

**Variation in Shorebird Nest Survival:
Proximate Pressures and Ultimate Constraints**

by
Paul Allen Smith

A thesis submitted to the Faculty of Graduate Studies and Research in partial
fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Biology
Carleton University
Ottawa, Ontario

May 2009
© Paul A. Smith, 2009



Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file *Votre référence*
ISBN: 978-0-494-52050-5
Our file *Notre référence*
ISBN: 978-0-494-52050-5

NOTICE:

The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protègent cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.


Canada

Abstract

Nest survival for shorebirds breeding in the arctic varies dramatically among species and years, but our understanding of this variation has been largely speculative. By finding and monitoring 1314 nests of 14 shorebird species, I have been able to assess patterns in nest survival that were unexplored. I tracked the timing of shorebirds' arrival and breeding over 11 years at four sites in the eastern Canadian Arctic. Although timing of arrival was relatively invariant, I found strong effects of local conditions on timing of breeding, with greater snow cover leading to delayed nesting, and a higher abundance of predators resulting in earlier nesting. Using logistic-exposure analyses, I found that the large variation in nest survival among years was related to the local abundance of predators. The pattern in nest survival among species was modelled most parsimoniously by distinguishing between species with uniparental and biparental incubation, with the former group having consistently lower rates of nest survival. For all species, nest survival was typically lowest in the middle of the nesting season but this pattern was not explained by the high densities of shorebird nests available at this time. Predators' access to other diet items, in addition to shorebird nests, may instead determine these temporal trends. I found that species with biparental incubation defended older nests more aggressively, and this may have contributed to the increase in nest survival with nest age that I observed. Finally, through nearly 800 days of behavioural observation on 11 species in arctic Canada and Siberia, I showed that more frequent breaks from incubation, or leaving the nest unattended for longer periods of time, increased the risk of nest predation. Total nest attendance explained 83% of the variability in nest survival among these 11 species, and incubation recesses and restless movements on the nest were more numerous at nests that would eventually fail versus those that were successful. Together,

these findings significantly advance our understanding of patterns in shorebird nest survival, and I conclude by discussing how this work can be used to better monitor shorebird populations.

Table of contents

Abstract	iii
List of tables	viii
List of figures	xi
Chapter 1. General introduction	14
Objectives and outline.....	5
Study sites	9
Shorebird species and their predators	9
Declaration.....	13
Chapter 2. Inter-annual variation in the breeding chronology of arctic shorebirds: effects of weather, snow melt and predators	15
Abstract.....	16
Introduction.....	17
Methods.....	20
<i>Study areas</i>	20
<i>Shorebirds and their predators</i>	22
<i>Monitoring weather and snow melt</i>	24
<i>Timing of arrival</i>	24
<i>Nest finding and ageing</i>	25
<i>Data analysis</i>	26
Results.....	27
<i>Weather and snow melt</i>	27
<i>Indices of predator abundance</i>	28
<i>Timing of arrival</i>	29
<i>Timing of nest initiation</i>	31
<i>Synchrony of nest initiation</i>	33
Discussion	33
<i>Timing of arrival</i>	34
<i>Timing of nest initiation</i>	35
<i>Synchrony of nest initiation</i>	40
Chapter 3. Predator abundance and incubation behaviour explain interannual and interspecific patterns of nest success for arctic breeding shorebirds	51
Abstract.....	52
Introduction.....	53
Methods.....	56
<i>Study areas</i>	56
<i>Shorebirds and their predators</i>	57
<i>Monitoring weather and snow melt</i>	58
<i>Artificial nests</i>	59
<i>Shorebird nest finding, ageing and monitoring</i>	60
<i>Data analysis</i>	61
Results.....	62

<i>Weather, snow melt and predators</i>	62
<i>Interspecific and temporal patterns of nest survival</i>	63
<i>Interannual patterns of nest survival</i>	65
<i>Artificial nest experiments</i>	67
Discussion	68
<i>Interspecific and temporal patterns of nest survival</i>	68
<i>Interannual patterns and predator abundance</i>	73
<i>Artificial nests</i>	75
<i>No evidence for an effect of lemming abundance</i>	76
Chapter 4. Intra-seasonal patterns in shorebird nest survival are related to nest age and defence behaviour	87
Abstract	88
Introduction.....	89
Methods.....	91
<i>Study area</i>	91
<i>Shorebirds and their predators</i>	92
<i>Shorebird nest finding, ageing and monitoring</i>	93
<i>Flush distance and nest defence</i>	94
<i>Nest density</i>	94
<i>Hypotheses and predictions</i>	95
<i>Data analysis</i>	97
Results.....	99
<i>Environmental conditions</i>	99
<i>Year and species effects</i>	100
<i>Effects of time and nest age</i>	101
<i>Effects of weather and predators</i>	102
<i>Nest density</i>	103
<i>Flush distance and nest defence</i>	103
Discussion	104
<i>Temporal patterns in shorebird nest survival</i>	104
<i>Factors determining temporal patterns in nest survival</i>	105
<i>Age-related patterns in shorebird nest survival</i>	108
Chapter 5. The influence of weather on uni- and biparental shorebird incubation	122
Abstract.....	123
Introduction.....	124
Methods.....	126
<i>Study area</i>	126
<i>Shorebird nest finding, ageing and monitoring</i>	127
<i>Monitoring incubation behaviour</i>	127
<i>Data analysis</i>	130
Results.....	132
<i>Behaviour of uniparental versus biparental incubators</i>	132
<i>Diel patterns</i>	133
<i>Temporal and weather related effects</i>	134

<i>Incidence of egg neglect</i>	137
Discussion	137
<i>Variation in incubation behaviour within days</i>	138
<i>Variation in incubation behaviour among days</i>	139
<i>Incidence of egg neglect</i>	140
<i>Effects of predators and diet?</i>	141
Chapter 6. Shorebird incubation behaviour and its influence on the risk of nest predation	151
Abstract.....	152
Introduction.....	153
Methods.....	155
<i>Study area</i>	155
<i>Shorebird nest finding, ageing and monitoring</i>	156
<i>Monitoring incubation behaviour</i>	157
<i>Timing of predation and observations of predators</i>	160
<i>Data analysis</i>	161
Results.....	163
<i>Nest survival and behaviour among species</i>	163
<i>Behaviour of incubators at successful versus failed nests</i>	165
<i>Time to failure</i>	165
<i>Analyses of paired observations</i>	166
<i>Timing of predation and observations of predators</i>	167
Discussion	169
Chapter 7. General discussion	184
<i>Predation and timing of breeding</i>	186
<i>Predation, predator abundance and alternative prey</i>	187
<i>Predation throughout the season</i>	189
<i>Predation and behaviour</i>	192
Future Directions	194
<i>Shorebirds as income-breeders</i>	194
<i>The evolution of shorebird life-history</i>	196
<i>Incubation behaviour in response to risk</i>	198
<i>Nest success versus fecundity</i>	199
Conservation Implications	200
Literature Cited	206

List of tables

Table 1.1. Body mass, social mating system, and incubation behaviour for the 10 shorebird species that are the focus of this thesis. Data are from this study, Thomas et al. (2006), Tulp (2006), and references therein.....	14
Table 2.1. Sample size (nests), first sightings and timing of breeding data for shorebirds breeding at four sites in the eastern low arctic. Data presented are means across years. *Limited data were available for Prince Charles Island in 1996 because staff arrived to the area in mid June.	43
Table 2.3. Results of an analysis of timing of breeding for shorebirds at East Bay Mainland and Coats Island, Nunavut. Separate General Linear Models were generated for the five timing metrics (earliest nests – latest nests) and for synchrony (measured as the standard deviation of initiation dates). Variables not found to be significant in any models include: mean temperature (°C, 10 – 30 June), mean daily windchill low (°C, 10 – 30 June) and mean wind speed (km / h, 10 – 30 June). Ns = not significant at $\alpha = 0.05$	47
Table 3.1. The total number of nests found of each species at the East Bay and Coats Island sites ('Total'), and the number used in analyses of daily nest survival ('Analysed'). Whether incubation is undertaken by one parent (uniparental) or both (biparental) is also displayed.	78
Table 3.2. Weather variables and the date of 50% snow clearance for the East Bay and Coats Island sites.....	79
Table 3.3. Summary of model selection results for an analysis of shorebird nest survival at East Bay, Nunavut, 2000-2007. The dependent variable was the daily rate of nest survival, AIC_c = Akaike's information criterion corrected for small samples, ΔAIC_c = the change in AIC_c relative to the top model, w_i = Akaike weight, a measure of relative support for the model, and deviance is the difference in the $-2 \log$ -likelihood between each model and the saturated model. The parameter abbreviations are as follows: S. = a single estimate of daily survival, species = a categorical variable denoting species, incub. = incubation system (biparental or uniparental), T, T^2 = time and time ² , Foxes, Jaegers, Lemmings = the encounter rate (sightings per observer*hour) of these species, temp = the mean daily temperature from 10 June – 25 July, snow = the Julian date of 50% snow clearance, and wind = the mean daily windchill low from 10 June – 25 July. A '+' indicates an additive effect, while a '*' indicates an interaction between two variables.....	80
Table 3.4. Parameter estimates, standard errors and lower and upper 95% confidence limits (LCL and UCL, respectively) for the top model of daily nest survival of shorebirds at East Bay, Nunavut, 2000-2007. The top model, as well as the	

abbreviations, appear in Table 3.3. Biparental incubation was coded as 0; the parameter estimate reflects the additive effect of uniparental incubation. 81

Table 3.5. Summary of model selection results for an analysis of shorebird nest survival at Coats Island, Nunavut, 2004-2006. AIC_c = Akaike's information criterion corrected for small samples, ΔAIC_c = the change in AIC_c relative to the top model, w_i = Akaike weight, a measure of relative support for the model, and deviance is the difference in the $-2 \log$ -likelihood between each model and the saturated model. Factors in the models included species, a single estimate of daily survival (S.), incubation system (biparental or uniparental, 'incub. '), time (T), time² (T²), and year. A '+' indicates an additive effect, while a '*' indicates an interaction between two variables. 81

Table 3.6. Parameter estimates, standard errors and lower and upper 95% confidence limits for the top model of daily nest survival of shorebirds at Coats Island, Nunavut, 2004-2006. The top model, as well as the abbreviations, appear in Table 3.5. Biparental incubation was coded as 0; the parameter estimate reflects the additive effect of uniparental incubation. 82

Table 4.1. The total number of shorebird nests found, and the sample used in the analyses of nest survival with Program MARK. 111

Table 4.2. Summary of model selection results for an analysis of shorebird nest survival at East Bay, Nunavut, 2000-2007. AIC_c = Akaike's information criterion corrected for small samples, ΔAIC_c = the change in AIC_c relative to the top model, w_i = Akaike weight, a measure of relative support for the model, K is the number of parameters, and deviance is the difference in the $-2 \log$ -likelihood between each model and the saturated model. The parameter abbreviations are as follows: Weather(d) represents the current day's weather, weather(d-1) represents the previous day's weather, jaegers represents the number of jaegers sighted per observer hour, and density is the daily count of active shorebird nests. These three variables were standardised within years to mean = 0 prior to analysis. A '+' indicates an additive effect, while a '*' indicates an interaction between two variables. 112

Table 4.3. Parameter estimates, standard errors and lower and upper 95% confidence limits for key variables associated with daily nest survival of shorebirds at East Bay, Nunavut, 2000-2007. All estimates were determined using model averaging based on the top 7 models in Table 4.2 and representing > 0.99 of the AIC_c weights. Estimates for time and time² were obtained using models 3 and 7 where they are included as a single additive effect. Uniparental incubation was coded as 0; the parameter estimates for incubation system therefore reflect the effects of biparental incubation. 114

Table 4.4. The mean distance at which birds flushed when their nests were approached, and the intensity of the nest defence they subsequently displayed. Species are

displayed with AOU 4-letter codes¹, and “behaviour code” included the following 5 categories: 0 = no response, 1 = scold from >10 m away from observer, 2 = scold from ≤ 10 m away, 3 = distraction display, 4 = attack (i.e. aerial mobbing)..... 115

Table 5.1. The number shorebird nests, and days of behavioural observation, included in the samples. Incubation is uniparental for the Red Phalarope and White-rumped Sandpiper and biparental for the remaining species. 143

Table 5.2. Summary of the incubation behaviour of shorebirds, based on the full dataset. Recesses for species with biparental incubation (Semipalmated Plover, Black-bellied Plover, American Golden-Plover, Ruddy Turnstone, Dunlin and Semipalmated Sandpiper) may have ended with the return of either parent. See text for a description of how movements were quantified. Means are displayed ± SE. 144

Table 5.3. Results of a general linear mixed model analysis to describe diel patterns in the incubation behaviour of shorebirds. Data were entered as an average value for each hour of the day, for each nest, and are based on the reduced dataset (where days with atypically long recesses (> 45 min) were filtered). Nest was entered as a random effect in all models..... 145

Table 5.4. Results of a general linear mixed model analysis to describe patterns among days in the incubation behaviour of shorebirds. Nest was entered as a random term in all models, while the remaining fixed effects were entered in a forward stepwise procedure. Analyses are based on the reduced dataset, where days with atypically long recesses (> 45 min) are omitted. The uniparental species were the White-rumped Sandpiper and the Red Phalarope, while the biparental species were the Semipalmated Plover, Black-Bellied Plover, American Golden-Plover, Ruddy Turnstone, Dunlin and Semipalmated Sandpiper. 146

Table 5.5. The variables that significantly increase the probability of temporary nest abandonment (i.e. absence > 45 min), and the direction of their effect, as determined by logistic regression. Results are displayed only for variables with $P \leq 0.05$ 148

Table 6.1. Sample sizes of nests found (included in analyses of nest survival), nests observed for incubation behaviour and days of observations collected. For each species, I also list whether incubation is uniparental or biparental, and whether the behavioural data include information on restless movements on the nest..... 177

Table 6.2. Sample sizes, means and standard errors for the six metrics of incubation behaviour from the sample where observations from unsuccessful nests are paired with observations from the same year, species and day, from successful nests. 179

List of figures

Figure 2.1. The four study sites in the eastern arctic, Nunavut, Canada. The East Bay Mainland and Island sites are separated by a distance of only 7 km.	48
Figure 2.2. The mean daily windchill low (°C) from 10 June – 30 June, for the East Bay Mainland site on Southampton Island, Nunavut, 1999 - 2007.	49
Figure 2.3. The number of predators and lemmings encountered in each year (sightings per observer hour) at the East Bay (a) and Coats Island (b) sites. Note that jaegers were the most abundant predator in all years; the encounter rate displayed in the figure is /10 to equalize the scale among species.	50
Figure 3.1, a-c. The predicted daily probability of nest survival for biparental and uniparental incubating shorebird species at East Bay, Southampton Island, Nunavut. All figures are based on the most parsimonious model, which includes effects of incubation type, a quadratic time effect, indices of fox and jaeger presence, and a fox*incubation type interaction effect. Panel a) shows the effect of time (day 1 = June 10) when predator presence is held constant at the observed mean, b) shows the effect of varying jaeger abundance half-way through the nesting season with fox abundance held constant at the observed mean and c) shows the effect of varying fox abundance half-way through the nesting season with jaeger abundance held constant at the observed mean. The range of variation in fox and jaeger abundance displayed in the figures reflects the range observed in the sample.	83
Figure 3.2. The probability of nest survival on each day of the nesting season (Day 1 = 11 June) for biparental and uniparental shorebird species, 2004-2006, at Coats Island, Nunavut. Estimates are based on a model including incubation system (uniparental versus biparental), a year effect, and a quadratic effect of time (see text).	84
Figure 3.3. The rate of daily nest survival on the median date of nest initiation, as predicted by the top models from the East Bay and Coats Island sites (see Tables 3.3 and 3.5). At East Bay, predictions were made with year specific values for fox and jaeger abundance, and the median date of nest initiation was 22 June. At Coats Island, the median date of nest initiation was 18 June.	85
Figure 3.4. The daily survival rate (\pm SE) of artificial nests containing four Japanese Quail (<i>Coturnix japonica</i>) eggs at East Bay (A) and Coats Island (B), Nunavut, 2004-2006. Overlaid is the predicted daily survival of real nests from the best models, calculated for 13 July (half-way through the artificial nest experiment) with year specific values for predator abundance. Note that the survival of real nests was much higher in all years, and is displayed on a different axis for clarity.	86

Figure 4.1. Temperature low, windchill low and windspeed high for each day of the shorebird breeding season at East Bay, Nunavut. Daily values are the means for all years \pm SE. Day 150 = 30 May.	116
Figure 4.2. The number of foxes and jaegers sighted per observer hour at East Bay, Nunavut. Daily values are the means for all years \pm SE. Note that jaegers were the most abundant predator on all days, and the values are divided by ten.	117
Figure 4.3. The temporal distribution of shorebird nest initiations throughout the breeding season. Day 1 is equal to 10 June here and in subsequent figures. Initiations were calculated for 472 of 574 nests.	118
Figure 4.4. The daily probability of nest survival for uniparental and biparental shorebirds at East Bay, Nunavut, based on the predictions of the most parsimonious model (see Table 4.2), which incorporates both time and nest-age effects. Predictions are displayed for a 21 day incubation period (i.e., nest age ranges from 1 to 21), initiated on the median date of nest initiation for uniparental (Day 17 = 26 June) or biparental (Day 10 = 19 June) species. Values represent the mean prediction \pm SE for all years.	119
Figure 4.5. Temporal patterns of nest survival, and their variation among years, for shorebird nests at East Bay, Nunavut, based on the predictions of the most parsimonious model (see Table 4.2). The predictions are for uniparental species in mid-incubation (nest-age = 10), and are displayed only for the intervals during which I monitored nests in each year. Day 1 = 10 June. Temporal patterns for biparental species have the same shapes, but less variation.	120
Figure 4.6. The index of relative shorebird nest density, 2000-2007. The index is standardised for differences in the total number of nests found each year, and was calculated as the number of active nests on a given day of the season divided by the mean number of active nests for all days in that year.	121
Figure 5.1. The number of incubation recesses or exchanges for each hour of the day, their mean duration (min), and the total time per hour where the nest was left unattended for uniparental species (panels a-c), or biparental species (d-f). See text for species included in the samples. Means are based on the full data set and are displayed \pm SE.	149
Figure 5.2. The number of restless movements of incubators on the nest (see text) for each hour of the day, their mean duration, and the total time per hour spent exhibiting restlessness for uniparental (panels a-c), or biparental species (d-f). See text for species included in the samples. Means are based on the full data set and are displayed \pm SE.	150
Figure 6.1. The study site at Medusa Bay, Russia.	181

Figure 6.2,a-f. The interspecific relationships between six measures of incubation behaviour (untransformed), and daily mortality rate of shorebird nests. Each data point represents a species; behavioural data include information about movements on the nest (panels d-f) for only 8/11 species.	182
Figure 6.3. The time of day at which nests were depredated at the East Bay, Coats Island and Medusa Bay sites. Data from Medusa Bay are adapted from Tulp and Schekkerman (2001).	183
Figure 7.1. A schematic representation of the effects identified in this thesis. Solid arrows denote significant effects demonstrated directly, while dashed arrows indicate hypothesised effects. Bold text denotes response variables that are a major focus of one or more chapters.	204
Figure 7.2. The decline in local abundance of Red Phalaropes on a 2.6 km ² plot at East Bay, Nunavut. Surveys were conducted in late June, 1999-2007.	205

Chapter 1. General introduction

Birds lay eggs, and this trait is as fundamental as it is obvious. The delicate embryo is furnished with the nutrients needed for development, suspended in a protective gel and shrouded in a calcareous shell. Then it is laid. From the elaborate and intricately woven nests of the weavers, to the simple dirt-pit of the White-rumped Sandpiper, birds invariably lay their eggs somewhere. By externalizing their embryos, birds are freed from the weighty burden of a pregnancy. However, in order for the eggs to hatch, embryos must still be provided with the appropriate conditions for development and protected from harm. When and where the eggs are laid, and how they are cared for once in the nest, form the basic features of avian reproductive ecology. This thesis examines how these decisions influence the success of a bird's nesting attempt.

Nest survival is a key component of fitness, and selection to maximize it should be strong (Ricklefs 1969, Martin 1992). However, maximizing nest survival does not necessarily maximize fitness; increasing parental investment yields benefits to current reproductive success, but may come at a cost to fitness over the life of the individual (e.g., Martin 1995, Wiebe and Martin 1998, Ghalambor and Martin 2001). An adaptive strategy must therefore balance investment in the current nesting attempt with risks to future attempts. Intra- and interspecific variation in how this balance is struck contributes to variation in rates of nest survival, and the strategy employed to mitigate the risk of egg loss may in fact underlie much of the variation in the life history of birds (e.g., Martin 1995).

Predation is the primary cause of nest failure in almost all bird species studied to date (e.g., Ricklefs 1969, Martin 1993). The best means of increasing nest survival is therefore to reduce the risk of predation. For many birds, predators that threaten the

clutch also pose a risk to incubating adults. Consequently, some traits that enhance nest success, such as aggressive nest defence or a concealed nest site (with compromised visibility), may be risky for adults (Brunton 1986, Wiebe and Martin 1998). Similarly, behaviours that reduce the likelihood of predation may bear energetic costs (Sasvari and Hegyi 2000). In broad terms, the risk of nest predation can be influenced by at least five factors: nest habitat, nest distribution, the crypsis of eggs and incubators, the behaviour of parent birds, and the abundance and behaviour of predators.

Across a wide range of species, and at a variety of scales, studies have shown that nest habitat is selected non-randomly (e.g., Colwell and Oring 1990, Rodrigues 1994, Clark and Shutler 1999). It is assumed that these nest site preferences are adaptive, yet explicit tests of this assumption are rare. Studies demonstrating effects of habitat on reproductive success typically take place where nest sites are limiting (e.g., Martin 1988). In the montane forests of Arizona, for instance, optimal nest sites are limited and nest sites in non-preferred microhabitats suffer higher predation (Martin 1998). In contrast, tundra breeding birds select nest sites on a relatively simple landscape that lacks the structural complexity of forests. For tundra breeding shorebirds, suitable nest sites are not limited and variation in nest predation is not explained by variation in nest habitat (Smith et al. 2007a). Here, variation in the microhabitat of occupied nests may simply reflect different strategies to optimize fitness under a variety of selective pressures.

When studying nest site selection, it is important to recognise that nests are placed not only in a habitat type, but also in a location with respect to neighbours. The spatial distribution of nests could affect reproductive success through a variety of mechanisms. If predators concentrate search effort in areas where they have found clutches previously,

selection may favour hyperdispersion of nests (e.g., Tinbergen et al. 1967, Page et al. 1983). Alternatively, aggregations of nests can result in a lower rate of predation through a “predator swamping” effect (Clark and Robertson 1979). For species with aggressive nest defence, colonial nesting may facilitate coordinated group response or early detection of predators (e.g., Andersson and Wiklund 1978, Larsen et al. 1996). Aggressive species may also affect the nest site selection of timid species. Many birds nest near more aggressive species in apparent protective associations (Durango 1949, Dyrce et al. 1981, Haemig 2001, Smith et al. 2007b). Several nesting associations have been reported for tundra breeding birds, with protector species ranging from large shorebirds (e.g., Paulson and Erckmann 1985) to Snowy Owls (*Nyctea scandiaca*; e.g., Summers et al. 1994).

Birds may also attempt to go unnoticed by matching the colouration or visual pattern of their surroundings. Camouflage as an adaptation to reduce predation is common throughout the animal kingdom, and especially prevalent in the plumage and eggs of ground nesting birds (Tinbergen et al. 1962, Montevicchi 1976, Bertram and Burger 1981, Solís and de Lope 1995, Yahner and Mahan 1996, Lloyd et al. 2000). The muted colours and mottling of the eggs and adult plumage of many shorebirds may serve to conceal them from visual predators.

My previous work on the reproductive ecology of arctic breeding shorebirds focussed on the factors above. I found clear evidence that nest sites were not selected randomly. That is, habitat of nest sites differed significantly from random sites, and from the nests of other species (Smith et al. 2007a). In some cases, this site selection acted to increase the visual match between the eggs and the nest site (J. Gobin, *unpublished*).

However, there was no evidence that variation in habitat or nest camouflage contributed to variation in nest success. Habitat did not differ between successful and failed nest sites, and artificial nest experiments suggested that interspecific patterns of nest predation are not related to habitat-specific risk. Similarly, the distribution of nests played no role in determining nest fate; nests in high-density areas did not have different rates of survival than those in low-density areas (Smith et al. 2007a). By nesting near aggressive Sabine's Gulls, some shorebirds were able to increase their rates of nest survival (Smith et al. 2007b), but this strategy was employed by relatively few individuals.

Despite my initial failure to find its source, variation in nest survival in this system was dramatic (Smith et al. 2007a, chapter 3). Nest survival varied more than 6-fold among species and across years. My previous work served to discount some of the possible sources of this variation, and building on this foundation, I defined a new set of hypotheses to test. In the chapters that follow, I present these hypotheses and demonstrate how they collectively explain a large proportion of the interspecific and interannual variation in the survival of shorebird nests.

Objectives and outline

The primary objective of this study was to identify the sources of variation in shorebird reproductive success. This objective is broad, and research projects addressed this theme both directly and indirectly. I began by evaluating the timing of shorebird breeding and the factors that influence it, because when to breed is among the first decisions made by individuals upon their return to the breeding grounds. I then assessed patterns in nest survival from broad interspecific or interannual scales to a finer, inter-individual scale. I organized my lines of inquiry into five chapters, based on the following questions:

- 1) What determines the timing and synchrony of shorebird nest initiation? What role do predators play in determining timing of breeding?
- 2) How does nest survival vary among species and years? How is this related to interspecific differences in the behaviour of shorebirds and interannual differences in the behaviour or abundance of predators?
- 3) How does nest survival vary within the season? Are patterns related to seasonal changes in the abundance of predators, or seasonal changes in the defence behaviours of shorebirds?
- 4) How does incubation behaviour differ among species and individuals, and how do shorebirds adjust incubation behaviour in response to environmental conditions?
- 5) After controlling for these effects of weather, does incubation behaviour influence the risk of predation?

Shorebirds in the arctic are faced with a comparatively short window of opportunity for breeding, bounded on both ends by freezing temperatures and snow covered ground. When they choose to breed can have important energetic consequences but also important consequences for nest survival, as demonstrated later in this thesis. In chapter two, I examine the variability among species and years in the timing of arrival, and the timing and synchrony of breeding. I then relate this variability to factors such as weather, snow cover and the abundance of predators to determine whether timing of breeding is driven by energetic needs and physiological constraints, or whether it is influenced by local conditions that could impact nest survival.

In chapter three, I evaluate patterns in nest survival among species and years, knowing *a priori* that variability was large (e.g., Smith et al. 2007a). I predicted that the abundance of predators would have an overriding effect on nest survival, and in this chapter I contrast predator effects with those of environmental factors such as weather and snowmelt. The arctic system studied here comprises relatively few species, and presents a unique opportunity to quantify the relationship between the abundance and activity of predators and the survival of the nests upon which they prey. My past work suggested that interspecific differences in nest survival might be related to incubation system. Here, I use modern analytic techniques and a large, long-term set of nest survival data to test whether uniparental species suffer higher nest predation than sympatric, biparental species.

Past studies of nest survival have faced a severe analytic limitation; nest survival was assumed to be constant through time because techniques to model temporal variation did not exist. In chapter four, I use Program Mark to assess the variation in nest survival within a breeding season. I compared models to identify the most parsimonious temporal trends, and used information on seasonal patterns in weather, predators, nest density and nest defence behaviour to determine the source of these trends. I predicted that nest survival would be lowest mid-season when the density of active shorebird nests was highest, due to a functional response of predators. I also predicted that nest survival might be higher for older nests, because the intensity of nest defence increases with nest age in a wide range of taxa.

In my previous work, I found preliminary evidence for a relationship between incubation behaviour and the risk of nest predation. However, incubation behaviour is

known to vary greatly in response to factors such as weather and the age of the nest (e.g., Tulp and Schekkerman 2006). In order to fully assess the relationship between incubation behaviour and nest survival, it was first necessary to understand the variation in my sample of behavioural data. In chapter five, I describe patterns in incubation behaviour within and among days, and assess how weather conditions influence these patterns. I quantify how incubation behaviour differs between species with uniparental and biparental incubation, and contrast the ways in which the behaviour of each group is influenced by weather conditions.

Incubation behaviour is highly variable even within species, and could influence nest survival. Secretive behaviour can decrease the detectability of the nest (Wiebe and Martin 1997, Martin et al. 2000), while conspicuous activities such as incubation feeding can serve as visual cues for predators (e.g., Lyon and Montgomerie 1987, Martin and Ghalambor 1999). Among shorebirds, uniparental species are energetically obligated to take more breaks from incubation than species with shared incubation. The added activity around the nest could increase the risk of predation, and this hypothesis is the foundation of chapter six. I used the understanding of incubation behaviour achieved in chapter five to control for confounding sources of variation, and tested whether metrics of behaviour such as the rate and duration of incubation recesses were related to the survival of nests. I examined the effects of behaviour within and among species, to determine the extent to which behaviour could account for the observed variation in shorebird nest survival.

These five research projects collectively explain a large proportion of the variation in nest survival among shorebird species and years, and provide a significantly

clearer understanding of these patterns than was available previously. In the final chapter, I synthesise the results of this work. I describe the trade-offs faced by shorebirds during the breeding season, and how these trade-offs could shape the evolution of life histories. This work was funded by Environment Canada, and the ultimate goal of these studies was to understand shorebird nest survival so that this understanding could be applied to the management of shorebird populations. I conclude by suggesting how insights gained here could be used to refine monitoring programs, and how this deeper understanding of nest survival could shed new light on the causes of shorebird population declines.

Study sites

My research was carried out primarily at two sites in the eastern Canadian arctic: Coats Island and East Bay, Southampton Island, Nunavut (see Fig. 2.1). In chapter two, I include information from a site at Prince Charles Island, Nunavut, and a second camp at East Bay. The research described in chapter five was carried out with colleagues from Europe, and here, data are included from a site at Medusa Bay on the Taimyr peninsula of arctic Siberia. Details of the sites are provided in the chapters in which they appear.

Shorebird species and their predators

Interpreting interspecific variation in rates of predation is often difficult, because of confounded interactions with life history, nest habitat and predator guild. Tundra breeding shorebirds offer a unique opportunity to control variation in some of these factors, because many basic features of reproductive ecology are shared by all species. All species typically lay four eggs in a simple scrape, incubate for roughly three weeks and are exposed to the same guild of nest predators. As they nest on the ground, in

structurally simple habitats, variation in nest habitat is also limited. While many basic nesting features are similar, tundra breeding shorebirds show considerable variation in mating system, incubation behaviour and rates of predation (Smith 2003, Smith et al. 2007a, this study).

A total of 15 shorebird species are considered in the various chapters of this thesis, with 10 species well represented in terms of nests found and monitored. These are the Semipalmated Plover (*Charadrius semipalmatus*), Black-bellied Plover (*Pluvialis squatarola*), American Golden-Plover (*Pluvialis dominica*), Red Phalarope (*Phalaropus fulicarius*), Ruddy Turnstone (*Arenaria interpres*), Dunlin (*Calidris alpina*), Curlew Sandpiper (*Calidris ferruginea*), Semipalmated Sandpiper (*Calidris pusilla*), White-rumped Sandpiper (*Calidris fuscicollis*), and Little Stint (*Calidris minuta*). A detailed review of the reproductive ecology of each is not appropriate here, but some brief details are provided below.

Semipalmated Plovers are monogamous, territorial and both parents incubate (termed 'biparental'; Nol and Blanken 1999). They are highly vigilant, and both parents take part in distraction displays or scolding (Sullivan Blanken and Nol 1998). On the breeding grounds, they feed primarily on dipteran larvae and adults (Baker 1977).

The Black-bellied Plover is large, territorial and monogamous, with both parents incubating and caring for chicks (Paulson 1995). They are highly vigilant and defend their nests aggressively from predators through aerial attack and distraction displays (Drury 1961, this study). They are visual foragers and peck invertebrates off the substrate, especially dipterans, beetles and spiders (Paulson 1995).

The American Golden-Plover is somewhat smaller than its Black-bellied congener, but is also territorial, monogamous and biparental (Johnson and Connors 1996). Their diet is similar to that of the other plovers, but may include a larger proportion of berries. They are also highly vigilant, but engage less in aggressive attacks of aerial predators than the larger Black-bellied Plover (Byrkjedal 1989).

The Red Phalarope exhibits facultative polyandry. Males are the sole incubators. They show no territoriality, distraction displays or aggression towards predators (Tracy et al. 2002). Red Phalaropes feed on a variety of aquatic and terrestrial invertebrate prey on the breeding grounds, especially the larvae and adults of chironomids and tipulids (Kitchinski and Chernov 1973, in Tracy et al. 2002).

The Ruddy Turnstone is monogamous and territorial. Incubation is shared, but the male's contribution varies geographically and seasonally (Nettleship 2000). Turnstones are highly vigilant and aggressively pursue predators. They feed primarily on dipterans, which they pick from the substrate or find by overturning stones (Macdonald and Parmelee 1962).

Dunlin are common across the circumpolar arctic; the race found in the eastern Canadian arctic is known as *Calidris alpina hudsonia*. They are monogamous and share the duties of incubation equally but only males care for chicks (Warnock and Gill 1996). They defend territories of variable size, through conspicuous flight displays and song. They feed primarily on adult and larval chironomids and tipulids by pecking them off the substrate or by probing with their long bill.

The Curlew Sandpiper is a bird of the old-world arctic, breeding primarily between the Yamal and Chuckchi peninsulas (Lappo and Tomkovich 2006). It has

uniparental incubation; males depart the breeding grounds by mid-season, leaving females to carry out all duties of incubation and chick rearing. Curlew sandpipers prefer to nest in drier areas or on slopes. They probe for tipulids early in the season, but later switch to surface-dwelling arthropods.

Semipalmated Sandpipers are common in the eastern Canadian arctic at low- to mid-latitudes. They are monogamous and have biparental incubation (Gratto-Trevor 1992). During the breeding season, they do not probe for food as much as some other sandpipers, and feed upon chironomids and arachnids. They often exhibit elaborate distraction displays, such as the “rodent run”, when predators approach the nest.

White-rumped Sandpipers are polygynous and territorial; only females provide parental care (Parmelee 1992). They feign injury when predators approach and select well concealed nest sites to avoid detection (Parmelee et al. 1968). They feed primarily by probing in moss for larvae (especially tipulids), but may also take spiders, beetles and adult tipulids from the substrate (Parmelee 1992).

The Little Stint is found across the full breadth of the old world arctic, and is locally abundant. Incubation is uniparental, and the mating system is unique. After laying a clutch for the male to incubate, the female typically moves farther north to lay a second clutch, which she will incubate (Tulp et al. 2002). They exhibit an amusing array of distraction displays, with various forms of jumping, squeaking and scurrying (Tulp 2007).

Potential nest predators are abundant at the study sites, but across the circumpolar arctic it is widely believed that predation on shorebird nests is carried out primarily by Parasitic Jaegers (*Stercorarius parasiticus*) and arctic foxes (*Alopex lagopus*) (Erckmann

1981, Schekkerman et al. 2004, Liebezeit and Zack 2008, this study). Potential predators observed regularly at the sites include Long-tailed Jaegers (*Stercorarius longicaudus*) and Herring Gulls (*Larus argentatus*), while Pomarine Jaegers (*Stercorarius pomarinus*), Glaucous Gulls (*Larus hyperboreus*), Sandhill Cranes (*Grus canadensis*), Peregrine Falcons (*Falco peregrinus*), Common Ravens (*Corvus corax*) and ermine (*Mustela erminea*) were observed infrequently.

Declaration

A project of this size requires many collaborators, and although I was responsible for all aspects of the study design, I did not collect all data myself. I oversaw data collection at East Bay and Coats Island until 2006. The field team in 2007 was led by Darryl Edwards. Data from Prince Charles Island, analysed in chapter 2, were provided by Jean-Louis Martin. Data from East Bay Island, also in chapter 2, were provided by Grant Gilchrist, Karel Allard and the East Bay field team. Those from Medusa Bay, analysed in chapter 6, were provided by Hans Schekkerman and Ingrid Tulp. All analyses and interpretation of the data were carried out by me, except the within-season models of nest survival in chapter 4, which were completed with the assistance of Scott Wilson. At the time of printing, no chapters of this thesis have been published elsewhere.

Table 1.1. Body mass, social mating system, and incubation behaviour for the 10 shorebird species that are the focus of this thesis. Data are from this study, Thomas et al. (2006), Tulp (2007), and references therein.

Species	Body Mass (g)	Social Mating System	Incubation System	Incubating Sex
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	47	monogamous	biparental	m & f
Black-bellied Plover (<i>Pluvialis squatarola</i>)	209	monogamous	biparental	m & f
American Golden-Plover (<i>Pluvialis dominica</i>)	147	monogamous	biparental	m & f
Red Phalarope (<i>Phalaropus fulicarius</i>)	45	polyandrous/monogamous	uniparental	m
Ruddy Turnstone (<i>Arenaria interpres</i>)	113	monogamous	biparental	m & f
Dunlin (<i>Calidris alpina</i>)	58	monogamous	biparental	m & f
Curlew Sandpiper (<i>Calidris ferruginea</i>)	58	polygynous	uniparental	f
Semipalmated Sandpiper (<i>Calidris pusilla</i>)	28	monogamous	biparental	m & f
White-rumped Sandpiper (<i>Calidris fuscicollis</i>)	44	polygynous	uniparental	f
Little Stint (<i>Calidris minuta</i>)	29	double-clutching	uniparental	m or f

Chapter 2. Inter-annual variation in the breeding chronology of arctic shorebirds: effects of weather, snow melt and predators

Abstract

Arctic breeding shorebirds travel thousands of kilometres between their wintering and breeding grounds, yet the period over which they arrive and begin to initiate nests spans only several weeks. I investigated the role of local conditions such as weather, snow cover and predator abundance on the timing of arrival and breeding for shorebirds at four sites in the eastern Canadian arctic. Over 11 years, I monitored the arrival of 12 species and found 821 nests. Weather was highly variable over the course of this study, and the date of 50% snow cover varied by up to three weeks between years. In contrast, timing of arrival varied by one week or less at the sites, and was not related to local conditions such as temperature, wind, or snow melt. Timing of breeding was best predicted by the date of 50% snow melt, with later snow melt resulting in delayed breeding. Higher predator abundance resulted in earlier nesting than would be predicted by snow cover alone. I hypothesise that when predation risk is high, the value of potential renesting exceeds the energetic risks of early breeding. Synchrony of breeding was not related to local weather conditions, but was significantly higher in late breeding years. These results suggest a relatively fixed date for the termination of nest initiation, after which nesting is no longer profitable.

Introduction

The breeding schedule of shorebirds nesting on the arctic tundra is bounded by extremes. The snow pack does not begin to melt and expose bare ground until late May in most arctic locations, imposing a limit on the earliest possibility for nest initiation in these ground nesting birds (e.g., Meltofte et al. 2007a). Because shorebirds are primarily income breeders (Klaassen et al. 2001, Morrison and Hobson 2004), limited availability of, or access to, their invertebrate prey on the frozen tundra can further constrain their ability to initiate nests (Meltofte et al. 2007b, but see Danks 1971). After a 2-3 month period of favourable weather, freezing temperatures return to the arctic. For successful reproduction, the final nests must be initiated with sufficient time for chicks to develop and migrate south before fall weather comes (Meltofte et al. 2007a).

Within these climatic boundaries, a number of variables may more subtly influence breeding schedules, including temperature, rate of snow melt and risk of predation. The energetic demands of homeothermy in the arctic are substantial (Piersma et al. 2003), and the added demands of egg production may be more difficult to meet in cold, wet, or windy breeding years. Although both clutch size and egg size are relatively invariant in shorebirds (Ricklefs 1984, Szekely et al. 1994), colder breeding seasons have been linked to both smaller clutch sizes and smaller eggs in some species (Meltofte et al. 1981 and Nol et al. 1997, and Sandercock et al. 1999, respectively). Increased energetic demands of homeothermy during the pre-breeding season could also result in delayed breeding (Morrison et al. 2005).

While total snow cover precludes nesting in some years (e.g., Mayfield 1978), partially snow covered ground may increase the risk of predation by concentrating the

search of predators (Byrkjedal 1980, Meltofte et al. 1981). In response to this increased risk, shorebirds could delay nest initiation until more snow-free ground is exposed. However, the impact of predators on timing of breeding might vary interspecifically. For example, some species are able to defend their nests from jaegers (*Stercorarius* spp.), such as the Black-bellied Plover (Paulson 1995, Drury 1961), and might therefore be less susceptible to predation than timid species if they nested early in snow-free patches.

The risk of predation also varies dramatically between years (e.g., Smith et al. 2007a). Populations of jaegers and arctic foxes fluctuate substantially in arctic systems. These fluctuations are in some cases known, or in most cases assumed, to be related to cycles in the abundance of their primary prey: lemmings (*Dicrostonyx* spp., *Lemmus* spp.). These cycles in predator abundance could play a role in determining the timing of nest initiation. Abundant predators may cause birds to delay the initiation of nests if risk of predation is greatest early in the nesting season, for example due to limited snow-free ground or lower total density of nests available to predators. Alternatively, a high presence of predators could contribute to earlier dates of nest initiation if birds attempt to maximize the time available for successful renesting in the event of nest depredation (Meltofte 1985, Meltofte et al. 2007a).

