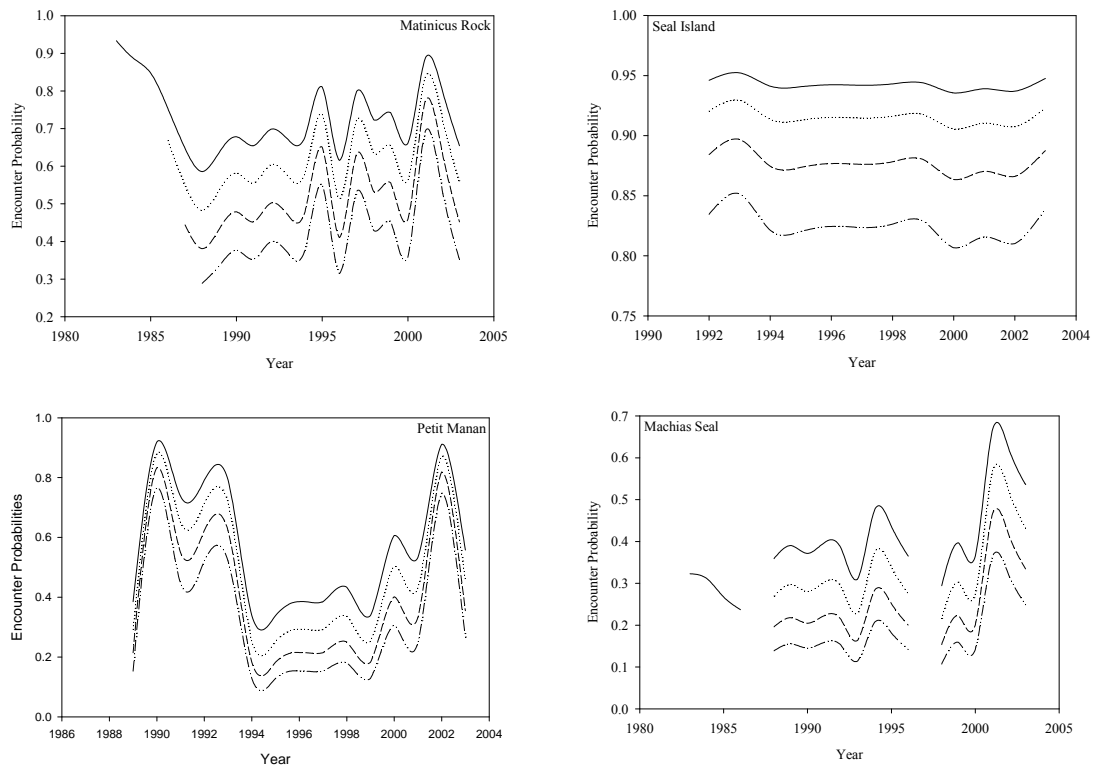
Fig. 3.2. Modeled averaged encounter probabilities (1983-2003) from the full

PBM model set (Table 3.5) for all islands and bands aged 3-5 (solid line), 6

(dotted), 7 (dashed), and 8 (dashed-dotted) years; ŜEs and 95% ĈIs are provided

in Table 3.6.

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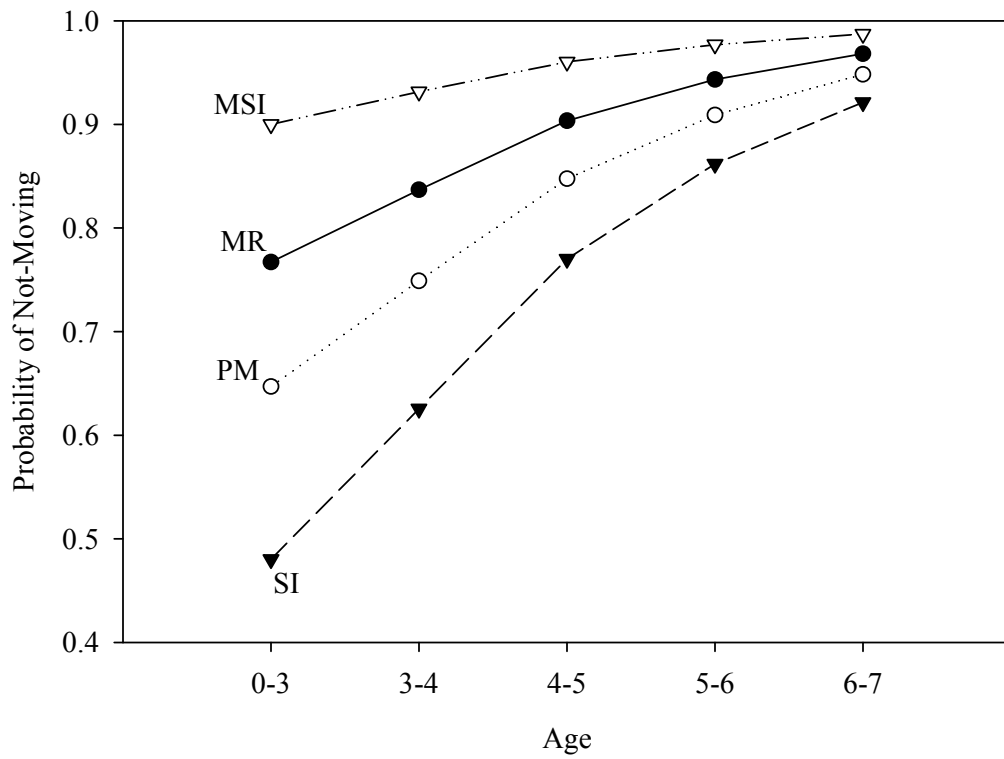
Fig. 3.3. Model averaged colony and age-specific probabilities of not moving

(e.g., B-B in Table 3.8) from the full PBM model set (Table 3.5); $\hat{S}Es$ and 95%

$\hat{C}Is$ are provided in Table 3.8.

Chapter 4

SURFACE WEAR ON INCOLOY AND DARVIC BANDS APPLIED TO ATLANTIC PUFFIN

(*FRATERCULA ARCTICA*) ADULTS AND CHICKS

Authorship: André R. Breton,[1,2] Antony W. Diamond,[1] and Stephen W. Kress [2]

[1]Atlantic Cooperative Wildlife Ecology Research Network (ACWERN),

University of New Brunswick, P.O. Box 45111, Fredericton, N.B. E3B 6E1,

Canada

[2] Seabird Restoration Program, National Audubon Society, 159 Sapsucker Woods

Road, Ithaca, NY, 14850 USA

Contribution of Authors: A. R. Breton designed study, performed analyses, and
wrote manuscript; A. W. Diamond primary editor, contributed some data from
Machias Seal Island; S. W. Kress editing, contributed all other data except data
from Petit Manan.

4.1 Abstract

Bands are a common marking method in bird studies. Often capture-mark-reencounter (CMR) models are used to analyze these data. Common to this family of models are two assumptions: marks do not fall off or become unreadable; 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 2nd or 3rd summer after hatching; consequently, probabilities of being worn were delayed on both band types by four years on bands applied to chicks compared to adults. Twenty-five percent and 87% of darvic bands applied to chicks and adults respectively were worn after five years. 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 five years on long-lived seabirds that are exposed to coarse substrates.

4.2   Introduction

Capture-mark-reencounter (CMR) is a method commonly used to gain insights about unobservable demographic processes including survival and emigration (Pollock *et al.* 1990). 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 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. Specifically, 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.

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 since adult life expectancies often exceed ten years and nesting substrates often consist of coarse material including sand, talus, and bedrock. Several studies on gulls and terns (Family Laridae, Order Charadriiformes) have reported loss rates (e.g.,

Kadlec and Drury 1969, Kadlec 1975, Spendelow *et al.* 1994) and rates of wear including comparisons between band types (e.g., 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 the species. Excluding those on gulls and terns, papers reporting band wear or loss rates in long-lived seabirds are uncommon (e.g., Anderson 1980, Wooller *et al.* 1985, Ludwig *et al.* 1995).

Atlantic Puffin (*Fratercula arctica*, Family Alcidae, Order Charadriiformes) are long-lived seabirds; average life expectancy once a bird has bred for the first time (age 3-6 years) is about 20 years (Harris 1984). At five colonies in the Gulf of Maine, USA and Canada, two types of field-readable bands, incoloy (nickel-chromium steel alloy) and darvic (rigid polyvinylchloride), 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.* in press); incoloy was introduced in 1999 as a potential solution. However, after only two years, 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.

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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' or 'worn', no noticeable wear and one or more characters difficult to read or obliterated respectively. Here we report results from two logistic regression analyses of these data. Our aims were to (1) measure the importance of the factors band age, bird age (chick or adult), and band type in the process of a band becoming 'worn' and (2) determine if 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.

4.3   Methods

4.3.1   Study Sites

Bands were applied and scored at five managed seabird colonies in the Gulf of Maine, USA and Canada: Eastern Egg Rock, Matinicus Rock, Seal Island National Wildlife Refuge (NWR), Petit Manan NWR, and Machias Seal Island. The landscape of these treeless islands is typically granite bedrock and boulder berms along the shore and herbaceous meadow covering the interior. Crevices within boulder piles are the primary nesting site for puffins in the region. Additional details including island locations are available in Breton *et al.* (in press).

4.3.2   Bird Age, Chick or Adult

About six weeks post-hatch, Atlantic Puffin chicks abandon colonies for the ocean (Harris 1984); the majority do not return to colonies, i.e., they remain at

sea, until their 2nd or 3rd summer after fledging (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, birds initially marked as chicks and adults were grouped separately prior to analysis. Adults in our analysis are birds identified as second-year or older on initial capture, i.e., individuals that were immediately susceptible to band wear.

4.3.3   Trapping and Marking

Chicks were captured by hand; adults were captured using noose mats, box traps, or by hand in nest cavities. Adults were trapped at any time during the field season, May through August; chicks were banded between middle July and late August. Between 1979 and 2004, 2001 chicks and 239 adults were marked with plastic field-readable leg bands on all islands; not all 'plastics' used were darvic, but all those analyzed here were. Although engraving design varied on these bands, all those analyzed here were engraved horizontally (numbers not stacked) and twice repeated, e.g., 1108-1108. Between 1999 and 2004, 2152 chicks and 615 adults were marked with incoloy field-readable bands; all of these were engraved two characters above and two below, e.g., AZ above 01, and twice repeated. All individuals received a United States Geological Survey (hereafter "federal") band engraved with eight or nine digits on the tarsus opposite the field-readable band. These banding data and resightings of marked birds are part of a continuing multi-site CMR study to estimate demographic parameters (Breton *et al.* 2005, Breton *et al.* in press).

Our incoloy (nickel-chromium steel alloy) bands are made of incoloy type 825; they are 9.0 mm tall, 30 mm long, and 0.85 mm thick. These were purchased directly from the manufacturer, Porzana Limited, East Sussex, England. Two-layered 1-½ mm x (ca.) 1 square meter darvic (rigid polyvinylchloride) sheet stock for forming bands was purchased, almost exclusively, from Kings Plastics and The Wildfowl Trust in Bristol and Slimbridge, England, respectively. Sheet stock was cut into 11 mm tall by 30 mm long sections prior to engraving. Engraving was made through the top layer exposing the inner layer. Each island used its own color scheme, e.g., Machias Seal Island used dark green with white engraved characters, i.e., outer plastic layer dark green and inner white.

4.3.4   Wear Scores

Between late May and early August 2003 and 2004, observers resighting puffin bands on all five islands were asked to score surface wear on as many bands as possible. Observers inspected wear on bands using spotting scopes from blinds at different locations throughout each colony. Four scores were used: no wear, (1); all characters easily read – 'light wear', (2); one or more characters difficult to read – 'moderate wear', (3); one or more characters illegible – 'severe wear', (4) (Fig. 4.1). Because engraving is twice repeated on both band types, we implemented 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. It was often necessary to read the federal band to identify birds wearing severely worn darvic bands.

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, e.g., 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 within a summer ($N = 135$) or in both 2003 and 2004 ($N = 175$). To ensure that observations were independent, we used only the most recent score for each band. Because band scores became less common with age, the most recent score was selected over other options.

4.3.5 <u>Analysis</u>

Our primary interest was in estimating the probability of a band becoming 'worn', which we define as any band acquiring moderate to severe surface wear (scores 3 and 4). Therefore, band wear scores were reduced to 'not worn', score 1-2, or 'worn', score 3-4, prior to analysis and subsequently analyzed using logistic regression. Although we had data for darvic bands applied to chicks and adults beyond five years post-application, data for incoloy bands was limited to only five years (see above) and scores for adult bands older than five years were sparse. In order to compare both band types and bird ages, we excluded all data beyond five years. Separately, we used logistic regression to analyse data extending to ten years from darvic bands applied to only chicks.

Goodness-of-fit (GOF) testing and model fitting were carried out using SAS (SAS Institute 2004). The global or starting model for each analysis contained all the factors that we thought might be important and were available: band age in weeks (since application) in both analyses; bird age (chick, adult) and band type (incoloy, darvic) in the 5-year analysis only. We tested GOF of our data to these models using a Hosmer and Lemeshow χ^2 test (Hosmer and Lemeshow 1989, Stokes *et al.* 2000). The null hypothesis is that observed and predicted values are equal. Therefore, fit is judged as adequate when the χ^2 test is not significant. In addition, we visually estimated GOF in the 5- and 10-year datasets by plotting 'observed' annual proportions ($\pm \hat{SE}$) on top of model 'predicted' probabilities of moderate to severe wear.

Following GOF testing, we constructed all possible models from our three factors. We used evidence ratios calculated from small sample Akaike's Information Criterion (AIC_c), model likelihoods and AIC_c weights, to determine support for competing models (Burnham and Anderson 2002). An evidence ratio of about 50:1 provides essentially zero support for the competing model (Burnham and Anderson 2002). Standard errors are provided as estimates of precision for effects in our top model.