The decision of when to breed is made by the individual, but the synchrony in timing of breeding can have important consequences at the level of the community (e.g., Clark and Robertson 1979). Synchronous breeding increases the density of nests available to predators, potentially diluting risk to the individual (but see Brown and Brown 2001), and facilitates group defence in species exhibiting mobbing behaviour (such as the Ruddy Turnstone, Nettleship 2000). While synchronous breeding could be

the product of social cues, it could also reflect the limited time available between the appearance of snow free land, and the latest possible opportunity for successful hatching and fledging of young prior to the onset of extreme weather. If time constraints determine synchrony, it should be greatest in years when the initiation of nests is most delayed (e.g., Green et al. 1977, Nol et al. 1997, Møller 2007b). Alternatively, if synchrony is constrained by the ability to access food and produce eggs, early years might facilitate synchronous breeding by masking differences in individual condition (Nol et al. 1997).

It is also important to consider how timing of arrival to the breeding grounds constrains the timing of nest initiation. Shorebirds nesting in the Canadian arctic are highly migratory, travelling thousands of kilometres from non-breeding areas as far south as Tierra Del Fuego. Because shorebirds require time to gather nutrients (Morrison and Hobson 2004), and a minimum interval of approximately 1 week for the development of eggs (Roudebush et al. 1979), the timing of shorebirds' breeding could be related to the timing of their arrival on the breeding grounds (e.g., Schamel and Tracy 1987, Schamel et al. 2002, Schekkerman et al. 2004). Arrival, in turn, could be influenced by climatic or other conditions encountered en route, and/or could be based on long-term averages of conditions in the arctic (Piersma et al. 1990). The timing of shorebird arrival, and how this relates to timing of breeding, has received little attention (Møller 1985, Morrison et al. 2005).

Few studies have tested explicitly for factors that influence the chronology of shorebird breeding because multi-year data sets are rare in the arctic (Nol et al. 1997, Møller et al. 2007a, Møller et al. 2007b). An understanding of long-term factors that

influence the timing of breeding in shorebirds is important for predicting how they might respond to future environmental change. Despite the relevance, I know of no community level analyses of nesting chronology for Nearctic shorebirds. Here, I present data for the timing of arrival and breeding at 4 sites, for 12 shorebird species and up to 9 years. I relate the timing of arrival, and both the timing and synchrony of nest initiation to factors such as snow melt, temperature and the abundance of predators.

Methods

Study areas

Research was conducted at four sites in the eastern Canadian arctic, spread across 700 km and 6° of latitude. The southernmost site was Coats Island, Nunavut (approximately 5500 km²), at the north end of Hudson Bay. Exposed outcroppings of Precambrian metamorphic rock dominate the northeast corner, while the remainder of the island is composed primarily of lowland tundra and exposed Palaeozoic sedimentary rocks (Heywood and Sanford 1976). Smaller areas of upland heath tundra, as well as raised beach deposits from the Holocene are also common across the island. Work at Coats Island was conducted from the beginning of June until the end of July, 2004-2006, at a camp located at N62° 51' W82° 29' (Fig. 2.1).

Two sites were located on the Northeast side of Southampton Island, Nunavut. This portion of the island consists of extensive tracts of coastal lowland tundra, and large expanses of unvegetated sedimentary rock farther inland. Raised beach deposits are very common as a result of substantial isostatic rebound, following the retreat of the Pleistocene ice sheets (Innes et al. 1968). Work in the area of East Bay, Southampton Island was conducted annually from the beginning of June until the end of July from

1999-2007, at a camp located at 63° 59'N 81° 40'W (Hereafter 'East Bay Mainland', Fig. 2.1). Habitat details and descriptions of the shorebird community at this site appear in Smith (2003) and Smith et al. (2007a).

Approximately 7 km away from this site, a research camp on a small island (hereafter 'East Bay Island', 64° 01'N 81° 47'W) was operated annually from late May until mid-August, 1999-2007. Shorebirds do not breed on this small island (24 ha); it is included in analyses because it is used heavily by shorebirds in the pre-breeding season in some years. Snow clears from this island much earlier than tundra wetlands on the mainland, presumably because its raised topography results in lower accumulation of snow.

The fourth site was on the Northwest side of Prince Charles Island, at 68° 11'N 76° 43'W (Fig. 2.1). Prince Charles Island, with an area of 9900 km², is notably flat, and consists of relatively young landforms also undergoing isostatic uplift (Gaston et al. 1986). The centre of Prince Charles Island is primarily unvegetated, broken shale. Raised beach features are common, and particularly so on the west coast. Most of the coastal area consists of lush wet tundra with numerous ponds. Work at Prince Charles Island was carried out from 19 June until 16 July, 1996, and 24 June until 17 July, 1997.

Climate differs substantially between the sites. Summer weather at Coats Island is comparatively mild, with climatic patterns influenced by the waters of Hudson Bay. Only 130 km to the Northeast, the East Bay Mainland and East Bay Island sites are dramatically colder, with a flora and climate more typical of mid-arctic regions (Edlund 1990). Summer temperatures here, and at Prince Charles Island 500 km to the North are

depressed by the cold and ice rich waters of the Foxe Basin; landfast ice persists until July, and coastal areas remain cool throughout the summer.

Shorebirds and their predators

Our study includes more than 3/4 of the shorebird species nesting in the eastern low- and mid-arctic. Those best represented in the samples include the American Golden-plover, Black-bellied Plover, Dunlin, Red Phalarope, Ruddy Turnstone, Semipalmated Plover, Semipalmated Sandpiper, and White-rumped Sandpiper. Observational data, and in particular nest records, are less abundant for the Baird's Sandpiper (*Calidris bairdii*), Pectoral Sandpiper (*Calidris melanotos*), Purple Sandpiper (*Calidris maritima*), Red Knot (*Calidris canutus*) and Sanderling (*Calidris alba*).

The shorebird species in this sample vary widely in a number of ecological characteristics that could influence timing of breeding, including range, mating system, territoriality, nest defence and foraging behaviour. While a complete review of each species' breeding ecology is not appropriate here, some relevant details are described below and further highlighted in the discussion. The majority of shorebird species are monogamous (Emlen and Oring 1977), but among the eight species common in the sample, the Red Phalarope exhibits facultative polyandry (Tracy et al. 2002), and the White-rumped Sandpiper is polygynous (Parmelee 1992). All of these species except the Red Phalarope defend territories to some extent, while aggressive nest defence is limited to the American Golden-plover, the Black-bellied Plover and the Ruddy Turnstone. The plovers (Charadriidae) are primarily visual foragers on terrestrial arthropods (Paulson 1995, Nol and Blanken 1999). In addition to gleaning terrestrial arthropods, the Red Phalarope also feeds on a wide variety of aquatic invertebrates, the White-rumped and

Semipalmated Sandpipers feed by probing in moss for larvae (especially tipulids, Parmelee 1992), and the Ruddy Turnstone searches for invertebrates by overturning stones (Macdonald and Parmelee 1962). Most of the eight species common in the sample are within the core of their range, but the Red Phalarope is near the southern limit of its breeding range on Coats Island, while the Semipalmated Sandpiper is approaching the northern limit of its distribution on Southampton Island.

The most significant nest predators at all sites were Parasitic Jaegers and arctic foxes. Herring Gulls were observed regularly, but are believed to eat shorebird eggs infrequently (Karel Allard, *pers. obs.*). Long-tailed Jaegers are included in jaeger counts, but are assumed to be of less importance than Parasitic Jaegers because they were on average 15 times less abundant, and are thought to eat lemmings principally (Wiley and Lee 1998). Pomarine Jaegers were encountered in both years at Prince Charles Island, but this species is uncommon at the other three sites. Other potential predators, assumed to be unimportant because of their scarcity, include: Peregrine Falcons, Glaucous Gulls, Sandhill Cranes and Common Ravens.

At East Bay Mainland and Coats Island, I recorded the number of arctic foxes and jaegers observed per person*hour, and used this as an index of relative predator abundance between years. On most days, these observations were made between 0700h and 1900h local time. This metric reflects both the abundance and level of activity of the predators, but provides an adequate index of predation pressure among years (Hochachka et al. 2000, Wilson and Bromley 2001). I also recorded the number of lemming (primarily *Dicrostonyx torquatus*) encounters at East Bay Mainland, and use this to reflect the abundance of potential alternative prey (e.g., Summers 1986, Summers and

Underhill 1987, Bêty et al. 2002). There are no lemmings on Coats Island (e.g., Gaston and Ouellet 1997).

Monitoring weather and snow melt

Weather data were collected at the camps by means of portable weather stations or hand-held instruments. Wind speed was measured at a height of 1-3 m, and was therefore higher than that which would be experienced by shorebirds at ground level. Although a number of weather variables were collected, I selected mean daily temperature from 10 – 30 June, mean daily wind speed from 10 – 30 June, and mean daily windchill low from 10 – 30 June, for use in analyses. Temperature during the pre-nesting period could affect the availability of surface-active arthropods to shorebirds (e.g., Hodkinson 2003), while the windchill temperature may more accurately reflect the energetic costs of homeothermy. I selected the period from 10 June – 30 June because weather records are sporadic before 10 June in some years, and because nearly all nests have been initiated by 30 June (see below). Snow-melt within the study sites was monitored by standing on raised beach ridges with an unobstructed view of the landscape and making daily estimates of the percentage of snow free ground in a fixed area (1.5 x 1.5 km).

Timing of arrival

The timing of shorebird arrival to the breeding grounds was monitored through standardised and opportunistic means. At the East Bay Island site, the perimeter of the island was walked once or twice daily by 1-2 observers, and all bird encounters were recorded. Given the small size of the island, and the number of staff present, it is likely that all shorebirds present were recorded. At the East Bay Mainland and Coats Island sites, 100 m wide belt transects 1 km – 1.5 km in length were walked daily by 2 observers

in locations consistent between years. Two transects were surveyed daily at East Bay Mainland, and one at Coats Island. Transect locations were selected to encompass the variety of habitats found at the site, and include areas that were known to melt earlier than surrounding tundra (e.g., river banks, areas of good drainage). In addition, I included any opportunistic sightings of arriving shorebirds. The slight differences in methods among sites are not problematic here because the goal was to compare arrival dates, and not relative densities, among sites.

No first sighting dates are available for Prince Charles Island, as field workers were not present until mid June in either year. At the remaining three sites, staff were typically present in the study areas before the arrival of any shorebird species. For the few instances when I believed that these first sightings did not represent the arrival of the species to the area, I omitted the sighting from analyses.

Nest finding and ageing

Workers searched for shorebird nests on foot at the East Bay Mainland, Coats Island and Prince Charles Island sites. As mentioned, shorebirds do not nest at the East Bay Island Site. Nests were found by observation, flushing birds while walking and by two people dragging a 30 m length of 5 mm diameter rope. In most years, nest searching began before shorebirds had begun to initiate nests. Search effort was not constant between sites or years.

Timing of nest initiation (the date when the first egg was laid) was rarely observed directly; it was usually estimated from clutch completion dates, hatch dates, or egg flotation characteristics. When nests were found with partial clutches, I assumed that one egg was laid per day in order to back-calculate the date of nest initiation (Sandercock

1998). When the date of nest initiation was calculated from hatch dates, I used species-specific data on incubation durations, from on-site recording where available or from literature values, if necessary. Nests that were found with complete clutches and were depredated before hatch were aged by the egg flotation method (Liebezeit et al. 2007). This method provides an unbiased estimate ± 4 days.

Data analysis

I limited detailed analyses to species for which I had a minimum of four nests in each year at a given site. Typically however, the samples for common species were much larger (Table 2.1). I recorded, for each species and year, the earliest, first quartile, median, third quartile and latest nests. I did this because shorebirds initiating nests at different times within the laying period may be responding to different conditions. I defined the total length of the laying period as the time between the initiation of the earliest and latest nests I observed, but also report the length of time between the first and third quartiles of nest initiation as an indication of peak laying. The synchrony of nest initiation within a species is represented by the standard deviation of nest initiation dates.

I assessed patterns in weather variables over the years of the study with linear regression. The relationship between weather and timing of arrival was also investigated with linear regression models and Bonferonni corrected α values for multiple tests. The five metrics of timing (earliest, first quartile, median, third quartile and latest nest initiations) and the metric of synchrony (standard deviation of nest initiation), were analysed separately as response variables in General Linear Models with SPSS 10.0.7 (SPSS Inc. 2000). Site was treated as a random effect, whereas species was included as a fixed effect. These variables were included in all subsequent models if they were

significant individually. Pearson correlation analyses revealed collinearity among some variables. The date of 50% snow melt was correlated inversely with the early season temperature ($R = -0.67, P < 0.001, n=12$ years total at East Bay Mainland and Coats Island), daily windchill lows ($R = -0.42, P < 0.01$), and average wind speeds ($R = -0.33, P < 0.05$). The abundance of jaegers was inversely correlated with average wind speed ($R = -0.66, P < 0.001$). To account for correlations between the variables, I used a forward stepwise approach, with Type I Sums of Squares. The strongest individual predictors were retained at each step, until no variables contributed significantly to explanatory power of the model. Interaction effects were considered only for variables with significant main effects. Where appropriate, post-hoc tests were conducted with Tukey's honestly significant difference tests. Unless otherwise noted, $\alpha = 0.05$ and means are reported \pm SE.

Results

Weather and snow melt

Weather varied markedly between years at all sites (Table 2.2). Over 9 years of observation at East Bay Mainland, the date of 50% snow cover varied by nearly 3 weeks, from 1 June until 19 June, with a mean of 11 June. The East Bay Island site was 50% free of snow at least 10.4 days earlier on average (range at least 4-16 days; snow cover < 50% upon arrival in some years) than the East Bay Mainland site, despite a separation of only 7 km. The areas surrounding these sites are predominantly tundra lowlands and raised beach complexes. Opportunistic work suggests that the East Bay Island site is free of snow earlier than any of the surrounding lowlands in most years, and particularly so in years of late snow melt (P. Smith, *pers. obs.*).

The Coats Island site had heavy snow cover in spring 2004, as did much of the eastern arctic that year (Meltofte et al. 2007a). The date of 50% snow cover was 18 days later in 2004 than in 2006, and the mean temperature between 10 June and 30 June was correspondingly lower (Table 2.2). Prince Charles Island had exceptionally late snowmelt in 1996, with a date of 50% snow clearance of 30 June.

I had nine consecutive years of weather data for the East Bay Mainland site, allowing for analyses of changes in local weather over time. No significant directional patterns were observed in dates of 50% snow melt, mean daily temperature or the mean daily wind speed high during the time of nest initiation (10 June – 30 June, all $R^2 < 0.03$, $P > 0.05$). However, the average daily windchill low from 10 June – 30 June, an index of the energetic cost of thermoregulation, showed a pronounced warming between 1999 – 2007 (Fig. 2.2, $R^2 = 0.85$, $P < 0.001$). Weather patterns were similar at the East Bay Island Site, although the mean temperatures were on average 1.0°C lower, presumably because the small island is surrounded by ice. The time series at the Coats and Prince Charles Island sites were not sufficiently long for analysis.

Indices of predator abundance

The abundance of predators and lemmings differed substantially between years at East Bay, and less so at Coats Island (Fig. 2.3). No such data were available for the East Bay Island site, and data were recorded with different methods at Prince Charles Island. At East Bay, numbers of arctic foxes were highest in 2006, while numbers of jaegers were highest in 2004 and 2005. There was no significant relationship between the numbers of lemmings and the number of foxes or jaegers at this site, either directly or with a time-lag of one year (all R values < 0.62 , all $P > 0.05$). At Coats Island, the number of predators

encountered by field staff were relatively stable between years. Both foxes and jaegers were most abundant in 2006. As mentioned, there were no lemmings on Coats Island. At Prince Charles Island, lemming abundance was high in 1996 (with 3 to 12 winter nests/ha in the most favourable habitats) and moderate in 1997 (0.5 to 4 winter nests/ha in the same habitats). Foxes, Long-tailed Jaegers and Pomarine Jaegers were common in both years. Five pairs of Long-tailed Jaegers, three pairs of Pomarine Jaegers and two arctic fox dens were recorded within an area of about 10 km² in 1996. In 1997, three pairs of Long-tailed Jaegers, one pair of Parasitic Jaegers, three pairs of Pomarine Jaegers and one fox den were present in the same area.

Weather variables were correlated with the abundance of predators at the East Bay Mainland and Coats Island sites; fox sightings were fewer in heavy snow years ($R = -0.32$, $P < 0.05$), and more numerous in years of cold windchill temperatures ($R = 0.73$, $P < 0.001$). Jaegers were less commonly encountered in years with high wind speeds ($R = -0.67$, $P < 0.001$).

Timing of arrival

In contrast to the highly variable weather and snow cover, the arrival dates of shorebirds were comparatively similar between years. The mean arrival date across all species varied between years from 4 June – 11 June for the East Bay Mainland Site, 30 May – 4 June for the East Bay Island site and 4 June – 10 June for the Coats Island Site (Table 2.1). None of the early season climatic variables related significantly to the mean arrival date for all species at either the East Bay Mainland or East Bay Island site (Linear regression models, all P values > 0.05). Although some weather variables were

significantly correlated with timing of arrival for some species at $\alpha = 0.05$, no significant relationships were identified using Bonferonni corrected α values.

Because I had only three years of data, such analyses were not possible for the Coats Island site. However, the date of 50% snow melt was 18 days later at this site in 2004 versus 2006, while the mean arrival date was only 6 days later. No timing of arrival data were available for Prince Charles Island.

Over all years, the earliest arriving species (common breeders only) at the East Bay Mainland site was the White-rumped Sandpiper (mean arrival: 4 June \pm 1 d), while the latest was the Red Phalarope (mean arrival: 8 June \pm 1 d). Similarly, at the East Bay Island site, the earliest arriving common bird was the White-rumped Sandpiper (31 May \pm 1 d) and the latest, the Red Phalarope (5 June \pm 1 d). On average, species arrived to the East Bay Island site 5 d earlier than the East Bay Mainland site, despite a separation of only seven kilometres. At Coats Island, the first of the common breeding species to arrive were the Dunlin and the American Golden-Plover (mean arrival: 3 June \pm 0 d), while the latest was the Red Phalarope (mean arrival: 7 June \pm 1 d).

Although the distribution of arrival times shifted from year to year, all species arrived typically within a span of one week (range 3 d – 11 d). The synchrony of arrival was not related to the mean arrival date nor the date of 50% snow cover at any site (e.g., date of 50% snow cover versus range of arrival dates at East Bay Mainland: $R^2 = 0.05$, $P > 0.05$, $n = 9$ years). Further, there was no latitudinal trend in arrival times. The mean date of arrival for all species and years was 6 June for Coats Island, the most southern site. At the East Bay Mainland site, the average arrival date was 6 June, while it was 2 June for the nearby East Bay Island site (Table 2.1).

Timing of nest initiation

I observed or estimated the date of nest initiation for 821 nests of 11 species. Nesting typically began in mid to late June at East Bay Mainland, and early to mid June at Coats Island and Prince Charles Island (Table 2.1). Averages, across species and years, for the earliest date of nest initiation were 16 June at East Bay Mainland and 12 June at Coats Island; these dates are 10 d and 5 d after the first sighting dates respectively. For Prince Charles Island in 1997, the average date of first nest initiation for all species was 12 June.

Both interspecific and inter-site differences were identified as significant in the models of timing of nest initiation. Nesting was on average 5 d earlier at Coats Island than at East Bay. The first species to nest at Coats Island was the Dunlin (mean: 10 June), while the latest was the American Golden-Plover (mean: 14 June). At the East Bay Mainland site, the Ruddy Turnstone was the first to initiate nests in each year, an average of 4 d earlier than any other species (11 June, Table 2.1). The latest of the common breeders at that site was the Red Phalarope, which initiated the first nests on 19 June, on average. In contrast, the Red Phalarope was among the earliest breeders at both Coats Island (12 June) and Prince Charles Island (9 June, Table 2.1).

The climate variable demonstrating the largest influence was the timing of snow clearance (Table 2.3), but this was after controlling for the inter-site and interspecific effects mentioned above. Later dates of 50% snow clearance corresponded to later dates for all metrics of timing of breeding. Climate variables were correlated, and with the effect of snow-melt date controlled, neither mean temperature during late June, nor the daily wind-chill lows during this period were significant predictors of timing of breeding (Table 2.3).

For nests initiated as late as the median initiation date, the number of predator sightings (foxes and jaegers combined) had a significant effect on initiation date. While snow cover had a strong overarching effect on timing of breeding, presence of abundant predators corresponded to earlier dates of nesting than would be predicted by snow cover alone (Table 2.3).

Only two years of data were available for Prince Charles Island, and the relationship between snow cover, temperature and timing of breeding was not assessed statistically. However, 1996 was a year of exceptionally heavy snow cover and the date of 50% clearance was 30 June. The median date of nest initiation in this year was 29 June. In contrast, snow cover was less than 1% on 25 June in 1997, and the median date of nest initiation was much earlier: 15 June.

Across all years, the date of first sighting was not a significant predictor of the timing of the initiation of the first nests ($R^2 = 0.16$, $P > 0.05$). This interval varied widely between species and years. At the East Bay Mainland site, the species displaying the smallest interval between arrival and first nests was the Ruddy Turnstone (6 ± 1 d), while the longest was the Black-bellied Plover (12 ± 1 d). The lowest mean interval for all species (8 ± 1 d) was observed in 2002, a year of warm temperatures and moderate snow cover, while the longest interval was observed in 2004 (12 ± 1 d), a year of moderate temperatures and late snow melt. A similar pattern was observed at Coats Island; the interval between arrival and laying was long (13 ± 2 d) in 2004, a late snow melt year, and much lower in the earlier melt years of 2005 and 2006 (5 ± 4 d, 4 ± 1 d, respectively).

Synchrony of nest initiation

The period over which nests were initiated was typically 2 – 4 weeks, with an average across species and years of 18 ± 1 d for East Bay Mainland, 15 ± 2 d for Coats Island and 11 d for Prince Charles Island (1997 only). However, most nests were initiated over a much narrower interval; the interval between the first and third quartile of nest initiation was 6 ± 1 d, 5 ± 1 d, and 4 ± 2 d for East Bay Mainland, Coats Island and Prince Charles Island, respectively. Nest initiation terminated in late June at Coats Island in 2005 and 2006 and Prince Charles Island in 1997. The final nests were later in the exceptionally late snow melt years of 2004 at Coats Island and 1996 at Prince Charles Island. The final dates of nest initiation were later at East Bay, with an average across species and years of 3 July.

Synchrony, measured as the standard deviation of nest initiation dates, was significantly higher at Coats Island than at East Bay ($SD_{\text{Coats}} = 4.8$ d, $SD_{\text{East Bay}} = 6.4$ d, $F_{1,29} = 6.4$, $P = 0.02$). I observed no significant interspecific differences in synchrony of breeding (7 species, 31 species*years, $F_{6,24} = 1.1$, $P > 0.05$). However, synchrony varied widely among years. In GLM analyses, only the date of the earliest nest initiation was significantly related to nesting synchrony, with earlier nesting leading to lower synchrony (i.e., higher SD). Predator abundance and weather variables, such as date of 50% snow melt, or temperature during the pre-breeding season, were not significantly related to synchrony of breeding.

Discussion

These results inform how nest initiation of several species of arctic-breeding shorebirds is affected by environmental and biological factors. Individual repeatability for clutch

completion dates is low for arctic breeding shorebirds (Nol et al. 1997), suggesting that local conditions might have a greater influence on timing of breeding in shorebirds than for other precocial species where repeatability is significant (e.g., Snow Geese *Chen caerulescens*, Findlay and Cooke 1982). Substantial variation, between species, years and sites, suggests that the pre-breeding and egg-laying periods are among the most responsive phases of the life-history cycle to environmental variation (Moltofte et al. 2007a). However, the factors influencing the timing of breeding have rarely been studied directly for shorebirds. These results demonstrate large variation in the timing of nest initiation among shorebirds in the eastern arctic, and show that both snow conditions and predator abundance have significant effects on the chronology of breeding.

Timing of arrival

Weather conditions encountered at the study sites were highly variable; dates of 50% snow cover at both the Coats Island and East Bay Island sites ranged by nearly 3 weeks. In comparison, the timing of shorebird arrival to the breeding grounds varied by a week or less. The weak correlation that I detected between local weather and timing of arrival is not surprising, as arctic-breeding shorebirds often stage at more temperate latitudes, where weather conditions are poorly correlated with those in the arctic (Piersma et al. 1990). Neither weather conditions on arctic breeding grounds, nor at the southern staging sites from which shorebirds depart, can predict the timing of arrival to the breeding grounds. Weather in Northeast Greenland was significantly correlated with timing of shorebird arrival for only 2 of 5 species, and no correlation was found between temperatures at European staging grounds and arrival of the birds in Greenland (Moltofte 1985). In sub-arctic Iceland, the arrival of shorebirds to breeding grounds was delayed in

some years when weather and wind conditions were unfavourable in Ireland and Scotland, but no overarching relationship with temperature at the staging grounds was apparent (Boyd and Petersen 2006). The timing of arrival may instead correspond to long-term averages of suitable weather conditions or access to invertebrate prey at arctic locations (Moltofte 1985, Piersma et al. 1990).

While in general the timing of arrival seems driven by long term averages, shorebirds have been observed to stop short of their breeding grounds in years of particularly late snow melt, either to wait for more suitable conditions, or to breed at more southerly latitudes (Schekkerman et al. 2004, Moltofte et al. 2007a). These observations suggest that, where possible, shorebirds will stage in snow-free areas near their nesting sites in years of late snow-melt. The East Bay Island is only 7 km away from the East Bay Mainland, but is 50% snow free nearly 10 days earlier on average. Shorebirds were seen earlier at the East Bay Island site than on the Mainland site, and particularly so in years of late snow melt. Similarly, large numbers of shorebirds were observed on a snow-free, south-facing slope on 8 June, 2000, 15 km east of the East Bay Mainland site (P. Smith and K. Allard, *pers. obs.*). At this time, the Mainland site was 99% snow covered, and no shorebirds had yet been seen. These observations suggest that birds arrive to the general vicinity of nesting areas, irrespective of local weather or snow conditions, and make use of available feeding areas nearby.

Timing of nest initiation

Shorebirds must acquire the nutrients for egg formation on the breeding grounds (Klaassen et al. 2001, Morrison and Hobson 2004), and there is a physiological limit for the speed at which eggs can be created (Roudybush et al. 1979). Within these

physiological constraints, laying date could be influenced by a number of local conditions, and the strongest effect documented in previous studies has been that of snow cover (e.g., Meltofte 1976, Green et al. 1977, Meltofte 1985, but see Meltofte 2007b). These results demonstrate that timing of nest initiation differed between species and sites, but was also strongly influenced by snow cover and the abundance of predators.

Interspecific differences in the timing of nest initiation were significant, with an average of 12 d separating the median initiation dates for the earliest and latest nesters at East Bay; the Ruddy Turnstone and the Red Phalarope, respectively. The differences were smaller among other species, and at other sites, with less than one week separating the median dates of nest initiation. These differences in timing of nest initiation were not a product of interspecific differences in the timing of arrival. The interval between the first sighting and the first nest varied by 100% or more between species at both the Coats Island and East Bay Mainland sites. Instead, these differences could reflect differences in the ability of shorebirds to gather sufficient food resources for egg formation.

In high arctic Greenland, Meltofte et al. (2007b) found invertebrate abundance to be a strong predictor of timing of breeding. Similarly, in a population of Semipalmated Plovers breeding in sub-arctic Canada, there was a strong correlation between temperature in the first week of June and the mean date of clutch completion (Nol et al. 1997). This relationship was attributed to greater availability of invertebrate prey. Temperature is indeed correlated with the availability of surface-active arthropods on arctic tundra (Tulp and Schekkerman 2008). As foraging behaviour varies widely among shorebirds, differential access to food resources could in part explain interspecific patterns in the timing of breeding seen here.

Ruddy Turnstones were the earliest breeders at the East Bay Mainland site, and similar observations have been made at sites in high arctic Greenland (Moltofte 1985, Moltofte et al. 2007b). Ruddy Turnstones, as their common name suggests, have the ability to overturn stones and plates of dry mud, thereby uncovering dormant arthropods (e.g., Nettleship 2000). While this behaviour is not entirely confined to this species (e.g., Danks 1971), it is certainly more highly developed among Ruddy Turnstones. This unique feeding mode may allow them to gain access to food resources earlier than other species, and facilitate early breeding. In contrast, Red Phalaropes feed primarily on aquatic invertebrates during the pre-breeding season (Ridley 1980), and the restricted access to these in years of late thaw could result in delayed breeding. I did not measure invertebrate abundance during the pre-nesting period, but found no relationship between temperature and timing of breeding. However, as snow cover at the time of nest initiation at these sites is similar to the location in Greenland, the importance of invertebrate abundance merits further study.

I also identified significant differences among sites in the timing of nest initiation. Breeding commenced 5 d later at East Bay Mainland than on Coats Island, 130 km to the South. Although I have only two years of data, the timing of breeding at Prince Charles Island, 500 km north of East Bay, was later than the mean for East Bay in the late year of 1996 and earlier than the mean for Coats Island, in the early year of 1997. In 2004-2006, when research was conducted at both the Coats Island and East Bay Mainland sites, Red Phalaropes nested 6 – 16 d earlier at the former, despite the small geographical separation. Similarly large discrepancies in timing have been observed between proximate, but climatically different, sites in Greenland (e.g., Green et al. 1977, Moltofte

1985), while little discrepancy was observed between the timing of breeding in Semipalmated Sandpipers in Alaska and Northern Manitoba, despite the large geographical separation (Gratto and Cooke 1987). These observations highlight the role of local conditions in determining the timing of shorebird breeding.

There were substantial differences in the interval between arrival and laying largely because timing of breeding varied more among sites and years than did timing of arrival. Despite a small geographical separation, the average interval between arrival and laying was 5 d longer at the colder, more snow-rich East Bay Mainland Site than at the Coats Island site. In 2004, when snow at Coats Island was atypically late to melt (less so at East Bay), the interval did not differ between sites. In 2005 and 2006, when snow melt was later at East Bay than at Coats Island, the interval was twice as long at East Bay than at Coats Island. Further, shorebirds feeding at the snow free sites within 20 km of the study sites in years of delayed “arrival” further supports the idea that shorebirds arrive to the general area of the breeding grounds at relatively fixed times, and adjust their breeding chronology to match local conditions.

The local condition considered to be of greatest importance in determining the timing of breeding is snow cover, with breeding delayed by up to 3 weeks in years of late snow melt (e.g., Green et al. 1977, Meltofte 1985, Meltofte et al. 2007a). In some years, complete snow cover well into the breeding season can preclude nesting altogether (e.g., Mayfield 1978). A heavy snow cover limits the availability of nest sites and delays the emergence of surface active arthropods. In my analyses, initiation of the earliest nests was delayed by 13 d in the very late snow melt year of 2004, versus 2005 or 2006, at Coats Island. Moreover, the date of 50% snow clearance was the strongest predictor for

all metrics of timing of breeding in these models. This work represents the first quantitative link between snow cover and timing of breeding for Nearctic shorebirds.

Snow covered ground limits the availability of nest sites, but might also increase the risk of nest loss when predators restrict their search to the snow free patches (Byrkjedal 1980, Møller et al. 1981). If predators employ this strategy successfully, shorebirds may choose to nest later when there is a high presence of predators. I documented large interannual fluctuations in the abundance of predators, and found that nesting was instead earlier than would be predicted by snow cover alone in years when predators were abundant. I also found strong evidence for an increased rate of nest survival early in the breeding season at these sites (chapter 3), in contradiction to the long-standing hypothesis above. By nesting early in years with abundant predators, shorebirds can capitalize on this reduced risk of predation early in the season, but also can take advantage of an increased opportunity for renesting should the need arise.

Renesting in the event of predation is common for shorebirds (e.g., Nol et al. 1997, Tulp et al. 2000, Møller et al. 2007a, R. Gates, *unpublished*), and individuals that initiate nests early maximize their opportunity for a successful second attempt at breeding. Early nesting is not without costs, however. The pre-breeding season is a time of significant energetic stress. Shorebirds must rebuild lean mass lost during migration (Tulp et al. 2009), alter their organ sizes and physiology in preparation for breeding (Morrison et al. 2005), feed in energetically challenging, exposed habitats (Piersma et al. 2003), gather the nutrients required for egg formation (Klaassen et al. 2001, Morrison and Hobson 2004), and amass energy stores in anticipation of incubation (Tulp et al. 2002, Tulp and Schekkerman 2006). Earlier nesting has been linked to reduced egg volume,

prolonged egg-laying intervals and prolonged incubation periods presumably because of the difficulty in meeting competing energetic demands (Reynolds 1987, Schamel 2000). Harsh early season weather can result in extended nest absences (Tomkovich 1988), longer incubation recesses, and adverse effects on body condition (Tulp and Schekkerman 2006). This prolongation of the nesting cycle exposes clutches to the risk of predation for longer periods of time, with adverse effects on nest success (e.g., Reynolds 1987). Thus, nesting earlier than is energetically optimal may only be warranted in years of high predator presence.

Synchrony of nest initiation

The synchrony of nesting should have a number of important consequences for breeding individuals. High synchrony results in greater densities of active nests, which in turn can facilitate group defence (Larsen et al. 1996), dilute the risk of predation to the individual by predator swamping (Ims 1990, but see Brown and Brown 2001), or increase the risk of predation through density dependent effects (e.g., Tinbergen et al. 1967). Low breeding synchrony among shorebirds nesting sympatrically may be the manifestation of differences in individual body condition, and reflect the difficulty of acquiring the resources for egg formation (Nol et al. 1997). There was no relationship between synchrony of breeding and weather variables, snowmelt or predator abundance. Instead, synchrony was related only to the timing of nest initiation, suggesting that it is merely a product of a variable start date and a relatively fixed end date to the period of nest initiation.

While I am confident in my interpretation that synchrony is influenced by this relatively fixed cut-off date, I should note the important influence of renesting on the

apparent synchrony of breeding. Second breeding attempts are necessarily initiated later than first nests. Thus, synchrony as measured here decreases in years of high renesting, which complicates interpretation of these results. Years of early breeding afford the greatest opportunity for renesting, and this may in part account for the apparent low synchrony in early-breeding years. Further, renesting is likely more common as nest predation increases. The higher synchrony of breeding observed at Coats Island and Prince Charles Island than at East Bay Mainland may in part reflect the higher nest success at the two former sites (see also chapter 3).

Regardless, nest synchrony relates to the proportion of late nests in the population of breeding birds. For individuals to breed successfully, their eggs must not only hatch, but their chicks must also develop, fledge and successfully start the long migration south before freezing temperatures reduce the availability of arthropods. I found that nest initiation ceases at the end of June or early July; a finding corroborated by other studies (Meltofte et al. 2007a,b and references therein). Chick growth is highest when nests hatch around the peak of arthropod abundance (Schekkerman et al. 2003) and chick survival declines when timing of egg hatching is late (Tulp and Schekkerman 2001, Ruthrauff and McCaffery 2005). Nests initiated later in the season also delay the departure of adults, such that they may miss the peak of food in non-breeding areas (e.g., Schneider and Harrington 1981), or encounter large numbers of predators en route (Lank et al. 2003). As the breeding season draws to a close, the value of initiating a nest decreases, while the costs to adults of remaining on the breeding grounds increases (*cf.* Forbes et al. 1994).

In summary, these results suggest that birds arrive to the breeding grounds at relatively fixed dates, and initiate nests when local conditions are suitable. Years of late snow melt resulted in delayed breeding, while breeding was earlier than would be predicted by snow cover alone when predators were locally abundant. This response to abundant predators might facilitate successful renesting in the event of predation. Synchrony of breeding was not influenced by weather, snow melt or predators, and instead reflected the variable dates of nest initiation and a fixed date after which few birds initiated nests. Presumably, abrupt cessation of nesting occurs because offspring from later nests would have insufficient time to hatch, fledge and prepare for southward migration.

Table 2.1. Sample size (nests), first sightings and timing of breeding data for shorebirds breeding at four sites in the eastern low arctic. Data presented are means across years. *Limited data were available for Prince Charles Island in 1996 because staff arrived to the area in mid June.

Species	East Bay Mainland (1999 - 2007)				Coats Island (2004 - 2006)			
	N	First Sighting	First Nest	Median Nest Initiation ± SD	N	First Sighting	First Nest	Median Nest Initiation ± SD
Semipalmated Plover	56	8 June	15 June	19 June ± 6	0	7 June	.	.
Black-bellied Plover	69	5 June	16 June	21 June ± 5	9	6 June	16 June	22 June ± 1
Red Phalarope	90	8 June	19 June	29 June ± 6	31	7 June	12 June	18 June ± 4
Ruddy Turnstone	178	6 June	11 June	17 June ± 6	0	7 June	.	.
Red Knot	2	6 June	15 June	.	0	12 June	.	.
White-rumped Sandpiper	51	4 June	15 June	23 June ± 7	14	6 June	14 June	10 June ± 4
Semipalmated Sandpiper	2	7 June	22 June	.	144	7 June	12 June	18 June ± 4
American Golden Plover	8	6 June	17 June	21 June ± 5	19	2 June	14 June	17 June ± 4
Sanderling	4	7 June	22 June	25 June ± 3	0	9 June	.	.
Dunlin	13	6 June	25 June	19 June ± 4	62	2 June	10 June	16 June ± 6
Purple Sandpiper	0	6 June	.	.	0	6 June	.	.
Pectoral Sandpiper	0	9 June	.	.	3	10 June	13 June	13 June ± 1
Baird's Sandpiper	0	8 June	.	.	0	.	.	.
All Species	473	7 June	18 June	22 June ± 5	282	7 June	13 June	16 June ± 4

Table 2.1. Continued.

Species	East Bay Island (1999 - 2007)				Prince Charles Island (1996*-1997)			
	N	First Sighting	First Nest	Median Nest Initiation ± SD	N	First Sighting	First Nest	Median Nest Initiation ± SD
Semipalmated Plover	0	4 June
Black-bellied Plover	0	4 June	.	.	6	.	11 June	15 June ± 3
Red Phalarope	0	5 June	.	.	29	.	9 June	16 June ± 4
Ruddy Turnstone	0	1 June	.	.	12	.	11 June	15 June ± 3
Red Knot	0	5 June
White-rumped Sandpiper	0	31 May	.	.	11	.	11 June	15 June ± 4
Semipalmated Sandpiper	0	30 May	.	.	2	.	16 June	.
American Golden Plover	0	30 May	.	.	4	.	14 June	16 June ± 2
Sanderling	0	2 June
Dunlin	0	1 June	.	.	2	.	14 June	.
Purple Sandpiper	0	3 June
Pectoral Sandpiper	0	3 June
Baird's Sandpiper	0	3 June
All Species	0	2 June			66		12 June	15 June ± 2

Table 2.2. Selected weather parameters for the four study sites in the eastern arctic, Nunavut.

Year	Prince Charles Island		East Bay Mainland	
	Mean Temp. (°C, 25 June - 30 June)	Date of 50% Snow Clearance	Mean Temp. (°C, 10 June - 30 June)	Date of 50% Snow Clearance
1996	7.0	30 June	.	.
1997	4.5	<25 June	.	.
1998
1999	.	.	2.7	18 June
2000	.	.	2.7	19 June
2001	.	.	4.7	1 June
2002	.	.	5.1	10 June
2003	.	.	3.0	13 June
2004	.	.	3.3	17 June
2005	.	.	5.5	14 June
2006	.	.	4.2	5 June
2007	.	.	1.7	15 June

Table 2.2. Continued.

Year	East Bay Island		Coats Island	
	Mean Temp. (°C, 10 June - 30 June)	Date of 50% Snow Clearance	Mean Temp. (°C, 10 June - 30 June)	Date of 50% Snow Clearance
1996
1997
1998
1999	3.0	8 June	.	.
2000	1.4	9 June	.	.
2001	3.0	< 23 May	.	.
2002	2.8	< 29 May	.	.
2003	2.4	4 June	.	.
2004	1.4	1 June	1.4	23 June
2005	.	< 30 May	4.9	< 7 June
2006	3.9	< 27 May	4.5	5 June
2007	1.8	11 June	.	.

Table 2.3. Results of an analysis of timing of breeding for shorebirds at East Bay Mainland and Coats Island, Nunavut. Separate General Linear Models were generated for the five timing metrics (earliest nests – latest nests) and for synchrony (measured as the standard deviation of initiation dates). Variables not found to be significant in any models include: mean temperature (°C, 10 – 30 June), mean daily windchill low (°C, 10 – 30 June) and mean wind speed (km / h, 10 – 30 June). Ns = not significant at $\alpha = 0.05$.