Improvement in annual wear resistance by incoloy bands over darvic is quantified as a percent difference ($\%\hat{D}$) using the estimator $\dfrac{\hat{p}_{1i} - \hat{p}_{2i}}{\hat{p}_{1i}} * 100$ where $\hat{p}_{1i}$ and $\hat{p}_{2i}$ are darvic and incoloy wear probabilities in the ith year respectively

from our top 5-year model. 95% confidence intervals are estimated

as $\%\hat{D} \pm (1.96 * \hat{SE}_{(\hat{p}_{1i} - \hat{p}_{2i})}) * 100$ where $\hat{SE}_{(\hat{p}_{1i} - \hat{p}_{2i})} = \sqrt{\dfrac{\hat{p}_{1i}(1 - \hat{p}_{1i})}{n_{1i}} + \dfrac{\hat{p}_{2i} - (1 - \hat{p}_{2i})}{n_{2i}}}$.

4.4   Results

4.4.1   Data

Scores from 386 bands were available for the 5-year analysis (Table 4.1). Our 10-year analysis includes scores from 275 darvic bands applied to chicks.

4.4.2   Logistic Regression

Fit of our 5-year data to the global model was not significant ($\chi^2_8 = 14.29$, $P = 0.08$). An evidence ratio supported the global model over the next best model by 299,000:1. Global model effect sizes ($\hat{\beta}$) and their precision ($\hat{SE}$) were: band age in weeks, $\hat{\beta} = 0.014 \pm 0.003$; bird age, $\hat{\beta} = -1.464 \pm 0.238$; band type, $\hat{\beta} = -1.064 \pm 0.228$; intercept $= -4.235 \pm 0.542$. Predicted estimates from this model are plotted in Figure 4.2 along with annual proportions ($\pm \hat{SE}$) of moderately to severely 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 five years to accumulate the same amount of band wear as adults accumulated in one (Table 4.2). Twenty-six percent (0.17, 0.37 95% $\hat{CI}s$) of darvic and 4% (0.02, 0.10 95% $\hat{CI}s$) of incoloy bands applied to chicks were moderately to severely worn after five years (Table 4.2). When applied to adults, 87% (0.69, 0.95 95% $\hat{CI}s$) and 43% (0.26, 0.64 95% $\hat{CI}s$) of darvic and incoloy bands respectively were worn after five years (Table 4.2). On average, moderate to severe wear was

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reduced on incoloy bands by about 87% and 71% annually relative to darvic bands worn by chicks and adults respectively (Table 4.2).

Fit of the 10-year 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 $\hat{SE}s$ from the global model were: band age in weeks, $\hat{\beta} = 0.014 \pm 0.002$; intercept, $\hat{\beta} = -4.75 \pm 0.539$. Predicted estimates are plotted in Figure 4.3 along with proportions of worn bands with $\hat{SE}s$. Overlap between observed proportions and predicted probabilities provide strong evidence that our data fit the model well. Within seven years, more than 50% (0.52, 0.70 95% $\hat{CI}s$) of darvic bands applied to chicks were worn.

4.5   Discussion

In 1961 and 62, Coulson (1963) applied rigid-polyvinylchloride, trade name 'darvic', to Black-legged Kittiwakes (*Rissa tridactyla*) and Shags (*Phalacrocorax aristotelis*) as an alternative non-metal bird band. Since this time, the use of darvic bands in bird studies has increased dramatically (Marion and Shamis 1977, Calvo and Furness 1992) but relatively few studies have reported on the performance of these bands in the field. Most have reported rates of band loss (e.g., Reese 1980, Nisbet 1991, Spendelow *et al.* 1994) or wear (e.g., 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

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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 is 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, which had been shown to degrade rapidly and fall off (Kadlec and Drury 1968, 1969). To our knowledge, titanium, incoloy, monel, and stainless steel are now used almost exclusively to form metal bands for marine birds. 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 that has attempted to identify factors that might modify the process of band wear experienced by incoloy bands.

All three factors that we tested, 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 four years with chicks as 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. Our study showed that resistance to wear over multiple years by incoloy is far superior to darvic.

In CMR studies, band loss or, equivalently, band illegibility, confounds estimates of survival, i.e., the survival estimate provided represents the product of survival and the unknown band retention rate (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, heterogeneity in detection probabilities from band wear will cause data to become 'overdispersed' and as a consequence, sampling variances estimated using CMR models would be underestimated (Anderson *et al.* 1994).

We defined and measured 'wear' as 'one or more characters on the band being difficult to read or obliterated'; and since engraving is repeated, bands may be readable even when one or more characters are obliterated. Because we double banded each individual, we also had the opportunity to read the federal band as field-readable bands wore out. These observations complicate our ability to say at what point probabilities of wear from this study, if ignored, would bias CMR model estimates.

To avoid this complication, we make the modest assumption here that biases ensue when the predicted wear probability for the sampled population reaches 0.50, which is equivalent to saying '50% of the population is wearing moderately to severely worn bands'. Since we are interested in the sampled population as opposed to the sample, we will identify the cut-off using lower

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95% $\hat{CI}$s rather than estimated wear probabilities. The lower confidence interval

that meets this criterion for darvic bands applied to adults and chicks is acquired

at four (0.57, 0.88) and seven years (0.52, 0.70) respectively. Incoloy bands worn

by chicks are far from the 50% cut-off after five years (0.02, 0.09), the extent of

our results for this band type. The lower $\hat{CI}$ for incoloy bands worn by adults is

26% after five years (0.26, 0.63).

Our modest approach (50% cut-off) and use of the lower 95% $\hat{CI}$ rather

than the estimated wear probability allows us to make a strong inference

concerning biases from wear probabilities observed in our study. Within four

years for adults and seven for chicks degradation of darvic bands from surface

wear will cause bias in CMR estimates unless either (1) birds are double banded

and the second mark does not wear or wears much slower or (2) worn bands do

not become completely illegible in this time. Both (1) and (2) also require that

effort spent trying to relocate marked animals is enough to detect the second band,

which is often a 'non-field-readable' federal type, or bands that are moderately to

severely worn. A combination of (1) and (2) could also be used to avoid or

minimize biases due to band wear. This combined approach was used

successfully by Breton *et al.* (2005) to avoid biases from rapidly degrading darvic

bands applied to adult Atlantic Puffins spanning ten years. In contrast, apparent

survival estimates from puffins marked as chicks reported by Breton *et al.* (in

press) appear to have been biased by band wear after five years, i.e., earlier than

our modest 50% cut-off predicts.

Based on our 50% criterion, data from incoloy bands applied to chicks spanning five years, experiencing the same amount of wear as our study, would not bias estimates in a CMR analysis. If the four-year delay in wear between bands on adults and chicks continued beyond our five years of data for incoloy bands, then we would expect that at least 26% (lower $\hat{CI}$) of incoloy bands applied to chicks would be worn after nine years. Wear on incoloy bands applied to adults roughly doubled annually. If this continued, and again we use the four-year delay observed between chick and adults, then we would expect incoloy bands applied to adults and chicks to reach the 50% cut-off at close to six and ten years respectively. These durations are much shorter than we would have predicted. However, these may be underestimates for two reasons.

First, details on the surface of an incoloy band are more difficult to detect than those on two-layered/colored darvic bands. As the dark colored surface layer on a darvic band is removed, it exposes the light colored underlying layer; alternatively, a light layer may be applied over a dark layer. Even if an observer is color blind, the contrast between dark/light or light/dark layers is easy to detect. In contrast, incoloy bands are a solid 'metallic' color and not even severe wear will produce a contrast such as that observed on darvic bands. We suspect that this lack of contrast on the surface of incoloy bands led to positively biased scoring errors, i.e., scores of 2 and 3 that should have been 1 and 2 respectively (no score 4s were recorded on incoloy bands). If these could somehow be demonstrated and taken into account, our estimates of six and ten years might be increased by several years.

Second, our top 5-year 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 four and five while the latter increase rapidly over the same period and substantially exceed the upper $95\%\ \hat{\text{CI}}\text{s}$ for the 5-year 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 six and ten years 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, Spendelow *et al.* 1994, Breton *et al.* 2005). Exactly which options are applied will depend on what is known about structure in the data that is due to band wear. Ancillary data in CMR studies can be very useful for correcting biases; e.g., data on band loss can be used to calculate a band retention rate (Spendelow *et al.* 1994). Multi-state models can be used to model an unobservable state such as when bands become completely unreadable (Lebreton *et al.* 2003). 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. in

press). Given these potential solutions and others (e.g., Pledger 2000), anyone experiencing or expecting problems should do a careful review of the literature to identify which data they should be collecting to correct for band wear.

Based on their poor performance over five (adults) and ten (chicks) years, 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 five years. Under these conditions, incoloy bands are preferable. In the absence of any corrections to account for wear, which 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 fifteen years.

4.6 Acknowledgements

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Table 4.1. Number of bands scored for wear ($N = 386$) and used in the 5-year

logistic regression analysis summarized by location (island) and year collected.

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

Table 4.2. Estimated probabilities with 95% $\hat{\text{CI}}$s of acquiring moderate to severe wear for darvic and incoloy bands aged one to five years applied to chicks and adults [a]. Also shown are percent differences ($\%\hat{\text{D}}$) between darvic and incoloy wear probabilities with 95% $\hat{\text{CI}}$s.

	Age of Band (yrs)					
Chicks	**1**	**2**	**3**	**4**	**5**	**Mean**
Darvic	0.02	0.04	0.08	0.14	0.26	-
95% $\hat{\text{CI}}$s [b]	0.01, 0.05	0.02, 0.08	0.05, 0.12	0.10, 0.21	0.17, 0.37	
Incoloy	0.002	0.005	0.01	0.02	0.04	-
95% $\hat{\text{CI}}$s	0.00, 0.01	0.00, 0.02	0.00, 0.03	0.01, 0.05	0.02, 0.10	
$\%\hat{\text{D}}$	87.89	87.67	87.24	86.37	84.65	86.76
95% $\hat{\text{CI}}$s	85.52, 90.26	84.35, 90.99	82.66, 91.82	80.23, 92.51	76.81, 92.49	
Adults						
Darvic	0.27	0.43	0.61	0.76	0.87	-
95% $\hat{\text{CI}}$s	0.14, 0.44	0.27, 0.61	0.43, 0.76	0.57, 0.88	0.69, 0.95	
Incoloy	0.04	0.08	0.16	0.27	0.43	-
95% $\hat{\text{CI}}$s	0.02, 0.10	0.04, 0.15	0.09, 0.25	0.16, 0.42	0.26, 0.64	
$\%\hat{\text{D}}$	84.38	80.84	74.47	64.16	50.04	70.78
95% $\hat{\text{CI}}$s	69.15, 99.61	63.57, 98.11	56.78, 92.16	47.48, 80.84	35.09, 64.99	

[a] Wear probabilities and their 95% $\hat{\text{CI}}$s are from the top model in the 5-year analysis.

[b] Confidence intervals were rounded-up to two significant digits; those reported here as 0.00 were between 0.0001 and 0.0044 prior to rounding.
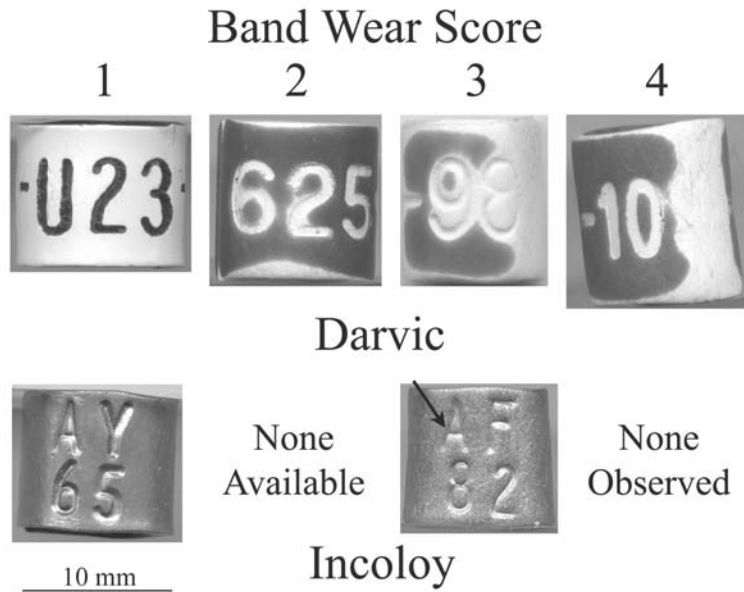
Fig. 4.1. Darvic and incoloy bands representing band wear scores 1 – 4: no wear, (1); all characters easily read – 'light wear', (2); one or more characters difficult to read – 'moderate wear', (3); one or more characters illegible – 'severe wear', (4). The arrow identifies a character on an incoloy band that may fit the criteria of 'difficult to read' in the field. No incoloy bands representing score 2 were available. Severe wear, score 4, has not been observed on an incoloy band.
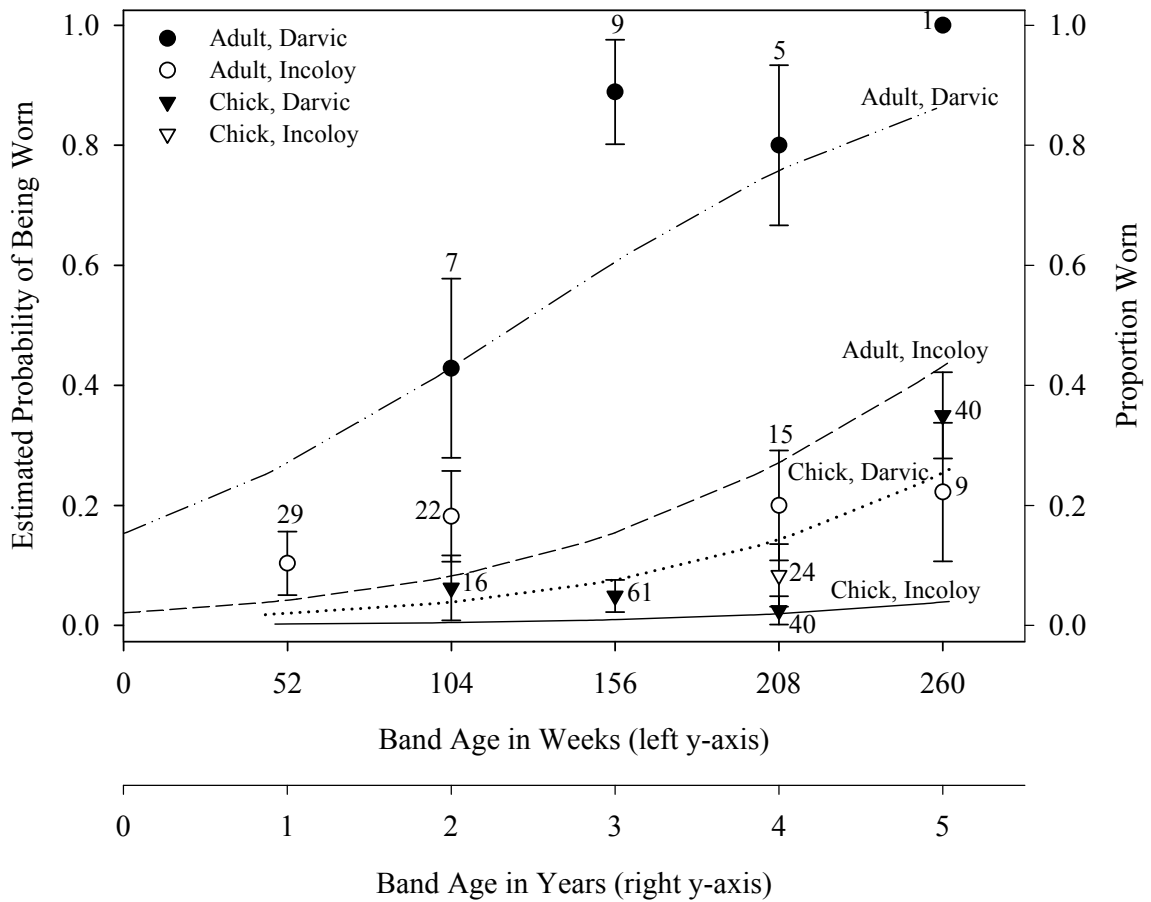
Fig. 4.2. Model predicted (lines; left y-axis) probabilities and annual proportions
($\pm \hat{S}E$; sample sizes provided) of 'worn' bands for both ages and band types
against band age in weeks and years respectively; annual proportions that were
zero are not shown.
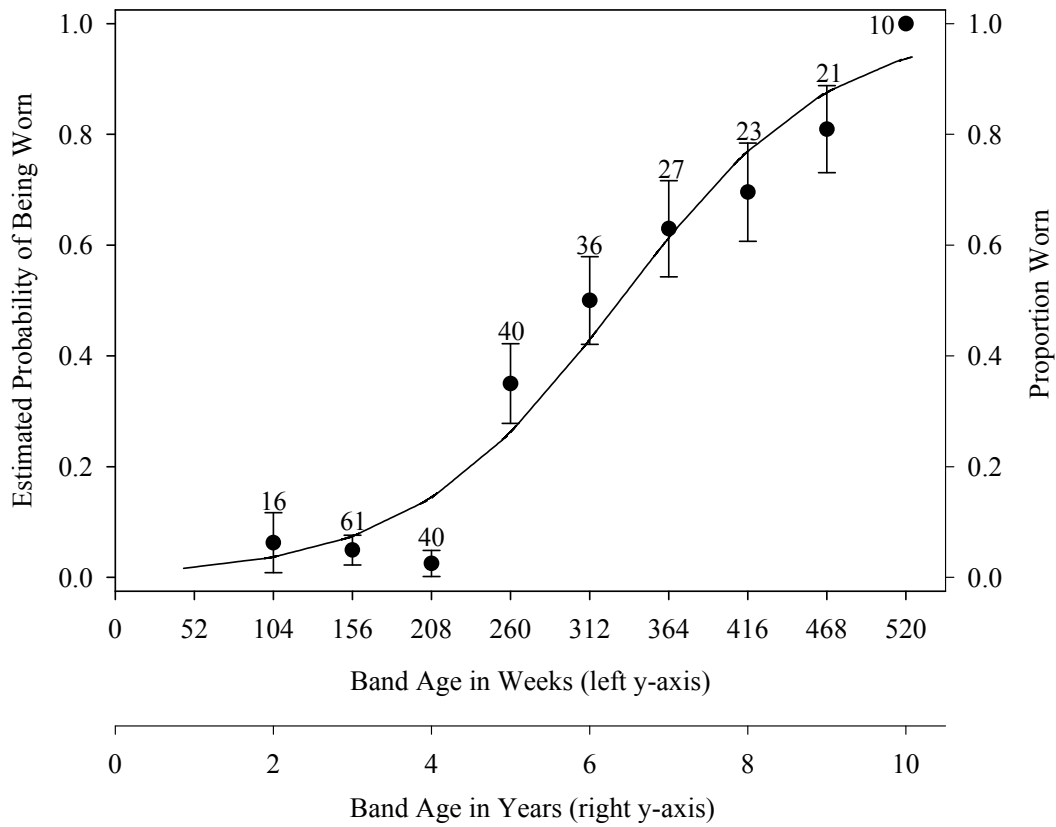
Fig. 4.3. Model predicted (line; left y-axis) probabilities and annual proportions
($\pm \hat{SE}$; sample sizes provided) of 'worn' darvic bands applied to chicks against
band age in weeks and years respectively; application year (0) and year one
annual proportions were zero, these are not shown.

Chapter 5

THE OVERLAP ASSUMPTION: AN IMPORTANT SOURCE OF BIAS IN STUDIES

OF MIGRATORY ANIMALS

Authorship: André R. Breton,[1,2] Antony W. Diamond,[1] and Stephen W. Kress [2]

[1]Atlantic Cooperative Wildlife Ecology Research Network (ACWERN),

University of New Brunswick, P.O. Box 45111, Fredericton, N.B. E3B 6E1,

Canada

[2] Seabird Restoration Program, National Audubon Society, 159 Sapsucker Woods

Road, Ithaca, NY, 14850 USA

Contribution of Authors: A. R. Breton original idea and all of the writing; A. W. Diamond primary editor; S. W. Kress editing.

5.1 Abstract

Wildlife and fisheries biologists routinely fit historical data to factors without careful, *a priori* consideration of how these might be related to the process of interest. Correlation is often assessed using some form of regression. Under the regression paradigm, several assumptions must be met otherwise results are unreliable. One assumption is that the data must be drawn randomly from the population of interest. We propose an extension of this assumption and refer to it as the overlap assumption to make explicit a source of bias that we believe has been overlooked with important consequences in studies of migratory animals: all randomly selected individuals from the sampled population experienced the factors fitted to the data. Three hypothetical scenarios are provided to reveal biases that can occur if data do not uphold the overlap assumption including false significant and non-significant results and slope coefficients that are too small or large. Three key pieces of information are necessary to determine if data are at risk of not upholding the overlap assumption: spatial extent of the effect; season of occurrence (origin) of the effect; and location of the sampled population when the effect occurred. When researchers fit factors to data without complete knowledge of extent, origin, and location, there is a risk of bias due to lack of overlap between the effect and the sample. For this reason, we recommend including incomplete knowledge of these variables along with other results. Next, we introduce three examples from the literature and demonstrate how their results may have been biased by overlap

failure. Given the generality of the problem, we propose that failure of the overlap assumption is a prevalent source of bias in wildlife and fisheries studies.

5.2 Introduction

In wildlife and fisheries research, factors are often selected and measured without careful, *a priori* consideration of how these might be related to the process of interest (Krebs 1989, Romesburg 1989, Anderson *et al.* 2001). At the analysis stage, fit is quantified to determine degree of agreement or correlation between data (response) and one or more factors (predictors). Typically, some form of regression involving a correlation statistic, such as R^2, and significance testing are used. Alternatively, Information-theoretic (IT) and Bayesian methods can be applied to the same problems (Royall 1997, Burnham and Anderson 2002). Below we develop our argument with reference primarily to simple, normal error, linear regression (Neter *et al.* 1996); however, IT, Bayesian and non-linear forms of regression including alternative error structures can easily be substituted.

Under the regression paradigm, a statistically significant fit, and the magnitude of the correlation statistic, can be used to assess consistency between an effect and a sampled process. For significant results, slope coefficients provide an estimate of the effect size or magnitude of change in the response resulting from a unit change in the predictor. In general, normal error linear regression has been shown to give reliable results as long as (1) the sample was drawn randomly, (2) sample size is not small, (3) sample units are independent, and (4) error and sampling distributions are normal with constant variance (Neter *et al.* 1996). We propose an extension of assumption (1) to make explicit a source of bias that we

believe has been overlooked with important consequences in studies of migratory animals: all randomly selected individuals from the sampled population experienced the factors fit to the data. For reasons that will become clear below, we prefer to describe this extended form of assumption (1) as 'the overlap assumption'.

Investigators must ask two basic questions for every assumption they invoke: do my data conform and if not, what are the consequences. Below we introduce the overlap assumption using three hypothetical scenarios. This leads naturally both to a way to assess conformity and to several consequences when data fail to do so. Our examples also allow an extension of the problem to other animal groups, including passive migrants and non-migratory species with extensive ranges. We conclude with three examples from the literature where overlap may not have been upheld.

5.3   The Overlap Assumption

Consider two contrasting scenarios: (A) 1000 individuals from a non-migratory animal population are captured at random in the breeding period and fitted with radio tags; survivors are located without fail over two weeks each spring for five consecutive years. The purpose of the study is to identify important mortality factors. Annual survival estimates from these data are fit to a factor that affects the entire sampling area, such as annual rainfall, to determine if this factor is correlated with annual survival. (B) 1000 individuals from a migratory seabird population are captured at random in the breeding period and fitted with radio tags; survivors are located without fail over two weeks each

spring for five consecutive years. Investigators know only roughly where their sampled population over-winters. Again, the purpose of the study is to identify important mortality factors. Annual survival estimates from these data are fit to a factor that affects the presumed wintering area, such as sea surface temperature (SST), to determine correlation with annual survival.

These two scenarios reveal three key pieces of information necessary for determining how well data conform to the overlap assumption. In scenario (A), investigators know the *extent* (area affected) and *origin* (period or season of occurrence, e.g., winter) of the factor they are testing and *location* of their sampled population when the factor, annual rainfall, occurred. Given this *a priori* knowledge, investigators know that the sampled population and factor overlapped completely, i.e., all animals did in fact experience the proposed mortality factor. A diagrammatic representation of this scenario is provided in Figure 5.1a: across five identical winter (*origin*) cells, *extent* of the factor and *location* of the sample, represented as a circle with cross-hairs and a hatched space within respectively, overlap completely; below each cell, an index of the magnitude of the factor, annual rainfall, is provided. To the right of this diagram, a plot of the hypothetical (observed) data and the actual underlying relationship (truth) are provided; in all scenarios (A-C), we assume truth is a simple linear relationship with a negative slope for the individuals that experience the effect. In scenario (A), the overlap assumption was met perfectly resulting in strong agreement between the observed data and truth.

In scenario (B), *extent* and *origin* (winter) of the mortality factor, SST, are known. However, *location* of the sampled population during the non-breeding period is only roughly known. As a result, overlap in this case is speculative. If all individuals did not experience the factor, the investigator in scenario (B) risks reporting biased results. Their results could be biased in many ways: SST may be falsely identified as not having an effect (not significant) or having an effect (significant). When a significant relationship is detected, estimated effect size may be too small, too large or in the wrong direction, e.g., positive when the true effect was negative. To motivate an understanding of how these biases can occur, we describe scenario (B) in greater depth and follow this with a new scenario, (C).

Imagine if, unknown to the investigators, half of the sampled population consistently over-winters a considerable distance away from the suspected wintering area (Fig. 1b); for simplicity, assume that individuals show complete fidelity to one wintering location. Those individuals that over-winter in the area where SST was measured (group A; Fig. 1b) do in fact experience inverse shifts in survival relative to SST; however, survival in the unknown wintering (group B; Fig. 1b) area is not related to SST. Consequently, estimates of survival from individuals sampled at random on the breeding grounds are a function of two unrelated systems. Due to incomplete overlap, this scenario could produce any result, most of them spurious.

If a line was fit to the observed data in Figure 1b, the result would be 'no effect', a spurious result: survival for those individuals that experienced the effect (group A) declined with increasing SST (truth) but this relationship was lost due

to the influence of group B survival. The origins of additional biases become evident, e.g., false positive and significant slope, if we assume truth for group B is also known (open circles, Fig. 1b). Notice that the observed data fall roughly between true survival for group A and B for each SST value (Fig. 1b); we would expect only a rough approximation since a random sample from the breeding population will not be representative. Now, imagine if by chance, survival had been much higher for group B at SSTs above the median than the median itself (Figure 1b); under these conditions, investigators would likely escape erroneously reporting 'no effect' but instead would report a positive slope when the true slope was negative. Additional manipulations of group B survival will lead to all possible errors including false significance and effects that are too small or large.

Since, in natural systems, *extent* of a factor and *location* of animals in a population are generally not fixed, we offer a third scenario. This time *extent* and *location* are allowed to vary over time and space; as before, *origin* of the effect is winter. In this scenario (C), 1000 individuals from a migratory seabird population are captured at random in the breeding period and fitted with radio tags; survivors are located without fail over two weeks each spring for five consecutive years. Annual survival estimates from these data are fit to a factor that affects only a small and variable section of the wintering area annually, such as quantity of oil released with bilge water at sea, to determine if this factor shows any correlation to annual survival. For simplicity, we will assume that the sampled population over-winters in a single group and one spill is released annually and reported.

Under this scenario, many degrees of overlap in each winter would be possible; one possibility over five winters is provided in Figure 1c. Given these conditions of overlap, we would expect mortality to be greatest in winter period 1 (complete overlap), slightly less in 5, a fraction of this in periods 3 and 4, and none in period 2 (no overlap). The observed data plotted in Figure 1c roughly approximate these expectations. As in scenario (B), contrast between the observed data and truth is severe (Fig. 1b and c) and consequently results from a regression analysis would give either a false non-significant result (scenario B), or a significant result with a biased slope (scenario C). However, unlike scenario (B), scenario (C) reveals how, due to space-time variation in overlap between a mortality factor and the sampled population, a false non-significant result could occur even when all animals died as a result of the factor being tested. This result can be visualized by adjusting overlap between winter cells in Figure 1c until the slope of the observed data is roughly zero.

Scenarios (A-C) were used to motivate an understanding of the overlap assumption including its consequences when data do not conform. We recognize that real systems will generally be more complex. However, biases resulting from incomplete overlap do not go away in these real systems. We expect, in most real cases, investigators will recognize their data fail to meet the overlap assumption but will be unable to untangle variation due to the factor(s) from variation due to overlap failure. Consequently, regression and other forms of analysis for determining consistency between data and factors will not give reliable results. In

these cases, researchers may be limited to reporting only estimates of parameters (such as survival) without insights into the process that produced them.