Predictor	Earliest Nests		1st Quartile		Median		3rd Quartile		Latest Nests		Predictor	Synchrony (SD)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>
Site	11.73	0.002	11.05	0.002	18.28	0.000	16.53	0.000	19.93	0.000	Site	16.74	0.000
Species	6.83	0.000	3.84	0.002	6.83	0.000	3.59	0.003	ns	ns	Earliest Nest Initiation	14.41	0.000
Date of 50% Snow Cover	119.98	0.000	73.19	0.000	42.27	0.000	21.80	0.000	4.62	0.037			
Fox and Jaeger Sightings / h	5.42	0.025	4.27	0.046	5.02	0.031	ns	ns	ns	ns			

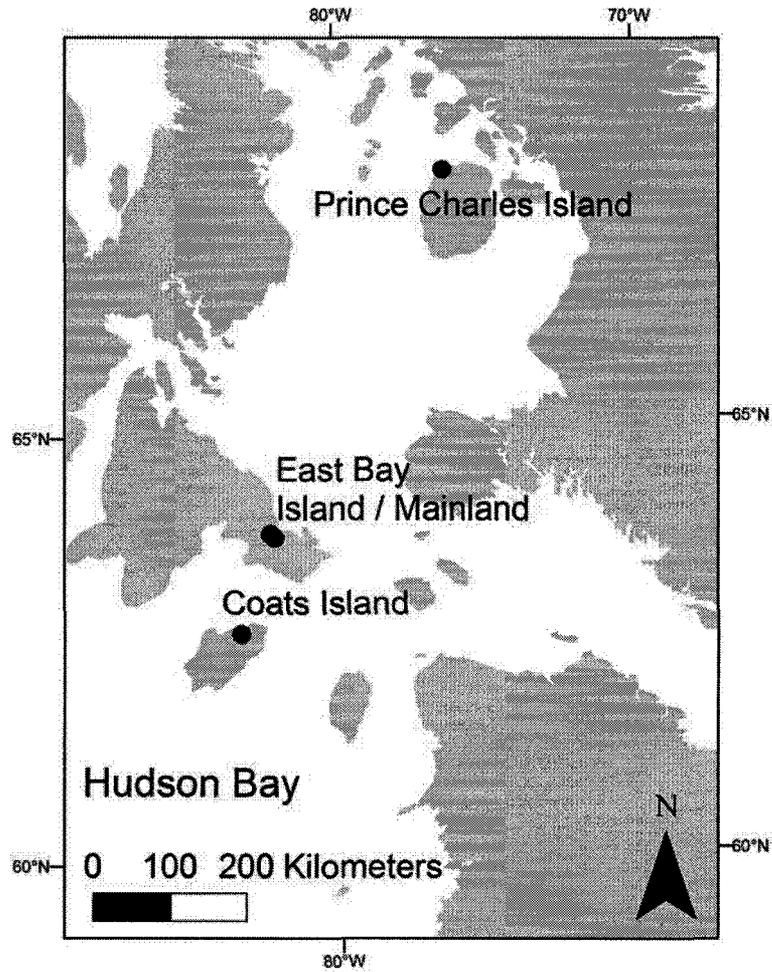


Figure 2.1. The four study sites in the eastern arctic, Nunavut, Canada. The East Bay Mainland and Island sites are separated by a distance of only 7 km.

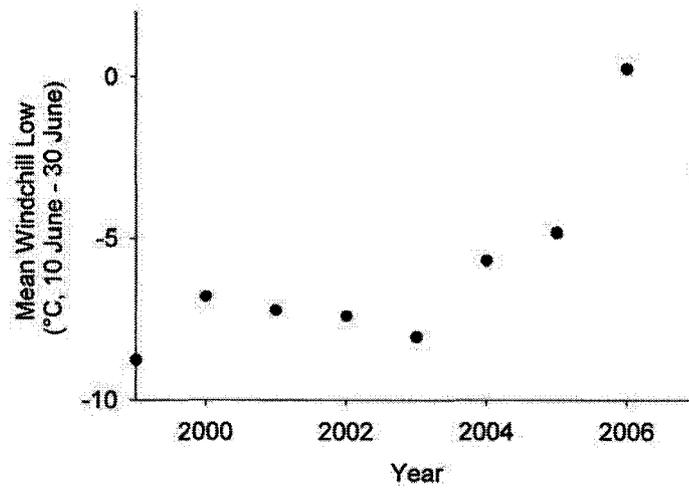


Figure 2.2. The mean daily windchill low (°C) from 10 June – 30 June, for the East Bay Mainland site on Southampton Island, Nunavut, 1999 - 2007.

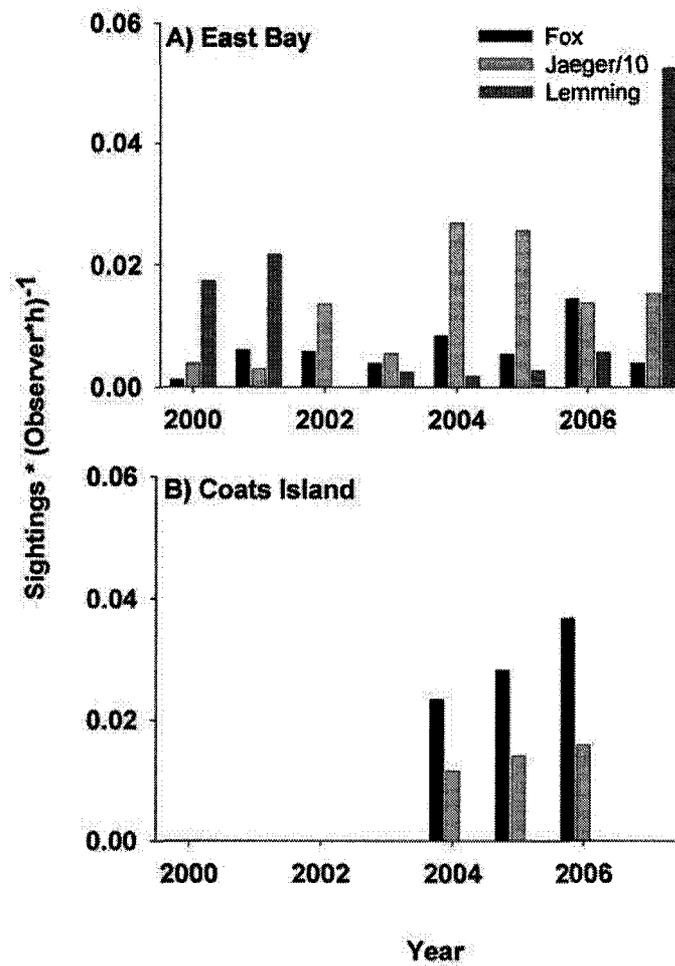


Figure 2.3. The number of predators and lemmings encountered in each year (sightings per observer hour) at the East Bay (a) and Coats Island (b) sites. Note that jaegers were the most abundant predator in all years; the encounter rate displayed in the figure is /10 to equalize the scale among species.

Chapter 3. Predator abundance and incubation behaviour explain interannual and interspecific patterns of nest success for arctic breeding shorebirds

Abstract

Abundance of predators is widely assumed to influence avian nest survival, but the expected relationship has rarely been tested empirically. I studied nest survival of shorebirds at two sites in the eastern Canadian arctic to determine whether natural fluctuations in predator abundance could explain the large interannual variation in nest survival, and contrasted this with the effects of variable weather on nest survival. This shorebird species assemblage also shows large interspecific variation in nest survival, and I tested the hypothesis that risk of predation is lower for biparental incubators than for those that incubate alone and leave the nest unattended during frequent recesses. From 2000-2007, I monitored 899 nests of 12 species, and used program Mark to assess patterns in daily nest survival. Most of the interspecific variation was explained by grouping species by incubation strategy, with uniparental species showing consistently lower nest survival. Over 8 years of study at East Bay, the average survival of nests from lay to hatch was 10% for uniparental species as compared to 42% for biparental species. Strong temporal patterns suggest that nest survival is highest early and late in the breeding season and depressed mid-season. Among years, variation in the abundance index of predators was an extremely strong predictor of nest survival. Models received little support if they contained effects of weather or abundance of lemmings, which is supposed to be a primary prey for tundra predators. Changes in arctic fox abundance explained variation in nest survival of biparental species whereas changes in abundance of jaegers explained variation in nest survival of uniparental species. These results demonstrate that increases in predator abundance indeed account for interannual variation

in shorebird nest survival, but that the relationship may be influenced by the behaviour of both the predators and the nesting shorebirds.

Introduction

The proportion of reproductive attempts that are unsuccessful varies widely within and among bird species, and understanding this variation is a cornerstone of avian research. This demographic variation has an important bearing on population dynamics, but understanding variation in nest survival is also important to make sense of varied avian life history strategies, and to assess how populations might respond to environmental change.

Variation in nest survival is commonly related to variation in nest-site characteristics, with the vast majority of studies demonstrating habitat differences between successful and failed nests (122/148, or 82% of published studies in a review by Clark and Shutler 1999). Despite the prevalence of significant effects in the literature, the factors that distinguish successful and failed nests are surprisingly inconsistent among and even within species (e.g., Filliater et al. 1994, Boulton et al. 2003). Even among waterfowl, where the active management of habitat to maximize nest success is a multi-million dollar industry, the critical habitat features for management are the subject of debate (e.g., Arnold et al. 2007). Moreover, studies of nest habitat do little to address the cause of the sometimes large inter-annual variation observed in nesting success within sites (e.g., Beletsky 1996, Schmidt and Ostfeld 2003, Clotfelter et al. 2007).

Patterns in nest success must, at some level, be attributed to the abundance or behaviour of predators, simply because predation is the primary cause of nest failure in almost all avian species studied to date (e.g., Ricklefs 1969, Martin 1993). Although

intuitive, explicit tests of this linkage between predator abundance and/or behaviour and rates of nest survival are few (Beauchamp et al. 1996, Côté and Sutherland 1997, Schmidt 2003, Schmidt et al. 2006, reviewed in Thompson 2007), and are often inter-site comparisons in disturbed or fragmented habitats (Anglestam 1986, Andrén 1992, Marzluff et al. 2007). An increasing abundance of predators should lead to greater nest mortality by increasing the encounter rate, but the nature of this relationship is difficult to assess when studies are complicated by a diverse array of predators (Marzluff et al. 2007), differential nest survival among vegetation layers (Martin 1993), or numerous features of inter-site variation. Even after controlling for these factors, the relationship between predator abundance and nest survival may be masked by the behaviour of the incubating birds themselves (Fontaine and Martin 2006a, Fontaine et al. 2007).

The behaviour of nesting birds can have a variety of positive or negative effects on nest survival. The active antipredator behaviours of some shorebirds, for example, are successful at dissuading or distracting predators and therefore have a positive influence (Gochfeld 1984, Larsen et al. 1996). However, the activity of parent birds near their nest also might increase the risk of predation if predators use their activity as a visual cue (Skutch 1949). Nest predation is higher for birds with greater rates of incubation feeding (Martin and Ghalambor 1999, Martin et al. 2000), and the rate of incubation recesses may have the same effect for species without mate feeding (Cresswell et al. 2003, Smith et al. 2007a). Risk of predation might be influenced by these behaviours, but the opposite may also be true: incubation behaviour might be modified in response to changes in the risk of predation. Incubation feeding may be suspended when predators are nearby (Ghalambor and Martin 2002), or increased when predators are experimentally removed (Fontaine and

Martin 2006a). Similarly, a shorebird nesting within the protective umbrella of an aggressive bird (lowered risk) took more frequent incubation recesses than individuals of the same species, nesting at the same site, in areas where the risk of predation was expected to be higher (Smith et al. 2007b). The relationship between predator and prey is thus two sided, and the link between predator abundance and nest survival is likely influenced by this interaction.

Arctic breeding shorebirds present a unique opportunity to study patterns of nest survival in a system with large, natural fluctuations in predator abundance, and dramatically different incubation behaviour among otherwise similar species. All shorebird species lay four eggs in a simple scrape in the ground but some incubate the eggs alone (uniparental incubators) whereas in other species (biparental incubators), incubation duties are divided between both pair members (Jönsson and Alerstam 1990). As a result of energetic constraints, uniparental incubators are known to leave the nest more frequently than biparental incubators change roles (e.g. Norton 1972), and in the case of uniparental incubators, the nest is left unattended.

Among shorebirds nesting in the Nearctic, there are two primary predators of eggs: arctic foxes and Parasitic Jaegers. The abundance of these predators fluctuates dramatically between years, potentially in response to yearly variation in the abundance of lemmings. I knew *a priori* that variation in nest survival among species and years was strong (Smith et al. 2007a), and attempted to explain these patterns among years by assessing the influence of factors that varied by year.

Here, I describe patterns of nest survival among 8 shorebird species, and quantify the relationship between the abundance and activity of predators and the survival of

shorebird nests. I predicted that nest survival would be more directly influenced by predator abundance than by abiotic factors that vary among years such as weather or snow melt. I modeled intra- and interspecific patterns of nest survival to identify seasonal trends and evaluate the influence of incubation behaviour on the risk of predation. Finally, I used artificial nests to evaluate interannual differences in nest survival with the effects of incubator behaviour experimentally removed.

Methods

Study areas

Research was conducted at two sites in the eastern Canadian arctic. Coats Island, Nunavut, lies at the north end of Hudson Bay. The research camp was located on the northeastern portion of the island, at $N62^{\circ} 51' W82^{\circ} 29'$ (Fig. 2.1). I worked at this site for June and July, 2004-2006, and searched for nests in a study plot measuring 6 km x 2 km. This plot was composed primarily of gramminoid dominated wetlands, ponds and small lakes. Willow and heath dominated uplands and raised beach habitats were less common. A small, newly established colony of roughly 500 pairs of Lesser Snow Geese was present on the northern end of the study plot during the years of this study. The second site was located on the shore of East Bay, Southampton Island, approximately 130 km to the northeast, at $63^{\circ} 59'N 81^{\circ} 40'W$ (Fig. 2.1). Work here was conducted from June - July, 2000-2007 in a study plot of 4 km x 3 km. This plot comprises a variety of coastal and inland habitats including intertidal mudflats, sedge dominated meadows, and hummocked areas of heath and exposed peat. More complete details of the sites' physiography appear in Smith (2003), Smith et al. (2007a) and chapter 2. Despite the small geographic separation, Coats Island and East Bay differ substantially in terms of

climate; the latter is influenced by the cold waters of the Foxe Basin and is more mid-arctic both in climate and flora.

Shorebirds and their predators

The shorebird species best represented in these samples include the Semipalmated Plover, Black-bellied Plover, American Golden-plover, Red Phalarope, Ruddy Turnstone, Dunlin, Semipalmated Sandpiper and White-rumped Sandpiper. Nest records were limited for the Purple Sandpiper, Red Knot, Sanderling and Pectoral Sandpiper.

All species share many basic reproductive traits (chapter 1). Typically, these species incubate for roughly three weeks (19-26 days). While subtle variation exists (see chapter 2), all breed at approximately the same time with peak laying in mid June. Most species are monogamous, biparental incubators, and share the duties of incubation more or less evenly. The Red Phalarope exhibits facultative polyandry (Tracy et al. 2002), and the White-rumped Sandpiper is polygynous (Parmelee 1992). Incubation is uniparental for these two species, and is carried out by the male for phalaropes and the female for White-rumped Sandpipers. The uniparental species have mean incubation bout lengths of approximately 45 min, and leave the nest unattended when they depart to feed (Cartar and Montgomerie 1985, Tulp and Schekkerman 2006, Smith et al. 2007b). In contrast, the biparental species sit for 3-4 h before one parent relieves the other by taking over incubation (Mayfield 1973, Sullivan Blanken and Nol 1998, Perkins 2004). Biparental species may leave the nest unattended for brief periods, but do not as a rule take breaks to feed until relieved from incubation by their mate.

The most significant nest predators at both sites were the Parasitic Jaeger, and arctic fox (See chapter 6). Herring Gulls were observed regularly at East Bay, but are

considered a minor predator of shorebird eggs (K. Allard, *pers. comm.*). Long-tailed Jaegers are included in jaeger counts, but are assumed to be less important than Parasitic Jaegers because they were on average 15 times less abundant, and are thought to eat primarily lemmings (Wiley and Lee 1998). Other potential predators, assumed to be unimportant because of their scarcity, include: Peregrine Falcons, Glaucous Gulls, Sandhill Cranes and Common Ravens. I recorded the number of arctic foxes and jaegers observed per person*hour, and use this as an index of relative predator abundance between years. This encounter rate metric reflects both the abundance and level of activity of the predators (i.e., total response), and provides an index of the potential for predation among years (Hochachka et al. 2000, Wilson and Bromley 2001). Total person*hours per season varied among years, but this did not bias our indices of predator abundance (linear regressions of total person hours vs. sightings per person*hour: all $P > 0.4$). I also recorded the number of lemming encounters at East Bay, and use this to reflect the abundance of potential alternative prey (e.g., Summers 1986, Summers and Underhill 1987, Bêty et al. 2002). No lemmings are present on Coats Island (e.g., Gaston and Ouellet 1997).

Monitoring weather and snow melt

I collected weather data at both camps with automated weather stations (Davis Vantage Pro). I collected a variety of weather data, but selected mean daily temperature and mean daily windchill low as the two variables with the most potential to influence nest survival (through effects on the energetic costs of homeothermy). I used the mean for the period 10 June – 25 July because this spans the incubation period for most individuals, and because weather records are inconsistent outside of this period in some years. Snow melt

influences timing of breeding (chapter 2), and was monitored by making daily estimates of the percentage of snow free ground in a fixed area within the study sites (see chapter 2).

Artificial nests

I conducted an artificial nest experiment in an attempt to remove effects of incubator behaviour and assess the interannual pattern of “ambient” predation risk, despite the severe limitations that have been noted with such experiments (reviewed in Burke et al. 2004). The experiment was conducted at both sites, from 2004-2006, using Japanese Quail (*Coturnix japonica*) eggs. Artificial nest locations were selected for another study in a stratified random (by habitat type) design. Sample sizes varied between years, in part due to breakage of eggs during transport to the arctic field sites. Artificial nests consisted of four eggs, and were exposed to predators for two periods of 9 d in early (deployed 3 - 6 July) and mid July (deployed 12 – 15 July). These times correspond to the late incubation period of natural nests in most years. Artificial nests were checked every third day, and the same sites were used in both rounds of experimentation. Nests with at least one egg damaged or removed were considered depredated.

Quail eggs closely resemble shorebird eggs in colouration and size. The depressions we created appeared similar to the simple scrapes used by shorebirds. A coloured nail was hidden under the eggs to facilitate finding the nest when predators took the eggs. I used observed nest losses divided by exposure days to calculate a daily mortality rate for artificial nests (Mayfield 1961). Nest loss was assumed to have occurred halfway between the 3 d intervals. Because I was modeling a constant survival

rate and had short intervals between checks, more complex models of nest success were unnecessary (Etterson and Bennett 2005, Johnson 2007).

Shorebird nest finding, ageing and monitoring

At both Coats Island and East Bay, I found nests by observing individuals on incubation recesses or by flushing birds either by walking or by dragging a 30 m length of 5 mm diameter rope. Search effort was not constant between sites or years, but was allocated evenly to 1 km blocks within the study plots to ensure that nest searching was not restricted to the highest quality habitats. When a nest was found, location was recorded \pm 3 m with a handheld Global Positioning System (Garmin eTrex™), and a nest marker was placed 10-15 m away so that the nest scrape could be revisited. Nests found during laying were monitored daily until the clutch was complete, and at least weekly thereafter until hatch. Nests found with complete clutches were aged (see below), and monitored at least weekly until 7 days before the predicted hatch date. All nests were monitored more closely as they approached hatch; every second day for nests showing signs of star-cracking, and daily until hatch for nests with pipped eggs.

Nest age was most often estimated using egg flotation characteristics because few nests were found during laying (Liebezeit et al. 2007). Two or more eggs from each clutch were immersed in water, and the angle and location of the egg in the water column were recorded to estimate nest age and predict hatch date (\pm 4 d or less in most cases). Nests were considered successful if one or more eggs hatched, and failed if they were depredated or abandoned. Nests were considered abandoned if the eggs were present but cold on two consecutive visits spanning at least 4 d. One egg of the clutch was positioned with the narrow end outwards to confirm that it had not been incubated (and

thus returned to the correct position) between our visits. I considered nests depredated if their contents disappeared before they could possibly have hatched. In the cases where nests disappeared but the fate could not be assigned with certainty, I recorded the fate as unknown, and used only the data up to the prior visit (as the nest was successful, i.e., not depredated or abandoned, over this interval).

Data analysis

Daily nest survival rates were modelled using Program Mark, version 5.0 (White 2007). Dates were scaled so day 1 was the date on which the first nest was found at each site, and sites were analysed separately. For each site, initial models were a single estimate of nest survival. I then considered the main effects of species and incubation strategy (uniparental versus biparental) separately. I selected one of these main effects models, and fit two additional additive models with linear and quadratic effects of time. I then added an interaction effect to test whether seasonal patterns in nest survival differed between incubation strategies. I did not test whether temporal patterns vary by year to limit the number of models evaluated. Nest age effects may also play a role in shorebird nest success (Dinsmore et al. 2002); these and other intraseasonal patterns in nest success are described separately (chapter 4).

Using the best model from these steps, I then considered models that varied by year. At East Bay, I had 8 years of data and was able to test directly the effects of year-specific covariates. I did this by adding the predator and weather variables individually to the time- and incubation system dependent model (see above). I also tested models including interactions between predators and incubation system because I predicted that predator effects should vary by incubation system (because for example some biparental

species are able to defend their nests from jaegers). I did not model the effects of year covariates formally for the Coats Island site, because I had only 3 years of data. Instead, I generated yearly estimates of nest success from the best model including time, species or incubation system effects, and compared these to the weather and predator observations to draw general conclusions.

In total I considered 16 candidate models for East Bay and seven for Coats Island. I used a logit link function for all models. I omitted rare species from the analyses (samples sizes for analyses appear in Table 3.1). At the East Bay site, analyses were restricted to the five most common species while at Coats Island, I excluded species*years for which there were fewer than 5 records. I also excluded nests that were active for only a single visit (24 cases); these nests cannot be utilised by Program Mark for estimation of nest survival.

Models were ranked with Akaike's information criterion for small samples (AIC_c), and ΔAIC_c and Akaike Weights (w_i) were used to infer support for models in the candidate set (Akaike 1973, Burnham and Anderson 2002). I identified a confidence set on the models by including those with $\Delta AIC_c \leq 6$. No goodness of fit test is currently available for the nest survival models in Program Mark (Dinsmore and Dinsmore 2007).

Results

Weather, snow melt and predators

Weather varied markedly between years at both sites (Table 3.2). The Coats Island site had heavy snow cover in the spring of 2004, as did much of the Eastern Arctic that year (Meltofte et al. 2007a). The date of 50% snow cover was 18 days later in 2004 than in 2006, and the mean temperature and wind-chill low were correspondingly lower (Table

3.2). Over eight years of observation at East Bay Mainland, the date of 50% snow cover varied by nearly 3 weeks, from 1 June until 19 June, with a mean of 11 June. The mean temperature from 10 June – 25 July varied by less than 3°C, and the mean daily wind-chill low by 9°C. See chapter 2 for a more complete description of interannual patterns in weather, and their effect on the timing of shorebird breeding.

The abundance of predators also differed substantially between years at East Bay and less so at Coats Island (Fig. 2.3a,b). At East Bay, encounters with arctic fox were most common in 2006, while the numbers of jaegers were highest in 2004 and 2005. Lemming abundance varied among years, but there was no significant relationship between the number of lemmings and the number of foxes or jaegers at this site, either directly, or with a time-lag of one year (all R values < 0.62 , all $P > 0.05$). At Coats Island, the number of jaegers encountered by field staff was relatively stable between years, while fox encounters increased from 2004-2006 (Fig. 2.3b). The number of fox encounters per observer hour was greater at Coats Island than at East Bay. There are no lemmings on Coats Island (e.g., Gaston and Ouellet 1997).

Interspecific and temporal patterns of nest survival

I found 574 nests of 11 species at the East Bay site, and 325 nests of 7 species at the Coats Island site (Table 3.1). Of these 899 nests, 351 (39%) successfully hatched one or more young, 453 (50%) were lost to predators, 15 (2%) were abandoned, and 80 (9%) could not be assigned a fate with certainty. As mentioned, 24 nests were only active for a single visit, and could therefore not contribute to the models of nest survival. After rare species were excluded, the sample used in analyses comprised 521 nests of 5 species at East Bay, and 303 nests of 6 species at Coats Island (Table 3.1).

At East Bay, differences in daily nest survival between species were substantial. The model including species effects was 47 AIC_c units better than the base model (Table 3.3). Much of this interspecific variation was captured by the division between uniparental and biparental incubators. When species effects were replaced by an effect of incubation system, the deviance was slightly higher, but the AIC_c lower; for building subsequent models I used the latter effect because it was more parsimonious (Table 3.3). This effect was negative in all models considered, suggesting lower nest survival for uniparental species (range of $\hat{\beta}$: -0.89 to -1.60 on a logit scale; Table 3.4).

Temporal patterns also substantially improved model fit. While there was little support for a linear time trend, inclusion of a quadratic time trend improved the model by 4 AIC_c units (Table 3.3). Models with these time trends included a negative parameter estimate for the linear term and a positive parameter estimate for the quadratic term (Table 3.4), suggesting that nest survival is highest early in the nesting season, lowest approximately mid-season, and moderately high later in the season (Fig. 3.1a). The drop amounts to a 3% decrease in daily nest survival for biparental species and an 8% decrease for uniparental species, with minima on 4 July. The process underlying this temporal pattern in nest survival is explored in more detail in chapter 4.

At Coats Island some species were poorly represented in some of the 3 years of recording. The uniparental incubators comprised only Red Phalaropes in 2004 and 2005, with a small sample in 2004 ($n = 5$ nests). White-rumped Sandpipers were present only in 2006 ($n = 15$ nests). Consequently, the results from this site should be interpreted with caution. Interspecific differences were less pronounced at Coats Island than at East Bay. Inclusion of a species effect reduced model deviance, but yielded a larger value of AIC_c .

(Table 3.5). The distinction between uniparental and biparental species was also weaker than at East Bay, although it was a marginal improvement over the base model, and a substantial improvement over the species-specific model (Table 3.5). As for East Bay, the parameter estimate was negative, suggesting lower nest survival for uniparental species (range of $\hat{\beta}$: -0.248 to -0.393 on a logit scale).

Temporal variation in nest survival at Coats Island was strong, and followed a curvilinear pattern similar to that at East Bay (Fig. 3.2). Including a quadratic time effect reduced the AIC_c value of the model by 3.8 units (Table 3.5). The parameter estimates again indicate a negative linear term and a positive quadratic term, although the 95% CI for the latter includes 0 (Table 3.6). The values of the parameter estimates were similar between the two sites, meaning that predicted temporal patterns match closely (2-8% drop in daily nest survival, minimum on 7 July).

Interannual patterns of nest survival

I knew *a priori* that variation in nest survival within species among years was strong at East Bay (Smith et al. 2007a). A long time series from this site allowed me to investigate the underlying cause of these patterns by modelling the effects of covariates that varied by year. Models including the mean daily temperature throughout the nesting season or the date of 50% snow clearance received no support (Table 3.3). The mean daily windchill low improved model fit substantially (an improvement of nearly 13 units of AIC_c , $\hat{\beta} = -0.09 \pm 0.02$); however, this effect was much weaker than the predator covariates and not retained in the final models. The influence of windchill on nest success and incubation behaviour is explored in chapters 4 and 5, respectively. The encounter rate of lemmings also improved the model fit (13 units of AIC_c improvement,

$\hat{\beta} = 15.1 \pm 4.1$), but was weaker than predator effects. The encounter rate of foxes and jaegers improved model fit dramatically; at least 20 units AIC_c better than models with no year-specific covariates and at least 7 AIC_c units better than the weather or lemming covariates (Table 3.3). All models in the confidence set indicate negative effects of fox and jaeger abundance on shorebird nest survival, in addition to a quadratic effect of time, and an effect of incubation system. The top model also includes an interaction between predator type and incubation system (Table 3.3). The top model alone has a weight (w_i) of 0.79 and the combined weight of the three models in the confidence set is 0.99, suggesting extremely strong support for the effects described above. Parameter estimates for the top model appear in Table 3.4, and predictions for all years on the basis of observed abundances of foxes and jaegers appear in Figure 3.3.

These models suggest that changes in fox abundance have a larger influence on the nest survival of biparental species, while changes in jaeger abundance have a more dramatic effect on the nest survival of uniparental species (Fig. 3.1b,c). Mid-season, and over the range of abundances observed during the study, an 11.4 fold increase in observed fox activity accounted for an estimated decrease in daily nest survival of 7.3% for biparental species and 4.6% for uniparental species. In contrast, 8.1 fold variation in jaeger abundance accounted for a decrease in daily nest survival of 3.0% for biparental species and 7.8% for uniparental species. These differences in daily nest survival represent a 1.4 – 3.8 fold increase in the daily risk of predation, and amount to very large differences in hatch success over the duration of incubation.

Because incubation durations vary by up to 7 days between species, daily nest survival does not fully reflect interspecific differences in the proportion of nests that

should hatch. Based on the nests analysed here, a weighted mean incubation duration for biparental species is 23.0 days, while for uniparental species it is 20.2 days. Further, the median date of nest initiation at the East Bay site differs by 7 days between biparental and uniparental incubators (19 June versus 26 June, respectively, See chapter 2). For a nest initiated on the median date, in a year of average jaeger and fox abundance, the probability of survival from lay to hatch is 42% for biparental species and 10% for uniparental species.

At Coats Island, I did not model the influence of year-specific covariates, but instead modelled the effect of year as a categorical covariate. Inclusion of year effects improved model fit by nearly 11 units AIC_c , despite the addition of two parameters. The parameter estimates show the lowest nest success in 2005 and the highest in 2004 ($\hat{\beta}$ 2004 vs. 2005 = -1.02 ± 0.28 , 2004 vs. 2006 = -0.63 ± 0.30 , on a logit scale, Table 3.6). Observations of predators (Fig. 2.3) do not explain why 2005 should have the lowest nest survival. However, the differences in nest success between years were more modest at Coats Island than at East Bay (Fig. 3.3). In 2004, snow melt was exceptionally late and the Snow Geese at this site, like many waterfowl across the Eastern Arctic, did not breed. The effect of this on my results is unknown.

Artificial nest experiments

At Coats Island, both real and artificial nests had the highest rates of daily survival in 2004 and the lowest in 2005 (Fig. 3.4). At East Bay, artificial nests had similar survival rates in 2004 and 2005, and lower rates in 2006. Real nests had a higher rate of survival in 2005 as compared to 2004 and 2006. Artificial nests were depredated at rates much higher than natural nests, with daily survival as low as 54% at Coats Island in 2005. The

relative rate of change between years was also greater for artificial nests. Although real nests had higher survival at Coats Island than at East Bay, the mean daily survival of artificial nests did not differ between sites (Coats Island: 0.75 ± 0.12 , East Bay: 0.74 ± 0.03). Given the high rate of depredation, the results of this artificial nest experiment should be viewed with caution. However, interannual patterns in survival of artificial nests bore a superficial resemblance to that of real nests.

Discussion

Interspecific and temporal patterns of nest survival

At East Bay, models suggest strong interspecific differences in nest survival. These differences were not masked by the large variation in nest survival among years. Large differences in nest predation rates among sympatric species have often been ascribed to habitat, and in particular, to variation in the risk of predation among nesting guilds (Lack 1948, Nice 1957, Martin 1993, 1995). However, here the variation in nest survival appears unrelated to habitat; all species nest in simple scrapes on the tundra and previous analyses of real and artificial nests revealed that macro- and micro-habitat characteristics did not predict nest survival within or between species (Smith et al. 2007a). The interspecific effects seen in these data were modelled most parsimoniously by grouping species as uniparental or biparental incubators. I suggest that the lower nest survival for uniparental species results from increased conspicuousness, due to a high rate of incubation recess.

Skutch hypothesised that the number of trips made to the nest to feed young could influence the risk of predation (Skutch 1949, Martin et al. 2000). Variation in nest survival has also been linked to the presence or rate of incubation feeding among

passerines with uniparental incubation (Lyon and Montgomerie 1987, Ghalambor and Martin 2002). While shorebirds do not exhibit incubation feeding, the rate of nest recesses is much higher for uniparental versus biparental incubators. The uniparental species at this site have mean incubation bout lengths of less than one hour, while the biparental species sit for several hours at a time (Cartar and Montgomerie 1985, Tulp and Schekkerman 2006, Smith et al. 2007b, Mayfield 1973, Sullivan Blanken and Nol 1998, Perkins 2004). The greater number of incubation recesses per day should make the nest sites of uniparental species more conspicuous to predators, and could account for the consistently lower nest survival they displayed. This hypothesis should be tested more conclusively by examining variation in incubation and nest survival within species (see chapter 6).

The distinction between species, and between uniparental and biparental incubators, was weaker at Coats Island than at East Bay. However, I had only three years of data for the former site and the representation of some species in some years was poor. The Mayfield estimate of hatch success for Red Phalaropes at Coats Island in 2006 was 58% ($n = 15$ nests, Smith *unpublished*), > 45% higher than estimates for either 2004 or 2005. The highest estimate of hatch success from East Bay was 35% (in 2001, Smith et al. 2007b), but a hatch success of 58% is within the range reported elsewhere in the arctic (18-77%, Tracy et al. 2002 and references therein). As a result of this atypically high nest survival, I observed higher nest survival for uniparental incubators versus biparental incubators in 2006, but the effect was reversed in 2004 and 2005. I did not model a year*incubation system interaction because of the limited number of years.

In addition to strong interspecific differences, models from both sites contained quadratic time effects. The coefficients for these time effects were similar between sites, predicting decreases in daily nest survival of 2-8% between the start of the nesting season and the minima in the first week of July. Examples from comparable studies are few, in part because the analytical tools for measuring continuous temporal change in nest survival were only developed recently (reviewed in Johnson 2007). However, a similar pattern of daily nest survival, with a similar magnitude of decrease was observed for Willow Ptarmigan in La Pérouse Bay, in subarctic Canada (Wilson et al. 2007), and a weaker quadratic time effect was observed for Mountain Plovers in Montana (Dinsmore et al. 2002). No one factor is likely to account for both the apparent decrease and subsequent increase in daily survival (see Figs 3.1 and 3.2). Several possible contributory factors include seasonal changes in density and functional responses of predators, individual heterogeneity of nest survival, and changes in parental behaviour as nests age (Emery et al. 2005).

As the density of a prey increases, it may become profitable for a predator to shift its focus towards this prey in a functional response (e.g., Holling 1959, 1961, Holt 1977). For foxes, this functional response involves a shift from cached eggs, carrion and lemmings to the eggs of birds as the nesting season progresses (Stickney 1991). For Parasitic Jaegers, the functional response may instead reflect the timing of arrival to the breeding grounds and the shift from foraging in marine habitats (Wiley and Lee 1999), or from searching for insects in tundra hummocks (P. Smith, *Pers. Obs.*), to searching for nests. Alternatively, or in addition to a functional response, increasing shorebird nest density could lead to lower nest survival through density-dependent predation (Tinbergen

et al. 1967, Lack 1968). If predators intensify their searches in areas where they have encountered success, risk of predation may be positively correlated with nest density. However, the functional responses previously observed in arctic foxes were such that predation was most intense immediately after nesting began (Stickney 1991), and studies in subarctic and temperate areas have not documented density-dependent predation at the nest densities found in this study (Göransson et al. 1975, Sugden and Beyersbergen 1986, O’Rielly and Hannon 1989, Schieck and Hannon 1993, Larivière and Messier 1998), although the thresholds for density dependence may be lower in tundra ecosystems. Further, I found no effects of nesting density on nest survival in a previous study at East Bay (Smith et al. 2007a). Despite these observations, a functional response of predators with increasing nest density is consistent with the curvilinear pattern of nest survival seen here, could explain the similarity of temporal effects between our two sites, and warrants further attention (see chapter 4).

If individual nests differ inherently in survival, the poorest nests may fail early resulting in a pattern of increasing nest survival over the season. This could not fully account for the quadratic pattern observed, but high repeatability of nest survival has been reported in other systems (e.g., Martin et al. 2000). Previous work found little evidence of habitat differences between successful and failed nests (Smith et al. 2007a), and therefore I expect the repeatability of nest survival to be low within species. However, here I demonstrated highly repeatable interspecific patterns of relative nest survival, and differences in timing of breeding between species could therefore lead to apparent temporal patterns of predation risk. For example, the Red Phalarope, a uniparental species, lays late relative to other species at East Bay (see chapter 2) and has

poor nest success, potentially leading to the appearance of depressed nest survival mid-season. It should be noted, however, that the interaction between temporal patterns and mating system did not significantly improve model fit, and similar quadratic patterns of nest survival have been observed in studies of single species (Dinsmore et al. 2002, Wilson et al. 2007).

Other factors thought important to nest survival such as time and nest age will be confounded to some degree because nest initiation is relatively synchronous (chapter 2). Both time and nest age should influence the behaviour of incubators, with concomitant effects on nest survival. Pectoral Sandpipers (a uniparental species) took more frequent and shorter recesses as the summer air temperatures warmed, and increased total duration of recesses as nests aged (Tulp and Schekkerman 2006). Three other uniparental species showed no relationship between nest age and incubation behaviour (Tulp and Schekkerman 2006). Semipalmated Sandpipers (a biparental species), increased bout length as nests aged, thereby reducing the conspicuousness of incubation behaviour. As nests age, the intensity with which the parents defend them is expected to increase (review in Montgomerie and Weatherhead 1988, Brunton 1990, but see Knight and Temple 1986). Subtle variation in incubation behaviour or nest defence may interact with time and nest age in a complex manner to influence patterns of nest survival (this relationship is explored in more detail in chapter 4).

Although these analyses were not designed to identify causal mechanisms behind these temporal patterns, the pattern itself is of interest. My observation of high nest survival early in the breeding season contradicts a long-standing hypothesis that survival of shorebird nests is lowest early in the season because predators can concentrate their

search in snow free patches (Byrkjedal 1980, Meltofte et al. 1981, 2007b). My recent finding that shorebirds nest earlier in years of high predator presence (chapter 2) further supports the contention that early nesting may in fact mitigate the risk of predation in some way.

Interannual patterns and predator abundance

Explicit tests of the relationship between predator activity and nest success are surprisingly few and show inconsistent results (see reviews in Chalfoun et al. 2002, Thompson 2007). For example, predation of artificial nests increased with increasing corvid density in one study (Andr n 1992), but predation of real nests was weakly related or unrelated to corvid density in another (Marzluff et al. 2007). Studies where predator abundance varies within a site, either naturally or experimentally, have shown a positive relationship between predator abundance and rates of nest predation (e.g., Schmidt et al. 2001b, Schmidt and Ostfeld 2003, Clotfelter et al. 2007), but here too the effects were sometimes less pronounced than predicted (Fontaine et al. 2007, Fontaine and Martin 2006a,b). In the present study, there were strong effects of predator abundance on the rate of nest survival. I also found that shorebird species differed in their susceptibility to avian vs. mammalian predator species, and an effect of incubator behaviour was implicated (Table 3.4 and 3.5).

Over the eight years of this study, predation accounted for 97% of nest losses. I observed abandonment for only 15 of 899 nests, despite the fact that these birds are nesting on the arctic tundra, in conditions that present severe energetic challenges (e.g., Piersma et al. 2003, Cresswell et al. 2004). Models including weather effects received little support. Instead, I found that interannual patterns in nest survival were best

predicted by the abundance and/or activity of predators, with a 1.4 – 3.8 fold increase in risk of predation (i.e. 3-8% decrease in daily nest survival) as a result of an 8.1 – 11.4 fold increase in the number of predators sighted per observer hour. While these changes in nest survival are substantial, they are less than the changes in predator abundance. This moderated rate of change in nest survival has been seen for passerine birds (Fontaine and Martin 2006a,b, Fontaine et al. 2007), and might be related to adaptive changes in parental behaviour in response to the perceived risk of predation. Among those passerine species, activity near the nest was reduced when predators were nearby (Martin and Ghalambor 1999, Ghalambor and Martin 2002), or increased when predator abundance was experimentally reduced (Fontaine et al. 2007). Similarly, Red Phalaropes nesting in a protective association with the aggressive Sabine's Gull had more conspicuous incubation behaviour (Smith et al. 2007b). If other species in the study area alter their incubation in response to changes in predator abundance, this behavioural response would partially mask the effects of predator abundance.

A behaviour exhibited by some shorebird species with a direct effect on nest survival is aggressive nest defence. Aggressive nest defence can deter some avian predators (Gochfeld 1984, Larsen et al. 1996), and is most prevalent among biparental shorebirds (Larsen 1991). Among the species considered here, Black-bellied Plovers and Ruddy Turnstones pursue jaegers aggressively (P. Smith, *Pers. Obs.*). The reduced susceptibility of biparental incubators to jaeger predation observed here may reflect the success of aggressive nest defence. The larger effect of increasing fox density on the nest survival of biparental species may reflect the spatial distribution of the nests of biparental species. Ruddy Turnstones and Semipalmated Plovers tend to nest closer to the coast,

where the nests of seabirds and waterfowl are more abundant. Although sightings of foxes are not stratified by habitat, the presence of larger eggs in these areas presumably makes them more attractive to foxes.