5.4   Why Not Sample the Affected Population?

A simple solution to the overlap issue is to randomly sample the population that experienced the effect. In our examples above, the affected population would be the non-breeding (winter) population rather than the breeding period population. Unfortunately, this alternative is not feasible for many animal groups including many seabirds, which over winter at low densities over the sea and typically far from shore (Gaston and Jones 1998), and anadromous fishes, which also spend a part of their lives at sea. When sampling these species and others, investigators will have to carefully assess how well their data conform to the overlap assumption and draw inference with respect to this assessment.

5.5   Studies at Risk and Suggestions

Whenever knowledge of *extent*, area affected by a factor, *origin*, timing of an effect, and *location* of the sampled population are incomplete, data are at risk of not satisfying the overlap assumption. Knowledge of *extent* and *origin* of factors should be easily attained relative to *location* of the sampled population. This is because the norm in wildlife and fisheries research has been to sample a population without careful consideration of the populations boundaries (Anderson 2001, Anderson *et al.* 2001). Consequently, a supplementary value of respecting the overlap assumption may be a general improvement of our knowledge of species population boundaries.

Although we focus above and below on migratory animals, we suspect that studies sampling other groups will also be susceptible to overlap failure, including passive migrants (e.g., marine plankton) and non-migratory species with extensive ranges. Similarly, we focus mainly on survival as the response variable. However, any response that is fit to an effect of unknown *extent* and *origin* will be susceptible to overlap biases. Susceptible responses include accumulation of energy reserves in birds prior to breeding (Mawhinney *et al.* 1999) and delayed vitellogenesis (Minagawa 1997) or ovulation (King and Pankhurst 2004) in crustaceans and Salmonids respectively.

Given the controlled aspect of experimental studies, it is hard to imagine how data from these studies would be susceptible to overlap failure; consequently, we expect primarily observational data will be at risk of not satisfying the overlap assumption. However, investigators should consider their designs carefully to make certain that incomplete overlap is not a potentially confounding effect.

We recommend investigators initiate study design with a simple question: 'to what population do I want to make inference?' Next, the geographic boundaries of this population (*location*) should be identified. If the population is migratory, boundaries at all times of the year should be at least roughly known. The *extent* of effects that they plan to test should then be compared to the appropriate population boundary, i.e., the boundary at some specific interval of a year from which each effect *origin*ated. Following this exercise, investigators will know how well or how poorly overlap has been achieved. When complete overlap is uncertain, investigators should include this along with other results. In

cases where overlap is known to be poor, we suggest excluding the factor from the analysis. Exclusion is suggested based on the high probability (not quantified here) of reporting biased results including false significance and non-significance and effect sizes that are too small or large.

5.6   Three Examples from the Literature

Below we review results from Harris *et al.* (1997), Ryding and Skalski (1999), and Solow *et al.* (2002); focal species are Atlantic Puffin (*Fratercula arctica*), coho salmon (*Oncorhynchus kisutch*), and green sea turtle (*Chelonia mydas*) respectively. Each reports an analysis of survival or remigration including factors that might be driving these processes and leaves open the possibility that their results could be biased by overlap failure. Our focus will be the latter and this includes implications for each case. Because our review focuses on unresolved biases, we feel it is important to point out that, regardless of the validity of our observations, each of these papers made significant contributions to wildlife or fisheries science.

5.6.1   <u>Atlantic Puffin</u>

Using capture-mark-reencounter (CMR) models, Harris *et al.* (1997) measured the consistency between annual survival rates from a sample of adult Atlantic Puffins and two environmental variables. The latter, frequency of gale force winds and SST, were confined to the North Sea and the August to February period. To justify testing these data, the authors report that "adults [from the study site, Isle of May, Scotland] are dispersed at a low density throughout the North Sea"; and out of 369 adult puffins marked and later found dead, less than

half (42%) were found "between January and February" (Harris *et al.* 1997). In their analysis, no "statistically significant" relationships between "puffin survival rates and estimates of…weather conditions" were detected (Harris *et al.* 1997).

Harris (1984) provides data from band recoveries that suggests overlap may be an issue with the data from Harris *et al.* (1997). Although "most older birds are [found dead] within 200 miles of colonies [in north-east Britain including the Isle of May]", some "have come from slightly further afield including" western Scotland, southern Ireland, the Channel Islands, northern France and the Bay of Biscay; and "[recently] puffins breeding on the British east coast [may be moving] further afield in winter [than previous years]". This evidence implicates both space and time as sources of variation in wintering area and therefore complicates the assumption made by Harris *et al.* (1997) that their sampled population over-winters in the North Sea. Also relevant here is the assumption made by Harris *et al.* (1997) that recoveries (their evidence that the sampled population over-winters in the North Sea) are equally probable in all areas of the species range; the CMR literature clearly shows that this assumption is false (White *et al.* 1982, Pollock *et al.* 1990, Lebreton *et al.* 1992).

These observations reveal that results reported by Harris *et al.* (1997) concerning the contribution of North Sea winter gales and SST to mortality may have been biased by overlap failure. Factors tested by Harris *et al.* (1997) may have affected puffin survival in a predictable way for those individuals that over-wintered in the North Sea. However, because some unknown number of individuals wintered outside of the North Sea, and likely this number varied from

one year to the next, the correlation between predictors and survival may have been concealed by variation that was due to overlap failure.

5.6.2 Coho Salmon

Ryding and Skalski (1999) used multivariate linear regression techniques to fit estimates of survival, from at-sea recoveries of coho salmon, to several environmental covariates including June and summer mean SSTs. SST was measured at a single offshore station about halfway between the mouth of the Columbia River and Juan de Fuca Strait. Coho salmon used in the analysis were released from 12 hatcheries distributed across three regions in Washington: Juan de Fuca Strait (north shore), coastal and Lower Columbia River (Pacific Coast).

Ryding and Skalski (1999) reported a significant simple linear relationship between mean summer temperature and survival; June SST was not significant. The authors also fitted a quadratic function to the data: the "mean of the quadratic term for the June SST…was not significant". However, when quadratic functions were fitted to data from each region separately, quadratic terms from the "Juan de Fuca Strait were significantly negative, the coast was significantly positive, and Lower Columbia River was positive but nonsignificant".

Weitkamp and Neely (2002) analyzed 1.47 million recoveries of coded-wire tagged coho salmon; these were marked and released from 90 hatcheries located within and between Northern California and Alaska; the purpose of the study was to identify both large and small scale at sea recovery patterns. Using a

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variety of analysis methods, they showed that over-wintering coho salmon inhabited 12 discrete coastal zones.

Recall that Ryding and Skalski (1999) sampled hatcheries from three regions, Juan de Fuca Straits, coastal, and Lower Columbia River. Weitkamp and Neely (2002) show that a high percentage of fish released from these three regions inhabit Puget Sound and the east Juan de Fuca Straits, coastal Washington and west Juan de Fuca Straits, and the Lower Columbia River respectively. Recall also that Ryding and Skalski (1999) measured SST at a single offshore station mid-way along the Washington coast. According to results from Weitkamp and Neely (2002), a large proportion of coho salmon released from two out of the three regions sampled by Ryding and Skalski (1999) probably did not experience the SSTs they fitted to their data.

We find it difficult to believe that spatial variation in mean summer and June SST does not exist among the narrow Juan de Fuca Straits and Puget Sound, along the Washington coast above the Columbia River, and at the mouth the Columbia. Instead, we suspect that coho salmon inhabiting these three regions experience different SSTs. If this is true, it is unlikely that data analyzed by Ryding and Skalski (1999) upheld the overlap assumption. Consequently, estimated slope coefficients and standard errors for SST effects may be too large or small and tests of significance of these parameters may be spurious. Failure of the overlap assumption would also explain why Ryding and Skalski (1999) found significant SST effects that were both positive and negative.

5.6.3   Green Sea Turtle

Solow *et al.* (2002) tested the effect of SST on 2-year remigration probabilities for female green sea turtles counted annually at Tortuguero, Costa Rica; remigration describes the 2 or 3-year delay between successive nesting attempts observed in this species. A winter index of annual SSTs was calculated from monthly data collected at La Parguera, in southwestern Puerto Rico, "the only long-term [recording station] in the Caribbean region" (Solow *et al.* 2002). Solow *et al.* (2002) compared the fit of two models using a likelihood ratio and null hypothesis test (H_0: no SST effect); one model included the SST constraint and the other did not. The null was rejected in favor of the model including an effect of SST on remigration probabilities.

During the winter period, when SST was expected to affect the turtles, "females from the Tortuguero stock [are] disperse[d] throughout the Greater Caribbean" (Solow *et al.* 2002). It seems highly improbable that turtles dispersing "throughout the Greater Caribbean" would experience the same SST conditions measured at La Parguera (Muller-Karger and Castro 1993). Consequently, data analyzed by Solow *et al.* (2002) would not be expected to uphold the overlap assumption. Therefore, estimates of the effect of SST on remigration probabilities may be too small or large and their conclusion that the SST effect was significant may be spurious.

5.7   Concluding Remarks

We suspect that failure of the overlap assumption is a prevalent source of bias in wildlife and fisheries studies. Consequently, overlap failure has likely led to many erroneous conclusions in peer-reviewed literature including false

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negatives, which may or may not (Bauchau 1997, Koricheva 2003) be underrepresented in science journals. In light of these observations, we recommend that wildlife and fisheries biologists reevaluate previous work with care to determine if important biases may be present.

5.8   Acknowledgements

5.9   Literature Cited

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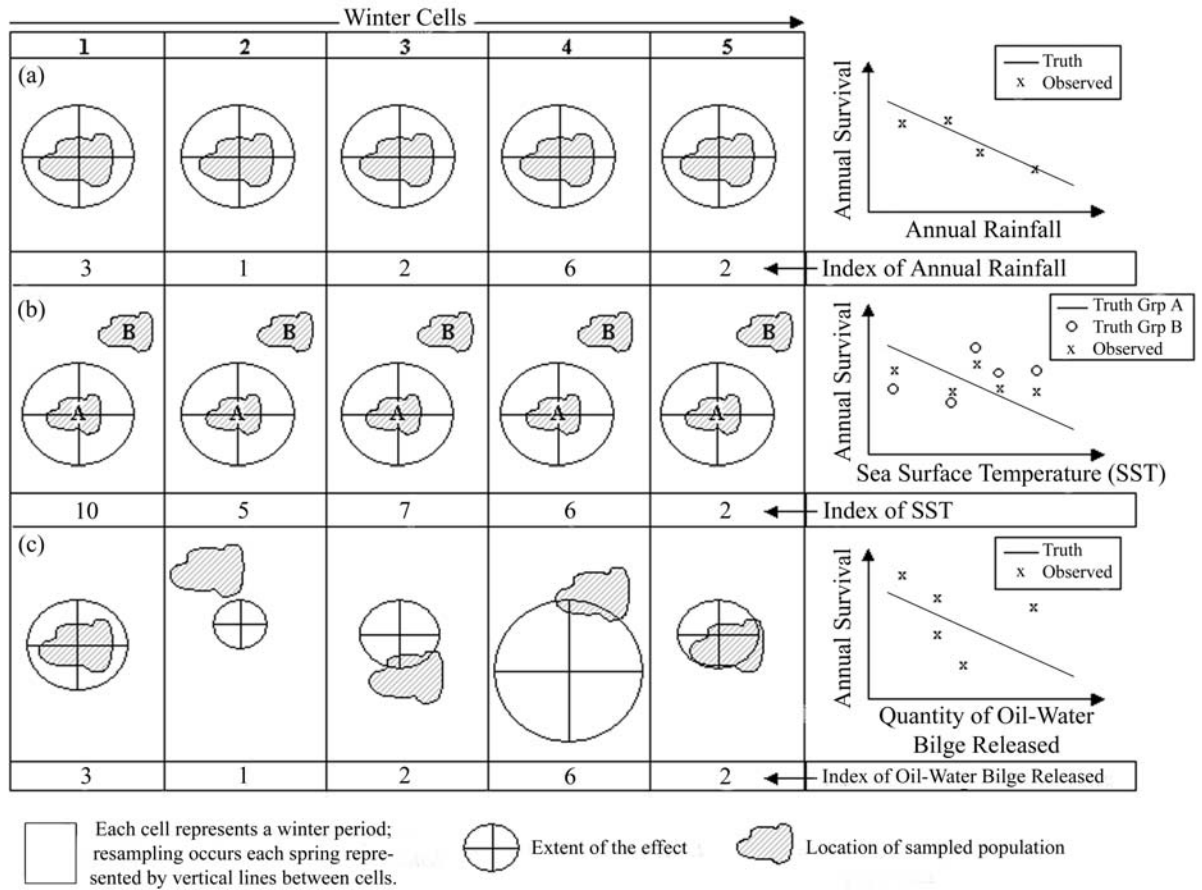
Fig. 5.1. See text for explanation.

Chapter 6

GENERAL DISCUSSION

6.1 Significance and Implications for Atlantic Puffins and other Long-lived Seabirds in the Region and Elsewhere

6.1.1 Significance

In order to demonstrate the significance of the survival and movement probabilities reported in this dissertation, I review what has been reported previously for the Atlantic Puffin. I am aware of only two previous estimates of adult survival and one for immatures in the Western Atlantic. Nettleship (1972 and pers. comm. in Hudson 1985) and Kress (1987) estimated adult survival in puffins breeding on Great Island, Newfoundland and Eastern Egg Rock, Maine respectively. Both of these estimates were calculated as 'return rates', which, as I have identified elsewhere, tend to underestimate true survival. Kress and Nettleship (1988) estimated immature survival and pre-breeding movement probabilities for puffins transplanted from Newfoundland to Maine and native to Matinicus Rock and Machias Seal Island. They also provided counts of puffins that dispersed among colonies. Although their results are valuable, the methods used to analyze the data did not account for difference in detection probabilities among islands and years. Movement estimates from Kress and Nettleship (1988) are the only estimates that I am aware of for the species in the Western Atlantic.

Elsewhere in the species range, estimates of adult survival are relatively abundant (e.g., Ashcroft 1979, Harris and Bailey 1992, Harris *et al.* 1997, Erikstad *et al.* 1998, Harris *et al.* 2000). I am aware of four studies that estimated immature survival for the species, Mead (1974) using recoveries from British colonies, Ashcroft (1979) and Hudson (1979) from Skomer Island, Wales, and

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Harris (1983) from the Isle of May, Scotland. Harris (1983, 1984) carried out two massive studies in the United Kingdom to determine movements by puffins among colonies and these provided estimates of both pre-breeding movement and natal dispersal. The only other estimates of natal dispersal and pre-breeding movement of which I am aware were provided by N. Brown and reported by Harris (1984). Nowhere in the species range has breeding dispersal (Greenwood and Harvey 1982) been detected (Harris and Wanless 1991). Patterns of migration, sometimes referred to as 'dispersal', have been reported by several authors (see review in Brown 1985) but this topic is outside of the focus of my dissertation.

Survival and movement probabilities from within or outside of the Gulf of Maine and Bay of Fundy region have rarely accounted for dispersal by sub-adults out of a single study site or detection probabilities. Estimates in this dissertation account for space and time variation in detection probabilities and dispersal to five out of eight colonies in the region. This achievement along with rare estimates of immature survival and dispersal make an important contribution to knowledge of demography of Atlantic Puffins, alcids, and long-lived seabirds in general. In addition, Chapter 3 is only the second seabird metapopulation study to come from the Western Atlantic; the first metapopulation study in the region was reported on Roseate Terns (*Sterna dougalli*) by Spendelow *et al*. 1995.

6.1.2   <u>Implications</u>

6.1.2.1   The Importance of Dispersal (and pre-breeding movement) in

Population Dynamics

Lidicker (1975) summarizes popular beliefs held by "population ecologists" before and during his lifetime: "commonly, dispersers have either been ignored or considered to be of little significance…" and "…population growth rates [have been] frequently defined in terms of birth and death rates only". Evidence in support of his view is overwhelming and includes the long tradition and wide use of 'life tables' to describe and predict changes in population size. Similarly, "The Natural Regulation of Animal Numbers" (Lack 1954), the celebrated text describing factors responsible for population changes in (mainly) birds, includes 24 chapters, none on dispersal. However, to say that influential authors, including Lack (1954) and others (e.g., Elton 1927, Nicholson 1933), did not recognize the potential for a role by dispersal would not be a fair statement. They were aware of the possibilities but chose to set them aside in favor of describing population change with the majority of data that were available, i.e., birth and death rates.

The importance of dispersal was clearly demonstrated by Darwin and Wallace (Wallace 1855, Darwin 1859) and refined by Mayr (1942, 1970) and others (e.g., Dobzhansky 1951) in the concept of speciation. However, since the context was not specifically 'animal abundance' but rather 'descent with modification' (Darwin 1859), animal demographers were slow to recognize the spatial structure of species populations revealed by these authors and its implications for the role of dispersal in population dynamics. Andrewartha and Birch (1954) committed a full chapter in their text, "The Distribution and Abundance of Animal Numbers", to dispersal. Elsewhere in this text, they

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provided an outline that foreshadowed what would later be coined a 'metapopulation' by Levins (1969, 1970). However, for almost two decades, the significance of their insights remained essentially ignored. Around 1970, the ideas of Andrewartha and Birch (1954) were recalled and expanded upon by authors including MacArthur and Wilson (1967), Levins (1969, 1970), Lidicker (1975) and later, Hanski and Gilpin (1991).

Andrewartha and Birch (1954) predicted that dispersal played a far greater role in modifying local population size than had been previously recognized. Although evidence accumulated in the last 30 years supports their view, it has been overwhelmingly theoretical (e.g., Fretwell and Lucas 1970, Pulliam 1988, Serrano and Tella 2003). The empirical evidence that does exist is generally on short-lived species, especially Lepidoptera (Hanski and Gilpin 1997). Strong colony-dependent variation in movement probabilities reported in this dissertation identifies natal dispersal and pre-breeding movement as key parameters affecting local population dynamics in a long-lived seabird. This important result has been replicated in all other multi-site studies of birds known to me (Hestbeck *et al.* 1991, Spendelow *et al.* 1995, Lindberg *et al.* 1998, Grosbois and Tavecchia 2003, Lebreton *et al.* 2003, Cam *et al.* 2004, Oro *et al.* 2004). Our combined results reveal that processes occurring among local populations may be responsible for modifying numbers at each local population. And since 'single site research' has been the norm in studies of birds (Wooller *et al.* 1992, Coulson 1991) and other groups (Lidicker 1975), this insight could have a considerable influence on the way population dynamics are measured in future research.

6.1.2.2   The Significance of Dispersal by Immature Seabirds

The tendency for immature members of animal populations to disperse more than adults or breeders is well known (Greenwood 1980). This immature dispersal bias is particularly problematic for studies monitoring marked individuals at a single local population. The main problem is that the spatial scale at which immature survival operates may be larger than the spatial scale of the study. Unless it can be shown that natal dispersal does not occur in the focal species, then the accuracy of immature survival probabilities will be necessarily suspect when studies are confined to a single local population. The best solution is cooperative studies that expand the spatial coverage that one team can manage. Nettleship (1991) anticipated the need for cooperative research in studies of seabirds. The alternative to broad scale cooperative studies, that is ignoring dispersal, cannot be expected to give reliable results.

Two components of this dissertation are relevant: First, dispersal by immature puffins was considerable, 8-25%, among the sampled colonies. By 'considerable' I mean more than enough, if these were ignored, to produce important biases in estimates of immature survival. Also relevant is the cooperative aspect of the work. This dissertation demonstrates that cooperative research among many agencies and organizations is an efficient and productive way to expand the spatial coverage of a study and obtain reliable estimates of immature survival and other demographic parameters.

6.1.2.3   The Role of Conspecific Attraction in Dispersal and PBM

Many hypotheses have been put forth to explain differential movement by animals including ideal-free distribution (Fretwell and Lucas 1970), source-sink habitats (Pulliam 1988), and conspecific attraction (Smith and Peacock 1990, Serrano and Tella 2003). Naturally, tests of these require overcoming the significant challenge of simultaneously monitoring two or more local populations; and for long-lived animals, the challenge must be maintained for multiple years. Studies that have overcome these challenges are rare relative to studies conducted at smaller spatial and shorter temporal scales. Two recent examples are Cam *et al.* (2004) and Lebreton *et al.* (2003).

Cam *et al.* (2004) monitored Audouins gulls (*Larus audouinii*) at two colonies in the Western Mediterranean from 1988-2001; their objective was to assess hypotheses concerning the role of breeding success and colony size in breeding dispersal. Results provided some support for source-sink dynamics, conspecific attraction and conspecific success attraction (Cam *et al.* 2004). Lebreton *et al.* (2003) monitored roseate terns (*Sterna dougalli*) at three colonies along the Atlantic coast off of New York, Connecticut, and Massachusetts. The strongest pattern in movement by adults and young was away from the least productive site to the nearest productive site. These results suggest that distance between local populations and conspecific success attraction might both be important in this metapopulation.

With so few multi-site studies available to compare, it is not possible to say at this time whether one hypothesis may be favored over another. And perhaps, as was demonstrated by Cam *et al.* (2004), the decision to move is not

always driven by the same factor. An additional complication is that results can be ambiguous concerning their support for competing hypotheses (Cam *et al.* 2004). This reveals the need for more critical thinking about predictions prior to conducting studies. I provide results from data on a long-lived seabird monitored at four islands for twenty-four years. Results implicate a role by conspecific attraction and distance between sites in movement probabilities. These results will be valuable when enough information has accumulated to attempt a meta-analysis on differential dispersal hypotheses.

6.1.2.4 *Shared Characteristics of Local Populations*

Managers seem comforted when they can say that 'all of their eggs are not in one basket'. This popular metaphor is reminiscent of the single large or several small (SLoSS) habitat patch size debate that raged in the late 70s and 80s (Quammen 1996). Admittedly, there is a logic to the 'several small' or 'eggs in many baskets' argument that seems to have an instinctual appeal. However, if the fate of the eggs, to continue the metaphor, is dependent on any shared factor, storage in insular baskets will not guarantee persistence of any one of them.

In Chapter 2, I introduced the concept of shared characteristics among local populations; and here and in Chapter 3, I focus primarily on the implications for colonial seabirds if two or more local populations (colonies) share the same mortality risk: (1) conspecifics from each colony may be over-wintering in the same location and consequently, (2) a single event, such as an oil spill, could reduce the species presence in the region considerably. Concerning shared mortality among the local populations measured in this thesis, my results suggest

colony is an important contributor to the survival process, and consequently, survival may not be a shared characteristic among managed puffin colonies in the Gulf of Maine and Bay of Fundy. However, this result, although well supported in Chapter 3, was not equivocal (Chapter 2). Apparently, given that this broad and long-term study failed to provide conclusive evidence, it will take a considerable effort to identify what demographic characteristics might be shared among local population so seabirds and other animals; but this insight may be critical for making reliable management decisions.

It is widely believed that mortality in alcids is essentially a winter phenomenon (Mead 1974, Harris 1984). This is consistent with anecdotal data available from the Gulf of Maine and Bay of Fundy, which includes very few instances of mortality in puffins and other alcids in summer (Kress unpubl. data, Diamond unpubl. data). Although colonies of puffins and other seabirds will always be vulnerable in the summer months, it may not be sufficient to protect and monitor birds only during this period. The possibility of shared risk in winter demonstrates the need by managers to expand the spatial scale of their efforts so that they include the breeding and wintering ranges of a species. This has recently been realized and effectively applied by the Canadian Wildlife Service in the Maritimes and Newfoundland[7]. Knowledge of their methods might be useful for planning and initiating the same monitoring effort for seabirds nesting in the Gulf of Maine and Bay of Fundy.

6.1.2.5 *Darvic Bands, Long-Lived Seabirds and Biases*

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[7] The Canadian Wildlife Service Atlantic Region Oil Spill Response Plan is available at http://www.atl.ec.gc.ca/reports/pdf/oil_spill_response.pdf.

Biases that band wear and loss cause in analyses of capture-mark-reencounter data are significant; I discuss these in detail in Chapters 2 and 4. Progress in gaining insights into population processes cannot be made if these biases are ignored. Unfortunately, band wear or loss seems to be a common problem in bird studies. In my own experience, I have seen evidence of considerable band loss on a diverse group of seabirds on three oceans; this includes loss of flipper tags in studies of pygocelids (brush-tail penguins). The continued use of bands under conditions that are known to cause band failure leads me to believe that there is a strong denial in the bird banding community that a problem even exists.

The use of bands in studies of long-lived seabirds is particularly problematic. For these species, the bands need to resist wear or loss for one or more decades. In addition, these species often nest adjacent to coarse substrates including sand, talus, and exposed bedrock. Results in Chapters 2 and 4 in this dissertation lead to only one conclusion, darvic bands should be abandoned as markers in studies of seabirds exposed to coarse substrates when study duration is above about five years. In their place, a wear resistant incoloy band is preferable, but even these may not resist problems for more than about 15 years. This means that a reliable solution for band wear is still unavailable. In my opinion, researchers marking long-lived birds should consider an alternative to bands; perhaps PIT-tags (Passive Integrated Transponder) or other devices that can be

detected remotely[8]; or DNA. These would provide many benefits including less need for human observers to detect marked birds, possibly higher detection probabilities, and no bias due to marker loss and wear.

6.2 Comparison of Survival and Dispersal Estimates from this Thesis to Other Conspecific Estimates

A comparison of adult survival estimates from this dissertation to other conspecific estimates is provided in Chapter 2, Section 2.5.3. Here I will make similar comparisons for estimates of immature survival and natal dispersal.

The only immature survival estimates[9] from the western Atlantic, prior to this dissertation, are 0%, 5%, and 9% from different cohorts reported by Kress and Nettleship 1988. Because these were estimated as return rates, they are likely underestimates of the true parameter. Also problematic is that these are estimates of survival to any age post-fledge. Using data from band recoveries, Mead (1974) suggested that 33% of the puffins marked as chicks survived their first year. An improved measure of immature survival is to estimate the parameter to the typical breeding age for the species (4 or 5 years) or for each age up to breeding age.

Harris (1983) estimated that 39% survived to breeding age (age 4); in calculating this estimate, Harris and Rothery (see appendix in Harris 1983) attempted to account for both detection probabilities and natal dispersal. For a long-lived species, like the Atlantic Puffin, 39% is very high suggesting either an overestimate or more likely, that "the Isle of May [was] an extremely good place

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[8] PIT-tag technology reading errors can occur when two or more tags are in close proximity. Also, PIT-tag readers must be within a few meters to detect the PIT-tag. These limitations will have to be overcome before PIT-tags can be used in most seabird studies.
[9] Here I'm referring only to estimates for native chicks not chicks transplanted from Newfoundland to the Gulf of Maine (Kress and Nettleship 1988).

to be a puffin [in the 1970's]" (Harris 1984). Based on age 0-3 and 3-4 immature survival estimates from this dissertation, immature survival to age four and five years is 46% and 41% respectively. These are consistent with estimates from Harris (1983) and suggest that conditions for survival of immature puffins have been very good for puffins born in the Gulf of Maine and Bay of Fundy from about 1982 to present. If we assume that the adult survival estimate from Chapter 2, 95%, can be applied to all managed colonies, then survival for puffins of all ages in the region is highly conducive to colony growth and expansion. This would explain why counts of breeding and non-breeding puffins at all colonies have increased and especially over the last ten years. One dramatic example of this is the increase from 7 to 290 breeding pairs at Seal Island from 1992 to 2004.

Kress and Nettleship (1988), Brown (reported by Harris 1984, pg. 173), and Harris (1983) all provide estimates of natal dispersal. However, the broad spatial scale and long time series provided by Harris (1983) probably comes closest to estimating the true value of the parameter. Harris (1983) monitored the movements of color-ringed puffins among several colonies in northeast Scotland from 1972 to the early 1980's. Data from this study provided a natal dispersal estimate of 23%. The arithmetic average from estimates in this study, excluding Seal Island, is 31%. If an estimate[10] for Seal Island calculated as 3/42 *100 = 7% is included, then the mean drops to 25%. The consistency between this estimate and the estimate from Harris (1983) is striking and suggests that the true *average* value for the species under similar conditions may be around 20-25%.