Artificial nests

Survival of artificial nests should be higher than that of real nests if incubation behaviour is risky and used by predators as a cue to locate nests. Instead, I found much lower survival for artificial nests than for real nests, with a daily survival rate as low as 0.54 at Coats Island in 2005. Lower survival of artificial nests is a common result (reviewed in Major and Kendal 1996, Burke et al. 2004), and might simply reflect an inability of researchers to select artificial nest sites that mimic those of real birds. Shorebirds show strong nest habitat preferences, and while variation in occupied habitat does not explain variation in nest survival, this may reflect strong selection, but no competition, for nest sites (Smith et al. 2007a). Our selection of artificial nest sites may place eggs in locations that would not be selected by shorebirds, and where eggs are overly conspicuous to predators. In an artificial nest experiment in 2002 with two quail eggs per nest, instead of the four used here, I found higher daily survival for artificial versus real nests (Smith et al. 2007a), suggesting that visual cues might influence the susceptibility of nests.

Alternatively, the distraction displays, aggressive nest defence and cryptic behaviour of incubators may have a positive effect on the survival of real nests (Burke et al. 2004); indeed these risky behaviours should have a fitness benefit.

The interannual patterns of survival found in artificial nests resembled that of real nests only superficially, and both the absolute and relative differences between years were larger for artificial nests. The results of these experiments add little to our

understanding of patterns in the survival of real nests despite my best efforts to mimic the nests of shorebirds with appropriately sized eggs, of appropriate coloration and mottling, which were handled carefully and placed in seemingly appropriate artificial scrapes.

No evidence for an effect of lemming abundance

The alternative prey hypothesis (Anglestam et al. 1984) posits that predators focus on lemmings in years of high lemming abundance, but prey more heavily on eggs in years of lemming scarcity, thereby producing cyclical effects in the reproductive success of birds. While this effect is well established on the Siberian tundra (e.g., Larson 1960, Summers 1986, Summers and Underhill 1987), studies from across arctic Alaska, Canada, and Greenland have shown equivocal support (Holmes 1966, Wilson 1997, Wilson and Bromley 2001, Gratto-Trevor *unpublished* in Meltofte et al. 2007a), or none at all (Day 1998, Stickney 1991, Nol *unpublished* in Meltofte et al. 2007a, Meltofte et al. 2008, but see Bêty et al. 2001).

I found no evidence for the numerical responses of predators predicted by the alternative prey hypothesis, nor evidence of tight correspondence between lemming abundance and predation of shorebird nests. Lemming abundance was not retained in the final models of nest survival. Moreover, I saw substantial fluctuations in both predator abundance and nest success at East Bay in four consecutive years when lemmings were extremely scarce. Nest success also was variable at Coats Island, despite the complete absence of lemmings from the island. In addition, my results suggest that Parasitic Jaegers have a substantial influence on shorebird nest survival. Although data are limited, this species is considered only an opportunistic lemming predator (Maher 1974, Taylor 1976, Wiley and Lee 1999). While I agree that shorebird nest survival might be

ameliorated in peak lemming years, I question the broad applicability of the specific predictions of the alternative prey hypothesis and feel that a reconsideration of the effects that lemming cycles have on the productivity of tundra nesting birds is warranted.

My work highlights the large variation in shorebird nest survival between years, species, and even within the nesting season. In this comparatively simple system, a great deal of the interannual variation in nest survival is explained by variation in the abundance of predators. Similarly, much of the interspecific variation is explained by grouping species on the basis of their incubation behaviour; behaviour that should influence their detectability by predators. Within these broad patterns, the interaction between predator abundance and nest survival is mediated by the behaviour of both predator and prey. Future studies should refine our understanding of the relationship between predators and nest survival by examining the role of behaviour directly (see chapter 6).

Table 3.1. The total number of nests found of each species at the East Bay and Coats Island sites ('Total'), and the number used in analyses of daily nest survival ('Analysed'). Whether incubation is undertaken by one parent (uniparental) or both (biparental) is also displayed.

Species	East Bay		Coats Island		Incubation System
	Total	Analysed	Total	Analysed	
American Golden-Plover	8	0	24	24	Biparental
Black-bellied Plover	80	77	11	6	Biparental
Dunlin	13	0	71	65	Biparental
Pectoral Sandpiper	0	0	3	0	Uniparental
Purple Sandpiper	1	0	0	0	Biparental
Red Knot	2	0	0	0	Biparental
Red Phalarope	113	111	36	36	Uniparental
Ruddy Turnstone	201	192	0	0	Biparental
Sanderling	4	0	0	0	Uniparental
Semipalmated Plover	73	69	0	0	Biparental
Semipalmated Sandpiper	3	0	162	157	Biparental
White-rumped Sandpiper	76	72	18	15	Uniparental
Total	574	521	325	303	

Table 3.2. Weather variables and the date of 50% snow clearance for the East Bay and Coats Island sites.

Year	East Bay			Coats Island		
	Mean Temp. (°C, 10 June - 25 July)	Mean Windchill Low (°C, 10 June - 25 July)	Date of 50% Snow Clearance	Mean Temp. (°C, 10 June - 25 July)	Mean Windchill Low (°C, 10 June - 25 July)	Date of 50% Snow Clearance
2000	6.9	-6.8	19 June	.	.	.
2001	6.6	-7.2	1 June	.	.	.
2002	6.9	-7.4	10 June	.	.	.
2003	5.8	-8.1	13 June	.	.	.
2004	5.8	-5.7	17 June	4.2	-2.1	23 June
2005	6.5	-4.8	14 June	6.0	0.0	< 7 June
2006	6.5	0.2	5 June	6.4	0.4	5 June
2007	4.0	-3.1	15 June	.	.	.

Table 3.3. Summary of model selection results for an analysis of shorebird nest survival at East Bay, Nunavut, 2000-2007. The dependent variable was the daily rate of nest survival, AIC_c = Akaike's information criterion corrected for small samples, ΔAIC_c = the change in AIC_c relative to the top model, w_i = Akaike weight, a measure of relative support for the model, and deviance is the difference in the $-2 \log$ -likelihood between each model and the saturated model. The parameter abbreviations are as follows: S. = a single estimate of daily survival, species = a categorical variable denoting species, incub. = incubation system (biparental or uniparental), T, T^2 = time and time², Foxes, Jaegers, Lemmings = the encounter rate (sightings per observer*hour) of these species, temp = the mean daily temperature from 10 June – 25 July, snow = the Julian date of 50% snow clearance, and wind = the mean daily windchill low from 10 June – 25 July. A '+' indicates an additive effect, while a '*' indicates an interaction between two variables.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Incub. + T^2 + Foxes + Jaegers + Foxes*Incub.	1390.6	0.0	0.79	7	1376.6
Incub. + T^2 + Foxes + Jaegers	1394.0	3.4	0.14	6	1382.0
Incub. + T^2 + Foxes + Jaegers + Jaegers*Incub.	1395.7	5.2	0.06	7	1381.7
Incub. + T^2 + Foxes	1405.4	14.8	0.00	5	1395.4
Incub. + T^2 + Jaegers	1411.4	20.8	0.00	5	1401.4
Incub. + T^2 + Lemmings	1418.3	27.7	0.00	5	1408.2
Incub. + T^2 + Wind	1418.9	28.3	0.00	5	1408.9
Incub. + T^2	1431.6	41.0	0.00	4	1423.6
Incub. + T^2 + Snow	1431.8	41.2	0.00	5	1421.7
Incub. + T^2 + Incub.* T^2	1433.1	42.5	0.00	6	1421.1
Incub. + T^2 + Temp.	1433.5	42.9	0.00	5	1423.5
Incub. + T + Incub.*T	1433.8	43.2	0.00	4	1425.8
Incub. + T	1433.8	43.2	0.00	3	1427.8
S. + Incub.	1435.7	45.1	0.00	2	1431.7
S. + Species	1436.8	46.2	0.00	5	1426.8
S.	1484.0	93.4	0.00	1	1482.0

Table 3.4. Parameter estimates, standard errors and lower and upper 95% confidence limits (LCL and UCL, respectively) for the top model of daily nest survival of shorebirds at East Bay, Nunavut, 2000-2007. The top model, as well as the abbreviations, appear in Table 3.3. Biparental incubation was coded as 0; the parameter estimate reflects the additive effect of uniparental incubation.

Label	Estimate	SE	LCL	UCL
Intercept	5.57	0.63	4.33	6.81
Incub. (bi = 0)	-1.60	0.27	-2.13	-1.07
T	-0.110	0.044	-0.196	-0.024
T ²	0.0022	0.0008	0.0006	0.0038
Fox	-110.34	21.59	-152.65	-68.03
Jaeger	-3.01	0.76	-4.51	-1.52
Fox*Incub.	77.88	33.68	11.87	143.90

Table 3.5. Summary of model selection results for an analysis of shorebird nest survival at Coats Island, Nunavut, 2004-2006. AIC_c = Akaike's information criterion corrected for small samples, ΔAIC_c = the change in AIC_c relative to the top model, w_i = Akaike weight, a measure of relative support for the model, and deviance is the difference in the -2 log-likelihood between each model and the saturated model. Factors in the models included species, a single estimate of daily survival (S.), incubation system (biparental or uniparental, 'incub. '), time (T), time² (T²), and year. A '+' indicates an additive effect, while a '*' indicates an interaction between two variables.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Incub. + T ² + Year	749.7	0.0	0.99	6	737.6
Incub. + T ²	760.3	10.7	0.00	4	752.3
Incub. + T ² + T ² *Incub.	764.0	14.4	0.00	6	752.0
S. + Incub.	764.1	14.4	0.00	2	760.1
S.	764.6	14.9	0.00	1	762.6
Incub. + T	765.5	15.9	0.00	3	759.5
S. + Species	768.2	18.5	0.00	6	756.1

Table 3.6. Parameter estimates, standard errors and lower and upper 95% confidence limits for the top model of daily nest survival of shorebirds at Coats Island, Nunavut, 2004-2006. The top model, as well as the abbreviations, appear in Table 3.5. Biparental incubation was coded as 0; the parameter estimate reflects the additive effect of uniparental incubation.

Label	Estimate	SE	LCL	UCL
Intercept	5.10	0.71	3.71	6.48
2006	-0.63	0.30	-1.21	-0.05
2005	-1.02	0.28	-1.56	-0.47
Incub. (bi = 0)	-0.39	0.24	-0.86	0.07
T	-0.114	0.060	-0.233	0.004
T ²	0.0021	0.0013	-0.0005	0.0047

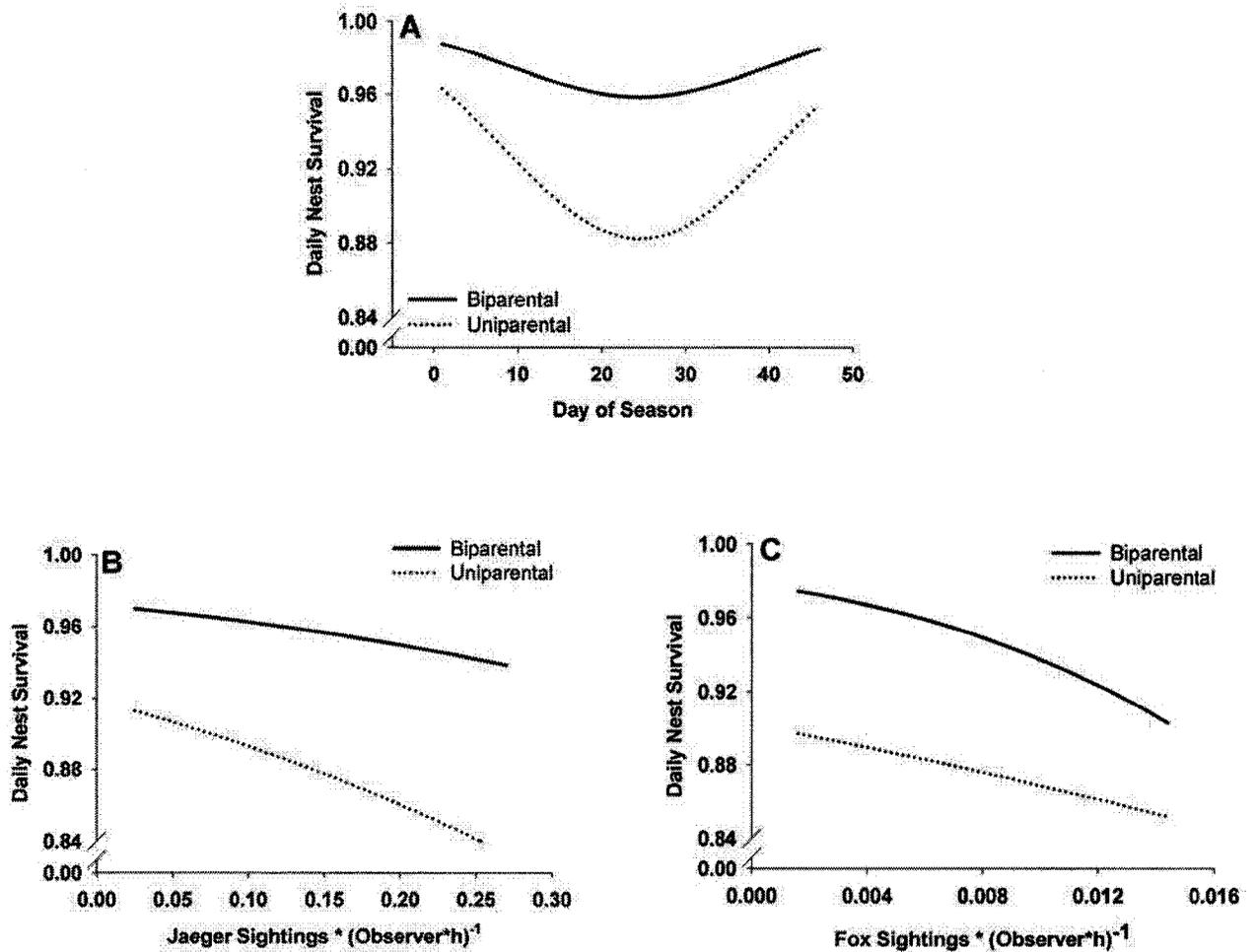


Figure 3.1, a-c. The predicted daily probability of nest survival for biparental and uniparental incubating shorebird species at East Bay, Southampton Island, Nunavut. All figures are based on the most parsimonious model, which includes effects of incubation type, a quadratic time effect, indices of fox and jaeger presence, and a fox*incubation type interaction effect. Panel a) shows the effect of time (day 1 = June 10) when predator presence is held constant at the observed mean, b) shows the effect of varying jaeger abundance half-way through the nesting season with fox abundance held constant at the observed mean and c) shows the effect of varying fox abundance half-way through the nesting season with jaeger abundance held constant at the observed mean. The range of variation in fox and jaeger abundance displayed in the figures reflects the range observed in the sample.

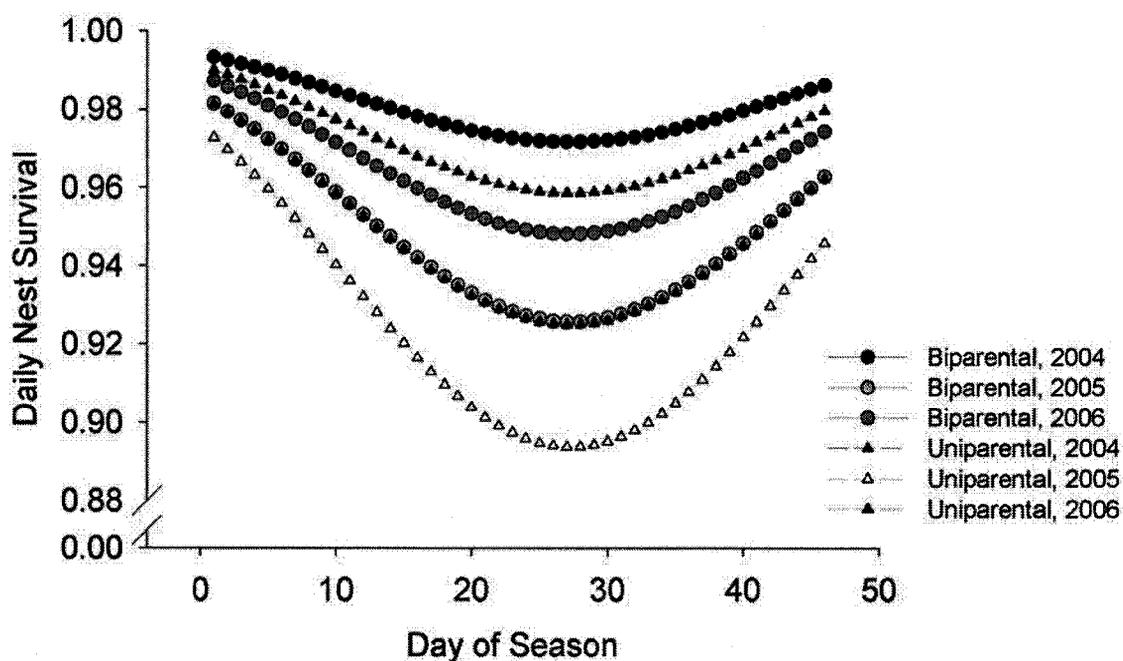


Figure 3.2. The probability of nest survival on each day of the nesting season (Day 1 = 11 June) for biparental and uniparental shorebird species, 2004-2006, at Coats Island, Nunavut. Estimates are based on a model including incubation system (uniparental versus biparental), a year effect, and a quadratic effect of time (see text).

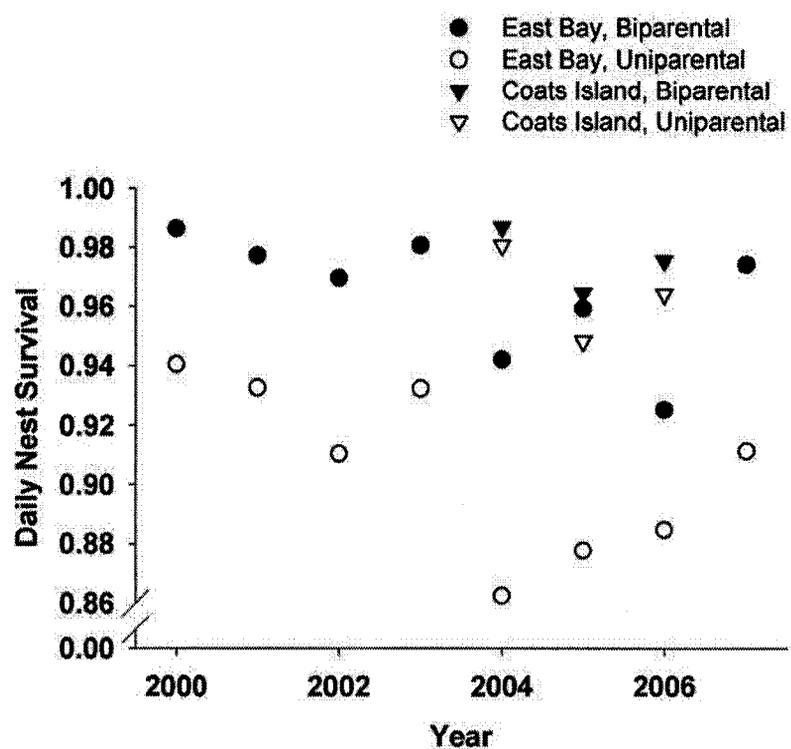


Figure 3.3. The rate of daily nest survival on the median date of nest initiation, as predicted by the top models from the East Bay and Coats Island sites (see Tables 3.3 and 3.5). At East Bay, predictions were made with year specific values for fox and jaeger abundance, and the median date of nest initiation was 22 June. At Coats Island, the median date of nest initiation was 18 June.

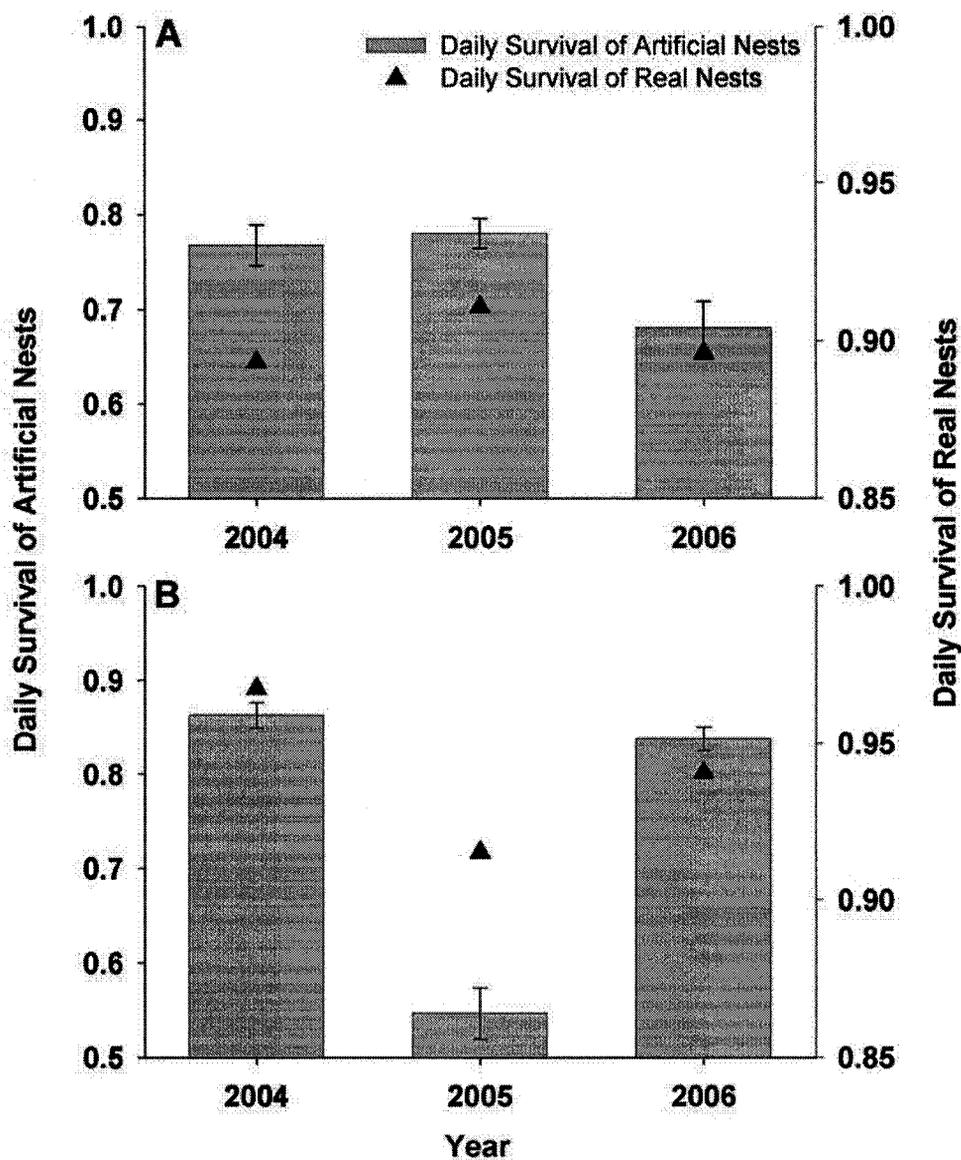


Figure 3.4. The daily survival rate (\pm SE) of artificial nests containing four Japanese Quail (*Coturnix japonica*) eggs at East Bay (A) and Coats Island (B), Nunavut, 2004-2006. Overlaid is the predicted daily survival of real nests from the best models, calculated for 13 July (half-way through the artificial nest experiment) with year specific values for predator abundance. Note that the survival of real nests was much higher in all years, and is displayed on a different axis for clarity.

Chapter 4. Intraseasonal patterns in shorebird nest survival are related to nest age and defence behaviour

Abstract

Nest survival may vary throughout the breeding season for many bird species, but the analytic methods to assess continuous temporal variation were developed only recently. I used Program Mark to model patterns in nest survival within the breeding season for shorebirds nesting on arctic tundra. I identified temporal patterns in nest survival and attempted to determine the mechanisms behind these patterns. Over eight years, I monitored 574 nests of 11 shorebird species and found strong evidence for variation in nest survival within a nesting season. Daily nest survival was lowest in the mid-season in five of eight years, but the timing and magnitude of the lows varied. I found no evidence that this quadratic time effect was driven by seasonal changes in weather or the abundance of predators. Contrary to my prediction, the risk of predation was not greatest when the density of active shorebird nests was highest. Although nest density reached a maximum near the middle of the breeding season, a daily index of shorebird nest density was not supported as a predictor of nest survival in the models. Predators' access to other diet items, in addition to shorebird nests, may instead determine the temporal patterns of nest predation. Nest survival also displayed a positive, linear relationship with nest-age; however, this effect was most pronounced among species with biparental incubation. Among biparental species, parents defended older nests with greater intensity. I did not detect a similar relationship among uniparental species, and conclude that the stronger relationship between nest age and both nest defence and nest survival for biparental species reflects that their nest defence is more effective.

Introduction

Studies of nest survival have contributed greatly to our understanding of avian demography and breeding ecology. Until recently, however, ecologists lacked the tools to rigorously study variation in nest survival within a season. The widely used Mayfield method and its derivatives assume that survival is constant over the interval of interest. Nests must be grouped for further analysis and this limits both sample sizes and statistical power (Johnson 2007). Novel analytical techniques have now been developed that allow nest survival to vary with time or other continuous covariates. Researchers have applied these new techniques to a variety of taxa in the last several years, and it has become apparent that nest survival is rarely constant throughout the season (e.g., Dinsmore et al. 2002, Wilson et al. 2007). However, in part because of the novelty of the results, the factors underlying within-season variation in nest survival have received little attention.

Predation is the primary cause of nest failure in almost all avian species studied to date (Ricklefs 1969, Martin 1993), including shorebirds breeding in the arctic (Smith et al. 2007a, chapter 3). Therefore, patterns in nest survival presumably are driven primarily by variation in the risk of predation. Beyond this, intraseasonal patterns can be grossly lumped into those that vary with time of the season and those that vary with the specific age of each nest. Factors that vary by time throughout the season and that could influence nest survival include nest density, the abundance or behaviour of predators, or the behavioural responses of incubating birds to seasonal changes in weather. In contrast, examples of age-dependent variables include heterogeneity in nest survival among nests, or changes in nest defence that vary with nest age. Time and nest age can be confounded, and the degree to which time- and age-dependent effects can be distinguished in analyses depends on the synchrony with which nests are initiated.

As time passes and the breeding season progresses, the density of active nests first increases and then decreases. The relationship between nest density and nest survival could be positive if predators become satiated, or negative if predators develop a search image for nests (Nams 1997), shift focus towards eggs in a functional response (e.g., Holling 1959, 1961, Holt 1977), or increase search effort in areas where they have found nests (Tinbergen et al. 1967). Even in the absence of a true response, increasing nest density necessarily increases the rate at which a systematically searching generalist predator encounters nests. While density and predator abundance and behaviour may influence nest survival, it may also be influenced by the behaviour of the incubators themselves.

The activity of parent birds near their nest may increase the risk of predation if predators use it as a visual cue (Skutch 1949). Birds making more frequent trips to the nest to feed mates suffer higher rates of predation (e.g., Martin and Ghalambor 1999, Martin et al. 2000), and more frequent incubation recesses may increase the risk of predation for species without mate feeding (Cresswell et al. 2003, Smith et al. 2007a). Shorebird incubation behaviour is constrained by energetic demands, and seasonal changes in weather are known to influence patterns of nest attendance (Cresswell et al. 2004, Tulp and Schekkerman 2006). Thus, weather could influence predation risk and nest survival indirectly by modifying nest attendance behaviour.

Changes in adult behaviour could also underlie age-related effects. As nests approach their date of hatch, their value to parents increases. This increased value, and the progressively diminished opportunity for renesting, may justify increased nest defence (review in Montgomerie and Weatherhead 1988, Forbes et al. 1994). However,

nest age could also appear to be related to nest survival if nests differ inherently in their susceptibility to predators. If the most susceptible nests fail early, heterogeneity of survival among nests could lead to a pattern of higher survival for older nests.

I monitored the nests of arctic breeding shorebirds to identify the patterns of nest survival within seasons and the factors that underlie them. Using the models available in Program Mark (White and Burnham 1999, Dinsmore et al. 2002), I simultaneously compared the influence of several covariates on the survival of shorebird nests. By testing *a priori* predictions, I assessed the influence of time-dependent effects such as nesting density, daily weather, and daily abundance of predators, as well the effects of nest age and age-dependent changes in nest defence, on the survival of shorebird nests.

Methods

Study area

Research was conducted from June-July, 2000-2007, at East Bay, Southampton Island, Nunavut (Fig. 2.1). The study plot (4 km x 3 km) comprises a variety of habitats including gramminoid-dominated wetlands, intertidal mudflats, hummocked areas of heath and raised beach ridges. A more complete account of the site's physiography appears in Smith (2003), Smith et al. (2007a) and chapter 2.

Weather data were collected at this site with an automated weather station (Davis Vantage Pro). A variety of weather data were collected (see chapter 2), but I selected daily windchill low as the variable with the most potential to influence nest survival (through effects on the energetic costs of homeothermy).

Shorebirds and their predators

Eleven shorebird species have been observed to breed at East Bay (Table 4.1), but five species represent >90% of nests and are the focus of this study: Semipalmated Plover, Black-bellied Plover, Red Phalarope, Ruddy Turnstone, and White-rumped Sandpiper.

These five species all nest in simple scrapes on the ground, lay four cryptically coloured eggs per clutch, and incubate for roughly three weeks (19-26 days). While subtle variation exists (see chapter 2), all breed at approximately the same time with peak laying in mid June. The Red Phalarope exhibits facultative polyandry (Tracy et al. 2002), and the White-rumped Sandpiper is polygynous (Parmelee 1992). Incubation is uniparental for these two species, and carried out by the male for phalaropes and the female for White-rumped Sandpipers. The remaining three species are monogamous, biparental incubators, and share incubation duties more or less evenly. Although accounts are primarily anecdotal, typical nest defence behaviour is thought to differ among the species. Red Phalaropes show no distraction displays or aggression towards predators (Tracy et al. 2002), White-rumped Sandpipers feign injury when predators approach (Parmelee et al. 1968), Ruddy Turnstones are highly vigilant and aggressively pursue predators (Nettleship 2000), Black-bellied Plover are highly vigilant and defend their nests aggressively from predators through aerial attack and distraction displays (Drury 1961), and Semipalmated Plovers are highly vigilant, with both parents taking part in distraction displays or scolding (Sullivan Blanken and Nol 1998).

The most significant nest predators at both sites were Parasitic Jaegers, and arctic foxes (See chapter 6). Long-tailed Jaegers were also included in counts of jaegers, but they were on average 15 times less abundant than their congener and are thought to eat lemmings primarily (Wiley and Lee 1998). Herring Gulls were observed regularly at

East Bay, but are considered a minor predator of shorebird eggs (K. Allard *pers. comm.*). Other potential predators, assumed to be unimportant because of their scarcity, include: Peregrine Falcons, Glaucous Gulls, Sandhill Cranes and Common Ravens. I recorded the number of arctic foxes and jaegers observed per person*hour, and used this to generate a daily index of the abundance and level of activity of predators (Hochachka et al. 2000, Wilson and Bromley 2001).

Shorebird nest finding, ageing and monitoring

I found nests by observing individuals on incubation recesses or by flushing birds, either by walking or by dragging a 30 m length of 5 mm diameter rope. Search effort was allocated evenly to 1 km blocks within the study plots to ensure that nest searching was not restricted to the highest quality habitats. When nests were found, their location was recorded ± 3 m with a handheld Global Positioning System (Garmin eTrex™), and a nest marker was placed 10-15 m away so that the nest scrape could be revisited. Nests found during laying were monitored daily until the clutch was complete, and at least weekly thereafter until hatch. Nests found with complete clutches were aged (see below), and monitored at least weekly until 7 days before the predicted hatch date. All nests were monitored more closely as they approached hatch; every second day for nests showing signs of star-cracking, and daily until hatch for nests with pipped eggs.

Few nests were found during laying, and nest age was most often estimated using egg flotation characteristics (Liebezeit et al. 2007). Two or more eggs from each clutch were immersed in water, and the angle and location of the egg in the water column was recorded to estimate nest age and predict hatch date (± 4 d or less in most cases). Nests were considered successful if one or more eggs hatched, and failed if they were

depredated or abandoned. Nests were considered abandoned if the eggs were cold on two consecutive visits spanning at least 4 days. One egg of the clutch was positioned with the narrow end outwards to confirm that it had not been incubated (and thus returned to the correct position) between our visits. I considered nests depredated if their contents disappeared before they could possibly have hatched. In the cases where nests disappeared but the fate could not be assigned with certainty, I recorded the fate as unknown, and used only the data up to the prior visit (as the nest was successful, i.e. not depredated or abandoned, until this point).

Flush distance and nest defence

In some years, workers measured the distance at which incubating birds flushed from the nest when nests were approached for checks. In 2002, this distance was measured with a handheld rangefinder, while in 2004-2006, it was estimated with a handheld GPS ($\pm 3\text{m}$), or measured by pacing for distances $<25\text{ m}$. From 2004-2006, I also recorded the behaviour of birds after they had flushed. This ordinal measure of nest defence included the following 5 categories: 0 = no response, 1 = scold from $>10\text{ m}$ away from observer, 2 = scold from $\leq 10\text{ m}$ away, 3 = distraction display, 4 = attack (i.e. aerial mobbing).

Distraction displays included both “broken-wing” and “rodent-run” displays (Gochfeld 1984), and were always displayed close to the observer ($< 5\text{ m}$). When both members of the pair were present and exhibiting nest defence, the highest code was used in analyses.

Nest density

I calculated a daily index of the density of shorebird nests by summing the number of active nests under observation for each day of the nesting season. Here, I considered nests to be active from the estimated date of initiation until the time they were observed

to hatch, or until the check before they failed. Nests for which I could not estimate age were considered to have been initiated at least three days prior to the time at which they were found with four eggs. Because the total number of nests found varied among years, I standardised these indices of density by dividing daily values for the number of active nests by the yearly mean.

Hypotheses and predictions

Intraseasonal patterns in nest survival could be driven by a large number of factors. To limit the number of models evaluated, I developed a set of *a priori* biological hypotheses and used these to guide the construction of models. The variables that I considered to have the most potential for influence, and upon which the analyses are based, are described below.

1) Year and Species Effects. My previous work identified strong interannual and interspecific variability in nest survival for arctic shorebirds (e.g., Smith et al. 2007a, chapter 3). The interspecific differences in nest survival have been most parsimoniously modelled by grouping species into those with uniparental and those with biparental incubation. By adding effects of year and incubation system to the models, I not only controlled for this substantial component of variation, but also allowed for models where intraseasonal patterns varied by year or species.

2) Nest Age. Several studies have identified a positive relationship between nest age and nest survival, and have suggested that this pattern arises because the most vulnerable nests are depredated early (Klett and Johnson 1982). I also predicted that shorebird nest survival would increase throughout the season, but as a result of intensification of nest defence. While both mechanisms predict a positive relationship,

the latter also predicts an interaction between nest age and incubation system, as biparental species are more aggressive, and more successful at defending their nests (Larsen 1991, Larsen 1996).

3) Temporal Variation. Most studies that allow for temporal variation find that nest survival varies throughout the season. My previous work suggested that nest survival might be depressed during mid-season (chapter 3). Here, I allowed for variation in temporal trends among years, and predicted that a quadratic effect of time would arise as the dominant pattern. Because time *per se* should not influence nest survival, I hypothesised that the temporal patterns would be explained by one or more of the covariates below.

4) Weather. Harsh weather could affect nest survival directly by leading to nest abandonment, or indirectly by influencing the behaviour of incubating adults. Recesses are longer and less numerous during adverse weather (Tulp and Schekkerman 2006, chapter 5), which should have a positive influence on nest survival. Adults show reduced body condition after periods of adverse weather (Tulp and Schekkerman 2006). This energy deficit may necessitate increased frequency or duration of incubation recesses, or adversely affect nest defence behaviour. Therefore, I also tested for a negative relationship between nest survival and weather on the previous day. I used the daily windchill low to index the putative energetic stress of weather conditions.

5) Predators. In the vast majority of instances, predators are the proximate cause of shorebird nest loss. Variation in the abundance of predators explains the variability in shorebird nest success among years (chapter 3), and I predicted that the index of daily

predator presence (sightings per observer hour) would be negatively related to the survival of nests on that day.

6) Nest Density. The density of active shorebird nests increases and then decreases over the breeding season, in a manner that could account for quadratic temporal patterns in nest survival. Even if the predation of shorebird nests is only incidental, higher nest densities should increase the encounter rate of predators and reduce nest survival. I predicted that the temporal patterns in nest survival would be a product of seasonal changes in nest density. To evaluate this prediction, I added the daily index of shorebird nest density to the models with and without the time effects included.

Data analysis

Daily nest survival rates were modelled using Program Mark, version 5.0 (White 2007). Dates were scaled so that day 1 was the date when the first nest was found (10 June). My initial model was a single estimate of nest survival. I controlled for year effects by modelling year as a categorical covariate. I then considered the main effects of species and then incubation strategy (uniparental versus biparental) to control for the substantial interspecific variation in nest survival that I have identified previously (Smith et al. 2007a, chapter 3). I selected the most parsimonious of these models, and tested for linear and then quadratic effects of time and nest age separately. I then added the most parsimonious effect of both nest age and time simultaneously, and examined the parameter estimates to ensure that these variables were not confounded (e.g., as a result of synchronous nest initiation). To this main effects model I added an interaction effect between incubation system and nest age to test my prediction of stronger age-related

changes in the nest survival of biparental birds. I then added an interaction effect between year and time effects, to allow for variability among years in temporal patterns.

To the best of these models, I added the four day-specific covariates individually: current day's windchill low, previous day's windchill low, the daily value for jaegers observed per observation hour, or the daily index of shorebird nest density. Observations of foxes were not included as a covariate because I recorded none on most days. These covariates were first standardised to have a mean of 0, because they varied among years, and year effects were included separately in the models. I then removed time effects from the models, but retained the density term to test whether temporal patterns arise from the effect of this covariate. Finally I included an interaction between year and density to allow for annual variability in the relationship.

In total I considered 17 candidate models. I used a logit link function for all models. Samples sizes for analyses appear in Table 4.1. Nests for which I had no estimate of initiation date (and hence age) were assigned a mean value (89 of 521 nests). Similarly, missing records in the daily covariates were substituted with means. Models were ranked with Akaike's information criterion for small samples (AIC_c), and ΔAIC_c and Akaike Weights (w_i) were used to infer support for models in the candidate set (Akaike 1973, Burnham and Anderson 2002). No goodness of fit test is currently available for the nest survival models in Program Mark (Dinsmore et al. 2002).

Time- or age-dependent patterns in nest survival could be related to changes in nest defence throughout the breeding season. I assessed the relationship between flush distance and date, nest age and the date of nest initiation with general linear models. There were a variable number of non-independent behaviour records for each nest, so I

randomly selected a single observation per nest for analysis. Flush distance was square-root transformed prior to analysis (Kolmogorov-Smirnov test of normality on transformed variable: $P > 0.05$). Uniparental and biparental species were analysed separately to correspond to the nest survival models generated in Program Mark. I tested year as a random effect, and did not include it in subsequent models where non-significant. Species was included as a fixed factor, and I used a forward-stepwise procedure with Type III sums of squares (probability of F to enter = 0.05) to identify significant predictors of flush distance.

Analysis of the ordinal codes for defence behaviour was also accomplished with general linear models (Zumbo and Zimmerman 1993). I analysed species with uniparental and biparental incubation separately, and randomly selected a single observation per nest. Year and species were tested as random and fixed effects respectively, and included in all subsequent models when they were significant individually. The covariates date of observation, nest age and the date of nest initiation were added in a forward stepwise fashion with Type III Sums of Squares. Means are displayed \pm SE.

Results

Environmental conditions

Weather conditions improved throughout the breeding season, with a linear increase in daily temperatures and daily windchill lows (Fig. 4.1). These linear relationships were significant (temperature: $R^2 = 0.39$, $P < 0.001$, windchill: $R^2 = 0.19$, $P < 0.001$), and describe increases in temperature and windchill temperature from -0.5°C to 7.7°C , and

–10.0°C to 1.1°C, respectively, over the period between 1 June and 31 July. The daily windspeed high showed a weak quadratic relationship with time ($R^2 = 0.03$, $P = 0.003$), with a peak in the first week of July.

Variation among years was significant for windchill low ($F_{7,367} = 14.8$, $P < 0.001$) and windspeed high ($F_{7,367} = 7.9$, $P < 0.001$), but not for daily temperature low ($F_{7,367} = 1.8$, $P > 0.05$). Tukey's post hoc tests showed higher windchill temperatures in 2001, 2006 and 2007, lower wind speeds in 2004 and higher wind speeds in 2006 and 2007.

Variation within seasons in the abundance of arctic foxes and jaegers showed no consistent patterns (Fig. 4.2). Parasitic Jaegers were more commonly encountered than foxes, and some were sighted on most days in most years (0.13 ± 0.01 sightings per observer hour). In contrast, I sighted foxes on only 45 of 306 observation days (0.006 ± 0.001 sightings per observer hour). Predator abundance varied among years, with 8 fold variation in the number of jaeger encounters and 11 fold variation in the number of fox encounters.

Variation among years in weather and predator abundance, and the effects of these on interannual patterns of shorebird nest success, are explored more fully in chapter 3. Here, I examine patterns in nest success within a season by controlling for year effects, and using standardised daily values for weather or the abundance of predators.