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[10] Three birds hatched on Seal Island bred on Eastern Egg Rock; 42 chicks were marked on Seal Island; 3/42 = 0.07.

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6.3   Ways to Improve the CMR Dataset and Other Suggestions for

   Managers in the Gulf of Maine and Bay of Fundy

   Suggestions outlined below and discussed in Chapters 2-5 are put forth on

the premise that all of us can improve. Although the results of this dissertation

are exciting and valuable, I believe that we can and should want to do better.

With these thoughts in mind, I hope that managers will not take any offense at my

suggestions and will try to implement any they decide might be valuable. After

five years of intimacy with the data that exist, study of estimation with CMR

models, and review of the animal demography literature, I believe that the reward

will be a future multi-site CMR analysis that is not overshadowed by a long list of

assumptions (Chapter 3) and that improves considerably on the predictive

component of this dissertation.

   Results in this dissertation and elsewhere (Kress and Nettleship 1988)

demonstrate that Atlantic Puffin colonies in the Gulf of Maine/Bay of Fundy

(GOM/BOF) region operate on a metapopulation scale. Therefore, it makes little

sense, with the exception of adult survival probabilities, for managers to estimate

demographic parameters using data from fewer than all five managed islands. For

this reason, I will assume, in the discussion that follows, that the goal of the three

teams managing puffins in the region is to repeat at some point in the future the

cooperative multi-site analysis presented in Chapter 3.

6.3.1   Bands, and Band Wear, Illegibility, and Loss

   Two suggestions I believe to be of particular importance are (1) use the

same band scheme, i.e., same field-readable band type, color, and engraving

pattern, on all islands and for all groups (chicks, adults, and others) and (2) apply a band that will resist problematic surface wear for close to the life expectancy of the bird. Of similar importance, managers should take more care when handling or resighting banded birds to note whether bands have been lost[11]; as noted elsewhere, these ancillary data are necessary for estimating band retention rates, which can be used to adjust survival probabilities that may otherwise be negatively biased due to band loss. These changes, alone, would significantly improve the quality of results from a future multi-site analysis; these changes would also make the analysis much more straightforward.

6.3.1.1   Use the Same Banding Scheme

Those deeply familiar with the full GOM/BOF dataset may have wondered why the analysis of known age birds in Chapter 3 included only about one-third ($n = 2,050$) of the 7,078 puffins marked as chicks in the region between 1973-2003 inclusive. Of those that were excluded, 1,832 were chicks transplanted from Great Island, Newfoundland (Kress 1997); many banding schemes were applied to these birds including multiple colored coils and engraved darvic bands. Nearly 2,000 ($n = 1,993$) were birds marked in recent years with metal field-readable leg bands. Those remaining were several hundred native chicks marked with either no field-readable band at all, or a combination of non-engraved colored coils.

Over two-thirds of the potential sample of chicks banded in the region (those just described) was excluded because of inconsistency in banding schemes

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[11] These can be conveniently recorded into Seabird Finder and onto accompanying capture/recapture field datasheets (Appendix 3); presence or absence of resighted bands could be recorded in the margin of the resightings field datasheet (Appendix 3).

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combined with sparse data and low resighting effort for some islands and years. To assure that all data can be used in future analyses, I strongly recommend applying the same field-readable band type, color, and engraving pattern to all age groups on all islands. This will assure that structure in detection probabilities that is a function of the band is consistent across all individuals. When these data are analyzed using CMR models, a minimal number of parameters will be required to account for this structure (White and Burnham 1999). Much will be gained including better precision (size of the $\hat{S}Es$) and more flexibility in models that can be considered in the analysis.

6.3.1.2 *Abandon Darvic Bands in Favor of a Wear Resistant Alternative*

As a graduate student at UNB, I was fortunate to attend two MARK workshops at Colorado State University. At both of these workshops, David Anderson, an expert in animal demography, CMR modeling and theory, stated that if your marks become illegible or fall off, "you might as well stay in bed". Band wear, loss and illegibility experienced by darvic bands applied to puffin adults and chicks in the GOM/BOF region will lead to biased estimates within fewer than ten years (Chapter 4). When these bands are applied to breeders (adults), survival estimates from these data might be biased low due to band wear within only five years (Chapter 4). Low adult survival probabilities reported in Chapter 3 (bands applied to chicks) likely resulted from bias due to band wear. This bias occurred within only six years after bands were applied to chicks, which is less than the seven years that I predicted in Chapter 4.

If managers are applying bands to puffins in the GOM/BOF region to estimate survival and movement among sites over the lifetime of a puffin, then engraved darvic field-readable bands need to be abandoned immediately as markers for these birds. In their place, a well applied, i.e., spins freely on the birds tarsus (see below), incoloy band is preferable; proper application may require seeking out an alternative-banding tool (see below). Managers should keep in mind that the loss in 'readability' of incoloy bands compared to darvic will be vastly outweighed by the increased longevity of these bands.

6.3.1.3 An Alternative Metal Field-readable Band with Improved Readability Features

With the issue of 'reduced readability' in mind, I have sought out the professional guidance of Rodney D. Breton (RDB), who has almost 40 years of experience in the trade of machining, tooling, and mold making, to develop a size five metal field-readable band with increased 'readability' features. Prototypes of these bands have been cut from stainless steel (grade 304-L[12]) as incoloy could not be located quickly (Fig. 6.1). New features are the following (Fig. 6.1): (1) engraved characters are thrice repeated; engraving pattern is identical to the current incoloy field-readables, i.e., two characters above, two below; (2) characters are filled with PermEnamel[13]; salt water resistance qualities of this material have not yet been determined; and (3) characters are engraved into bands that are juxtaposed between raised ridges. Improved readability features include

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[12] This grade may be susceptible to corrosion in salt water; for this reason, a higher grade, 316,is being considered.
[13] Manufactured by Delta Technical Coatings, Inc., Whittier CA 90601; purchased in a local crafts supply store.

(1) no opportunity to view a blank area on the band and much improved contrast between characters and the band by (2) filling the engraved area with colored material and (3) producing shadows via the raised and sunken features of the bands surface. Although the 'raised ridges' feature of the band improves readability, this feature was initially developed to deflect abrasion away from the engraved characters; whether or not this feature will actually reduce rate of band wear will require some form of testing.

In order that these, or the incoloy bands currently in use, could be applied easily and properly, i.e., free spinning on the bird's tarsus, RDB is also developing two sets of pliers. With these pliers, we hope to accomplish a tight butt between the two ends of the band while maintaining a visually precise round band shape. All of this we hope to accomplish with only a single squeeze on the new pliers. Prior to writing the first draft of this dissertation, RDB had made significant progress in developing pliers for closing the incoloy and prototype bands. Our long-term goal is to demonstrate that these alternative bands and pliers can be manufactured at a reasonable cost and subsequently made available to seabird researchers worldwide[14].

6.3.1.4   How Well a Band is applied May Affect How Quickly it Wears

It is important that bands spin freely on a birds tarsus. Recall from Chapter 4 that of the incoloy bands applied to puffin adults 43% may have been worn within five years (Table 4.2). Also recall that annual proportions suggested that model fitted values for incoloy bands applied to adults might have been

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[14] Using specially designed pliers, 200 of these new bands (cut from 304-L stainless steel) were applied in 2005, 100 on MSI and 100 on Seabird Restoration Program Islands.

positively biased (Figure 4.1): annual proportions remained relatively stable between two and five years post-application while fitted values steadily increase (Figure 4.1). If proportions were approximately stable over this period, then one explanation would be that a subset of incoloy bands applied to adults was uniquely susceptible to wear, and how well bands were applied could produce such a subset.

In order for bands to spin properly, it is important that the band retain its circular shape during application. Bands that are compressed or flattened on one or more sides during application will not spin properly; as a result, wear on the band surface will be distributed unevenly and will favor corners where the circular shape of the band has been jeopardized. If it were assumed that most bands applied to adults retained their circular shape during application and a small subset did not, then we would expect the smaller subset to wear at a faster rate than the larger subset. If both sets were analyzed together we would expect a rapid increase in wear, non-circular bands wear quickly, followed by a plateau, all non-circular bands worn; this is exactly the pattern we see in annual proportions in Figure 4.1.

Data were not available to test whether or not band wear was a function of how well bands were applied. However, bands with flattened sides have been observed in the population and these appear to be more noticeably worn compared to bands that retained their circular shape; as expected, wear on flattened bands is concentrated on corners (Karel Allard pers. comm.). Based on these observations and the pattern observed in annual proportions, it is possible that two subsets were

pooled in the analysis of incoloy bands applied to adults and as a result, model

estimates, for the majority of the incoloy bands in the population, may have been

positively biased. If applied properly, incoloy bands, in the GOM/BOF region,

might persist for ten or more years when applied to puffin adults. If band shape

was occasionally jeopardized during application to chicks, and there is no reason

to believe that it wasn't, incoloy bands applied to this part of the population may

resist problematic wear for fifteen or more years.

6.3.2   Sample Size

Data in a capture-mark-reencounter study come from *four* sources, number

of sampling occasions, number of newly marked individuals, encounters with

previously marked individuals, and covariates such as an index of resighting

effort (Pollock *et al*. 1990). Availability of these data, which represent 'the

sample', will dictate (1) the precision (size of the $\hat{S}Es$) of the estimates and (2)

complexity (number of parameters) of the CMR models that can be considered.

For example, if the sample is sparse, a test of time-dependence in survival

probabilities may not be possible. Explicitly, the analyst may experience

convergence failure when attempting to run the time-dependent model.

Convergence failure is a condition where by the numerical search procedure used

to solve the underlying log likelihood function of all CMR models is unable to

locate the peak of the function (Burnham and Anderson 2002). When this occurs,

the log likelihood function cannot be solved and consequently, estimates from the

model remain unavailable.

As these insights suggest, at the analysis stage, models and precision are limited by the sample as well as than the imagination of the person doing the analysis. For this reason and others, careful *a priori* thinking and planning are critical components of a CMR study. The architect of program MARK, Gary White, provided the following relevant advice at the 2004 MARK Workshop at Colorado State University, "be disappointed now not after the study is over."

6.3.2.1   Use Simulators to Avoid Sample Size Problems

Published results of extensive simulations are a valuable aid for avoiding problems in CMR studies and may be all that is needed in some cases (e.g., see Pollock *et al.* 1990 and below). Alternatively, investigators can perform their own simulations. Two simulation tools can be accessed in program MARK (White and Burnham 1999). Success with these tools will require a commitment to comprehend a rich CMR literature and terminology; but the payoff will include highly precise estimates of important demographic parameters and enough information (data) to run highly parameterized CMR models. The best resources I'm aware of to initiate a study of the method of CMR are the program MARK manual, written by Cooch and White (2001), and notes available online from a course taught by David Anderson (or recently by Ken Burnham) and Gary White at Colorado State University, http://www.cnr.colostate.edu/class_info/fw663/. After about six to eight months of committed study, anyone serious about doing CMR analyses should consider signing up for the weeklong workshop provided by the experts at Colorado State. Workshop announcements are posted at the

program MARK webpage, http://www.cnr.colostate.edu/class_info/fw663/,

maintained by Gary White.

6.3.2.2   Do Not Neglect the Biggest Payoff in CMR Studies – Detection

Probabilities

"The big law" in CMR studies is to "get p high"; alternatively, "p beats

the hell out of sampling more birds" (David Anderson, Mark Workshops in 2003

and 2004). Lower case 'p' is the model notation used to describe detection

probabilities; detections are achieved by many methods including resight,

recapture, and recover. Advice in quotes is based on results from hundreds of

simulations including those presented by Pollock *et al.* (1990) and others (e.g.,

Burnham *et al.* 1987).

In section 8.3 of the monograph by Pollock *et al.* (1990), the authors lay

out several plots of the coefficient of variation (CV) of a parameter, population

size (N) or survival (ϕ) or birth number (B), against detection probabilities. The

coefficient of variation of a parameter ($\hat{C}V_{\hat{\theta}}$) is equal to the ratio of the standard

error of that parameter to the estimate of the parameter itself, $\hat{C}V_{\hat{\theta}} = \dfrac{\hat{SE}_{\hat{\theta}}}{\hat{\theta}}$, where

the hat means values given are estimates[15] and theta ($\hat{\theta}$) is a generic symbol for a

parameter. As the $\hat{SE}$ declines, so does the $\hat{CV}$ and precision of $\hat{\theta}$. As a result,

inference from the sample to the sampled population, the ultimate goal of the

study, becomes more reliable.

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[15] For example, $\hat{SE}$ is an estimate of the true parameter SE where SE = standard error.

Across a range of N, ϕ, and B, Pollock *et al.* (1990) demonstrate that the relationship between the $\hat{CV}$ and detection probabilities is inverse exponential[16] until some point where higher detection probabilities provide no further reduction in the $\hat{CV}$. Their figures suggest a minimum detection probability of between 0.40 and 0.60 are desirable when survival probabilities of the focal animal are about 0.90; this is close to the rate experienced by adult puffins (Table 2.3). The authors suggest that these minimums should be enough to acquire a "reasonable" $\hat{CV}$, i.e., one at or below 20% (Pollock *et al.* 1990).

Their logic is revealed if we consider an example, say $\hat{\theta} = 0.80 \pm 0.16$ where 0.16 is $1\hat{SE}$; note that $\dfrac{0.16}{0.80} * 100 = 20\% = \hat{CV}$. An approximate 95% confidence interval for this estimate is $0.80 \pm 1.96 * 0.16 = 0.49, 1.0$. The interval, 0.49 to 1.0, reveals that even when the $\hat{CV}$ is 20%, the precision of the estimate is marginal. If, in this example, the $\hat{CV}$ attained was 10%, the $\hat{SE}$ would be 0.08 and 95% $\hat{CI}$, 0.64, 0.96. Notice that precision has been improved substantially, but ability to draw inference from the point estimate of the parameter to the sampled population remains marginal. This line of reasoning leads me to suggest that managers monitoring puffins in the GOM/BOF region maintain annual resighting (detection) probabilities at or above (ideally) 0.60 on all islands in order to achieve $\hat{CV}$s close to or (ideally) below 10%.

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[16] The relationship between the CV and detection probabilities describes a steep decline followed by a plateau of roughly equal lengths.