Year and species effects

In total, 574 nests of 11 species were found. All nests were used in the calculation of daily indices of nest density; however, the sample used in the analyses of nest survival comprised 521 nests of 5 species (4951 exposure days, Table 4.1). Of these, 11 were abandoned, 288 were lost to predators and 182 hatched one or more young. The fate

could not be determined for 40 nests. Twenty-two nests could not contribute to the models in Program MARK because they were found while hatching, and thus contributed no exposure days.

Year effects were strong, and the addition of the 7 year parameters reduced the AIC value by nearly 30 units (Table 4.2, Table 4.3). Estimates from the best model suggest that the mean daily survival rate over the period during which nests were monitored varied by up to 0.11 among years. The effect of species also was strong. A model with species divided into uniparental and biparental incubators was 56 AIC units better than the model with only year effects, and 1.5 AIC units better than the model with a parameter for each species (Table 4.2). Parameter estimates for the additive effect of biparental versus uniparental incubation were positive in all models considered. The best model also contained an interaction between incubation system and nest age. Model averaged parameter estimates appear in Table 4.3.

Effects of time and nest age

In each year, nests were initiated over a period of 19 – 31 days (mean 26 days, Fig 4.3). The sample therefore includes nests of various ages throughout the breeding season, so that effects of time and nest age could be estimated separately. I found strong support for linear effects of nest age; a model containing this effect was 17 AIC units better than the model containing only effects of year and incubation system (Table 4.2). The interaction between incubation system and nest age also improved model fit. The relationship between nest age and nest survival was positive in all models considered, but parameter estimates from the best model suggest that the relationship is weak for uniparental species and stronger for biparental species (Table 4.3, Fig. 4.4).

I found no support for linear effects of time, but strong support for quadratic temporal effects. Inclusion of a single quadratic time effect for all years reduced the AIC value by 5 units. Parameter estimates for these models suggested that daily nest survival was lowest during mid-season. Allowing the quadratic temporal trends to vary by year required 14 additional parameters. Model deviance was substantially reduced by their inclusion (29 units), but after correction for the additional parameters the AIC value was only marginally lower (Table 4.2). However, this step changed the interpretation of the temporal patterns; nest survival was depressed mid-season in 5 of 8 years, and was elevated in the remaining three (Fig. 4.5). Precision of the parameter estimates was poor for these three years (2000, 2001, 2003, Table 4.3). Among the years with depressed nest survival mid-season, the timing of the low in daily survival rate varied from 30 June (Day 21) in 2006 to 9 July (Day 30) in 2002, and occurred 10 – 17 days after the mean date of nest initiation, or 2 – 11 days after the peak in the index of nest density in each year (see also Fig. 4.6).

Effects of weather and predators

The best model without day-specific covariates included an intercept, linear time term and quadratic time term for each year, as well as a linear effect of nest age, a categorical variable denoting incubation system and an interaction between incubation system and nest age. The addition of day-specific covariates did not improve model fit in any case. Current daily windchill low, the previous day's windchill low, and the daily abundance of jaegers all had negligible effects on model deviance and resulted in higher AIC values. I did not test the effect of fox abundance because none was recorded on most days. Inclusion of these covariates did not alter the parameter estimates for the time² or nest

age variables. These results suggest that the temporal and age-related patterns are not driven by daily changes in weather or predator abundance.

Nest density

The relative density of active nests was greatest mid-season (Fig. 4.6), a time which corresponded to the period of lowest nest survival in most years (Fig. 4.5). The apparent quadratic temporal trends could therefore be a product of a negative linear relationship between density and nest survival. I first added density to the model including time effects, and found no support for an additive effect of nest density (Table 4.2). Next, I removed the temporal effects to test whether density accounts for the quadratic relationship between nest survival and day of the nesting season. This model had an AIC value 18 units larger than the model with time effects. Finally, I allowed the relationship between nest density and nest survival to vary among years. This model too found no support. I therefore conclude that the observed temporal patterns in nest survival are not related to the density of active shorebird nests.

Flush distance and nest defence

Flush distance differed significantly among species ($F_{4,145} = 76.5, P < 0.001$). Biparental species flushed from greater distances than uniparental species (mean for uniparental species = 11 ± 0 m, biparental = 71 ± 29 m, Table 4.4). Among uniparental species, there was no relationship between flush distance (square-root transformed) and date of observation, nest age, or date of nest initiation. Further, there were no differences among years, or between the two uniparental species (All P s > 0.05). For the three biparental species, species explained a significant proportion of the variance in flush distance ($F_{2,78}$

= 24.3, $P < 0.001$). Year effects, nest age, date of observation and date of nest initiation were not significantly related to flush distance for biparental species.

Defence behaviour was variable within species. Even species that characteristically perform distraction displays (such as the Semipalmated Plover and White-rumped Sandpiper) showed a range of behaviour including many instances of no defence or distant scolding. Means for the observed defence behaviour appear in Table 4.4. Defence behaviour differed among species, but not among years, for both uniparental and biparental species (Uniparental, Species: $F_{1,31} = 16.0$, $P < 0.001$, Year: $F_{1,31} = 0.8$, $P > 0.05$; Biparental, Species: $F_{2,51} = 5.2$, $P < 0.01$, Year: $F_{1,52} = 0.8$, $P > 0.05$). For uniparental species, nest defence behaviour was not influenced by the date of the observation, the date of nest initiation, nor the age of the nest (All P 's > 0.05). In contrast the defence behaviour of biparental species intensified as nests aged ($F_{1,50} = 11.1$, $P < 0.01$) and as the season progressed ($F_{1,50} = 10.9$, $P < 0.01$). Nest age and date of observation were correlated in this sample ($R = 0.77$, $P < 0.001$), and when the effect of one was controlled in the models, the additive effect of the other was non-significant. I identified no significant interaction between species and any of the covariates for either uniparental or biparental species.

Discussion

Temporal patterns in shorebird nest survival

Recent studies of nest survival have detected intraseasonal variation, but the patterns identified have been inconsistent. Some have found that nest survival declines mid-season (Dinsmore et al. 2002, Wilson et al. 2007), while others have found positive (e.g., Grant et al. 2005), negative (Burhans et al. 2002, Jehle et al. 2004), or no relationship

between time and nest survival (Traylor et al. 2004, Walker et al. 2005). I found that, among ground nesting shorebirds, nest survival typically was lowest in mid-season, and that the pattern varied among years. Although I tested several plausible hypotheses to account for these temporal patterns, I found no evidence for effects of weather, predator abundance, or the density of active shorebird nests. My results suggest that some more complex aspect of predator behaviour, perhaps due to seasonal changes in the availability of other prey, acts to depress shorebird nest survival during the mid-season in most years.

I investigated linear and quadratic effects of time, and found support only for the latter. Still, temporal patterns did vary among years; nest survival was depressed during the mid-season in five of eight years while it was higher in the remaining three.

Among the 5 years, the date when the lowest values of daily survival was reached differed by 10 days, but this date was not correlated with either the mean date of nest initiation, nor the date of peak nesting density for shorebirds. The earliest date of the low value for nest survival occurred in 2006, a year of early shorebird breeding and early peak density, while the latest value for the low occurred in 2002, a year with moderate dates for mean nest initiation and peak density. Temporal patterns in nest survival were therefore not driven by variation in the timing of breeding.

Factors determining temporal patterns in nest survival

Weather could influence nest survival directly if birds abandon their nests during storms. However, abandonment was rare in the sample (11 of 521 nests, or 2%). Weather events can also influence nest survival indirectly by altering the incubation behaviour of birds. Among the uniparental species considered here, incubation recesses are less numerous during periods of adverse weather (chapter 5). A decrease in the number of incubation

recesses could make nests less visible to predators (Skutch 1949, Martin and Ghalambor 1999, Martin et al. 2000). However, harsh weather results in a negative energy balance and decreased body condition (Tulp and Schekkerman 2006), and could therefore necessitate an increased rate of nest recesses on the following day. Relationships between weather and incubation behaviour might be weaker for biparental species, because they have more time available for foraging (Norton 1972, Cresswell et al. 2003, chapter 5). Although there were many days of harsh weather during this study, I found no effect of current or previous days' weather on the survival of either uni- or biparental shorebird nests. Further, the general improvement of weather conditions throughout the breeding season could not explain the quadratic patterns of nest survival observed.

Predators are the proximate cause of 98% of the nest failures that I observed, and I predicted that the daily abundance or activity of predators should influence the survival of shorebird nests. If predators relied solely on shorebird nests as prey, shorebird nest survival should be tightly correlated with predator activity. Although it varied day to day, the index of predator activity showed no consistent patterns throughout the season that could account for the temporal trends in nest survival that I observed. No foxes were observed on most days, and variability in the number of jaegers sighted per observer*hour was high. Assuming that sightings per observer hour is a reasonable index of abundance or activity (Hochachka et al. 2000), the lack of a relationship between my predator abundance index and shorebird nest survival suggests that predators at these sites rely primarily on other food sources.

The density of active shorebird nests could influence the probability that nests are depredated through several means. High nest density could increase nest survival if

predators become swamped or satiated (Ims 1990). This is perhaps unlikely because arctic foxes cache the majority of the eggs that they find (Stickney 1991). Instead, nest survival could be lower when nest density is high if predators develop a search image for nests (Allen 1989, Nams 1997), intensify search effort in areas where they have found nests (area-restricted search, Tinbergen et al. 1967), or if they shift attention towards eggs in a functional response (e.g., Holling 1959, 1961, Holt 1977). Even in the absence of any behavioural response by the predators, higher nesting density increases the rate at which nests are encountered by a generalist predator that searches systematically (Taylor 1976).

In this study, the density of active nests was low early and late in the breeding season, and greatest approximately mid-season. The pattern in nest density over time therefore had a similar shape to the observed temporal patterns in nest survival, where predation was highest mid-season (Fig. 4.5). However, the timing of the peak in shorebird nest density was not related to the timing of the low in nest survival, nor was there support for density as a predictor of nest survival in the models. Even mid-season, the density of shorebird nests is low in comparison to the thresholds for density dependence identified in other studies (Göransson et al. 1975, Sugden and Beyersbergen 1986, O'Rielly and Hannon 1989, Schieck and Hannon 1993, Larivière and Messier 1998), and I demonstrated previously that the survival of shorebird nests at East Bay was not influenced by distance to the nearest nests of shorebirds or other species (Smith et al. 2007a). Shorebird eggs form only a portion of the diet of jaegers and foxes, and the lack of a relationship between shorebird nest density and shorebird nest predation suggests that other foods may be more important.

The diet of arctic foxes in spring consists of cached eggs that have overwintered, carrion and lemmings. As the eggs of migratory birds become available, this diet shifts; in a waterfowl nesting area, predation on birds' nests was intense as soon as nesting began and eggs dominated the diet throughout the nesting period (Stickney 1991). For Parasitic Jaegers, a diet shift occurs when they leave marine feeding habitats and begin to breed and forage in terrestrial habitats (Wiley and Lee 1999). The relative contribution of shorebird eggs to the diet is unknown, although both jaegers and foxes frequently consume the eggs of larger birds such as Snow Geese, Gulls, and Loons (*Gavia* spp.) (Wiley and Lee 1999, Stickney 1991). The average mass of a shorebird clutch ranges from 32g for the Red Phalarope (Tracy et al. 2002) to 132g for the Black-bellied Plover (Paulson 1995). A typical Snow Goose clutch has a mass of 522g (Cooke et al. 1995), 4 – 16 times greater than that of a shorebird. Because shorebirds are less able to defend their nests from predators than larger birds, their eggs may contribute to the diet of these predators more than egg mass would suggest. Regardless, because shorebird nests are only one component of predators' diets, temporal patterns in nest survival are likely to reflect the availability of all diet items.

Age-related patterns in shorebird nest survival

Age is specific to individual nests, and in contrast to trends throughout the season which are time-dependent, the mechanism underlying an age-related trend is more likely to act at the individual level. Age of nests was not confounded with time of season in this study because nests were initiated throughout the season. I found that the daily probability of survival was higher for older nests. Patterns of increasing survival for older nests have been previously ascribed to heterogeneity in nest survival, rather than age effects *per se*

(Klett and Johnson 1982, Martin et al. 2000). If the most vulnerable nests fail early, survival will appear to increase with increasing nest age. Such a pattern can arise, for example, if nest sites differ in their risk of predation (Martin et al. 2000).

At this location, nest site characteristics of shorebirds do not differ between successful and failed nests (Smith et al. 2007a). The large differences in predation risk among species could introduce heterogeneity, but I controlled for this by considering species effects in the models. Most importantly, individual heterogeneity in nest survival cannot explain the strong support I found for an interaction between nest age and incubation system. Consequently, I do not believe that the relationship between nest age and nest survival found here is an artefact of heterogeneity, and instead propose that incubating adults change their behaviour as nests age to increase the probability of nest survival.

Nests are increasingly more valuable to their parents as they age because the probability of survival to hatch is a product of both daily survival rate and days until hatch. Further, the opportunity for renesting successfully declines because chicks hatching from nests initiated late in the season are unlikely to fledge (Meltofte et al. 2007, chapter 2). As a nest ages and its relative value increases, parents can increase their investment by defending it more aggressively (reviewed in Montgomerie and Weatherhead 1988, Forbes et al. 1994). Aggressive forms of nest defence are typically more common and more successful among monogamous, biparental incubators (Larsen 1991, Larsen et al. 1996). I found the level of nest defence (i.e., from no defence to aggressive attack) to be variable within and among species, but its intensity increased significantly throughout the breeding season only among biparental species. This

stronger increase in intensity of defence was accompanied by a stronger age-related increase in nest survival among biparental versus uniparental species. In contrast, I found that the Red Phalarope and White-rumped Sandpiper (uniparental species) flushed from much shorter distances than the three species with biparental incubation. This observation, and their highly concealed nest sites (Smith et al. 2007a), suggest that these species may instead rely on cryptic behaviour to avoid detection.

Analytic techniques such as those employed here now enable researchers to describe and explore patterns in nest survival in a way that was not possible previously. My results show that shorebird nest survival varies among species and years, but also within a single nesting season. I found that strong temporal patterns in which nest survival declined mid-season were not related to seasonal changes in weather, the abundance of predators, nor the density of active shorebird nests. These patterns are more likely to be driven by a complex relationship between predator abundance and the full suite of diet items available to them. The survival of shorebird nests also increases as they age, and this pattern appears to be related to parent birds' increased defence of older, more valuable nests.

Table 4.1. The total number of shorebird nests found, and the sample used in the analyses of nest survival with Program MARK.

Species	East Bay	
	Total	Analysed
American Golden-Plover	8	0
Black-bellied Plover	80	77
Dunlin	13	0
Purple Sandpiper	1	0
Red Knot	2	0
Red Phalarope	113	111
Ruddy Turnstone	201	192
Sanderling	4	0
Semipalmated Plover	73	69
Semipalmated Sandpiper	3	0
White-rumped Sandpiper	76	72
Total	574	521

Table 4.2. Summary of model selection results for an analysis of shorebird nest survival at East Bay, Nunavut, 2000-2007. AIC_c = Akaike's information criterion corrected for small samples, ΔAIC_c = the change in AIC_c relative to the top model, w_i = Akaike weight, a measure of relative support for the model, K is the number of parameters, and deviance is the difference in the -2 log-likelihood between each model and the saturated model. The parameter abbreviations are as follows: Weather(d) represents the current day's weather, weather(d-1) represents the previous day's weather, jaegers represents the number of jaegers sighted per observer hour, and density is the daily count of active shorebird nests. These three variables were standardised within years to mean = 0 prior to analysis. A '+' indicates an additive effect, while a '*' indicates an interaction between two variables.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Year*Time ² + Incubation System + Nest Age + Incubation System*Nest Age	1358.0	0.0	0.25	27	1303.7
Year*Time ² + Incubation System + Nest Age + Incubation System*Nest Age + Density	1358.3	0.3	0.22	28	1302.0
Year + Time ² + Incubation System + Nest Age + Incubation System*Nest Age	1358.6	0.6	0.19	13	1332.5
Year*Time ² + Incubation System + Nest Age + Incubation System*Nest Age + Weather(d-1)	1359.3	1.3	0.13	28	1302.9
Year*Time ² + Incubation System + Nest Age + Incubation System*Nest Age + Weather(d)	1359.9	1.9	0.10	28	1303.5
Year*Time ² + Incubation System + Nest Age + Incubation System*Nest Age + Jaegers	1360.0	2.0	0.09	28	1303.6
Year + Time ² + Incubation System + Nest Age	1364.0	6.0	0.01	12	1339.9
Year + Incubation System + Nest Age	1375.9	17.9	0.00	10	1355.8
Year + Incubation System + Nest Age + Incubation System*Nest Age + Density	1377.0	19.0	0.00	12	1353.0
Year + Incubation System + Nest Age ²	1377.9	19.9	0.00	11	1355.8

Table 4.2. Continued.

Model	AICc	Δ AICc	w_i	K	Deviance
Year*Density + Incubation System + Nest Age + Incubation System*Nest Age	1383.2	25.2	0.00	19	1345.0
Year + Incubation System + Time ²	1388.1	30.1	0.00	11	1366.1
Year + Incubation System	1393.1	35.1	0.00	9	1375.0
Year + Incubation System + Time	1393.9	35.9	0.00	10	1373.8
Year + Species	1394.5	36.5	0.00	12	1370.4
Year	1449.1	91.1	0.00	8	1433.0
Null Model	1476.7	118.7	0.00	1	1474.7

Table 4.3. Parameter estimates, standard errors and lower and upper 95% confidence limits for key variables associated with daily nest survival of shorebirds at East Bay, Nunavut, 2000-2007. All estimates were determined using model averaging based on the top 7 models in Table 4.2 and representing > 0.99 of the AIC_c weights. Estimates for time and $time^2$ were obtained using models 3 and 7 where they are included as a single additive effect. Uniparental incubation was coded as 0; the parameter estimates for incubation system therefore reflect the effects of biparental incubation.

Parameter	$\hat{\beta}$	SE	95% C.L.	
			Lower	Upper
Time	-0.176	0.043	-0.260	-0.092
Time ²	0.003	0.001	0.001	0.005
Nest Age	0.025	0.018	-0.010	0.060
Incubation System	0.382	0.217	-0.043	0.807
Nest Age * Incubation System	0.064	0.022	0.021	0.107

Table 4.4. The mean distance at which birds flushed when their nests were approached, and the intensity of the nest defence they subsequently displayed. Species are displayed with AOU 4-letter codes¹, and “behaviour code” included the following 5 categories: 0 = no response, 1 = scold from >10 m away from observer, 2 = scold from ≤ 10 m away, 3 = distraction display, 4 = attack (i. e. aerial mobbing).

Species	Flush Distance (m)		Behaviour Code	
	N	Mean ± SE	N	Mean ± SE
SEPL	16	39.1 ± 5.5	8	2.6 ± 0.3
BBPL	32	116.5 ± 10.1	20	1.8 ± 0.3
REPH	41	11.0 ± 1.9	15	0.6 ± 0.2
RUTU	33	56.1 ± 6.0	27	1.1 ± 0.1
WRSA	28	10.9 ± 2.1	18	2.3 ± 0.3

¹ SEPL = Semipalmated Plover *Charadrius semipalmatus*, BBPL = Black-bellied Plover *Pluvialis squatarola*, REPH = Red Phalarope *Phalaropus fulicarius*, RUTU = Ruddy Turnstone *Arenaria interpres*, WRSA = White-rumped Sandpiper *Calidris fuscicollis*.

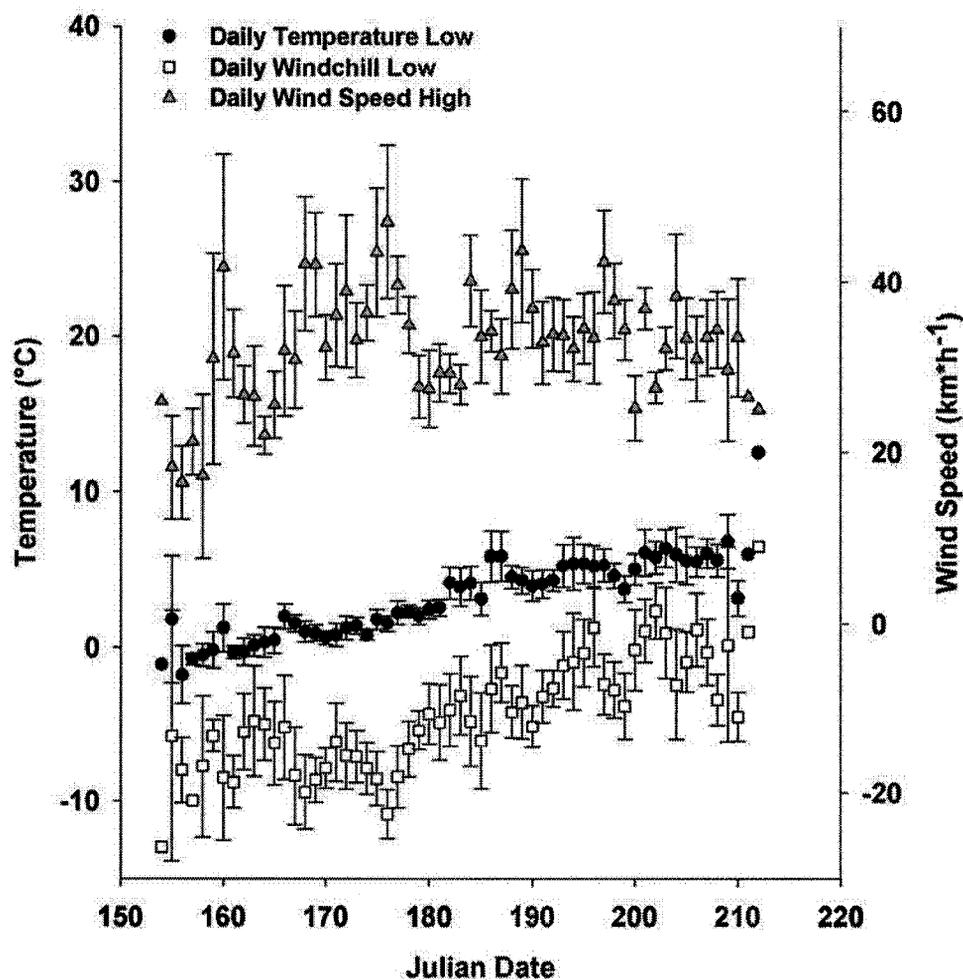


Figure 4.1. Temperature low, windchill low and windspeed high for each day of the shorebird breeding season at East Bay, Nunavut. Daily values are the means for all years \pm SE. Day 150 = 30 May.

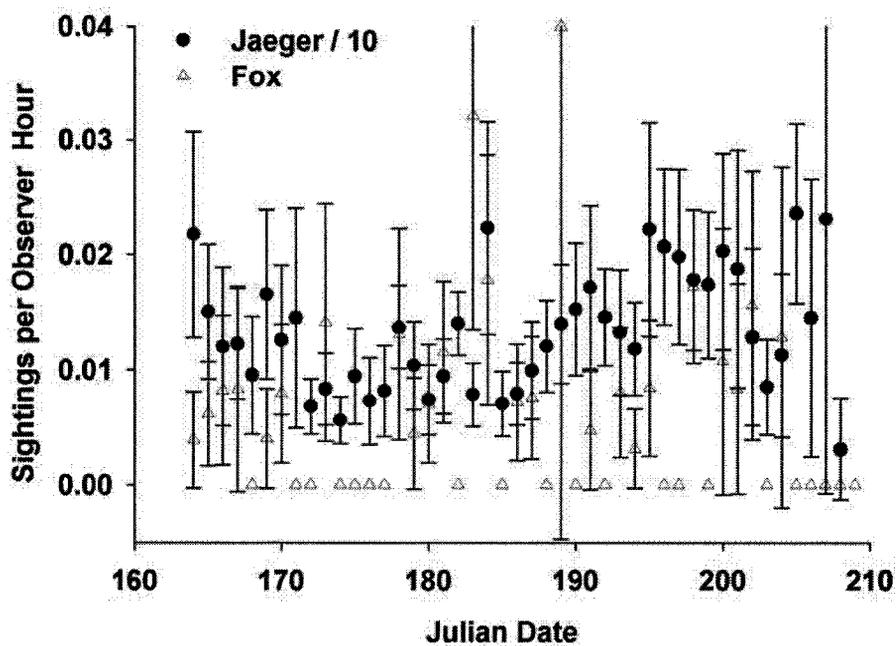


Figure 4.2. The number of foxes and jaegers sighted per observer hour at East Bay, Nunavut. Daily values are the means for all years \pm SE. Note that jaegers were the most abundant predator on all days, and the values are divided by ten.

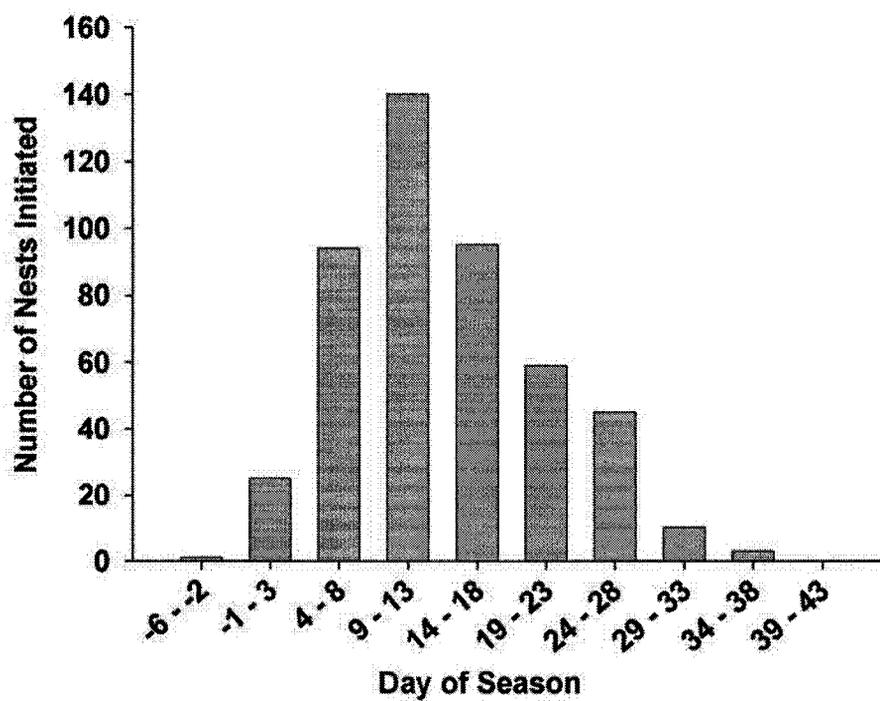


Figure 4.3. The temporal distribution of shorebird nest initiations throughout the breeding season. Day 1 is equal to 10 June here and in subsequent figures. Initiations were calculated for 472 of 574 nests.

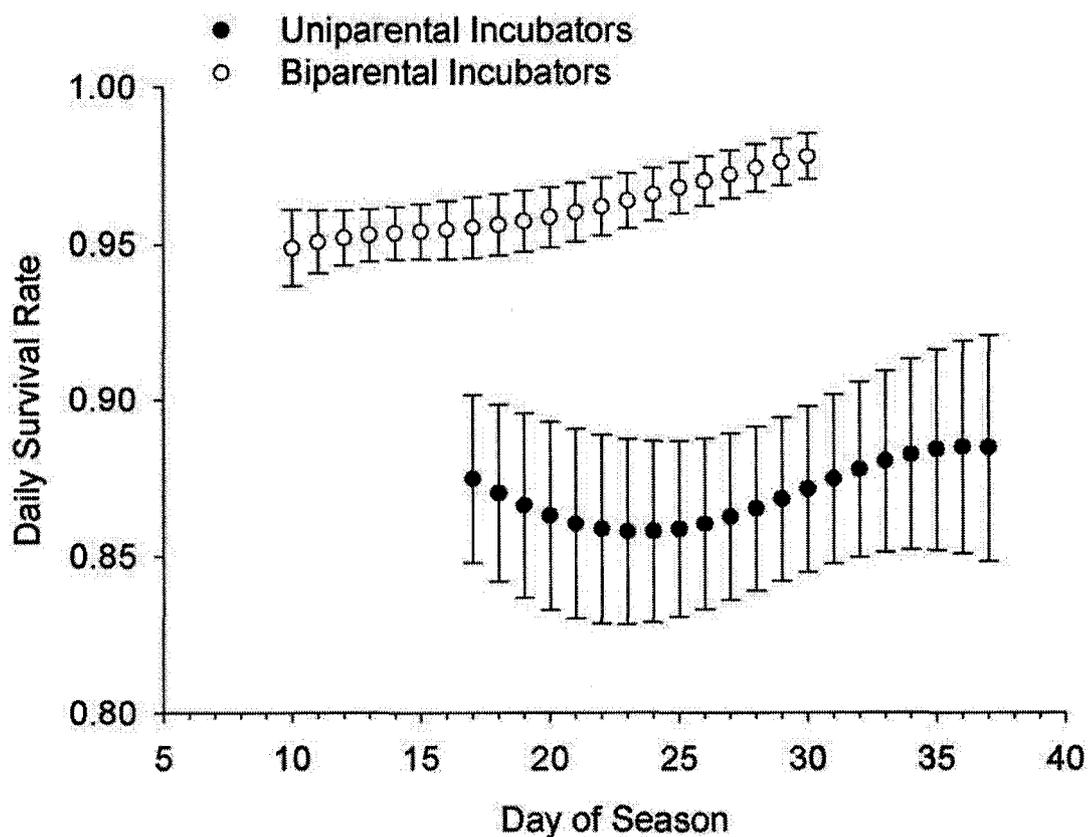


Figure 4.4. The daily probability of nest survival for uniparental and biparental shorebirds at East Bay, Nunavut, based on the predictions of the most parsimonious model (see Table 4.2), which incorporates both time and nest-age effects. Predictions are displayed for a 21 day incubation period (i.e., nest age ranges from 1 to 21), initiated on the median date of nest initiation for uniparental (Day 17 = 26 June) or biparental (Day 10 = 19 June) species. Values represent the mean prediction \pm SE for all years.

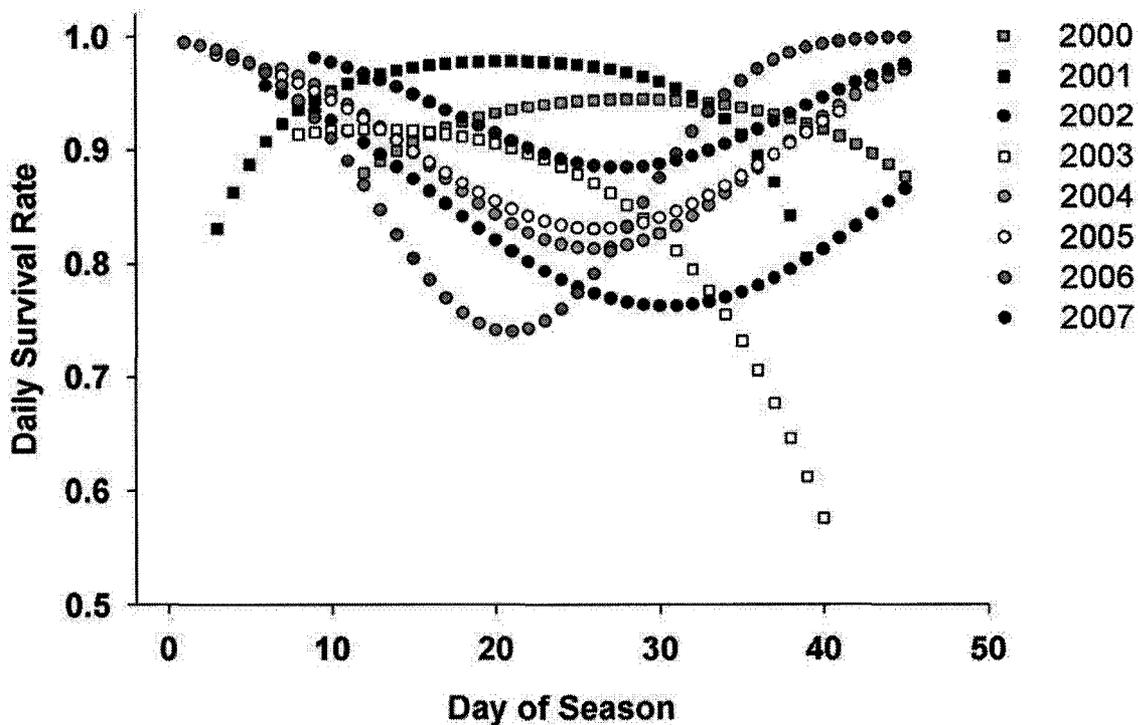


Figure 4.5. Temporal patterns of nest survival, and their variation among years, for shorebird nests at East Bay, Nunavut, based on the predictions of the most parsimonious model (see Table 4.2). The predictions are for uniparental species in mid-incubation (nest-age = 10), and are displayed only for the intervals during which I monitored nests in each year. Day 1 = 10 June. Temporal patterns for biparental species have the same shapes, but less variation.

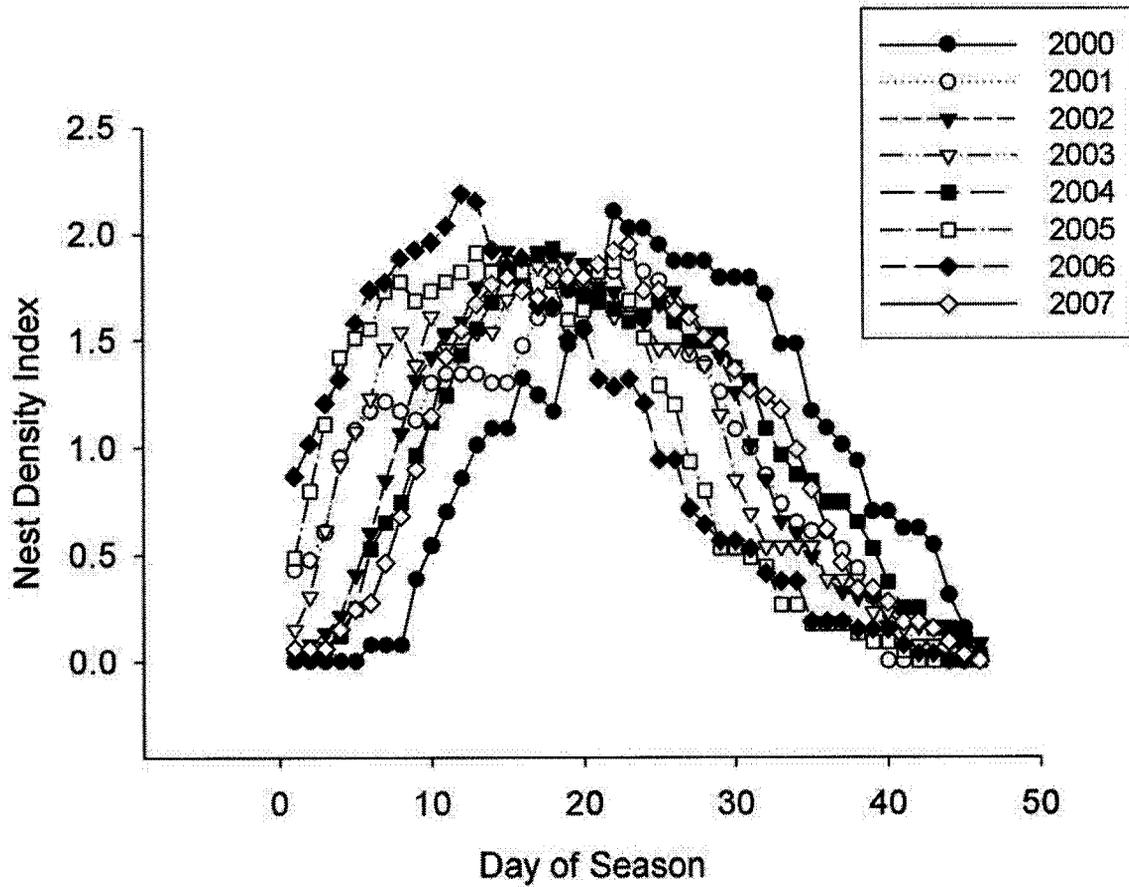


Figure 4.6. The index of relative shorebird nest density, 2000-2007. The index is standardised for differences in the total number of nests found each year, and was calculated as the number of active nests on a given day of the season divided by the mean number of active nests for all days in that year.

Chapter 5. The influence of weather on uni- and biparental shorebird incubation

Abstract

For some shorebird species, incubation is shared between both members of the pair, while for others, it is undertaken individually. How incubation is altered to meet energetic demands under changing weather conditions may be influenced by this life history difference. I used video and nest-temperature recordings to quantify the incubation behaviour of eight species of shorebirds breeding at two sites in the eastern Canadian arctic. From 2002-2006, I obtained 419 days of behavioural records from 99 nests. Despite nearly continuous daylight, diel patterns in incubation behaviour were pronounced for uniparental species, with a significant trend for more and longer incubation recesses during the afternoon. Biparental species exhibited more restless movements on the nest during the afternoon, but diel patterns were weaker in general. Incubation behaviour was variable among days, and uniparental species took fewer recesses and spent more time on the nest when weather conditions were poor. In contrast, windier conditions caused biparental species to leave the nest unattended for longer periods. At 22/58 (38%) nests of uniparental species, I observed temporary instances of egg neglect (defined as absences >45 min) and the probability of these prolonged absences was higher when weather conditions were cold and windy. These results suggest that uniparental species usually rely on capital energy reserves to withstand periods of adverse weather, but temporarily abandon their nests when reserves are insufficient. Biparental species instead respond to increases in energetic costs of incubation by increasing their potential foraging time. After controlling for the effects of weather, I found that all species leave the nest unattended for shorter periods of time as

nests age. This may serve to protect embryos at a time when they are less resistant to chilling or relatively more valuable to their parents.

Introduction

Although birds inhabit nearly every corner of the globe, the range of environmental conditions that ensure the hatching of their eggs is quite narrow. The optimal temperature for embryonic development, for example, ranges from only 36 – 38°C across a wide variety of species (Lundy 1969, Drent 1975, Webb 1987). Consequently, birds have evolved numerous traits to control both the temperature and the gaseous environment of the nest. For shorebirds breeding in the arctic, significant energy must be expended to maintain eggs within this optimal range when ambient temperatures are well below it (Piersma et al. 2003). To limit the energy required to heat eggs, shorebirds actively select nest sites with appropriate microclimate (e.g., Smith et al. 2007a), nest depth (Tulp 2007), and nest lining materials (Reid et al. 2002a). Appropriate habitat selection can minimise the amount of heat lost to the environment, but most bird species also must regulate the amount of heat provided to their eggs through their incubation behaviour.

Eggs develop most quickly when they are continuously maintained within the range of optimal temperatures, but time spent incubating is time unavailable for foraging. Birds must balance the needs of their eggs with their own energetic requirements, and how this balance is resolved can be influenced by ultimate and proximate factors (Webb 1987, Williams 1996). Among shorebirds, incubation can be shared between both members of the pair (biparental incubation), or can be undertaken by a single bird (uniparental incubation). For uniparental species, the amount of time spent on the nest

necessarily reduces the time available for foraging, while amongst biparental species, each member a pair could forage 50% of the time even with constant incubation. Thus, patterns in incubation behaviour, both within and among days, may be expected to differ for uniparental versus biparental species.

Among days, weather has been suggested to play a dominant role in the organisation of incubation behaviour (e.g., Norton 1972, Cartar and Montgomerie 1987, Tulp and Schekkerman 2006). Weather conditions can influence energetic costs on and off the nest and, for shorebirds breeding in the arctic, weather plays a significant role in determining daily energy expenditure (Piersma and Morrison 1994, Piersma et al. 2003). Cold temperatures increase the cost of homeothermy for shorebirds, but also reduce the activity and availability of arthropods which are their primary prey (Schekkerman et al. 1998, 2003, Tulp 2007). Because foraging in exposed tundra habitats is more expensive than incubating (Piersma et al. 2003, Cresswell et al. 2004), and less profitable when weather conditions are poor, shorebirds could decide to forgo foraging until weather conditions improve if they carry sufficient energy stores to do so.

Previous studies with shorebirds have shown inconsistent results, but for birds in general, it has frequently been suggested that energetic limitation is more likely for uniparental species because of the limited time available for foraging (Bryan and Bryant 1999, Reid et al. 2002b, Tulp and Schekkerman 2006). Here, I compare patterns in incubation behaviour within and among days for biparental and uniparental shorebirds breeding at two sites in the Canadian arctic. Using video recordings and temperature probes, I describe the rate, duration and timing of breaks in incubation, as well as restless movements on the nest. I relate incubation behaviour to weather patterns to assess how

shorebirds respond to conditions that could influence their daily energy expenditure, and ask how changes in incubation behaviour differ among species with uniparental and biparental incubation.

Methods

Study area

I collected data on the incubation behaviour of shorebirds at two sites in the eastern Canadian arctic between 2002-2006 (Fig. 2.1). Work at Coats Island (62° 51'N 82° 29'W) took place from the beginning of June until the end of July, 2004-2006. At East Bay (63° 59'N 81° 40'W), work was carried out from late May until late July in 2002, 2005 and 2006. Workers searched for nests over an area of 12 km² at both sites, in wet lowlands, upland heath tundra, raised beach ridges and coastal habitat types typical for these latitudes. The physiography of the sites is described in more detail elsewhere (Smith et al. 2007a, chapter 2).