Effort expended in resighting puffins marked with *darvic* bands has produced resighting probabilities near or above 0.60 on all islands in recent years (Table 3.6). From a partial analysis of adults marked with either darvic or incoloy bands, I determined that the same amount of effort produced about 20% fewer sightings of incoloy compared to darvic bands. Therefore, if 100 hours were required to detect 80% (resighting probability = 0.80) of a cohort of puffins marked with darvic bands, I would expect that 120 hours would be needed to detect the same number of incoloy bands. These insights should be useful for determining how many hours are needed to achieve desired resighting probabilities of 0.60 or greater for incoloy or some other wear resistant field-readable band.

6.3.2.3 Adults Banded as 'Unknown Age' May Provide only Marginal Data for Estimating Survival Probabilities

The assumption of 'no heterogeneity in survival probabilities among groups'[17] is a common assumption of CMR models (Lebreton *et al.* 1992). When heterogeneity is present in a dataset, standard errors are underestimated (Anderson *et al.* 1994). Consequently, parameter estimates are reported with inflated precision. In addition, the estimates given represent an average for the group, which may or may be biologically meaningful.

In Chapters 2 and 3, I provide strong evidence that puffin survival probabilities from four of the five managed colonies are age-dependent (Table 3.7). Over the period studied, age 0-3, 3-4, 4-5, and above (adults) survival

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[17] Heterogeneity refers to differences in survival (or detection or some other parameter) probabilities among individuals within groups.

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probabilities were 0.60 (0.04 (1SE)), 0.77 (0.05), 0.87 (0.06), and 0.95 (0.01; Table 2.2) respectively. Notice that the arithmetic mean of these estimates, 0.80, tells us little about the demography of this species. If CMR data from a group of puffins captured, marked and released as 'after-hatch-year', meaning at least one year old, were analyzed, the survival estimate might look a lot like this arithmetic mean; and would similarly, tell us little or nothing about the species biology.

All of the management teams routinely mark adult puffins of unknown age. These are often aged as 'after-hatch-year, second-year, or third-year'. Unless these individuals are also identified as known breeders, CMR data accumulated from these animals will not provide useful estimates of demographic parameters. If birds are identified as known breeders, then these fall into a group that has biological meaning, i.e., an estimate of annual survival experienced by breeders would be useful for understanding the species demography. In order to avoid collecting marginal data, I recommend managers discontinue marking puffins of unknown age unless they are known breeders; if breeders, be sure to record this along with other data on the field datasheet and subsequently into Seabird Finder (see below). Alternatively, managers might seek-out (or develop) quantitative criteria, such as bill grooves (Harris 1984), for aging adults of unknown age; qualitative criteria such as presence of a brood patch would also be valuable. If these can be acquired with CMR data, I recommend carefully recording how each bird was aged. If aged accurately, these will be available, along with birds marked as chicks, for valuable known-age analyses.

6.3.2.4   Try to Mark More Chicks on Eastern Egg Rock, Petit Manan, and Seal

   Island

Recall that Eastern Egg Rock was excluded from the analysis of known

age birds presented in Chapter 3. Also, estimated resighting probabilities from

Petit Manan and Seal Island and dispersal probabilities from Petit Manan had

poor precision (Tables 3.6, 3.11). All of these problems resulted from too few

chicks marked and released from the three islands[18]. Egg Rock released fewer

than 20 chicks between 1981 and 2003 inclusive. Inclusion of Egg Rock with so

few data would have resulted in convergence failure of many models (see above).

Seal and Petit Manan each released about 80 chicks between 1987 and 2003

inclusive.

Managers should attempt to mark at least 10 chicks and ideally 20 or more

at both Eastern Egg Rock and Petit Manan annually. The long-term goal on all

islands should be to mark between 150 and 200 chicks annually. If detection

probabilities can be maintained at or above 0.60 (see above), this many chicks

marked annually will provide precise parameter estimates. Effort spent banding

more than about 200 chicks annually would be better spent resighting previously

marked birds.

6.3.2.5   When Should Another Multi-Site Analysis be Carried-out?

I recommend that the next analysis be performed after data have been

collected in 2009. This will allow time for ten years of CMR data to accumulate

on field-readable incoloy bands; this assumes that managers continue to apply this

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[18] Note that precision at Seal Island was better than Petit Manan. This is because resighting effort
was higher at the former.

band type. These data could be combined with data on darvic bands analyzed in

Chapter 3. Of course, detection probabilities for darvic and incoloy bands will be

different and these will have to be accounted for in the CMR analysis.

6.3.3   Data Collection and Management

6.3.3.1   Increase Commitment to Training to Ensure that Datasheets are Filled

Out Properly

Several columns on the resighting and capture/recapture field datasheets

have been either ignored or carelessly filled by observers (sample datasheets are

provided in Appendix 3). These datasheets were developed to accommodate

individual island work plans (for puffins) and accompany Seabird Finder, custom

software for managing CMR and ancillary puffin data. On the resighting

datasheet, band color, engraving color, special feature, and time under the 'band

description' have been left blank. Due to the complex history of banding schemes

applied in the GOM/BOF region *all columns* listed under 'band description' are

required to identify an individual band. Even when observers think a part of this

information is 'obvious', they should fill the columns as presented on the sheet.

What is 'obvious' at the moment may be far from obvious five, ten or more years

into the future.

Location and proximity under 'bird contact details' have also been

neglected. These are very useful for identifying if a banded adult is a breeder (see

above). When these ancillary CMR data are known, birds that were marked as

unknown adults can be lumped into a group described as 'breeders'; as detailed

above, CMR data from unknown adults may not otherwise be useful.

Subsequently, survival rates and other important demographic parameters for these breeders can be estimated (e.g., see Chapter 2).

Although records of 'behavior', another column in the bird contact details section, are not required by most island work plans, behavior records can be valuable for identifying if an adult is a breeder. Behaviors of relevant interest include carrying nest material, entering or exiting a known nest site, and carrying fish to a nest site (feeding). Breeders used to estimate adult survival probabilities in Chapter 2 were identified using location, proximity, and behavior. If this information had not been available, this analysis would not have been possible.

Two columns for recording details concerning band wear have also been neglected on the resighting field datasheet. Assuming that darvic bands are replaced by incoloy or an alternative, I recommend continuing to record band scores for these alternative bands for several years. An analysis of band wear data on incoloy bands aged ten years or more would make a valuable contribution to the CMR literature[19].

Columns neglected on the capture/recapture field datasheet are time, proximity, trap method, age, how aged, sex, and how sexed[20] in the section, bird contact details. Proximity along with location can be used (as above) to determine if a bird aged 'after-hatch-year, second-year, or third-year' might be a breeder. Chapters 2 and 3 demonstrate that survival and movement (prior to

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[19] Managers should consider recording the mass of bands before application and once bands are removed as an alternative to the subjective band wear scores that are currently in use. Rates of band wear calculated from these measurements are not uncommon in the literature (see list of references in Chapter 4).

[20] I include sex and how sexed in this discussion but recognize that these will often not be available when a bird is captured. However, managers should consider taking feather samples (or some alternative) to sex birds and subsequently fill this information (sex, how sexed) onto the datasheet.

breeding) are both functions of age (see also Newton 1995). Sex has been

identified as an important predictor of many variables including survival (e.g.,

Brooke 1978, Nichols *et al.* 2004) and dispersal (Greenwood and Harvey 1982).

Information about the capture/recapture 'stint' itself, i.e., the period-spent

trapping puffins, has occasionally been left completely blank. The time required

to fill out this section, once an observer has spent a few minutes becoming

familiar with the datasheet, is about one minute. These data provide estimates of

trapping effort and a record of where these activities were carried out.

I think the primary reason why some data are not recorded is

unwillingness by observers to spend 20 minutes to an hour becoming familiar

with each datasheet prior to resighting or trapping puffins. This probably leads to

confusion and either blank datasheet columns or columns filled with the wrong

information. Every detail of both datasheets is described in the key on the

datasheet itself and in the comprehensive manual for Seabird Finder. To remedy

these problems, I suggest either making the manual required reading for all

observers or requiring that island supervisors review the contents of all datasheets

prior to asking observers to record data.

6.3.3.2 *Increase Commitment to Training to Ensure that Data are Transcribed*
       Properly into Seabird Finder

Another reason for requiring that all observers read the manual is to

reduce errors made when entering data into Seabird Finder. Three of the most

serious problems that I have encountered have been typing over an existing record

when entering a new observer, failing to mark bands as removed, and not

recording (on database comment logs) errors made when entering new birds into the database. Chapter 5 of the Seabird Finder manual is dedicated entirely to teaching observers how to enter new observers (or staff) into the database. Part of Chapter 3 outlines how to update a band that has been removed or lost. Apparently, Seabird Finder users are not reading these and other important sections of the manual or making efficient use of the database comment log.

Although many database features, including drop down fields and input masks, go a long way to protect the integrity of data stored in Seabird Finder, sloppy data collection and careless data entry will over-time reduce the quality of the database. Thorough training for new observers is an efficient solution requiring relatively little effort. I believe the rewards of this effort will include more time rather than less for other responsibilities and high quality CMR and ancillary data for future analyses. To aid managers, I put together two training files for Seabird Finder, a comprehensive PowerPoint presentation and accompanying Word file, and distributed these to project partners in the spring of 2003. In 2004, the Word file was added to the manual as Supplement 2. As part of the manual, this file might be a useful aid for on-island training by supervisors.

6.3.4   The Value of Predicting versus Describing in Science

In a famous passage, R. A. MacArthur (1972) wrote "to do science is to search for repeated pattern, not simply to accumulate facts…". Pattern in nature is all around us and it is this phenomenon that allows for generalizations in science. However, the pinnacle of scientific achievement is not the elucidation of pattern. If science were to end here, then it would be a discipline limited to only

describing. Elucidation of the mechanisms behind the pattern is the highest

achievement that can be attained because this allows science to predict. I do not

believe that R. A. MacArthur intended, in his statement above, to focus science

practitioners on pattern at the expense of identifying 'cause and effect'

relationships. However, the desire to predict, at least in Ecology, seems to have

fallen far behind the desire to describe (Romesberg, 1981, Keppie 1990, Krebs

1995, Anderson 2001).

6.3.4.1   More Critical Thinking is Needed to Identify and Properly Record

Factors that Might Affect Puffin Demography

On the islands in the GOM/BOF, it is easy to apply bands to puffins and

subsequently resight them. If these activities produce high quality data, then

estimates of demographic parameters, e.g., survival or dispersal, can also be

attained with relative ease. What is difficult is identifying factors that might be

responsible for changes in demographic parameters. A quick search through the

literature will turn up an impressive list of papers estimating survival in long-lived

species. Fewer papers estimate dispersal but these are quickly growing in

number. However, this valuable research falls short of identifying factors in the

majority of cases. Progress, therefore, lies in elucidating factors that are driving

population vital rates as opposed to adding another 'brick', i.e., rates without

mechanisms, to the temple of animal demography and science in general

(Forscher 1963). I suggest that managers set aside a significant amount of time to

think critically separately, and as a group, about mechanisms, such as burrow

density and habitat availability, and then carefully plan how they will collect these

ancillary data simultaneously with CMR data. Otherwise, results from future analyses will be limited to estimates of survival and dispersal in puffins without insights into the processes that produced them.

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Fig. 6.1. Prototypes of an alternative size five field-readable metal band being developed by A. R. and R. D. Breton.

Appendices

Appendix 1

Permission to Reprint from Journals

Permission from The Auk (Chapter 2):

December 13, 2004

Mr. Breton:

Although your manuscript has not as yet been accepted formally [(see below)], if it is, The Auk will have no problem if you include a chapter in the Ph. D. thesis based on the paper submitted to The Auk.

All the best with your work.

Best wishes,
Spencer G. Sealy
Editor, The Auk

January 04, 2005

Dear Mr. Breton,

Thank you for submitting your revised manuscript, ADULT SURVIVAL ESTIMATES FROM TWO ATLANTIC PUFFIN (Fratercula arctica) COLONIES IN THE GULF OF MAINE, for publication in The Auk. Associate Editor Alan E. Burger and I reviewed this version and I am pleased to accept your work for publication in the July 2005 issue of The Auk. Thank you for your hard work on this manuscript…

Sincerely,
Spencer G. Sealy

Permission from Ecological Monographs (Chapter 3):

June 29th, 2005

Andre, yes, you have permission to reprint your paper in your thesis.

With best wishes,

Steve

Stephen Buckland
Subject Matter Editor
Journals of the Ecological Society of America
CREEM, The Observatory, Buchanan Gardens, St Andrews KY16 9LZ, Scotland
Tel.   +44-(0)1334-461841   Secretary +44-(0)1334-461842
Fax   +44-(0)1334-461800   e-mail   steve@mcs.st-and.ac.uk

Appendix 2

Information shared by Joe Nocera and Ted D'Eon via email concerning puffin

activity on Round and Noddy Islands, Mud Island Group, and Green Island,

Tusket Island Group, Nova Scotia

Sent to Ted from André Thursday, August 8th, 2002 3:00PM

Cheers Ted,

We met at a winter GOMSWG meeting in 2000/01 on Campobello Island. I am a student with Dr. Antony Diamond at the University of New Brunswick...our work (and Dr. Kress) focuses on survival and emigration rates in Atlantic puffin for the Gulf of Maine. We spoke about Noddy and Green Islands at that meeting.
You must be pleased with your census of the puffin colonies at both islands. It is good to hear some solid information concerning numbers and potential emigration from other colonies for Green and Noddy.

I was hoping to get some clarification for a few descriptions you made below...

1) Throughout the email, you often use the words 'at' and 'on' to describe sightings of puffins at the colonies. My question is 'do the numbers presented (e.g. you wrote..."90 puffins on Green Rock" - Aug 1st) include birds in the water and if so, how many (roughly)'.
2) Next, have you seen puffins carrying fish to either island...? Maybe during your on-island stint to Noddy?
3) Did you make your August 1st observations at Green Island from shore or from a boat?

I wonder if you've made it back to Noddy? Could you put me on your mailing list if you do and then send out a report similar to the one below?
My Best,
andre

Received from Ted Sunday, August 11th, 2002 10:47 PM

André:

The puffins seem to be doing well. The Roseate Terns on The Brothers, really great. (0 Roseate Tern nests with a minimum of 62 chicks and very little mortality.

My figures (e.g. "90 puffins on Green Rock" - Aug 1st) should really have been "at Green Rock", meaning "on and around". The same applied to Noddy and Round islands.

I could not read the characters on the puffin leg bands. The green bands looked like green over white plastic. The characters appeared white, however, it looked like some of the green had rubbed off and white areas showed through.

I have seen puffins carrying at all 3 locations this summer. On Round Island, June 29, one adult puffin stayed under the boulders while we were searching for evidence of chicks or eggs. It must have known it was safe under the rocks beyond our reach.

On August 1 on Green Rock while I was at one of the nesting sites, I could hear purring sound of puffins in the boulders, though I could not locate them. I only would see them as they were coming out from the boulders.

My Aug 1 observations at Green Rock were both from the boat and on land. My photos were from land. There are puffins at two distinct areas of Green Rock; a small islet at the south end where most of the puffins were seen and also an area below and to the west of the lighthouse. The lighthouse colony was only viewed from the boat.

Thanks for the note. I look forward to meeting you again in the future. Perhaps next summer I can take you to these islands. I would love to do it.

Ted C. D'Eon
c/o PHARMASAVE West Pubnico
P.O. Box 100, West Pubnico,
Nova Scotia B0W 3S0   Canada
Phone 1-902-762-2097 at home, 1-902-762-2793 at work
FAX 1-902-762-2885
E-Mail ted@ns.sympatico.ca
Internet address http://pages.ca.inter.net/~deonted/

Sent to Ted from André Tuesday, March 25th, 2003 5:37 PM

Good Day Ted...

I am currently working on a paper concerning adult survival rates for Atlantic puffin in the Gulf of Maine. In it, I give some history of puffin colonies for the region. The information you have already given has been extremely helpful...in fact, it seems that you are the only person who knows anything about ATPU colonies off southwest NS. Therefore, I am exceptionally grateful for your insights...

I wonder, for the three colonies you have made me aware of (Green Rock, Round and Noddy Islands), can you tell me:

(1) If they were occupied by ATPU prior to the last century...
(2) When birds (that you are now seeing) might have colonized...

At this point, I'm guessing that all islands were previously occupied by the species (19th century) and as a result, their arrival their in last century is a recolonization

event rather than an occupation of new territory. As well, I'm guessing that they recolonized in the last 20 years...can you help me clarify any of this?
My Best,
andre

Received from Ted Sunday, March 30th, 2003 10:35 PM

Hello André:

Good to hear from you. I am not sure if I can help you much. Most of what I know of the history of the puffins around here came from Roby Tufts "the Birds of Nova Scotia". A link to its puffin page is http://museum.gov.ns.ca/mnh/nature/nsbirds/bns0200.htm (from the NS Museum web site).

From what I have gathered from the local fishermen there may have always been a few pairs of puffins nesting on Green Island (a.k.a. Green Rock) and on Noddy Island even between the early 1900s and the 1980s. I do not know where the truth lies. Tuft does not mention these islands and there are no puffins on Seal Island now. Even today, many lobster fishermen fishing in the bay even close to Noddy Island tell me they have never ever seen a puffin. They used to be exclusive to the southwestern cove of Noddy I. The fishermen fishing on this side of Noddy have known about the puffins for a long time (a couple of decades, perhaps). From my general observations of last year, I can say that their activity at Noddy now includes the east side of the island also. I believe their nesting area is on the increase. Only a few puffins nest on the east side of Round Island.

That is about all I know. I will be doing more observations on the puffins this spring and summer. I am especially interested in leg bands and definitely will be checking for Razorbill nesting activity with the puffins of Green Rock.

Likely, my observations will be posted on my puffin web pages so you can keep tab on my activities.
Ted

Correspondence Between Joe Nocera and Myself by Email:

Sent to Joe from André Monday, February 02, 2004 3:22 PM

You suggested (I think) that "Round Island" [(Mud Island Group, Nova Scotia)] was 'not currently' active...is this true? Perhaps if you have 5 minutes, call me on this one (454-5275). – andre

Received from Joe Tuesday, February 10th, 2004 4:51 PM

Yup, you are correct that I said that. When I was on that island in 2001, I saw no sign of puffin breeding. Likewise, dozens of local fishermen that stay on Seal Island (with the ABO) have all said that they have not seen them on Round Island for years either.

Noddy Island does have a few pairs. I found a few burrows in 2001, and you can predictably see puffins loafing there. The fishermen are always going there to watch them.

Joe

Sent to Joe from André Tuesday, February 10, 2004 8:32 PM

Thanks Joe...this is a nice catch before any of my papers get (we hope!) published. Tony [Diamond] and I will have to discuss this...and make (minor) changes to both of my manuscripts. I do have a few questions, can you tell me the date, time of day, and duration spent on Round Island that you mention below (2001). How well you feel you searched (briefly). Lastly, did you see any birds close by in the water? I'll likely be asked all of these questions at some point! Cheers, - andre

Received from Joe Wednesday, February 11th, 2004 11:39 AM

Hi Andre,

I'll try to answer your questions.
Date = exact date unknown, late May 2001.
Time of Day = mid-morning (say ~9:00ish).
Duration = maybe 2 hours.
Searching = quite well.
Birds in nearby water = none.

The island [(Round)] is very small, and has numerous half-buried oil drums, which are meant to provide protection to eider nests from the numerous sheep that live on the island (and trample nests). Our job was to investigate every barrel, nook, and cranny on the island looking for eider nests. As well as to beat bush looking for grass-nesting eiders. So between myself and the 6 others that were with me, we had our hands and heads in EVERY hole and boulder crevice on that island. We found a few guillemots (they are on just about every island out that way), but no other alcids.

In addition, we go by this island just about every time we head to Seal Island to get Trinas crew set up. Never in my approximately 15-20 trips by this island have I ever seen a puffin nearby. I have indeed seen them almost every time I go by Noddy. (It is worth noting that Noddy has no sheep or rats).

An additional point of anecdotal evidence is that several fishermen that live on Seal Island run trap lines through the "Muds". So, they go through those islands every two days for the entire spring. They have all said they have never seen "puffins on there"; only on Noddy. This likewise holds true for the fishermen that live on Seal for the summer. Although they are not running trap lines (that I can tell you about!), they are often in boats around the Muds for several reasons...and again maintain there are no puffins there.

Given all this I'd say it is unlikely that they have been on Round in the recent past (since 2001 anyway). There certainly is a chance we/I missed a pair or two... I can't discount that. But I'd bet my last dollar there is no "colony" there... only on Noddy. I would say that 7-10 active burrows on Noddy would be a good estimate.

Cheers,
Joe

Appendix 3

Sample Field Datasheets:

Resighting *and* Capture/Recapture

| Island Alpha: | Year: | | | Stint Type: Sighting | | | | | | | | | *Use on SINWR and EER* | | | Band Wear | |

Stint Details (Date like mm/dd/yy)					Band Description				Bird Contact Details				Interacting Bird Band Desc.			Present/Wear Score	
*Obs.	Location (Blind)	Start	End	Date	Btype	BClr	EClr/SF	AlphaNum	Time	Loc/Px	S/H	Beh(s)	Btype	BClr	AlphaNum	FRB	BBL
ARB	Loafing Ledge Blind	12:00	15:00	01/30/00	PFR	Y	Blk/HR	656	09:36	B100/1	M/2	F,B	PFR	R	212	Y/2	Y/U
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*Please Identify Observers with Initials

ARB - Andre R Breton

Comments:

KEY: (use codes on lookup sheet when available)

*Obs=Observer initials	Sf=Special Feature	FRB = Field Readable Band
Start=Time Start	AlphaNum=AlphaNumeric	BBL = USFWS Band
End=Time End	Loc=Location	Present = Yes(Y) or No (N)
Btype=BandType	Px=Proximity to Location	Wear Score = 1 - 4 or U (unk)
BClr=Band Color	S/H=Sex/How Sexed	
EClr=Engraving Color	Beh=Behaviors	

CAPTURE/RECAPTURE FIELD DATASHEET for ATPU   Formatted to accommodate all SRP workplans   *NEW* **Field Readable Band**   *NEW* **BBL Band**   Pg ____

| *Supervisor Initials: | | Island: | | Year: | | Date Start: | | Date End: | | | BClr: EClr: Sfeat: | | | | of ____ |

BClr: EClr: Sfeat:

Stint	Bird Contact Details (military time only)						Measurements (mass in grams and lengths in millimeters)												NEW Field Readable Band		NEW BBL Band		~Recapture
**St#	Time	Loc	Prox	TrM	Age/H	Sex/H	*MB	Mass	WC	Cul	Blen	Bdep	HB	***FS	Tars	Btype	BClr	AlphaNum	Tars	AlphaNum	reference
1	23:59	B100	2	3	ATY/2	M/2	ARB	600	136	48.5	39.6	40.4	81.6	1	L	PFR	R	ZZ01	R	0705-55065	ZZ01
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**Stint #1	**Stint #2	**Stint #3	KEY: (use codes on lookup sheet when available)		
Location:	Location:	Location:	**St# = Stint Number	Cul = culmen	EClr=Engraving Color
Date (mm/dd/yy):	Date (mm/dd/yy):	Date (mm/dd/yy):	Loc=Location	Blen=Bill Length	Sfeat=Special Feature
Time Start-End:	Time Start-End:	Time Start-End:	Prox=Proximity to Location	Bdep=Bill Depth	AlphaNum=AlphaNumeric
Stint Type:	Stint Type:	Stint Type:	TrM=Trap Method	HB=Head-Bill	BBL=Bird Banding Lab or service band
^Trap Type/#, Loc., time set/remove:	^Trap Type/#, Loc., time set/remove:	^Trap Type/#, Loc., time set/remove:	Age/H=Age/How Aged	FS=Feather Score	~Recapture reference = a reference to old
			Sex/H=Sex/How Sexed	Tars=Tarsus	bands and band wear recorded on the
			*MB=Measured By	Btype=BandType	back of this datasheet; use *new* field
			WC=Wing Cord	BClr=Band Color	readable band alpha numeric or integer.
*Please Identify Initials (like ARB - Andre R Breton):			Notes:		

*Please identify initials above.
**Summarize additional Stints on the back of the datasheet.

***FS = Feather Score (1=no down, 10=all down).
^If trap type is grubbing or pursue, then # traps = # of participants.

ANDRÉ R. BRETON
Curriculum Vitae

Education:

Ph. D. – University of New Brunswick (UNB)   2000 – 2005
B.A. – Massachusetts College of Liberal Arts (MCLA; Biology major)
                                                         1990 - 1994
6 Credits – Dean Junior College, Massachusetts   1989 - 1990

Conference Presentations:

2005 Pacific Seabird Group and Waterbird Society Joint Meeting. Portland,
Oregon. Encounter, survival, and movement probabilities from an Atlantic
Puffin (*Fratercula arctica*) metapopulation. **Breton, A. R.**, A. W.
Diamond, & S.W. Kress

9th Annual Atlantic Cooperative Wildlife Ecology Research Network (ACWERN)
Conference. UNB, 2004. Encounter, survival, and movement probabilities
from an Atlantic Puffin (*Fratercula arctica*) metapopulation. **Breton, A.
R.**, A. W. Diamond, & S.W. Kress

8th Annual ACWERN Conference. Acadia University, Nova Scotia. 2003.
Challenges in estimating seabird demographic parameters: *insights and
uncertainty*. **Breton, A. R. & C. Devlin**

2003 Annual Northeast Wildlife Graduate Student Conference (NWGSC).
University of Prince Edward Island. Evaluating the reliability of covariate
analysis using survival rates from colony-based studies. **Breton, A. R.**

11th Annual Graduate Student Association Conference On Student Research.
UNB, 2003. What is science? **Breton, A. R.**

2002 Annual NWGSC. UNB. Adult survival of a long-lived seabird, the Atlantic
Puffin *(Fratercula arctica),* in the Gulf of Maine. **Breton, A. R.**, A. W.
Diamond, & S.W. Kress

6th Annual ACWERN Conference. Sackville, New Brunswick. 2001. Estimating
age-specific survival and distribution of emigrants between colonies of
Atlantic Puffin (*Fratercula arctica*) in the Gulf of Maine. **Breton, A. R.**,
A. W. Diamond, & S.W. Kress

2001 Annual NWGSC. University of New Hampshire. Colony and year effects on
survival, intercolony movement, and emigration of Atlantic Puffins
(*Fratercula arctica*) in the Gulf of Maine. **Breton, A. R.**, A. W. Diamond,
& S.W. Kress

5th Annual ACWERN Conference. Huntsman Marine Lab, New Brunswick. 2000.
Sub-adult survival and intercolony movement of Atlantic Puffins
(*Fratercula arctica)* in the Gulf of Maine. **Breton, A. R.**, A. W. Diamond,
& S.W. Kress

Publications:

Refereed publications – *in press*

Breton, A. R., A. W. Diamond, & S.W. Kress. Adult survival rates of Atlantic Puffin (*Fratercula arctica*) at two colonies in the Gulf of Maine. ***The Auk***, July 2005 Issue.

Breton, A. R., A. W. Diamond, & S.W. Kress. Encounter, survival, and movement probabilities from an Atlantic Puffin (*Fratercula arctica*) metapopulation. ***Ecological Monographs***.

Refereed publications – *Submitted or Invited for Resubmission (IFR)*

Breton, A. R., A. W. Diamond, & S.W. Kress. Surface wear on incoloy and darvic bands applied to Atlantic Puffin (*Fratercula arctica*) adults and chicks. ***Journal of Field Ornithology***, **IFR** on 29 April 2005.

Breton, A. R., A. W. Diamond, & S.W. Kress. The overlap assumption: an important source of bias in studies of migratory animals. ***Journal of Wildlife Management***, **IFR** on 10 April 2005.

Allard, K. A., **A. R. Breton**, H. G. Gilchrist, & A. W. Diamond. Adult survival in an Arctic breeding herring gull (*Larus argentatus*) population. ***Waterbirds***, **Submitted** 24 June 2005.

Keeler, R., **A. R. Breton**, D. Peterson, & R. Cunjak. Survival and movement of slimy sculpin, *Cottus cognatus*, in five New Brunswick streams. ***Transactions of the American Fisheries Society***, **Submitted** on 24 May 2005.