Weather data were collected at this site with an automated weather station (Davis Vantage Pro, see chapter 2). For the analyses described below, I used mean daily temperature, the mean of the observed windspeeds at 0800h and 2000h each day, the daily windchill low and a categorical variable denoting whether or not there was precipitation on a given day.

The sample includes behavioural data from eight species: the Semipalmated Plover, Black-bellied Plover, American Golden-Plover, Red Phalarope, Ruddy Turnstone, Dunlin, Semipalmated Sandpiper and the White-rumped Sandpiper. Together, these species represent > 95% of the breeding individuals at these two sites (chapter 3). All species nest in simple scrapes on the ground, have a modal (and

relatively invariant) clutch size of four eggs, incubate for approximately three weeks (19-26 days), and have a median date of clutch initiation in mid June (chapter 2). While these basic reproductive traits are shared, the incubation system differs among species.

Incubation is carried out solely by the male for the polyandrous Red Phalarope (Tracy et al. 2002), and by the female for the polygynous White-rumped Sandpiper (Parmelee 1992). The remaining six species are monogamous, biparental incubators, and both sexes share the duties of incubation. The contribution of each sex is poorly documented, but male Semipalmated Plovers at Churchill, Manitoba, Canada, have longer incubation shift lengths (Sullivan-Blanken and Nol 1998), and the contribution of male Ruddy Turnstones varies geographically and seasonally (Nettleship 2000, Perkins 2004).

Shorebird nest finding, ageing and monitoring

Methods for finding, ageing and monitoring nests are described in detail in chapter 2. In brief, nests were found by observing individuals on incubation recesses or by flushing birds, either on foot or by dragging a 30 m length of 5 mm diameter rope. Search effort was intentionally allocated evenly across the study areas, and nest locations were recorded ± 3 m with a handheld Global Positioning System (Garmin eTrex™). Nests found during laying were monitored daily until the clutch was complete, and at least weekly thereafter until hatch.

Monitoring incubation behaviour

The equipment used to monitor incubation behaviour differed for species with uniparental and biparental incubation. For uniparental species, thermistor probes were placed amongst the eggs to capture the temperature changes when birds departed from the nest (Norton 1972, Erckmann 1981). The probes consisted of a 10 K Ω Curve-G

thermistor on a 15 m, 24 AWG cable, with a $10\text{ K}\Omega$ ($\pm 1\%$) reference resistor loop, on a 2.5 mm stereo jack and were attached to a Hobo H8 data logger (Onset Instrument Corporation, Pocasset, Massachusetts). The tip of the probe (2 mm x 5 mm) was centred in the nest and was level with the top surface of the eggs. Because the probe was near the brood patch, temperatures approached 40°C when the incubating bird was present, and dropped sharply to ambient temperature (-2°C to $+21^\circ\text{C}$) when the incubator departed (see below). Readings were taken every 30 s, allowing for more than 11 d of continuous records. Loggers were placed 15 m from the nest in a camouflaged, waterproof housing, and the cable between them was buried or concealed. The entire placement procedure lasted less than 10 min.

Observations (24 h total) on two nests before and after deployment of the logger system revealed that the probes had no detectable effect on incubator behaviour and that they accurately captured departures of the incubator to within ± 30 s. Moreover, I observed no recesses of less than 30 s. Based on simultaneous observations and recordings of temperatures at these nests, I defined any temperature changes $\pm 2^\circ\text{C}$ as continuous incubation. Any sudden (± 30 s) change of $> 2^\circ\text{C}$ but $< 9^\circ\text{C}$ in the recorded temperature was defined as movements such as egg rolling, cup maintenance, or restless incubation. Any drop exceeding 9°C was considered a recess. The beginning and end of incubation recesses (± 30 s) were identified manually by examining the data logger output. Nest recesses were generally unambiguous. Occasionally, the tip of the probe was displaced and temperature readings became difficult to interpret. Readings also became erratic when eggs were pipping, usually within < 3 days of hatch. Such records were discarded.

The above method is inappropriate for monitoring the incubation of biparental species because the changeovers between sexes could happen too rapidly to be captured by the thermistor probe. Instead, I used commercially available surveillance equipment to develop portable video recording systems. The systems consisted of a small (10cm x 2cm), weatherproof, low-lux, CMOS camera, connected to a 40 GB hard-drive based digital video recorder. Using a 21 Ah (circa 10 kg) lead acid battery, these comparatively economical systems could record full-motion video of incubating birds for continuous periods of > 36 h. Cameras were placed approximately 10 m from nests, and were elevated 30-40 cm above the ground with tripods made of 2 mm thick wire. The wire legs of the tripods were pressed into the ground to stabilize the camera. The battery and recorder were concealed in a camouflage-painted waterproof housing (30 cm x 20 cm x 10 cm) and placed another 10 m further from the nest. To analyse videos, I watched them at 4x speed with DivX (DivX Inc., San Diego, CA) computer software, and paused when necessary to record behaviours ± 1 s.

Despite the differences in the method of data collection, I derived the same measures of incubation behaviour for both uniparental and biparental species. For all species, I calculated the frequency and duration of nest absences, and the proportion of time that nests were left unattended. For biparental species, these absences could end with the return of either parent; in some cases the sexes or individuals could be distinguished while in others they could not. I also quantified the frequency and duration of movements, and the proportion of each hour or day that these movements amounted to. For uniparental species, these were defined on the basis of temperature records (see above). For biparental species, "movements" constituted nest maintenance, egg rolling,

feeding from the incubating position, preening, and repositioning. I monitored behaviour at nests with complete clutches only.

Data analysis

I analysed patterns in incubation behaviour separately for uniparental and biparental species. Among uniparental species, some individuals took atypically long recess (>45 min) on some days. To limit the influence of these outliers, for some analyses I created a reduced dataset by omitting days on which these long absences took place. Such long absences were not a feature of biparental incubation; rather, fog and strong winds occasionally reduced the quality of the video and impaired my ability to record the full suite of incubation movements (if recesses and changeovers could not be reliably identified, I discarded the video from all analyses). I therefore created a reduced dataset for analysing incubation movements that consisted of only video footage where I was confident that all behaviours could be identified. The full dataset, based on all videos, therefore represents a minimum number for incubation movements, while the reduced dataset may be biased by exclusion of some videos on days with very wet or windy conditions. To better satisfy the assumptions of normality, I log-transformed the counts of recesses and movements and arcsine transformed the proportions of time a bird spent engaged in these activities prior to analysis.

To describe diel patterns, I calculated an average value for each measure of incubation behaviour for each hour, for each nest, using the reduced datasets for both uniparental and biparental species. These means were used as response variables in linear models using the mixed models procedure in SAS version 9.1 (PROC MIXED, SAS Inc. 2003). Nest was entered as a random effect, and species, hour, hour², and hour³

were tested as fixed effects. Effects were estimated with the residual maximum likelihood method, and tested for significance with Type III tests.

I tested for effects of weather, nest age, date and timing of nest initiation on incubation behaviour by using daily values, based on the reduced data sets. I expressed the daily rate of nest recesses or movements as observations/hour because records did not all span complete 24 h periods. I calculated an average duration of incubation recesses or movements over the day. I also calculated the proportion of the observation period (i.e., usually 24 h) during which the incubator was restless or absent from the nest. Using these response variables, I constructed separate mixed models (PROC MIXED, SAS Inc. 2003) for uniparental and biparental species. To account for repeated observations on individual nests, nest was added as a random effect in all models. Species was added as a fixed effect, and retained only if significant. For uniparental species, site (Coats versus East Bay) was tested as a fixed effect. Site was not included in models for biparental species, as it was confounded entirely with species (Table 5.1). I found no evidence of year effects, and lumped years for analyses. Weather variables, nest age, date of observation, and date of nest initiation were added to the models in a forward stepwise procedure (P of F to enter = 0.05, to remove = 0.10). Post-hoc comparisons among groups were computed with Tukey's adjustment of the pairwise differences of least-squares means.

Days when uniparental incubators took extended incubation recesses were omitted from the above analyses. To determine the circumstances that led to these long recesses, I identified days when long recesses occurred, and used this occurrence as the response variable in a logistic regression (PROC LOGISTIC, SAS 2003). I tested for

effects of the weather variables, species, nest age and date of observation using a forward stepwise approach. Means are displayed \pm SE.

Results

Behaviour of uniparental versus biparental incubators

I monitored incubation behaviour at 99 nests for a total of 419 days of observation.

Sample sizes were larger for uniparental species than for biparental species (Table 5.1), both because I had more temperature logger units and because the analysis of video footage was much more time consuming than the analysis of temperature traces. A summary of incubation behaviour for all species appears in Table 5.2.

The frequency with which the nest was left unattended differed among species, and the overall mean number of absences (i.e., recesses or exchanges) per hour was significantly lower for biparental species than for uniparental species (biparental: 0.58 ± 0.06 recesses per hour, uniparental: 1.02 ± 0.02 , $t = 6.5$, $P < 0.0001$). Absences for biparental species were also shorter than those of the uniparental species (4.4 ± 0.4 min versus 12.3 ± 0.7 min, $t = 9.5$, $P < 0.0001$), resulting in higher nest attentiveness by biparental species (0.96 ± 0.01 vs. 0.83 ± 0.00 , $t = 16.8$, $P < 0.0001$).

Although these differences between biparental and uniparental species are significant, they are smaller than I expected *a priori*. The range of nest behaviour was frequently overlapping among biparental and uniparental species, and the largest number of nest absences was in fact observed in the small sample of Semipalmated Plover nests (a biparental species). For biparental species, I was sometimes able to determine whether a departure from the nest was a recess or an exchange if dimorphic plumage could be discerned in the videos, or both parents were visible in the field of view. At least 22% of

nest absences were known to be recesses, when the same parent left and then returned to the nest, versus 19% where parents were observed to alternate roles.

The frequency of movements also differed among species, but the distinction between uniparental and biparental species was less clear (Table 5.2). The number of movements per hour was higher for biparental species (1.15 ± 0.14 vs. 0.75 ± 0.05 , $t = 2.6$, $P = 0.01$), but there was no significant difference in the duration of movements, nor in the proportion of each day occupied by movement behaviours. However, the values reported for the frequency of movements should be regarded as minimums. For some recordings of biparental species, subtle movements were difficult to detect, and in particular, at the highly concealed nest sites of Dunlin and Semipalmated Sandpipers. More detailed analyses of movements are based on the reduced data set, which includes only data where all behaviours could be accurately recorded. For uniparental species, some movements may not have altered nest temperature, and I have no means of quantifying these missed behaviours. Thus, comparisons of relative patterns (e.g. patterns throughout the day) in movements between uniparental and biparental species are more reliable than comparisons of absolute values.

Diel patterns

Despite the nearly continuous daylight at these sites, I found strong evidence for diel patterns in incubation rhythms. For the two uniparental species, recesses were most numerous midday and least numerous in the early hours of the morning (Fig. 5.1a). This quadratic pattern in the number of recesses was reflected in the model results, where hour and hour² were significant predictors of the number of incubation recesses taken (Table 5.3). The duration of recesses showed a similar pattern, with the longest recesses

occurring in the afternoon and evening. Long recesses also tended to occur in the early morning hours (Fig. 5.1b). After controlling for random effects of individual nests, and the effect of species (Red Phalaropes took longer recesses, see Table 5.2, Table 5.3), I found that recess duration was significantly related to hour, hour² and hour³. Uniparental incubators also displayed diel patterns in the rate of movements, with more restless movements made during the afternoon. However, the patterns were weaker than for recesses (Fig. 5.1a-c, Fig. 5.2a-c). Movements for uniparental species were typically short, and displayed little variation in duration. The variation observed was not related to species, hour, hour² or hour³.

Within-day patterns in the rate of incubation recesses or exchanges were weak for biparental species, in contrast to the strong patterns observed for uniparental species. The number of recesses or exchanges differed significantly among species (Table 5.3, see also Table 5.2), but was only marginally related to hour of the day, and unrelated to hour² or hour³. Models suggested longer recesses in the early morning hours, but again, patterns were not as pronounced as for uniparental species (Fig. 5.1e). Restless movements on the nest did show pronounced diel variation, and the rate was higher throughout the day than during the night (Fig. 5.2d, Table 5.3). The duration of restless movements showed a similar pattern, with longer movements during the day. Thus, biparental species showed stronger diel patterns in movement frequency and duration than uniparental species, but weaker patterns in the rate and duration of incubation recesses or exchanges.

Temporal and weather related effects

I also found patterns among days in the organisation of incubation behaviour. Using means for each day of observation in the reduced data sets, I tested the influence of

species, weather, nest age, and date on the rate and duration of incubation recesses or restless movements. Among uniparental species, I found that the rate of incubation recesses was significantly related to species, date of observation, and daily windchill low (Table 5.4). White-rumped Sandpipers took more recesses than Red Phalaropes, incubation recesses were more numerous on days with warmer windchill lows and, even after controlling for this effect of weather, recesses were more numerous later in the nesting season. Over the range of windchill low temperatures and dates in this sample (-15°C to 8.5°C, 13 June – 19 July), these effects describe differences of 11 and 9 recesses per day respectively for Red Phalaropes, and 13 and 11 recesses per day for White-rumped Sandpipers.

The duration of incubation recesses was shorter for White-rumped Sandpipers than for Red Phalaropes (see Table 5.2 for means from full data set, Table 5.4 for model results for reduced data), and they were also significantly shorter as nests aged. Though the effects were significant, the differences predicted by the models were modest. From the onset of incubation to the date of chick hatch, the duration of individual recesses was predicted to decrease by 2.3 min. Recesses were predicted to be 2.0 min shorter for Red Phalaropes than for White-rumped Sandpipers, and were also predicted to be 2.0 min shorter at East Bay than they were at Coats Island.

The proportion of time that an incubator is absent from the nest reflects both the rate and duration of incubation recesses. In this sample, total absence was positively related to the daily windchill low, positively related to date, was higher for Red Phalaropes than for White-rumped Sandpipers, and was higher at Coats Island than at East Bay. The differences among sites and species were modest (1-2%), but differences

across the range of windchill temperatures and dates encountered resulted in 5% differences in the total proportion of time that nests were incubated.

I identified a significant influence of weather on the incubation behaviour of biparental species as well. Recesses were longer with higher windchill temperatures (2.3 – 7.1 min over the -5°C to $+8.5^{\circ}\text{C}$ windchill low temperatures observed in the sample), and marginally shorter as incubation progressed (5.2 min at onset of incubation, 2.9 min at hatch). The total proportion of time that neither parent was on the nest was greater at greater mean daily windspeeds, with a change from 1.6% absence with winds of 3 km/h to 9.4% absence with 53 km/h winds. The frequency of incubation recesses or exchanges was not influenced by weather, but post-hoc tests of least-squares means suggest that recesses were significantly more numerous for Ruddy Turnstones than for Dunlin or Semipalmated Sandpipers.

Despite the strong patterns in frequency and duration of movements within days, I found no effects of weather, nest age, or date on restless movements of either biparental or uniparental species. Species effects were evident in the total proportion of time that uniparental incubators were restless, with Red Phalaropes exhibiting a greater proportion of restless behaviour than White-rumped Sandpipers. Among biparental species, Dunlin exhibited significantly fewer movements than all species except Semipalmated Sandpipers, and Semipalmated Sandpipers exhibited fewer movements than Ruddy Turnstones. The models detected no other variables with influence on the rate or duration of restless movements.

Incidence of egg neglect

The overall mean recess length for uniparental species was 12.3 ± 0.7 min, but I observed numerous recesses in excess of 45 min, and classified these as long recesses. These bouts of egg neglect were observed at 19/37 Red Phalarope nests (47/243 observation days), and 3/21 (3/99 observation days) White-rumped Sandpiper nests. These long recesses exceeded 4 h on 15 occasions, and were as long as 494 min. Even in this extreme case, all four eggs hatched successfully.

I investigated the probability that a long recess would occur with logistic regression, and found significant effects of species, nest age, temperature and windspeed (Table 5.5). Long recesses were more likely to occur among Red Phalaropes than White-rumped Sandpipers, were less likely as nests aged, and were more likely on cold or windy days. These long absences were not observed among species with biparental incubation.

Discussion

An optimal incubation schedule balances the energetic budget of incubators against the need for eggs to be kept suitably warm. This complex balance can be driven by a variety of factors such as changing energetic demands of incubation, availability of prey, and the tolerance of eggs to chilling. My results demonstrate strong diel patterns in incubation behaviour despite nearly continuous daylight. Across larger time scales, the organisation of these behaviours was influenced both by intrinsic factors such as the age of the nest, and environmental factors such as weather. Not surprisingly however, the most fundamental differences in shorebird incubation behaviour arise from whether or not the duties of incubation are shared among members of the pair.

Breeding in the arctic is challenging, and arctic shorebirds have among the highest energetic outputs of any avian species recorded (e.g., Piersma and Morrison 1994, Piersma et al. 2003, Cresswell et al. 2004). When incubation is carried out by both members of the breeding pair, either can forage freely when the other is incubating. A uniparental incubator must take more and/or longer breaks from incubation to meet metabolic demands, irrespective of any extrinsic factors, and this is indeed what I found. In the sample, uniparental incubators were on the nest 83% of the time, leaving a maximum of 17% of time available for foraging, in comparison to the 52% of time available to each member of a biparental pair. As expected, I found that uniparental incubators took twice as many incubation recesses, and three times longer recesses than did biparental pairs. Moreover, their incubation behaviour showed greater variation within days, and was influenced more by environmental conditions that could increase energy expenditure or reduce food intake rate.

Variation in incubation behaviour within days

The within-day variation in incubation behaviour that I observed among uniparental incubators and, to a lesser extent, among biparental incubators may reflect the relatively predictable patterns in temperature and solar radiation throughout the day. Recesses were longest and most numerous in the warmest hours of the day, and nests were incubated more constantly during the night and early hours of the morning. The energetic cost of foraging in exposed habitats is greater than the cost of incubation (Piersma et al. 2003, Cresswell et al. 2004), and it may be too energetically costly to forage, and/or re-warm the chilled eggs, during the coldest portions of the day. However, the variation in temperature within a day is small in comparison to that experienced throughout the

breeding season, and it is therefore likely that other factors also regulate the diel pattern in nest attendance.

Invertebrates are more active and rates of emergence typically greater during the warmer and brighter afternoon hours (Danks and Oliver 1972), and greater invertebrate activity increases the foraging success of shorebirds (Schekkerman et al. 2003, Tulp 2007). Concentrating the incubation recesses in the afternoon hours may also give shorebirds better access to prey. The observation that recess frequency peaks earlier in the day than recess duration suggests that shorebirds may initiate more recesses mid-day, when they expect invertebrates to be most active, and extend their recesses when they begin to encounter good foraging conditions. Both uni- and biparental species also took long recesses in the morning, potentially reflecting bouts of feeding to recover from more constant incubation through the relatively cold conditions and difficult foraging of the night.

Variation in incubation behaviour among days

Patterns in incubation behaviour among days also suggested an influence of both weather conditions and foraging efficiency. Incubation recesses were longer or more numerous, and nest attentiveness lower, when temperatures were higher. Similar decreases in nest attentiveness in response to increasing temperatures have been observed in a range of avian taxa (reviewed in White and Kinney 1974), but are opposite to what would be predicted if birds manage their energy budget on a short time scale. Incubating shorebirds maintain energy reserves that allow them to withstand periods of harsh weather (Tulp et al. 2002), and body condition is reduced in some species after enduring these weather events (Tulp and Schekkerman 2006). Moreover, incubation behaviour in

White-rumped Sandpipers was influenced by behaviour on the preceding day (Cartar and Montgomerie 1987). Like these studies, my finding that uniparental shorebirds have higher nest attentiveness during periods of poor weather also suggests that they optimize their energy budget over a time scale longer than a single day, and forage more on days when it is most profitable to do so. This finding is contrary to some previous evidence that uniparental shorebirds increase recess time during periods of poor weather (Norton 1972, Erckmann 1981, Tulp and Schekkerman 2006).

I identified strong effects of weather on the organisation of incubation behaviour, but also found that incubation behaviour varied over time and with the age of the nest. For all species, after controlling for effects of weather which generally improve throughout the season (see chapter 4), recesses were shorter as nests aged. Among uniparental species, recesses were also more numerous later in the season. A trend towards shorter, more numerous breaks from incubation in older nests may reflect the needs of the developing embryo. Older embryos are more susceptible to chilling than younger ones (e.g., Romanoff and Romanoff 1972), and more but shorter trips off the nest may serve to regulate nest temperature within a narrower range as the date of hatching approaches (Cartar and Montgomerie 1987).

Incidence of egg neglect

Incubation behaviour is thus influenced by a number of factors, and it may at times be difficult for adults to balance energy intake with the thermal needs of the eggs. I found that a substantial proportion of uniparental incubators occasionally left the nest for a prolonged period, and that the probability of this temporary egg neglect was higher when conditions were cold and/or windy. Because these birds generally reduced their time off

the nest during adverse weather, and presumably relied on body stores to do so, these prolonged absences may suggest a threshold beyond which birds prioritise their own body condition over the needs of their eggs (Mallory and Weatherhead 1993). While these prolonged absences increase the duration of the incubation period, and thus increases exposure to the risk of predation, rarely are they fatal for embryos (Hildén 1979, Meltofte et al. 2007, this study). I also found that prolonged absences were less common later in the incubation period, when embryos are less resistant to chilling and the need for insurance against harsh weather is diminished, both due to reductions in the remaining incubation time, and the improvement of weather conditions (Tulp et al. 2002).

Effects of predators and diet?

A shortcoming of my analyses was that the behaviour of birds while absent from the nest was not monitored. Nest defence is more common among biparental species (Larsen 1991), and they tend to be more vigilant and select more open nest sites (Larsen et al. 1996, Whittingham et al. 2002, Smith et al. 2007a). Undoubtedly, some of the incubation recesses observed by us were initiated in response to approaching predators, and potentially more so for biparental species than for uniparental species. The larger variance in the number of recesses observed among biparental species (see Fig. 5.1d), and the higher rate of nest departures for the aggressive Ruddy Turnstone than for the placid Semipalmated Sandpiper or Dunlin, may be a reflection of this (Table 5.2). Antipredator departures from the nest are typically short (1-2 min, Perkins 2004), and it is likely that such departures influenced the results for the rate of incubation breaks more so than for total nest attentiveness. Moreover, 50% of my records (38/76 observation days) come

from the Semipalmated Sandpiper and Dunlin, which are similar to the uniparental species in their antipredator behaviour.

I have identified a number of consistent patterns relating incubation behaviour to factors such as weather and nest age, but some results suggest that more complex interactions may also be involved. For example, White-rumped Sandpipers had higher nest attendance than Red Phalaropes, despite having smaller body sizes (Female White-rumped Sandpipers = 42.4g - 45.8g; Parmelee 1992, Parmelee et al. 1967, Male Red Phalaropes = 49.1g – 53.5g; Tracy et al. 2002) and larger eggs (37g clutch, Parmelee 1992 versus 32g, Tracy et al. 2002) which should be more costly to warm (Deeming 2001). White-rumped Sandpipers feed primarily by probing in moss for larvae (especially Tipulidae, Parmelee 1992), while Red Phalaropes commonly feed on aquatic invertebrates such as larval Chironomidae (Tracy et al. 2002). Differences in diet and foraging methods could necessitate foraging bouts of different lengths or frequencies, and may in part determine patterns of incubation behaviour.

Finally, movements to and from the nest may attract the attention of predators, and limiting nest recesses may reduce the risk of predation (Martin et al. 2000, chapter 6). Because the risk of predation is high for shorebirds, incubation behaviour may be modified away from an energetic optimum to increase nest survival. While I have shown that incubation behaviour is adjusted in response to the thermal requirements of eggs and the weather conditions experienced by incubators, a more complete understanding of patterns in incubation behaviour could be gained by examining the more complex relationships between behaviour, prey availability, body mass dynamics, and the risk of predation.

Table 5.1. The number shorebird nests, and days of behavioural observation, included in the samples. Incubation is uniparental for the Red Phalarope and White-rumped Sandpiper and biparental for the remaining species.

Species	East Bay (2002, 2005-2006)		Coats Island (2004-2006)	
	Nests	Days	Nests	Days
Semipalmated Plover	2	3		
Black-bellied Plover	4	7		
American Golden-Plover			6	14
Red Phalarope ^a	14	96	23	147
Ruddy Turnstone	8	14		
Dunlin			6	12
Semipalmated Sandpiper			14	26
White-rumped Sandpiper ^b	9	33	13	67
Total	37	153	62	266

^a Uniparental incubation by male

^b Uniparental incubation by female

Table 5.2. Summary of the incubation behaviour of shorebirds, based on the full dataset. Recesses for species with biparental incubation (Semipalmated Plover, Black-bellied Plover, American Golden-Plover, Ruddy Turnstone, Dunlin and Semipalmated Sandpiper) may have ended with the return of either parent. See text for a description of how movements were quantified. Means are displayed \pm SE.

Species	Recesses			Movements		
	Number/h	Mean Duration (min)	% Absent	Number/h	Mean Duration (min)	% Restless
Semipalmated Plover	1.33 \pm 0.54	1.89 \pm 1.10	0.04 \pm 0.02	1.92 \pm 0.37	0.20 \pm 0.01	0.01 \pm 0.00
Black-bellied Plover	0.80 \pm 0.24	4.70 \pm 1.57	0.05 \pm 0.02	1.75 \pm 0.41	0.82 \pm 0.30	0.03 \pm 0.01
American Golden-Plover	0.57 \pm 0.21	4.17 \pm 0.69	0.05 \pm 0.02	2.06 \pm 0.36	0.38 \pm 0.08	0.01 \pm 0.00
Red Phalarope	0.96 \pm 0.03	14.06 \pm 1.01	0.18 \pm 0.01	0.83 \pm 0.06	0.77 \pm 0.07	0.01 \pm 0.00
Ruddy Turnstone	0.88 \pm 0.09	4.72 \pm 1.18	0.07 \pm 0.02	2.22 \pm 0.29	0.62 \pm 0.06	0.02 \pm 0.00
Dunlin	0.25 \pm 0.04	5.67 \pm 1.17	0.03 \pm 0.01	0.16 \pm 0.07	1.57 \pm 0.82	0.01 \pm 0.00
Semipalmated Sandpiper	0.42 \pm 0.08	3.64 \pm 0.47	0.03 \pm 0.01	0.17 \pm 0.06	0.22 \pm 0.03	0.00 \pm 0.00
White-rumped Sandpiper	1.16 \pm 0.04	7.98 \pm 0.37	0.14 \pm 0.00	0.56 \pm 0.04	0.56 \pm 0.02	0.01 \pm 0.00

Table 5.3. Results of a general linear mixed model analysis to describe diel patterns in the incubation behaviour of shorebirds. Data were entered as an average value for each hour of the day, for each nest, and are based on the reduced dataset (where days with atypically long recesses (> 45 min) were filtered). Nest was entered as a random effect in all models.

	Number of Recesses		Duration of Recesses		Number of Movements		Duration of Movements	
	F	P	F	P	F	P	F	P
Uniparental Species	.	.	31.46	<0.0001	7.25	<0.001	.	.
Hour	181.54	<0.0001	4.57	0.033	10.23	0.001	.	.
Hour ²	125.68	<0.0001	21.81	<0.0001	11.00	<0.01	.	.
Hour ³	.	.	34.1	<0.0001
Biparental Species	19.04	<0.0001	.	.	12.59	<0.0001	.	.
Hour	4.30	0.039	16.53	<0.0001	13.61	<0.001	8.77	<0.01
Hour ²	.	.	11.52	0.001	14.59	<0.001	10.39	0.001
Hour ³

Table 5.4. Results of a general linear mixed model analysis to describe patterns among days in the incubation behaviour of shorebirds. Nest was entered as a random term in all models, while the remaining fixed effects were entered in a forward stepwise procedure. Analyses are based on the reduced dataset, where days with atypically long recesses (> 45 min) are omitted. The uniparental species were the White-rumped Sandpiper and the Red Phalarope, while the biparental species were the Semipalmated Plover, Black-Bellied Plover, American Golden-Plover, Ruddy Turnstone, Dunlin and Semipalmated Sandpiper.

Effect	Number of Recesses			Duration of Recesses			% Absence		
	Direction of Effect	F	P	Direction of Effect	F	P	Direction of Effect	F	P
Uni- Species	REPH<WRSA	5.98	0.019	REPH>WRSA	15.87	0.00	REPH>WRSA	3.48	0.07
parental Nest Age (d)				-	10.56	0.00			
Date of Observation	+	6.25	0.014				+	3.48	0.07
Mean Temperature (°C)									
Daily Windchill Low (°C)	+	14.13	0.0002				+	13.41	0.00
Mean Daily Windspeed (km/h)									
Precipitation (Y/N)									
Site				Coats > East Bay	23.69	0.00	Coats>East Bay	5.86	0.02

Table 5.4. Continued.

Effect		Number of Recesses			Duration of Recesses			% Absence		
		Direction of Effect	F	P	Direction of Effect	F	P	Direction of Effect	F	P
Bi-parental	Species	RUTU>DUNL, RUTU>SESA	3.39	0.012						
	Nest Age (d)				-	3	0.09			
	Date of Observation									
	Mean Temperature (°C)									
	Daily Windchill Low (°C)				+	14.37	0.00			
	Mean Daily Windspeed (km/h)							+	5.52	0.02
	Precipitation (Y/N)									

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 5.5. The variables that significantly increase the probability of temporary nest abandonment (i.e. absence > 45 min), and the direction of their effect, as determined by logistic regression. Results are displayed only for variables with $P \leq 0.05$.

	Direction of Effect	X^2	P
Species	REPH > WRSA	13.16	0.0003
Nest Age (d)	-	4.69	0.03
Julian Date of Observation	.	.	.
Mean Temperature (°C)	-	5.26	0.022
Daily Windchill Low (°C)	.	.	.
Mean Daily Windspeed (km/h)	+	7.634	0.0003
Precipitation (Y/N)	.	.	.
Site	.	.	.

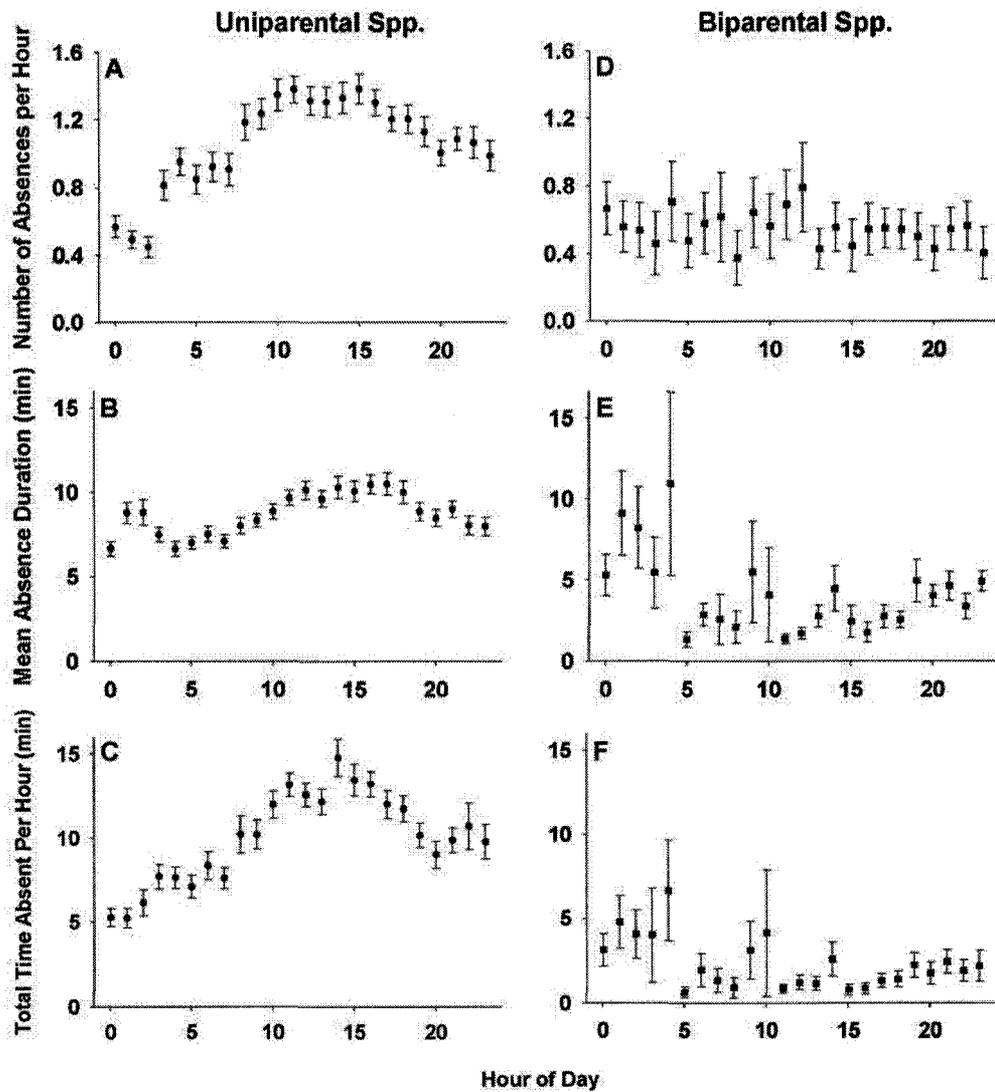


Figure 5.1. The number of incubation recesses or exchanges for each hour of the day, their mean duration (min), and the total time per hour where the nest was left unattended for uniparental species (panels a-c), or biparental species (d-f). See text for species included in the samples. Means are based on the full data set and are displayed \pm SE.

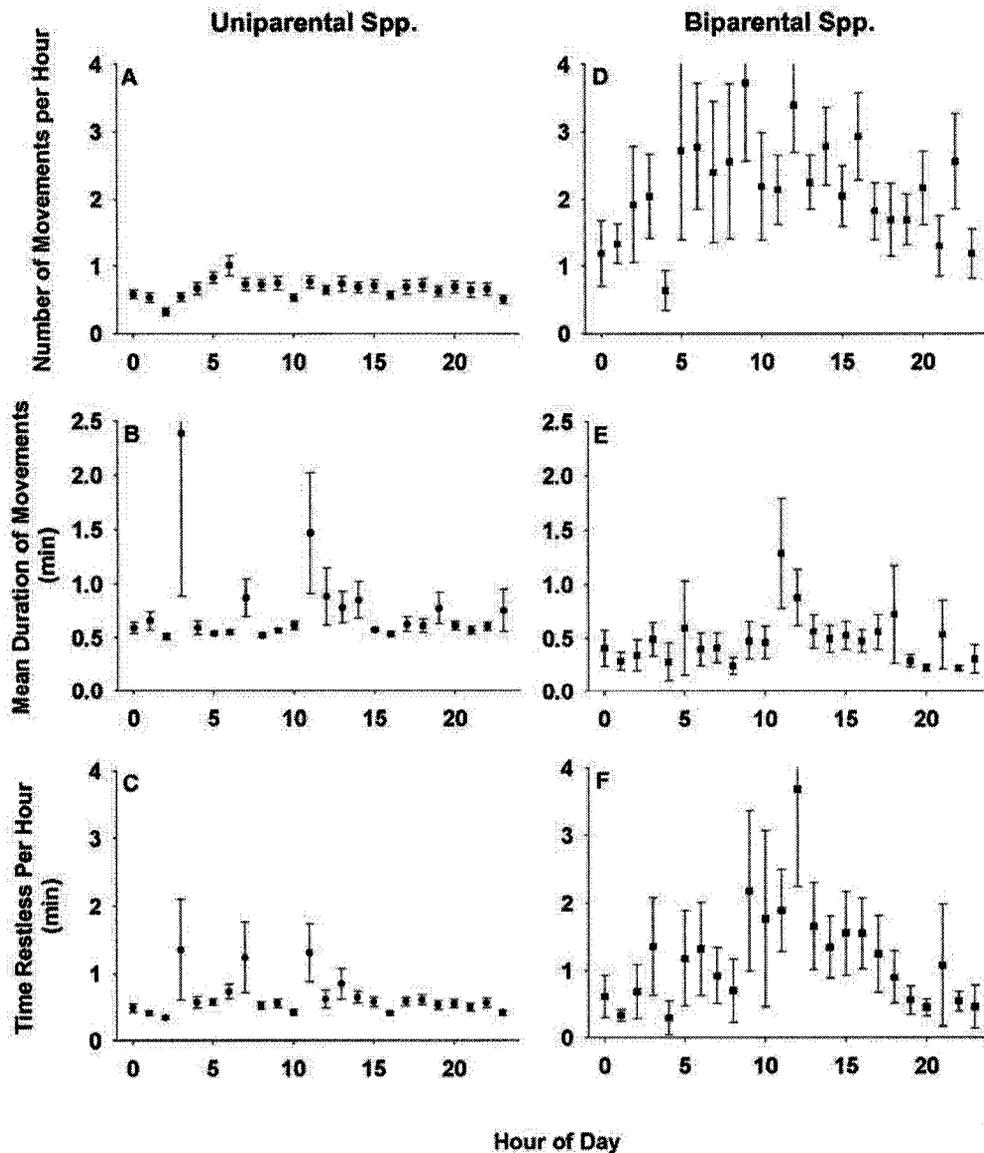


Figure 5.2. The number of restless movements of incubators on the nest (see text) for each hour of the day, their mean duration, and the total time per hour spent exhibiting restlessness for uniparental (panels a-c), or biparental species (d-f). See text for species included in the samples. Means are based on the full data set and are displayed \pm SE.

Chapter 6. Shorebird incubation behaviour and its influence on the risk of nest predation

Abstract

Both nest survival and incubation behaviour are highly variable among shorebirds, and I tested whether more conspicuous incubation behaviour increased the risk of nest predation. From 2000-2006, I monitored 901 shorebird nests at three study sites across the circumpolar arctic. Using miniature video recorders and nest temperature sensors, I obtained 782 days of behavioural data for 161 nests of 11 species. I related nest fate to the rate and duration of nest absences or restless movements on the nest, as well as the total proportion of each day engaged in these activities. I also summarise direct observations of predation events, obtained incidentally during the recording of incubation behaviour. I found that nest predation was positively related to the proportion of time each species left the nest unattended. After controlling for species effects, the likelihood of a successful nesting attempt was lower for individuals that spent more time off the nest, but among failed nests, the number of days that a nest survived prior to depredation was not significantly predicted by my measures of incubation behaviour. To control for weather or seasonal effects, I paired observations from nests that were ultimately depredated with observations from successful nests of the same species on the same day. In this paired sample, both incubation recesses and restless movements were more numerous among failed versus successful nests. These results suggest that more conspicuous incubation behaviour is indeed related to a higher risk of nest predation, and that this relationship may underlie patterns of nest survival within and among shorebird species.

Introduction

Parents must balance the costs to themselves of providing care with the benefits to their offspring of being cared for (Clutton-Brock 1991, Stearns 1992). A fundamental parental care behaviour among birds is the incubation of eggs, and because a large proportion of eggs do not survive until hatch in most species (e.g., Ricklefs 1969), parent birds could realise benefits by increasing their investment in incubation. In most previous studies of incubation behaviour, the costs to parents are measured in terms of time and energy, and balanced against the need to maintain the eggs at a suitable temperature for embryonic development (Mallory and Weatherhead 1993, Williams 1996, Tulp and Schekkerman 2006, chapter 5). However, because predation is the primary cause of nest failure in almost all avian species studied to date (e.g., Martin 1993), incubation behaviour also may be modified to reduce the risk of nest predation.

Increased activity of parent birds around the nest can increase the risk of predation if predators locate nests by sight (Skutch 1949). For species with incubation feeding, more frequent feeding trips have been linked to reduced nest survival, and feeding trips are suspended when parents are faced with an immediate risk of nest predation (Martin and Ghalambor 1999, Martin and Ghalambor 2002, Martin et al. 2000). For species without incubation feeding, more frequent incubation recesses may increase the risk of predation (Cresswell et al. 2003, Smith et al. 2007a), but this effect has not yet been demonstrated directly.

Shorebirds do not exhibit incubation feeding, but do vary dramatically in their incubation behaviour. Within days or throughout the season, shorebird incubation behaviour varies in response to environmental conditions and energetic demands (Norton

1972, Cartar and Montgomerie 1987, Cresswell et al. 2004, Tulp and Schekkerman 2006, chapter 5). However, incubation behaviour is constrained at a higher level by mating system; ecologically similar species breeding in sympatry show strategies ranging from completely uniparental incubation, by females or by males, to incubation shared evenly between both parent birds (Pitelka et al. 1974). Uniparental incubators leave the nest more frequently to feed than do members of a biparental pair (e.g., Norton 1972, chapter 5), and previous studies suggest that uniparental birds may suffer higher rates of nest predation in most years (Smith et al. 2007a, chapter 3). There is considerable variation in incubation behaviour even within groups of species with uni- or biparental incubation (Tulp and Schekkerman 2006, chapter 5), and how this variation may contribute to interspecific variation in nest survival remains unknown.

I simultaneously monitored the nest survival and incubation behaviour of shorebirds to determine whether more conspicuous behaviour increases the risk of nest predation, and whether this relationship underlies patterns of nest survival within and among species. Data were collected on the rate and duration of incubation recesses, as well as the rate and duration of restless movements on the nest for 11 shorebird species varying widely in incubation behaviour. I related patterns in behaviour among species to interspecific patterns in nest survival, to contrast the effect of biparental versus uniparental incubation with the effect of incubation behaviour *per se*. I also asked whether successful and failed nests within species differed in the conspicuousness of adult behaviour on the nest. I then paired observations from nests that eventually failed with observations from successful nests of the same species on the same day. This enabled me to evaluate whether differences in behaviour could explain differences in nest

fate, while controlling for seasonal or weather related variation in incubation. Finally, I summarise observations of interactions between shorebirds and their predators, obtained incidentally while recording behaviour at the nest.

Methods

Study area

Fieldwork was conducted between 2000 – 2006, at three sites across the circumpolar arctic. At Coats Island, Nunavut (N62° 51' W82° 29', Fig. 2.1), work was carried out from the beginning of June until the end of July, 2004-2006. At East Bay, Nunavut (63° 59'N 81° 40'W, Fig. 2.1), it was completed from late May until late July in 2002, 2005 and 2006. At both of these sites, workers searched for nests over an area of 12 km² in wet lowlands, upland heath tundra, raised beach ridges and coastal habitat types typical for these latitudes. The third site was located at Medusa Bay, on the Taimyr Peninsula, Russia (73° 20'N 80° 30'E, Fig. 6.1). Work here was led by I. Tulp and H. Schekkerman, and was carried out June – August, 2000 and 2001, in a 4 km² area of hilly tundra interspersed with wet sedge meadows and scattered, stony ridges. The physiography of the Canadian and Siberian field sites are described in more detail elsewhere (Smith et al. 2007, chapter 2, and Tulp 2007, respectively).

The sample includes behavioural data from eleven species: Semipalmated Plover, Black-bellied Plover, American Golden-Plover, Red Phalarope, Ruddy Turnstone, Dunlin, Curlew Sandpiper, Semipalmated Sandpiper, White-rumped Sandpiper, Little Stint, and Pectoral Sandpiper. The relative abundance of nests found at each of the sites, and the composition of the sample of behavioural data, appears in Table 6.1. At the Canadian sites, I collected behavioural data for all of the species that breed in significant

numbers, together representing >95% of all breeding individuals. At Medusa Bay, behavioural data were collected only for species with uniparental incubation (see below), and thus some important species are not represented in the sample (Ringed Plover *Charadrius hiaticula*, Pacific Golden-Plover *Pluvialis fulva*, and Dunlin).

All species share many basic features of reproductive ecology, with a typical clutch of four eggs laid in a simple scrape on the ground and incubated for approximately three weeks (19-26 days). Though these traits are shared, the incubation system differs among species. Incubation is carried out solely by the male for the polyandrous Red Phalarope (Tracy et al. 2002), and by the female for the Curlew Sandpiper, Little Stint, White-rumped Sandpiper and Pectoral Sandpiper. The remaining six species are monogamous, biparental incubators, and share the duties of incubation. The organisation of incubation behaviour is complex; all species considered here alter their incubation dramatically throughout the day and in response to weather conditions (chapter 5, Tulp and Schekkerman 2006), and these responses may differ for uniparental versus biparental species, or for nests in early versus late incubation (chapter 5). Overall, uniparental species take more and longer recesses, and leave the nest uncovered for a greater proportion of each day than biparental species, although variation among species is pronounced (chapter 5).

Shorebird nest finding, ageing and monitoring

Methods for finding, ageing and monitoring nests are described in detail elsewhere (chapter 3, Tulp 2007). Nests found with complete clutches were aged with the egg flotation method (Liebezeit et al. 2007), which provides accuracy ± 4 d or less in most instances. Nests were considered successful if one or more eggs hatched, and failed if

they were depredated or abandoned. Nests were considered abandoned if the eggs were cold on two consecutive visits spanning at least 4 days. One egg of the clutch was positioned with the narrow end outwards to confirm that it had not been incubated (and thus returned to the correct position) between visits. I considered nests depredated if their contents disappeared before they could possibly have hatched. In the cases where nests disappeared but the fate could not be assigned with certainty, I recorded the fate as unknown.

Species-specific estimates of nest survival were calculated using the Mayfield 50%- method (Mayfield 1961), with standard errors calculated following Johnson (1979). I calculated an estimate of the daily mortality rate for each species using all nests found at all sites over the years of this study (see Table 6.1). Mayfield exposure days were terminated at the last active date for nests of unknown fate, and halfway between the last active and first inactive date for nests of known fate found empty (Manolis et al. 2000).

Monitoring incubation behaviour

The equipment used to monitor incubation behaviour differed for species with uniparental and biparental incubation. For uniparental species, I placed thermistor probes amongst the eggs to capture the temperature changes when birds departed the nest (Norton 1972, Erckmann 1981). At Coats Island and East Bay, I constructed the probes using a 10 K Ω Curve-G thermistor on a 15 m, 24 AWG cable, with a 10 K Ω (\pm 1 %) reference resistor loop, on a 2.5 mm stereo jack, and attached these probes to a Hobo H8 data logger (Onset Instrument Corporation, Pocasset, Massachusetts, USA). At Medusa Bay, similar probes were obtained commercially and attached to Gemini Tiny Tag data loggers (Gemini Data Loggers Inc., West Sussex, UK). Loggers were placed 15 m from

the nest in a camouflaged, waterproof housing, and the cable between them was buried or concealed. The placement procedure lasted less than 10 min, and observations from portable blinds (24 h total) on two nests before and after deployment of the logger systems revealed that the probes had no detectable effect on incubator behaviour.

Temperature readings were taken every 30 s at East Bay and Coats Island, and every minute at Medusa Bay. The thermistors accurately captured departures of the incubator (i.e., drops in temperature) within this time frame, and visual observations suggest that nest absences shorter than 1 minute were rare. At East Bay, I based interpretation of the temperature records on the 24 h of visual observations mentioned above. I defined any temperature changes $\pm 2^{\circ}\text{C}$ as continuous incubation. Any drop exceeding 9°C was considered a recess. The beginning and end of incubation recesses (± 30 s) were identified manually by examining graphs of temperature over time. Any sudden change of $>2^{\circ}\text{C}$ in the recorded temperature was defined as movements such as egg rolling, cup maintenance, or restless incubation. At Medusa Bay, large drops in temperature were classified as recesses but no effort was made to identify movements on the nest or restless incubation (see Tulp and Schekkerman 2006 for details).

Temperature readings were generally unambiguous because the probes were placed such that they were near to the warm brood patches when the bird was incubating. Occasionally however, the tip of the probe was displaced and temperature readings became difficult to interpret. Readings also became erratic when eggs began to pip and chicks began to thermoregulate. Erratic temperature data were discarded prior to analysis.

The incubation of biparental species cannot be monitored adequately with the above method because changeovers between pair members could happen too rapidly to be detected by a drop in temperature. Instead, I used portable video recording systems consisting of a small (10cm x 2cm), weatherproof, low-lux, CMOS camera, connected to a 40 GB hard-drive based digital video recorder. Using a 21 Ah (circa 10 kg) lead acid battery, these comparatively economical systems could record full-motion video of incubating birds for continuous periods of > 36 h. Cameras were placed approximately 10 m away from nests, and were elevated 30 - 40 cm above the ground with wire tripods. The wire legs of the tripods were pressed into the ground to stabilize the camera. The battery and recorder were concealed in a camouflage-painted waterproof housing and placed another 10 m further from the nest. To analyse videos, I watched them at 4x speed with DivX[®] computer software, and paused when necessary to record behaviours \pm 1 s. These video systems were only deployed at East Bay and Coast Island.

Although the methods of data collection differed among biparental and uniparental species, I derived similar measures of incubation behaviour for both. For all species, I calculated the frequency and duration of nest absences, and the proportion of time that nests were left unattended. For biparental species, these absences could end with the return of either parent; in some cases the sexes or individuals could be distinguished while in others they could not. At Coats Island and East Bay, I also quantified the frequency and duration of movements, and the proportion of each day that these movements comprised. For uniparental species, these were defined on the basis of the temperature records (see above). For biparental species, "movements" constituted

nest maintenance, egg rolling, feeding from the incubating position, preening, and repositioning.

Fog and strong winds occasionally reduced the quality of the video and impaired my ability to record the full suite of incubation movements. In these instances, the value for number of movements represents a minimum. If the quality of the recording was so poor that recesses and changeovers could not be reliably identified, I discarded the video from all analyses. Incubation behaviour can be erratic during laying (Norton 1972), so I monitored behaviour when clutches were complete.

Timing of predation and observations of predators

For nests that were monitored with video systems, the timing and nature of predation was observed directly. The video footage also documented instances when predators were near nests but did not depredate them. For nests of uniparental species, where I did not have video footage, I used the temperature traces to identify the timing of predation. From nest monitoring, the timing of nest predation was typically known ± 3 days. The temperature trace in the intervening time was scrutinized to identify the exact timing of predation. A nest containing warm eggs cools more slowly than an empty cup, and the flush of an incubator followed by a rapid decrease to ambient temperature and the cessation of incubation, was interpreted as a predation event. In many instances, the exact moment (± 30 s) that the eggs were removed could be identified as an acceleration of the cooling curve in the temperature trace. The timing of predation events for uniparental species at Medusa Bay, Russia, was obtained in a similar manner, and has been summarised previously in Tulp and Schekkerman (2001).

For each failed nest I also calculated the duration of time between the onset of incubation and nest failure (time to failure). The onset of incubation was either observed or estimated from nest age (see above). Observations of the exact timing of predation were used where available. Otherwise, I assumed that the nest was depredated half-way between the last visit upon which it was observed as active, and the first visit upon which it was noted to have failed.

Data analysis

Incubation behaviour is highly variable, and the effects of interest here could be masked by the complex interactions with time of day, weather, nest age, and species. I therefore relied on multiple lines of evidence to quantify the relationship between incubation behaviour and the risk of predation. To account for diel patterns in incubation behaviour, all analyses are based on records spanning 24 h. To better satisfy the assumptions of normality, I log-transformed the counts of recesses and movements and arcsine transformed the proportions of time birds spent engaged in these activities prior to parametric analyses. For logistic regression models, I used the untransformed data.

Interspecific differences in nest survival are strong, and I first asked whether these differences in the risk of predation were related to interspecific differences in incubation behaviour. I entered the species-specific daily mortality rate as the dependent variable in a general linear model (GLM) and tested the influence of the metrics of behaviour as covariates. Because some are correlated (e.g., time per recess * recess frequency = 1-incubation constancy), I used a forward stepwise procedure and Type I sums of squares. I had data on rates and durations of movements on the nest for only 8/11 species; I conducted one analysis on all species using only recess data, and a second analysis on

these eight species using all six measures of incubation behaviour. Both nest survival and incubation behaviour may vary by mating system (see chapter 3, chapter 5), and spurious correlations between behaviour and nest survival could result from the effect of mating system. I therefore tested whether a fixed effect of uniparental versus biparental incubation changed the interpretation of the model results.

I then asked whether the behaviour of birds at nests that were ultimately successful differed from that of birds at nests that eventually failed. I used logistic regression with fate as the dependent variable, and the metrics of incubation behaviour as predictors. I accounted for differences in nest survival among years and species by including them as fixed effects. Because I had a variable number of repeated observations from individual nests, I used means per nest for the measures of behaviour in this analysis. I first tested the behavioural metrics individually for a significant influence on nest fate. Then, as above, I conducted one model building analysis including all species but only the data for incubation recesses, and a second analysis including 8/11 species which also included the data for incubation movements.

Some nests fail faster than others, and I tested whether those nests which failed the fastest had the most conspicuous incubation behaviour. Analyses were limited to failed nests, and time to failure (in days) was treated as the dependent variable in a mixed model. Each nest had a single value for time to failure, and I used means per nest to include the metrics of behaviour as covariates. Because interspecific differences in nest survival could create interspecific differences in time to failure, I added species to the model as a fixed effect. Interannual variability was controlled by including year as a random effect.

Finally, I conducted analyses on paired records, where observations for depredated nests were matched with observations from similar, but successful, nests. For each day of observation on a failed nest, I selected an observation from the same site, year and day, for a successful nest of the same species. Nest age was matched as closely as possible (mean difference \pm SE = 1.8 ± 0.4 d), and records from successful nests were used more than once if unsuccessful nests outnumbered successful nests on a given day of observation. While greatly reducing sample size, this approach eliminates entirely the confounding influence of day to day variation in incubation behaviour.

To analyse these paired records, I first compared the means of the six indices of incubation behaviour among successful and failed nests using paired t-tests. I then asked whether fate could be predicted on the basis of incubation behaviour by using binary logistic regression with nest fate (successful versus failed) as the dependent variable for this reduced data set. The categorical variables species and year were included as fixed effects and the influence of the metrics of behaviour was assessed by testing them as covariates. Separate models were constructed for recess and movement data. All analyses were conducted with SAS 9.1 (SAS Inc.) and means are displayed \pm SE.

Results

Nest survival and behaviour among species

I found and monitored a total of 901 nests of 11 species. Five of these species have uniparental incubation, while incubation is shared in the remaining six (Table 6.1). I obtained behavioural data for 161 nests and a total of 782 nest*days of observation (Table 6.1).

Of 852 nests for which fate was known, 522 (61%) were depredated and only 23 (3%) were abandoned. Estimates of the daily mortality rate varied among species, from a low of 0.040 ± 0.007 for the Black-bellied Plover to a high of 0.155 ± 0.040 for the Curlew Sandpiper. Rates of nest mortality differ among years, and interannual variation in predation is explored in detail elsewhere (chapter 3, 4, Tulp and Schekkerman 2001, Schekkerman et al. 2002).

Among the 11 species, daily mortality rate was positively related to the duration of incubation recesses ($F_{1,9} = 12.2, P < 0.01$) and also the proportion of time that the nest was left unattended (arcsine transformed, $F_{1,9} = 44.3, P < 0.0001, R^2 = 0.83$, Fig. 6.2,a-c). Whether a species has uniparental versus biparental incubation was marginally related to daily mortality rate ($F_{1,9} = 5.4, P < 0.05$). Neither the effect of time per recess, nor incubation system remained significant when added to a model containing the proportion of time spent off the nest.

Thus, some of the large variation in nest predation among species was related to incubation behaviour, with those species spending more time off the nest suffering greater rates of predation. This relationship is not simply a product of differences in the rate of nest predation for uniparental versus biparental incubators (as indicated by a non-significant effect of incubation system in the above GLM), and was apparent despite the potential for the large interannual variation in mortality rate to obscure the effects of interest.

In contrast, I found no evidence that the rate or duration of movements, or the total proportion of time spent exhibiting movements at the nest influenced nest predation (Fig. 6.2, d-e). Among the eight species for which I had movement data, no measures of

incubation movements were significant predictors of daily mortality rate in the GLM (all P s > 0.4).

Behaviour of incubators at successful versus failed nests

I had behavioural data for 161 nests, and fate was known for 149 of these. Among these, 93 (62%) failed. This value is nearly identical to the proportion of nest failures observed in the full sample of nests (61% nest failure among 852 nests), suggesting that the deployment of data logging devices at nest sites did not increase the risk of predation.

In logistic regression analyses, the fate of a nesting attempt (successful vs. unsuccessful) was weakly related to year as a categorical variable ($n = 6$ years, $X^2_5 = 11.4$, $P = 0.043$). Although significant differences in the rate of nest predation among species are evident in the larger sample of nests, species was not a significant predictor of nest fate for the sample of 161 nests for which I had behavioural data ($X^2_{10} = 14.0$, $P = 0.17$). In contrast, more frequent incubation recesses ($X^2_1 = 5.4$, $P = 0.021$), and a greater amount of time spent off the nest ($X^2_1 = 7.5$, $P = 0.006$) were associated with nest failure. Year did not remain significant when added to either the model containing recess rate, or the model containing the proportion of time spent off the nest. For the reduced set of eight species for which I had movement data, nest mortality was only marginally positively related to the rate of movements on the nest ($X^2_1 = 2.8$, $P = 0.09$).

Time to failure

For the sample of 93 failed nests for which I had behavioural data, I measured the time from the onset of incubation until the nest was depredated. In 80 cases, the exact time of predation was known, but for the remaining 13 I assumed that predation happened mid-

way between the penultimate and final visit. This time to failure varied widely, from 2 d - 26 d, with a mean of 12.1 ± 0.6 d.

Variation in time to failure among the restricted sample of nests was not related to species ($F_{10,76} = 1.0, P = 0.43$), nor was it related to year ($F_{5,81} = 2.0, P = 0.09$), despite both year and species effects being detected in the daily risk of nest mortality in the larger sample of nests (see above). None of the six metrics of incubation behaviour (transformed as appropriate) was related to time to failure (all F 's < 2.3 , P 's > 0.14).

Analyses of paired observations

Incubation behaviour varies dramatically among species and days, and the use of paired records from successful and failed nests of a given species on a given day is an effective means of accounting for this variation. However, sample size is limited dramatically by this approach, and the sample of paired records included 85 nests and a total of 211 pairs of observation days, with some species poorly represented (Table 6.2). When the mean behaviour of incubators at all failed nests was compared to their paired records of incubators at successful nests, I found that both the rate of incubation recesses and the rate of movements on the nest differed (recess rate, log transformed: $t_{210} = 2.1, P = 0.03$, movement rate, log transformed: $t_{109} = 2.2, P = 0.03$). The sample is dominated by records for Red Phalaropes and Little Stints (Table 6.2). For both of these species, all measures of incubation behaviour were larger for individuals whose nests failed, suggesting that more conspicuous behaviour may have increased the risk of predation. Results for other species, particularly those with very small samples, are more variable. For example, because so few White-rumped Sandpiper nests were successful, 13 of 16 paired records were drawn from a single successful nest. This individual had atypically

conspicuous behaviour, and the results for White-rumped Sandpiper should therefore be viewed with caution.

I then used logistic regression to test whether incubation behaviour could be used to predict fate in this paired sample of successful and failed nests. Neither species nor year effects were significant predictors individually because the paired design meant that exactly 50% of nests failed for each species and year. Year and species effects remained non-significant predictors of nest fate when added to models including behavioural covariates. In contrast, nest fate was significantly related to the rate of incubation recesses ($X^2_1 = 6.4, P = 0.012$), and the strongest model suggested that nest failure was predicted by more frequent and longer recesses ($X^2_2 = 11.2, P = 0.004$). The relationship between restless movements and the risk of nest predation was less pronounced. The mean values for the rate, duration and total proportion of time exhibiting movements was higher for failed than for successful nests in 12 of 15 contrasts (3 metrics * 5 species, Table 6.2), but variability was large and no measure of movement was a significant predictor of nest fate in this sample ($X^2_1 < 1.6, P > 0.2$).

Timing of predation and observations of predators

The exact time of predation was known for 39 nests that failed at Coats Island and East Bay (of the 52 failed nests at these sites for which I had behavioural data). Among these, predation appeared somewhat more common in the early morning and evening, but patterns were not strong (Fig. 6.3). The timing of predation was known for a large proportion of the nests from Medusa Bay used here. Timing of predation of these and other nests from this site in 2000 and 2001 are summarised fully in Tulp and

Schekkerman (2001). I present these data here for comparison with those obtained at East Bay and Coats Island (Fig. 6.3).

Our video footage at biparental nests yielded a number of interesting observations of predators, and because of the rarity of such observations, I summarise them here. Five predation events were recorded directly, and all were perpetrated by arctic foxes. These occurred at 0213h, 0232h, 0418h, 0702h, and 2215h. In three instances, all eggs were consumed immediately. In one instance, individual eggs were taken away from the nest site singly and presumably cached. After caching two of the eggs, the fox apparently could not find the remaining two and left them in the nest cup (parents later returned to incubate them). In another instance, the fox cached two eggs, returned to smell the nest cup and left the remaining two eggs intact. In addition to these direct observations of predation events, I recorded several instances when predators came near nests but did not find them.

I recorded footage of foxes unsuccessfully searching for nests on six occasions, and they came within several metres of the nest on three of these. In one case, the fox walked directly over the nest of a Ruddy Turnstone, while in another, it came within 1 m of the nest of a Semipalmated Sandpiper, with its nose to the ground; in both cases the nests went unnoticed. These six observations of nest searching among foxes were recorded at 0005h, 0255h, 0330h, 1456h, 1725h, and 2251h.

In one instance, I recorded an avian predator (a Parasitic Jaeger) hovering several meters above a nest (at 0040h). The incubating bird (a Black-bellied Plover) retracted its neck, lay flat on the ground, and apparently cowered. I observed this same behaviour on

five other occasions, but did not observe the predator directly in these cases. These observations occurred at 0027h, 1041h, 1124h, 1347h and 1521h.

On one occasion, a Canada Goose (*Branta canadensis*) approached the nest of a Ruddy Turnstone and was chased away aggressively; Canada Geese are known to eat eggs occasionally. Long-tailed ducks (*Clangula hyemalis*) or king eiders (*Somateria spectabilis*), which are not known to eat eggs, came near nests on at least three occasions and incubating birds showed no response.

Discussion

Bird eggs develop optimally within a narrow range of environmental conditions (Lundy 1969, Webb 1987), and incubation behaviour for all birds must, at some level, balance the need to provide a suitable environment for eggs with the need for self-maintenance (Williams 1996). Shorebirds nesting in the arctic can mitigate the high costs of incubation by selecting sheltered, well-insulated nest sites (Tulp 2007, Reid et al. 2002a), but they still have among the highest energetic outputs of any species recorded (e.g., Piersma and Morrison 1994, Piersma et al. 2003, Cresswell et al. 2004). To balance their energy budget, shorebirds must leave the nest to feed frequently, with some species spending 15% or more of the day off the nest (Ch 4, Tulp and Schekkerman 2006). These breaks in incubation have traditionally been viewed as the means by which the costs of incubation are recouped. However my results suggest these trips also entail costs, with more frequent or longer incubation recesses increasing the risk of nest predation. This finding has obvious bearing on studies of incubation behaviour or nest survival, but because the rate and duration of incubation recesses also depends on

whether a species has uniparental or shared incubation, this finding also has important implications for the study of life history evolution.

Variation in nest survival among species of shorebirds is large, and it has been shown previously that much of this variation is accounted for by distinguishing between species with uniparental and biparental incubation (Smith et al. 2007a, chapter 3). Here, the results suggest that this distinction is not a product of shared versus single-parent incubation *per se*, but rather a product of increased risk of predation for species that take longer incubation recesses and/or leave the nest uncovered for a greater proportion of time.

I found similar effects within species, where the fate of a nest could be predicted by the rate of incubation recesses and the total proportion of time spent off the nest. Even among paired records, where the confounding influence of variation in environmental conditions is controlled, I found that recesses and movements were significantly more numerous among failed versus successful nests, and that the rate and duration of breaks in incubation were positively related to nest failure. Thus, through a variety of analyses, I demonstrated that the rate and duration of nest recesses, and the total proportion of time that a nest is left unattended, play important roles in determining nest fate. Although these metrics of incubation are correlated, the mechanism by which they could influence the risk of predation varies.

Frequent trips to and from the nest could disclose its location to predators that use visual cues. Skutch (1949) first hypothesised this relationship in the context of trips to feed altricial nestlings, and the effect has since been demonstrated in a variety of species (e.g., Martin and Ghalambor 1999, Martin et al. 2000, but see Roper and Goldstein

1997). Other conspicuous activities, such as trips on and off the nest or restless movements while incubating, may have the same negative effect. In the analyses of paired records, for example, Red Phalaropes incubating nests that would ultimately succeed took 17% fewer recesses than those with nests that ultimately failed. While the effects of restless movements during incubation (such as egg rolling, nest maintenance and preening) were less pronounced, the results also suggest that an increased rate of movement on the nest increases the risk of nest failure due to predation. Among Red Phalaropes again, 14% fewer movements were observed among successful versus failed nests. These conspicuous behaviours may act as cues for predators, directly disclosing the location of the nest. However, time spent off the nest may also influence the probability that a nest will be found by predators, if shorebirds encounter predators while foraging.

Shorebird nest sites are typically more sheltered than the exposed habitats in which the adults forage (e.g., Smith et al. 2007a), and more time spent in exposed habitats (e.g., pond edges) may increase the likelihood of being seen by a predator. One of the techniques that researched as human “predators” employ while searching for nests is to watch foraging birds from a distance and follow them back to the nest site; it seems intuitive that predators could profit from a similar approach. The proportion of time that a nest was left unattended, and then returned to, varied from 3-19%, and accounted for 83% of the variation in nest survival. Because incubation is shared for biparental species, they undertake much of their foraging while their mate is incubating. As experienced nest searchers, I recognise that it is less profitable to watch a foraging bird if it is a species with biparental incubation. Whether predators discern between shorebird species

and focus on those nests that are easier to find is unknown, but may also contribute to the differences observed in nest survival.

Whether incubation is biparental or uniparental, leaving the nest unattended could also increase the risk of predation by leaving the eggs uncovered or by compromising a bird's ability to defend its nest aggressively. By sitting on the nest, birds with cryptic plumage and conspicuous eggs can camouflage their nest contents (Martin 1992 and references therein). Studies with artificial nests mimicking those of shorebirds have shown inconsistent results, with both higher (Erckmann 1981, Ch 2) and lower (Ashkenazie and Safriel 1979, Safriel 1980) rates of nest survival for unattended versus real, active nests. Given the general criticism of artificial nest studies (e.g., Major and Kendal 1996, Burke et al. 2004), these results are difficult to interpret. However, shorebird eggs have muted background colours and heavy mottling; common adaptations among ground nesting birds to provide camouflage and reduce nest predation (Tinbergen et al. 1962, Montevecchi 1976, Bertram and Burger 1981, Solís and de Lope 1995, Yahner and Mahan 1996, Lloyd et al. 2000). Therefore it seems unlikely that eggs would be markedly more conspicuous than an incubating parent. Studies of nest, egg and incubator crypsis in this system are ongoing (Smith *in prep.*), and at present I cannot discount the possibility that eggs are conspicuous and that leaving them uncovered increases the risk of nest predation.

By remaining on the nest, birds also ensure that they are present to defend it when predators approach. Nest defence is common in a wide variety of bird species (Montgomerie and Weatherhead 1988), and shorebirds exhibit defence behaviours ranging from aggressive mobbing to distraction displays (Gochfeld 1984). Aggressive

nest defence is most prevalent among biparental shorebirds (Larsen 1991, Larsen et al. 1996), but of the species considered here, only Black-bellied Plovers and Ruddy Turnstones pursue avian predators aggressively (P. Smith, *pers. obs.*). Semipalmated Plovers, American Golden-Plovers, White-rumped Sandpipers and Little Stints characteristically exhibit distraction displays. The effectiveness of nest defence depends on early detection of predators (e.g., McLean et al. 1986, Martin 1992, Götmark et al. 1995), and limiting time away from the nest ensures that a parent is able to respond appropriately when predators are nearby.

The above arguments, and indeed any potential links between incubation behaviour and nest predation, are predicated on the assumption that predators use visual cues to locate nests. The primary nest predators at the three study sites are arctic foxes, and Long-tailed and Parasitic Jaegers, with a variety of other predators including Pomarine Jaegers, Gulls, Common Ravens and ermine encountered less frequently. Avian predators hunt by sight, and jaegers are routinely observed flying low over the tundra, searching for eggs, lemmings or birds (Maher 1974, Wiley and Lee 1999). Although I directly observed only five instances of shorebird nest predation, all were by arctic foxes. My video recordings of predator behaviour suggest that jaegers may hunt more during the day, and foxes more at night. At East Bay and Coats Island, I observed more nest failures between the evening and morning hours, suggesting that arctic foxes may have been the dominant predator. Tulp and Schekkerman (2001) reached similar conclusions from their observations at Medusa Bay.

Although foxes are known to use olfaction (and often scent mark nests after depredation), my video recordings of predation events suggest that visual cues may also

play a role. I observed foxes coming within several meters of shorebird nests, but failing to find them, on seven occasions (versus 5 successful predation events). In two of these, the fox came within 1 m of the nest, and in another, it failed to find the remaining two eggs of the four-egg clutch after caching the first two. If olfaction is the primary means by which foxes search for nests, locating them at such short distances should not be problematic. Instead, I argue that foxes are opportunistic foragers, and use any visual or olfactory cues available to them to locate food.

In the same way that predators may respond to conspicuous behaviour of their prey, the prey may alter behaviour in response to the presence of predators. Many species exhibit adaptive changes in behaviour in response to a perceived risk of predation (review in Lima and Dill 1990), and indeed the incubation feeding hypothesised by Skutch (1949) to be a risky behaviour is suspended when predators are nearby (Ghalambor and Martin 2002), and increased when predators are experimentally removed (Fontaine and Martin 2006a). Similarly, for Red Phalaropes at the East Bay study site, individuals nesting within the protective umbrella of aggressive Sabine's Gulls behaved less cryptically, taking more and longer recesses, than those in areas with a higher risk of predation (Smith et al. 2007b). Because these results are based upon observed behaviour and observed risk of predation, responses by shorebirds to modify their behaviour could influence the interpretation of the results.

For example, some studies suggest that incubation recesses are shorter as nests age, and shorter than the improvement in weather conditions alone predict (chapter 5, but see Tulp and Schekkerman 2006). The value of a nesting attempt to parents increases as nests approach hatch, and shorter incubation recesses for older nests could reflect the

desire for parents to remain nearer to their nests. At the same time, the intensity of nest defence increases with nest age, and perhaps as a result of these behavioural changes, higher nest survival is realised (chapter 3). A reduction in the duration of nest absences throughout the season would strengthen the relationship between recess duration and nest survival as measured here. In contrast, other changes in incubation behaviour may weaken my ability to test the prediction that conspicuous behaviour increases the risk of nest predation.

For species that exhibit nest defence, departures from the nest could be initiated in response to approaching predators. At East Bay and Coats Island, rates of nest departure were higher for the aggressive Ruddy Turnstone than for the placid Semipalmated Sandpiper and Dunlin (chapter 5). Defence behaviours were rarely recorded within the field of the camera's view, and I have little ability to assess the impact that nest defence had on the measures of incubation behaviour. If such departures constitute a large proportion of the apparent incubation recesses, the relationships between the conspicuousness of incubation behaviour, as measured here, and the risk of nest predation would be weakened. However, because such departures from the nest are typically short (1-2 min in the case of the Ruddy Turnstone, Perkins 2004), they should have a minimal influence on measures of total nest attentiveness. Further, to overcome this and other potentially confounding variation in behaviour, I have based conclusions on a variety of tests among several species, within species and between paired records for successful and unsuccessful nests.

I have demonstrated that more frequent or longer breaks in incubation, leaving the nest unattended for a greater proportion of time, and/or exhibiting more restless

movement on the nest can increase the risk of nest predation for ground-nesting shorebirds. This result suggests that shorebirds could increase their nest survival by reducing the conspicuousness of their incubation behaviour. However, shorebirds' ability to do so might be constrained by several facets of their ecology and life history. Species with uniparental incubation (typically polygamous) must leave the nest to feed, and this constraint imposes a limit on the possible levels of nest attendance. Incubators manage their energy reserves by foraging at appropriate intervals, and reserves are depleted if nest attendance is increased or foraging efficiency reduced (Cresswell et al. 2004, Tulp and Schekkerman 2006). Because each member of a biparental pair (always monogamous) can feed while its mate is incubating, energetic limitation is less severe among these species. However, even here, energetic limitation can necessitate reduced incubation bout lengths (Cresswell et al. 2003). The potential for plasticity in incubation behaviour, and the ability of parent birds to reduce their risk of predation by modifying it, is therefore influenced by mating system. The evolution of mating system has traditionally been viewed in relation to access to mates and resources (e.g., Lack 1968, Emlen and Oring 1977), but the constraints that mating systems impose on nest survival, through constraints on incubation behaviour, may represent an additional selective pressure to be considered.

Table 6.1. Sample sizes of nests found (included in analyses of nest survival), nests observed for incubation behaviour and days of observations collected. For each species, I also list whether incubation is uniparental or biparental, and whether the behavioural data include information on restless movements on the nest.

	East Bay (2002,2005,2006)			Coats Island (2004,2005,2006)			Medusa Bay (2000,2001)			Incubation System	Movement Data?
	Nests Found	Nests Observed	Nest*Days of Records	Nests Found	Nests Observed	Nest*Days of Records	Nests Found	Nests Observed	Nest*Days of Records		
Semipalmated Plover	37	2	3							Biparental	Yes
Black-bellied Plover	45	4	7	11						Biparental	Yes
American Golden-Plover	1			24	6	12				Biparental	Yes
Red Phalarope	40	14	96	36	23	147	13	2	13	Uniparental	Yes
Ruddy Turnstone	89	8	14				10			Biparental	Yes

Table 6.1. Continued.

	East Bay (2002,2005,2006)			Coats Island (2004,2005,2006)			Medusa Bay (2000,2001)			Incubation System	Movement Data?
	Nests Found	Nests Observed	Nest*Days of Records	Nests Found	Nests Observed	Nest*Days of Records	Nests Found	Nests Observed	Nest*Days of Records		
Dunlin	6			71	6	12	54			Biparental	Yes
Curlew Sandpiper							29	15	91	Uniparental	No
Semipalmated Sandpiper				162	14	26				Biparental	Yes
White-rumped Sandpiper	36	9	33	18	13	67				Uniparental	Yes
Little Stint							204	38	197	Uniparental	No
Pectoral Sandpiper				3			12	7	64	Uniparental	No

Table 6.2. Sample sizes, means and standard errors for the six metrics of incubation behaviour from the sample where observations from unsuccessful nests are paired with observations from the same year, species and day, from successful nests.

Species	Fate	n nests	n paired records (days)	recesses/hr ± SE	moves/hr ± SE	% off nest ± SE	% moving ± SE	time per recess (min) ± SE	time per movement (min) ± SE
American Golden-Plover	Succ.	1	1	0.29±.	3.79 ± .	0.02±.	0.06 ± .	3.70±.	0.91 ± .
	Failed	1		0.31±.	2.62 ± .	0.05±.	0.01 ± .	9.07±.	0.23 ± .
Curlew Sandpiper	Succ.	3	21	0.88±0.04		0.21±0.01		15.30±2.00	
	Failed	6		0.92±0.07		0.14±0.01		9.40±0.60	
Little Stint	Succ.	8	68	1.27±0.03		0.19±0.01		9.90±0.94	
	Failed	18		1.41±0.06		0.20±0.01		10.81±1.44	
Pectoral Sandpiper	Succ.	2	12	1.17±0.07		0.01±0.00		11.70±1.87	
	Failed	3		1.11±0.08		0.01±0.00		10.61±2.16	

Table 6.2. Continued.

Species	Fate	n nests	n paired records (days)	recesses/hr ± SE	moves/hr ± SE	% off nest ± SE	% moving ± SE	time per recess (min) ± SE	time per movement (min) ± SE
Red Phalarope	Succ.	10	89	0.86±0.03	0.86±0.13	0.16±0.01	0.01±0.00	11.70±0.86	0.66±0.03
	Failed	18		1.04±0.05	1.00±0.14	0.19±0.01	0.01±0.00	14.05±1.58	0.97±0.20
Ruddy Turnstone	Succ.	2	3	0.94±0.21	1.64±0.68	0.05±0.02	0.02±0.01	3.21±1.15	0.61±0.18
	Failed	2		0.97±0.24	2.26±0.65	0.05±0.02	0.03±0.01	3.35±1.12	0.67±0.26
Semipalmated Plover	Succ.	1	1	2.20±	1.40±	0.05±	0.00±	1.49±	0.19±
	Failed	1		1.00±	1.91±	0.01±	0.01±	0.58±	0.19±
White-rumped Sandpiper	Succ.	3	16	1.08±0.09	0.56±0.06	0.13±0.01	0.00±0.00	7.13±0.16	0.52±0.00
	Failed	6		0.87±0.07	0.91±0.08	0.14±0.01	0.01±0.00	9.85±0.55	0.57±0.04

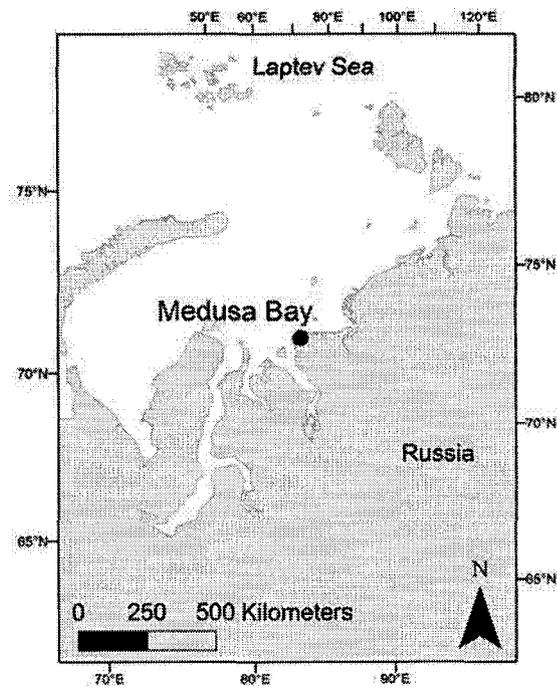


Figure 6.1. The study site at Medusa Bay, Russia.

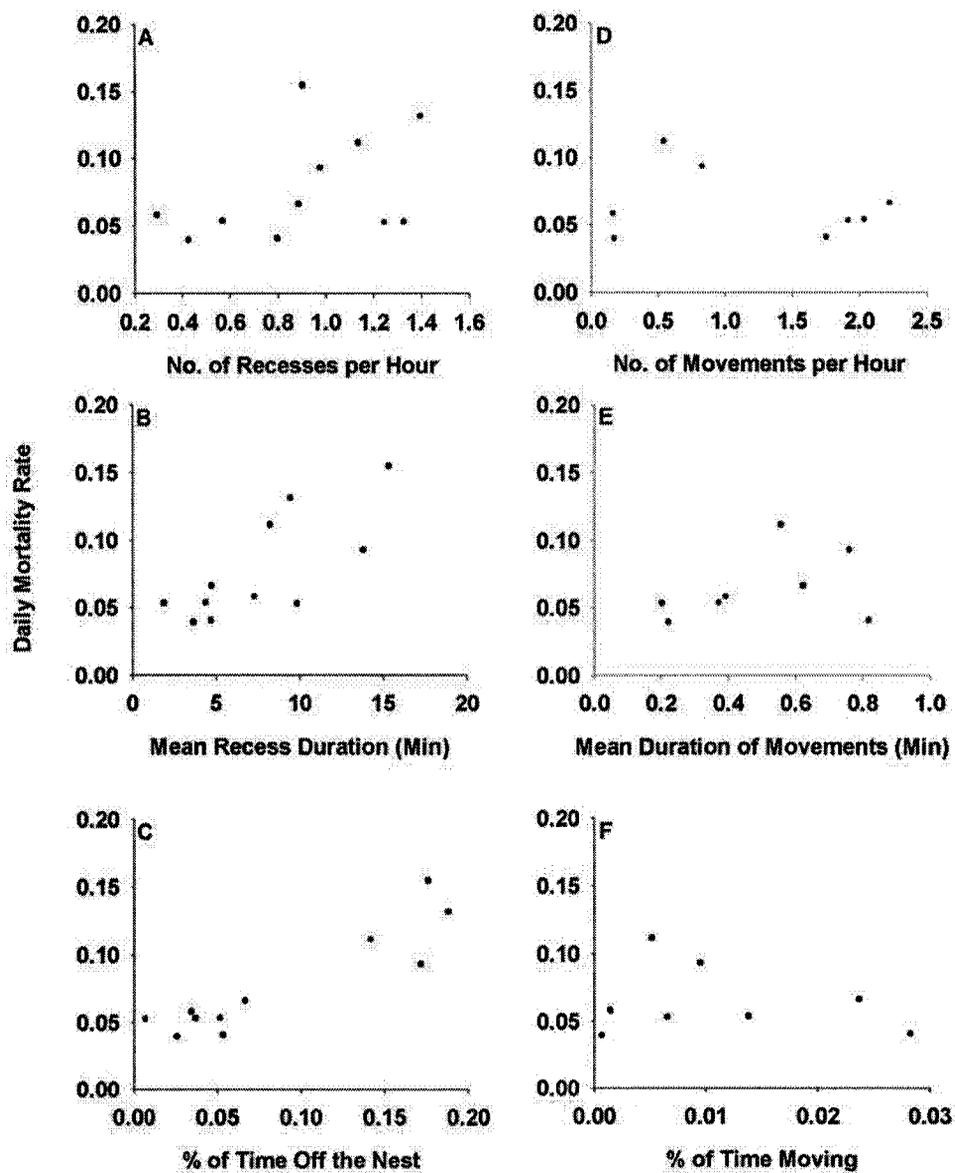


Figure 6.2,a-f. The interspecific relationships between six measures of incubation behaviour (untransformed), and daily mortality rate of shorebird nests. Each data point represents a species; behavioural data include information about movements on the nest (panels d-f) for only 8/11 species.

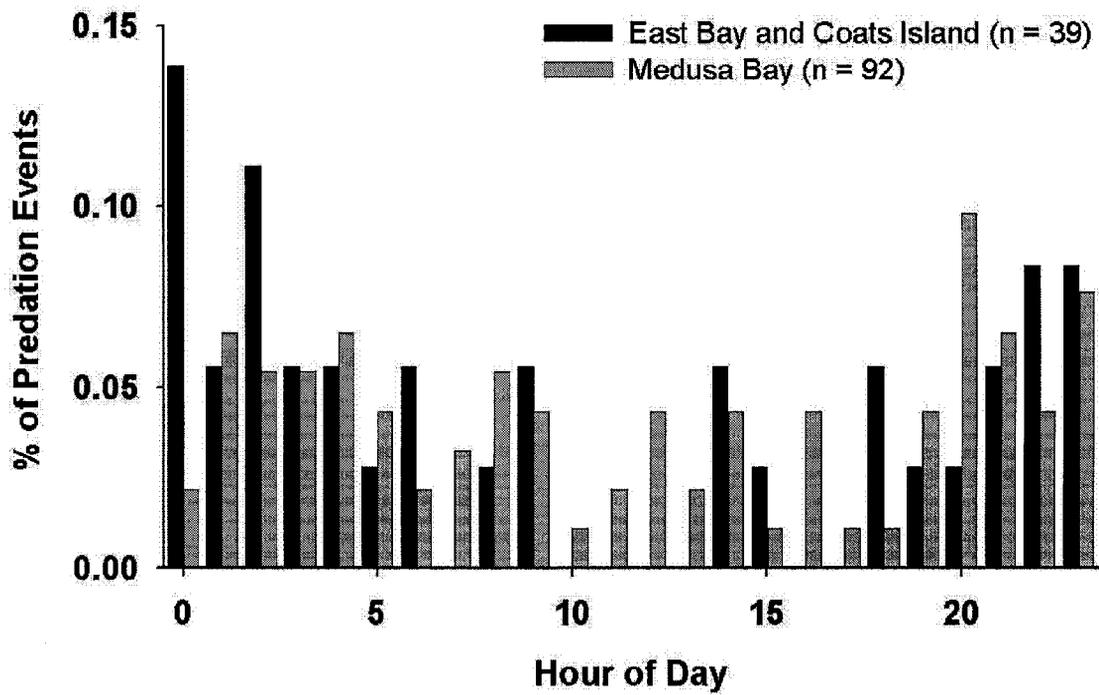


Figure 6.3. The time of day at which nests were depredated at the East Bay, Coats Island and Medusa Bay sites. Data from Medusa Bay are adapted from Tulp and Schekkerman (2001).

Chapter 7. General discussion

The study of breeding ecology is a rich field in ornithology, and many patterns in nest survival have yet to be explained. The risk of nest predation can be influenced by the attributes of nest sites, and relating variation in nest predation to nest site characteristics has been a traditional focus of studies of nest survival (e.g., Nice 1957, Ricklefs 1969, Collias and Collias 1984, Martin 1993). However, when bird densities are low and competition for nest sites in optimal habitat is unlikely, all birds should be free to select ideal nest sites that maximize fitness (Fretwell and Lucas 1970). It remains unclear whether nest habitat selection has a genetic or learned basis (Martin 1995, see also Jaenike and Holt 1991), but in either case, adaptive responses should serve to limit the variation in nest survival that stems from variation in nest habitat (Clark and Shutler 1999). Arctic shorebirds nest on the ground, in simple scrapes, and at low densities. It is perhaps not surprising then that in previous studies, I found little evidence for an effect of nest habitat on shorebird nest survival (Smith 2003, Smith et al. 2007a).

In the absence of habitat effects, nest predation may be influenced more by biotic factors such as the behaviour of incubating adults, or the behaviour and abundance of predators. Variation in these factors, in turn, may stem from proximate forces such as weather, snow melt, and the availability of alternate prey, or from ultimate pressures such as the division of labour among incubating birds. It is intuitive that behavioural interactions between predators and the guardians of the eggs upon which they prey should have important consequences for the outcome of a nesting attempt, but the nature of these interactions have rarely been studied for whole communities. This study of a community of arctic breeding shorebirds demonstrates the importance of these behavioural interactions. I present evidence that shorebird behaviours, from elaborate

nest defence to basic traits of incubation, influence or are influenced by the risk of nest predation. The local abundance of predators is strongly related to the survival of nests, and even the timing of shorebird breeding may be altered in response to this perceived risk (Fig. 7.1). This study expands our knowledge about patterns in shorebird nest survival, and in particular, yields new insights into effects of shorebird behaviour on survival of their nests. Sample sizes in some analyses are unprecedented, and the implications of this new understanding are far reaching. Several areas where these findings have significantly altered our understanding of avian breeding ecology are discussed below.

Predation and timing of breeding

Shorebirds travel great distances from wintering areas to their breeding areas, and their decision to begin northward migration is made with little information about the conditions they will encounter on the breeding grounds. I found that the timing of shorebirds' arrival varied by one week or less at three arctic breeding sites, despite highly variable weather conditions among years (chapter 2). Timing of arrival was not correlated with local conditions. In contrast, I found strong effects of local conditions on timing of breeding, with greater snow cover leading to delayed nesting, and a higher abundance of predators resulting in earlier nesting (see Fig. 7.1).

Snow cover has been proposed as the primary determinant of the timing of shorebird breeding at several Palearctic locations (e.g., Meltofte 1976, 1985, Green et al. 1977), and my results suggest that this is also the case in the Nearctic. While complete snow cover imposes an obvious constraint on these ground-nesting birds (e.g., Mayfield 1978), I found that shorebirds arrived after the area was partially free of snow in many

years. Thus snow cover, *per se*, should not preclude early breeding in most years.

Instead, snow cover might influence timing of breeding by limiting the access to, or the activity of, invertebrate prey (Moltofte et al. 2007b, Tulp 2007, Tulp and Schekkerman 2008).

The timing of nest initiation could also be influenced by the risk of nest predation. Many previous studies have suggested that nesting in snow free patches could increase the risk of nest predation by allowing predators to focus their hunting efforts. The common claim that breeding should be delayed in years of late snowmelt to avoid this high risk of nest predation can be traced back to a single study, based on a small sample of artificial nests, in the mountains of southern Norway (Byrkjedal 1980). Concerns about artificial nests aside, this area receives greater amounts of snow than the comparatively arid polar regions. If snow free patches are very small and limited in number at a time when shorebirds begin to initiate nests, such an effect may well be important. However, I found that when shorebirds were faced with a high local abundance of predators, they initiated nests earlier than snow cover alone would predict; a response that increases their opportunity for successful renesting (chapter 2). Moreover, I found that nest survival was highest early in the season in most years (chapter 4). Thus, the claim that high predation on snow free patches influences the timing of shorebird breeding may not be as general as once believed.

Predation, predator abundance and alternative prey

Another common arctic paradigm is that the cyclical populations of lemmings have a keystone effect on arctic ecosystems and indirectly influence the population dynamics of birds. In some areas, and particularly the Russian arctic, almost complete breeding

failure occurs in waterfowl and some shorebirds in some years (e.g., Summers 1986, Summers and Underhill 1987, Underhill et al. 1993). Populations of lemmings and voles (*Microtus* and *Clethrionomys* spp.) vary greatly in size over time, with fluctuations following periods of three to five years (Krebs 1964, Hanski and Korpimäki 1995). When rodents are abundant at these sites, they are the primary prey of arctic foxes and jaegers (especially Pomarine and Long-tailed Jaeger; Wiley and Lee 1998). Predator populations can respond to this abundance both functionally and numerically (Wilson and Bromley 2001, Anglestam et al. 1984). When rodent densities decline, so the story goes, bolstered populations of predators turn to the eggs and young of birds as alternative prey (Larson 1960, Martin and Baird 1988, Bêty et al. 2002).

The evidence for this relationship is strong for some bird species on the Taimyr Peninsula of Siberia, where the production of juvenile Brant and their subsequent resighting on the wintering grounds, is tightly correlated with the abundance of lemmings (Dhondt 1987). However, evidence from elsewhere is less compelling. At Bylot Island, Nunavut, fox predation on nests in a large colony of Greater Snow Geese (*Chen caerulescens atlanticus*) tends to be higher in years with a greater abundance of lemmings (Bêty et al. 2001). However, even on Bylot Island, in perhaps the best Nearctic example of the alternative prey hypothesis, the relationship varies among sites and is obscured by inverse density dependence in nest survival. Studies from elsewhere in arctic Alaska, Canada, and Greenland have shown equivocal support (e.g., Holmes 1966, Wilson 1997, Wilson and Bromley 2001, Gratto-Trevor *unpublished* in Meltofte et al. 2007a), or none at all (e.g., Day 1998, Stickney 1991, Nol *unpublished* in Meltofte et

al. 2007a, Meltofte et al. 2008, this study), for the patterns predicted by the alternative prey hypothesis.

I found no relationship between the abundance or activity of predators and the abundance of lemmings (chapter 3). To the contrary, I saw substantial fluctuations in the abundance of both arctic foxes and jaegers at East Bay in four consecutive years when lemmings were extremely scarce. Moreover, I saw nearly two fold variation in predator abundance among only three years at Coats Island; an island which is entirely free from lemmings or any other small herbivorous mammals. These indices of predator abundance were tightly correlated with shorebird nest survival, while I found no support for an effect of lemming abundance in any of my nest survival models. At these sites, the abundance of predators does vary and this variation does drive variation in shorebird nest survival. However, I found no support for the widely held belief that this variation in predation is driven by lemming abundance.

Predation throughout the season

Previous studies of nest survival, although numerous, suffer from a common analytical limitation. Until recently, nest success was estimated using apparent survival or a daily survival rate from the “Mayfield Method” (Mayfield 1961). Nest survival could only be compared among groups of nests by assuming constant survival within the group; relationships with continuous covariates such as time could not be assessed. The development of logistic exposure techniques with maximum likelihood parameter estimation overcame this limitation and ushered in a new era of studies of nest survival (e.g., Dinsmore et al. 2002, Shaffer 2004). It has since become apparent that nest survival is rarely constant throughout the season, but no consistent temporal patterns have

emerged. In some studies nest survival is depressed mid-season (Dinsmore et al. 2002, Wilson et al. 2007), while others have found positive (e.g., Grant et al. 2005), negative (Burhans et al. 2002, Jehle et al. 2004), or no relationship between time and nest survival (Traylor et al. 2004, Walker et al. 2005). Until this study, nest survival for arctic breeding shorebirds had not been rigorously assessed with modern analytic methods.

I found that nest survival was depressed mid-season in most years, but the pattern was variable among years (chapter 4). This pattern was not explained by the high abundance of shorebird nests available mid-season, as I found no support for an index of the relative density of active nests as a predictor of nest survival. Even when they are most abundant, the density of shorebird nests is low in comparison to the thresholds for density dependence identified in other studies (Göransson et al. 1975, Sugden and Beyersbergen 1986, O'Rielly and Hannon 1989, Schieck and Hannon 1993, Larivière and Messier 1998). Also, I demonstrated previously that the survival of shorebird nests at East Bay was not influenced by distance to the nearest nests of shorebirds or other species (Smith et al. 2007a). Neither were these temporal patterns influenced by day-to-day variation in the abundance or activity of predators in the study area. This quantity was highly variable and showed no seasonal trend. Instead, my results suggest that predation on shorebird nests may be related to the availability of the full suite of diet items available to predators, including the eggs of waterfowl, small mammals, invertebrates and even marine resources.

Shorebird clutches are small, and typically 4-16 times smaller than an average clutch of snow goose eggs (see chapter 4). The relative contribution of shorebird nests to the diet of these predators is unknown, but because of their small size, they may be

consumed incidentally rather than targeted specifically. In contrast, waterfowl eggs are known to be an important component of the diet of tundra predators, and dominate the diet of foxes throughout the nesting period (regardless of lemming abundance, Stickney 1991, Samelius and Alisauskas 2000). Shorebird nest predation might be higher when other prey items become less available, such as when vulnerable goose nests have already been taken. Similarly, shorebird nest predation might be lower early in the season if foxes focus on carrion at this time (e.g., Stickney 1991). Whether seasonal variation in predators' diets explain the seasonal variation in shorebird nest survival remains a mystery, and will require a more thorough investigation of both the diet of predators, and the specific predators of shorebird nests.

While shorebirds have little control over the diet preferences of predators, they can reduce the risk of their eggs becoming a diet item by actively defending the nest. Defence behaviours are risky (Brunton 1986, Brunton 1990), and this cost must be weighed against the value of a nest to its parents. As nests age, this value increases both because the hatch date grows progressively nearer, and because opportunities for successful renesting progressively diminish (see chapter 2). This increasing value could justify increased investment in nest defence, and such a relationship has been observed in several species (reviewed in Montgomerie and Weatherhead 1988, tested in Forbes et al. 1994).

Shorebirds do exhibit a variety of distraction displays and aggressive defence, but interspecific variation in these behaviours does not explain interspecific patterns in nest survival (Smith et al. 2007a); it has merely been assumed that these behaviours increase nest success. I found that defence behaviour intensified as nests aged for biparental, but

not uniparental, species (chapter 4). At the same time, I found that nest survival increased with nest age to a greater extent for biparental versus uniparental species. These results suggest that nest defence behaviours are indeed a worthwhile investment, and may underlie the significant increase in survival with nest age observed among these arctic breeding shorebirds (see Fig. 7.1).

Predation and behaviour

Aggressive behaviours are not the only behavioural means of protecting a nesting attempt. Parents may also modify their risk by avoiding conspicuous behaviours near the nest. Skutch (1949) proposed that feeding nestlings might increase the risk of nest predation, and that this risk might influence optimal life history traits of birds. Since this time, it has often been suggested that any behaviour near the nest could increase the risk of predation, but tests of this hypothesis are exceedingly rare. Ghalambor and Martin provided experimental evidence for increased risk with increased rates of incubation feeding (e.g., Martin and Ghalambor 1999, Martin et al. 2000, Ghalambor and Martin 2002). Among species without incubation feeding, and for shorebirds in particular, evidence for this effect is weaker or lacking (Wiebe and Martin 1997, Cresswell et al. 2003). In general, the organisation of incubation behaviour continues to be viewed primarily from an energetic standpoint, with the energy requirements of incubators being traded off against the thermal needs of eggs. I found that weather conditions indeed influence the organisation of incubation behaviour, but that these behaviours also affect the risk of nest predation.

That incubation behaviour may be altered in response to prevailing weather conditions is not a new idea, and not even for shorebirds in the arctic (e.g., Norton 1972,

Cartar and Montgomerie 1987, Tulp and Schekkerman 2006). However, never has a study been conducted on this scale with simultaneous observations of shorebirds with uniparental and biparental incubation. It has been widely suggested that energetic limitation is more likely for species with uniparental incubation (Bryan and Bryant 1999, Reid et al. 2002b, Tulp and Schekkerman 2006), but I found that biparental species also altered their incubation behaviour in response to changing weather conditions (chapter 5). Among uniparental species, incubation behaviour was organized over a time-scale longer than a single day; time spent off the nest was reduced during periods of poor weather, when foraging in exposed habitats is energetically expensive and unprofitable (chapter 5, Fig. 7.1). This increased nest attentiveness during harsh weather could compromise body condition, and indeed I found that some individuals temporarily abandoned their nests when conditions were too cold or windy. This implied threshold of acceptable body condition might vary among species with differing life histories in ways that have not yet been explored. Although several of these insights into incubation behaviour are novel, my primary interest in incubation behaviour was its effect on the risk of nest predation.

An interesting result of my previous work (Smith 2003, Smith et al. 2007a, chapter 3) is that nest survival is lower among uniparental versus biparental species. I have long believed that the source of this variation is interspecific differences in incubation behaviour. In chapter 6, I demonstrated that a single measure of incubation behaviour (constancy) explained 83% of the variability in nest survival among 11 shorebird species distributed widely across the arctic. With nearly 900 nests and 800 days of behavioural observation considered, this result is compelling. I also found that incubation behaviour could significantly predict the fate of individual nests, and that

incubation behaviour on a given day was more conspicuous at nests that would ultimately fail versus nests that would ultimately succeed. Taken together, these results provide strong evidence that conspicuous incubation behaviour can increase the risk of nest predation. This work substantially improves our understanding of interspecific patterns in nest survival, and introduces a new selective pressure that should be considered in the study of shorebird life-history evolution.

Future Directions

Shorebirds as income-breeders

Shorebirds are considered to be income breeders, and egg production should therefore be limited by food intake (Klaassen et al. 2001, Morrison and Hobson 2004). Møller et al. (2007b) demonstrated that timing of shorebird breeding was determined in part by insect abundance; after controlling for effects of snow cover, nesting was earlier in years with more abundant invertebrates. Because nutrients for egg production must be gathered “locally”, a theoretical minimum of 5-8 days exists between timing of arrival and timing of breeding based on the physiological limits of egg production (Roudebush et al. 1979). The interval between arrival and breeding has received little attention, because observers are rarely on-site to witness the arrival of shorebirds to the arctic breeding grounds. I found intervals between arrival and laying shorter than this theoretical minimum in numerous cases, and for the Ruddy Turnstone, the mean interval was scarcely within this range (5.5 ± 1.1 d; chapter 2). It is unlikely that I missed early arriving individuals of this conspicuous, semi-colonial species. What this result might suggest is that the scale for

“local” acquisition of food for these putative income-breeding species might need to be revisited.

It is becoming increasingly clear that shorebirds stop short of the breeding grounds to forage and await snow-melt at some locations in some years (e.g., Tulp 2007, Meltofte et al. 2007a,b, this study). I observed this directly, when shorebirds stopped on a snow-free eider colony (East Bay Island) to forage in years when heavy snow melt blanketed their breeding areas, or when Baird’s Sandpipers, a species which typically breeds at higher latitudes, were observed foraging in large numbers on a snow-free slope 30 km from the East Bay study sites. Similarly, band re-sighting data from Siberia suggest that shorebirds approach the breeding grounds in “short hops” as opposed “long leaps” (Tulp 2007). Collectively, these observations suggest that shorebirds might be foraging and regaining body condition in the final stages of the northward migration.

Our understanding of shorebirds as income breeders comes from two studies of the carbon isotope ratios of adult feathers, eggs, and natal down (Klaassen et al. 2001, Morrison and Hobson 2004). These studies relied on the discrepancy in isotope ratios between prey of marine and terrestrial origins, and had no ability to discern between local and distant food sources *per se*. Even here, there were traces of marine sources evident in the earliest laid eggs of the Ruddy Turnstone (Morrison and Hobson 2004). Both studies predate the use of stable isotopes to determine latitude of origin (K. Hobson, *unpublished*), and this technique could shed light on the true origin of the nutrients required for egg formation. Satellite transmitters have now been deployed on the largest shorebirds (B. Truitt, *unpublished*), and early results confirm my suggestion that numerous stops are made in tundra habitats en route to the breeding grounds. Data-

logging geolocators have already been deployed on smaller shorebirds, and should be retrieved next summer (B. Andres, *pers. comm.*). As these modern data loggers begin to provide a more detailed picture of migratory behaviour, our understanding of how and where shorebirds gather nutrients for egg formation will likely change.

The evolution of shorebird life-history

It is widely believed that the mating systems of birds have evolved against a backdrop of spatial and temporal variation in the abundance of resources and mates (e.g., Lack 1968, Pitelka et al. 1974, Emlen and Oring 1977). Monogamy is thought to represent a conservative strategy, evolving or being maintained when resources for egg production and self-maintenance are limited, or access to mates is restricted. As many as 98% of avian species have a monogamous mating system (Lack 1968), and monogamy with bi-parental care is the ancestral condition in shorebirds (Székely and Reynolds 1995, Borowik and McLennan 1999). However, the diversity of mating systems within the shorebirds is atypically high, ranging from lek breeders with uni-parental female care, to polyandrous species with uni-parental male care. While food and resources may influence the evolution of mating systems, variation in risk of predation could also play a role, and has received little attention.

In many passerine species, access to food limits fecundity, which in turn influences adult survival through the costs of reproduction (Martin 1987). Increased access to food can allow for greater annual fecundity without a cost to adult survival. However, annual fecundity in shorebirds is relatively fixed; most are determinate layers of four eggs regardless of food abundance, and opportunities for second broods are rare because of short breeding seasons (Sandercock 1997, Arnold 1999). This low annual

fecundity is offset by comparatively long life spans, with individuals of some species commonly living over 10 years. Lifetime reproductive success in shorebirds thus depends primarily on adult survival and nest success.

Nest success in turn, is determined primarily by the risk of predation. While energetic stress under extreme weather conditions may cause shorebird nest abandonment, such instances are rare (Hill 1983). Shorebird nest failure is attributable almost entirely to predation (e.g., Smith et al. 2007a, chapter 3), and the risk of predation may be influenced by incubation behaviour. Whether a bird undertakes incubation singly or jointly, an important life-history division among shorebirds, can substantially influence the risk of predation in ways that were previously unknown.

Social monogamy with bi-parental care remains dominant in the plovers (Charadriidae). In contrast, a great diversity of polygamous mating systems and unequal parental care strategies has evolved in the sandpipers (Scolopacidae) (Székely and Reynolds 1995, Borowik and McLennan 1999). Monogamous, biparental species typically have long incubation shifts (chapter 5), flush early when predators approach, and often engage in coordinated aggressive nest defence (which increases in intensity over the nesting season, chapter 4). Species with uniparental incubation, in contrast, have shorter incubation bouts, and rely more on evading detection than dissuading predators through nest defence. For either group, predation risk could potentially be reduced by limiting the number of trips to and from the nest, but a uniparental incubator is more constrained and may not have the energetic capacity to do so.

This constraint is offset by a benefit, however. The polygamous sex of a uniparental species has a greater opportunity for multiple broods, and fecundity could be

higher than for biparental species if predation risk can be mitigated. Low risk of nest predation, either due to periodic lows in predator abundance (chapter 3) or annual or geographic variability in the weather conditions that influence incubation, might favour the evolution of uniparental incubation. While this idea requires further development, acknowledging the role of nest predation was a critical paradigm shift in the study of passerine life-histories (e.g., Martin 1995). The interplay between mating system, incubation behaviour, and predation of nests had not been demonstrated previously for shorebirds, and could shed new light on the evolution of diverse mating systems in this taxa.

Incubation behaviour in response to risk

I presented evidence for a link between conspicuous incubation behaviour and increased risk of nest predation, but incubation behaviour may also be modified in response to risk. Adaptive changes in behaviour in response to a perceived risk of predation are common across the animal kingdom (reviewed in Lima and Dill 1990), and among birds, conspicuous incubation feeding is suspended when predators are nearby (Ghalambor and Martin 2002), and increased when predators are experimentally removed (Fontaine and Martin 2006a). Further, species suffering higher rates of predation showed more willingness to reduce incubation feeding in the face of perceived risk than those that have lower rates of nest predation (Ghalambor and Martin 2002).

In an earlier study, I found that Red Phalaropes exhibited more conspicuous incubation behaviour, taking more and longer recesses, when nesting within the protective umbrella of the aggressive Sabine's Gull than when nesting in areas with a greater risk of predation. Thus, shorebirds too may match their incubation behaviour to

their perception of the risk of nest predation. The degree to which species can alter their behaviour may differ for uni- versus biparental species, may be constrained by energetic demands, or may reflect the relative value of the nesting attempt. Experimental presentation of predator models and simultaneous monitoring of incubation behaviour at these and at control nests could answer these questions, and may further demonstrate the link between behaviour and shorebird nest survival.

Nest success versus fecundity

The largest shortcoming of this study, and indeed of the vast majority of studies of shorebirds, is that monitoring stops when the nest hatches. Shorebird chicks leave the nest within hours of hatching and are notoriously difficult to follow thereafter. The roughly four-week period between hatching and fledging is perhaps the most poorly understood in the life cycle of many shorebirds. I found that uniparental species had consistently lower nest survival than biparental species, but the claim that reproductive success *per se* differs among these groups would be strengthened by measures of fledging success.

A complete understanding of shorebird demography also requires measures of breeding propensity, rates of re-nesting and juvenile and adult survival. Exquisite examples of in-depth demographic studies exist for shorebirds (e.g., the work of E. Nol or B. Sandercock); however, this time consuming work has never been attempted for a diverse community of arctic shorebirds. It could be argued that patterns in nest survival are now well understood at the East Bay site, and could be monitored on an ongoing basis with smaller samples of nests than I have aimed for previously. I would argue that in the

coming years, less effort should be expended on finding nests, and more effort should be devoted to banding the adults and chicks to monitor vital rates.

Conservation Implications

Across North America, shorebirds appear to be in a state of widespread decline. Of the 35 shorebird species for which we have reasonable survey data, 28 species (80%) show negative trends, and 19 species show statistically significant declines from 1970s population levels (Morrison et al. 2001). Arctic breeding species are particularly at risk, and the Red Knot, for example, was recently recommended for listing as endangered owing to dramatic declines. Population decline in this species is the subject of much research, and is thought to stem from over-harvesting of the horseshoe crabs whose eggs provide important food for Knots migrating through Delaware Bay. Declines in other species have also been dramatic, but in nearly all cases, the causes remain unknown.

Through the implementation of initiatives such as the Program for Regional and International Shorebird Monitoring (PRISM: Bart, Johnston, Smith, et al. *submitted*), Canada is making great progress at monitoring arctic shorebirds. Population surveys on the breeding grounds are most accurate when conducted during the late courtship and early incubation periods (Moltofte 2001, Nebel and McCaffery 2003), and the timing of these are currently predicted only by expert opinion. My results demonstrate that timing of breeding can be related with reasonable accuracy to local conditions such as snow cover and predator abundance. Remotely sensed estimates of snow cover are widely available, and could aid in the timing of future shorebird surveys. Also, as each year's surveys are conducted at new locations, the quantitative relationship between local conditions and timing of breeding can be refined.

The accuracy of the surveys also depends on an understanding of rates of predation, because the number of nests found in an intensively surveyed sub-sample of plots is used to calculate a detection rate. Nests that fail before being found potentially bias the estimates of shorebird densities (Smith et al. *In Press*). The results I've presented here suggest that, for instance, surveyors should expend particular effort to find the nests of uniparental species early in the season, prior to their failure. Also, these intensively sampled plots often contain too few nests to accurately estimate nest survival. Instead, the abundance of jaegers or foxes in the area could be recorded as an index of predation risk, to address this possible source of bias.

While the recent development of survey programs has increased our ability to detect changes in shorebird populations, we have done relatively little to increase our understanding of the causes of declines. It is widely assumed that changes in adult survival should have the greatest effect on population trajectories of shorebirds, because they are relatively long-lived and have low fecundity. Consequently, little attention has been paid to the possibility that declining reproductive success on the arctic breeding range could be influencing population size.

I've showed here that nest survival is highly variable, and that some species suffer higher predation than others. A disturbing observation, however, is that nest survival is low in many years. At East Bay, for example, the nest survival from lay to hatch over eight years was 42% for biparental species and 10% for uniparental species. Other vital rates are unknown for these species, but if I assume that they are similar to an intensively studied population of Upland Sandpipers in Kansas (B. Sandercock, *unpublished*) it is apparent that these rates of nest survival may be cause for concern. Among these Upland

Sandpipers, adult apparent survival is estimated at 80%, nest survival ranges from 10-30%, and renesting is common because of a long breeding season. With these vital rates, the population is declining. Adult survival is likely lower at my arctic site (published estimates for arctic species are typically closer to 0.7), and rates of renesting, fledging success, and juvenile survival are also likely to be lower. Moreover, some shorebirds with particularly poor reproductive success are showing alarming local declines. Over eight years of surveys for breeding birds on a standardised plot, the density of Red Phalaropes has dropped from a high of 28 birds / km² in 2000 to a low of 0 in 2006 (Fig. 7.2).

Clearly, more detailed study of demography at these arctic sites would be required to make the claim that low breeding success is causing the widespread declines in shorebird populations. However, several plausible mechanisms for declines in breeding success can be imagined. Reductions in fox harvest for a weakening fur industry, bolstered predator populations because of over abundant snow geese, or reductions in the availability of seal carrion (a preferred food of foxes) during the shorebird nesting season because of reduced sea ice could all lead to more, or hungrier, predators.

I also found that shorebird nest survival varies with time of the season. If the timing of shorebirds' breeding has responded differently to a warming arctic than other components of their predators' diet, a functional response of predators could place shorebird nests at greater risk at certain times throughout the season. Although the Arctic is largely uninhabited, it would be naïve to suggest that the far reaching effects of humans are not felt there. A metanalysis of published estimates of nest survival, past and current,

is warranted to evaluate the role that breeding success might play in the decline of shorebird populations.

Global environmental change is showing widespread effects on wildlife, and there is demonstrated interest in predicting the impacts of this change on our already declining shorebird populations (Rehfishch and Crick 2003). Arctic breeding shorebirds are long-distance migrants as a rule, and these globe-spanning migrations make it difficult to identify the source of problems (Piersma and Lindström 2004). Through awareness campaigns, habitat protection, increased capacity for monitoring and targeted research, we are making headway towards shorebird conservation. By better understanding patterns in the survival of nests on the arctic breeding grounds, we clarify the role that a changing Arctic might play in the widespread and alarming population declines of shorebirds.

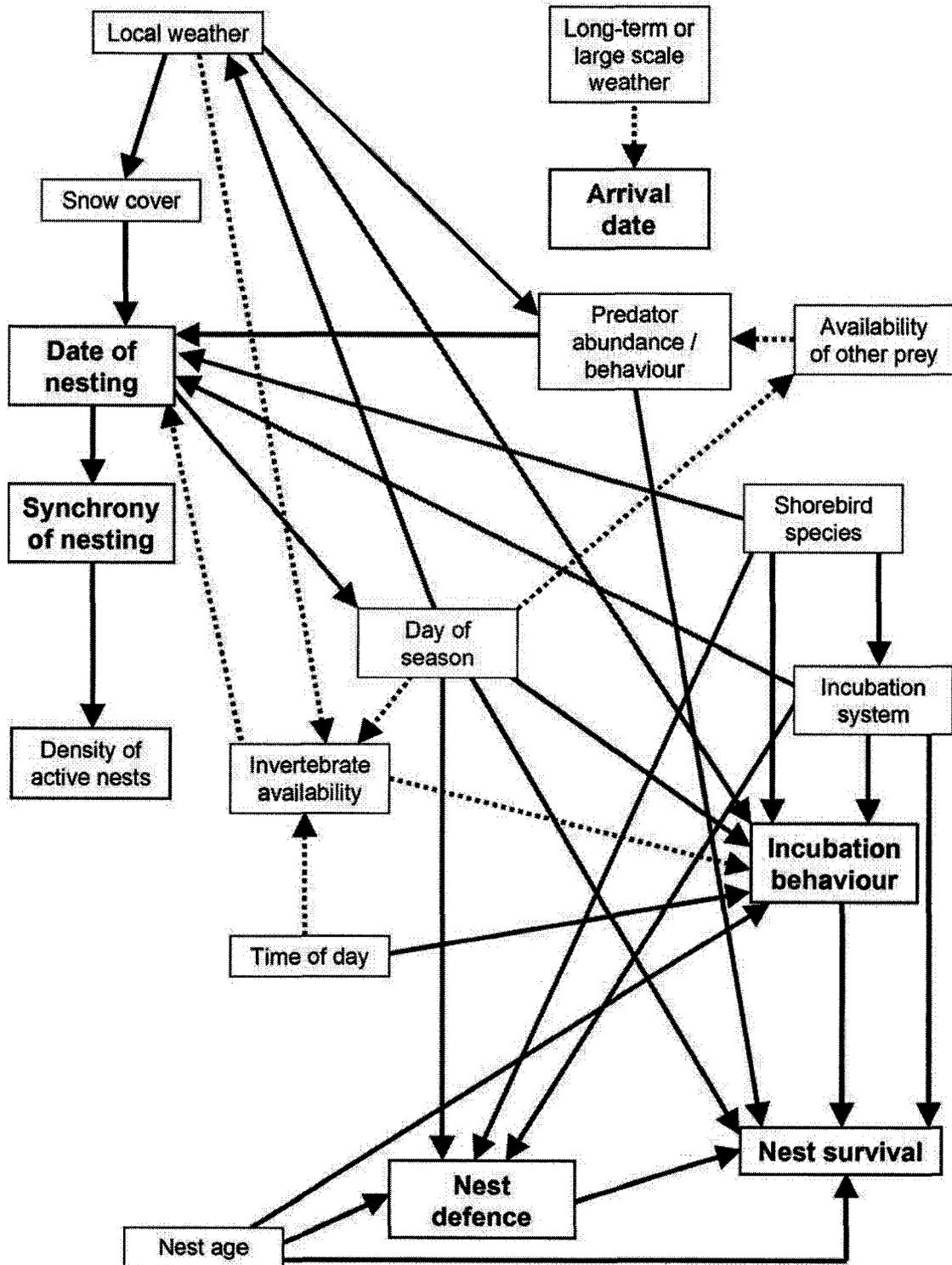


Figure 7.1. A schematic representation of the effects identified in this thesis. Solid arrows denote significant effects demonstrated directly, while dashed arrows indicate hypothesised effects. Bold text denotes response variables that are a major focus of one or more chapters.

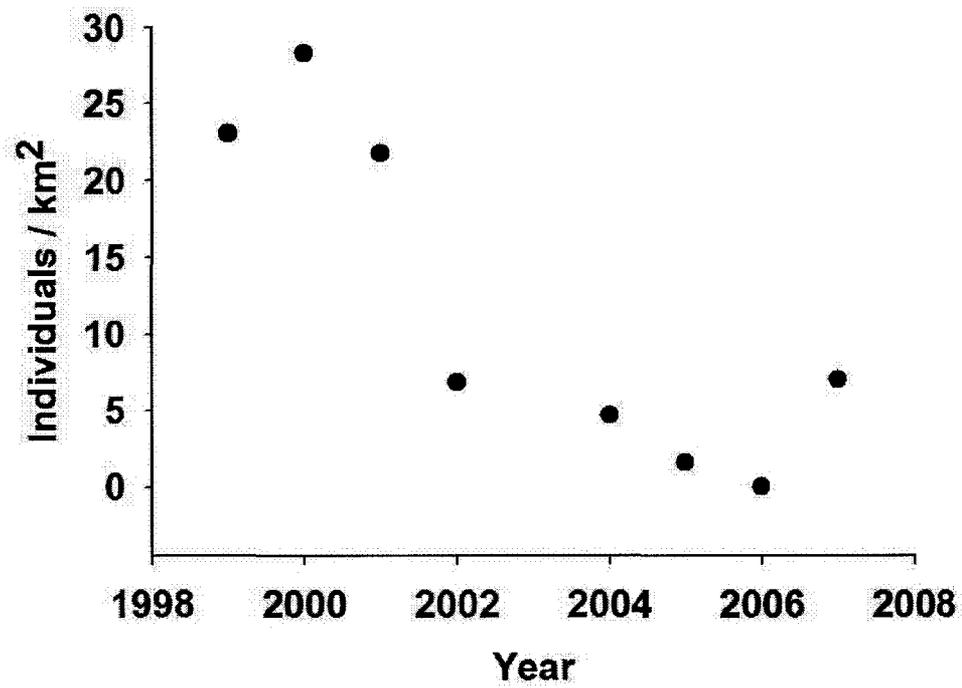


Figure 7.2. The decline in local abundance of Red Phalaropes on a 2.6 km² plot at East Bay, Nunavut. Surveys were conducted in late June, 1999-2007.

Literature Cited

Ackerman, J. T., A. L. Blackmer, and J. M. Eadie. 2004. Is nest predation on waterfowl nests density-dependent? Tests at three spatial scales. *Oikos* 107: 128-140.

Aebischer, N. J. 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* 46: S22-S31.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 In B. N. Petran and F. Csaki [eds.]. *International symposium on information theory*. Second edition. Akademiai Kiado, Budapest, Hungary.

Allen, J. A. 1989. Searching for search image. *TREE* 4: 361.

Andersson, M., and C. G. Wiklund. 1978. Clumping versus spacing out: experiments on nest predation in Fieldfares (*Turdus pilaris*). *Animal Behaviour* 26:1207-1212.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73: 794-804.

Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator density and habitat edge. *Oikos* 47: 365-373.

Angelstam, P., E. Lindström, and P. Widén. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62: 99–208.

Arnold, T. W. 1999. What limits clutch size in waders? *Journal of Avian Biology* 30: 216-220.

Arnold, T. W., L. M. Craig-Moore, L. M. Armstrong, D. W. Howerter, J. H. Devries, B. L. Joynt, R. B. Emery, M. G. Anderson. 2007. Waterfowl use of dense nesting cover in the Canadian Parklands. *Journal of Wildlife Management* 71: 2542-2549.

Ashkenazie, S., and U. N. Safriel. 1979. Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* 60: 783-799.

Baker, M. C. 1977. Shorebird food habits in the eastern Canadian arctic. *Condor* 79: 56-62.

Bart, J., V. Johnston, P. Smith, A. Manning, J. Rausch, and S. Brown. *Submitted*. Design of a long-term survey for shorebirds in the arctic. Submitted to *Ecological Applications* May, 2008 (#08-0717).

Beauchamp, W. D., T. D. Nudds, and R. G. Clark. 1996. Duck nest success declines with and without predator management. *Journal of Wildlife Management* 60: 258-264.

- Beletsky, L. D. 1996. The Red-winged Blackbird. The biology of a strongly polygynous songbird. Academic Press, San Diego, CA.
- Bertram, B. C. R., and A. E. Burger. 1981. Are ostrich *Struthio camelus* eggs the wrong color? *Ibis* 123: 207–210.
- Bêty J., G. Gauthier, E. Korpimäki, and J.-F. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. *Journal of Animal Ecology* 71: 88-98.
- Bêty, J., G. Gauthier, J.-F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos* 93: 388-400.
- Borowik, O, and D. A. McLennan. 1999. Phylogenetic patterns of parental care in calidridine sandpipers. *Auk* 116:1107-1117.
- Boulton, R. L., P. Cassey, C. Schipper, and M. F. Clarke. 2003. Nest-site selection by yellow-faced honeyeaters *Lichenostomus chrysops*. *Journal of Avian Biology* 34:267-274.
- Boyd, H. and A. Petersen. 2006. Spring arrivals of migrant waders in Iceland. *Ringing and Migration* 23: 107-115.

Brown, C. R., and M. B. Brown. 2001. Avian coloniality: progress and problems. Pp. 1-82 in *Current Ornithology*, Vol. 16 (V. Nolan and C. F. Thompson, eds.). Plenum, New York.

Brunton, D. H. 1986. Fatal antipredator behaviour by Killdeer. *Wilson Bulletin* 98: 605-607.

Brunton, D. H. 1990. The effects of nesting stage, sex and type of predator on parental defense by killdeer (*Charadrius vociferous*): testing models of avian parental defense. *Behavioural Ecology and Sociobiology* 26: 181-190.

Bryan, S. and D. M. Bryant. 1999. Heating nest boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*. *Proceedings of the Royal Society of London, Series B* 266: 157-162.

Burhans, D. E., D. Dearborn, F. R. Thompson III, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management* 66: 240-249.

Burke, D. M., K. Elliott, L. Moore, W. Dunford, E. Nol, J. Phillips, S. Holmes, and K. Freemark. 2004. Patterns of nest predation on natural and artificial nests in forests. *Conservation Biology* 18: 381-388.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, New York, USA.

Byrkjedal, I. 1980. Nest predation in relation to snow-cover – a possible factor influencing the start of breeding in shorebirds. *Ornis Scandinavica* 11: 249-252.

Byrkjedal, I. 1989. Nest defense behaviour of Lesser Golden-Plovers. *Wilson Bulletin* 101: 93-96.

Cartar, R. V., and R. D. Montgomerie. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicolis*): a uniparental incubator in a cold environment. *Behaviour* 95: 261-289.

Cartar, R. V., and R. D. Montgomerie. 1987. Day-to-day variation in nest attentiveness of White-rumped Sandpipers. *Condor* 89: 252-260.

Chalfoun, A. D., F. R. Thompson III, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16: 306-318.

Clark, K. L., and R. J. Robertson. 1979. Spatial and temporal multi-species nesting aggregations in birds as anti-parasite and anti-predator defense. *Behavioural Ecology and Sociobiology* 5: 359-371.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks. *Ecology* 80: 272-287.

Clotfelter, E. D., A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan Jr., and E. D. Ketterson. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia* 154: 493-503.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey.

Collias, N. E., and E. C. Collias. 1984. Nest building and bird behaviour. Princeton University Press, Princeton, N. J.

Colwell, M. A., and L. W. Oring. 1990. Nest-site characteristics of prairie shorebirds. *Canadian Journal of Zoology* 68: 297-302.

Cooke, F., R. F. Rockwell, and D. B. Lank 1995. The Snow Geese of La Pérouse Bay: natural selection in the wild. Oxford Univ. Press, Oxford, U.K.

Côté, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11: 395-405.

Cramp, S., and K. E. L. Simmons. 1983. The birds of the western Palearctic Vol. 3: Waders to gulls. Oxford University Press.

Cresswell, W., S. Holt, J. M. Reid, D. P. Whitfield, and R. J. Møller. 2003. Do energetic demands constrain incubation scheduling in a biparental species? *Behavioral Ecology* 14: 97-102.

Cresswell, W., S. Holt, J. M. Reid, D. P. Whitfield, R. J. Møller, D. Norton, and S. Waldron. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine energy expenditure in the pectoral sandpiper. *Behavioral Ecology* 15: 498-507.

Danks, H. V. 1971. A note on the early season food of arctic migrants. *Canadian Field Naturalist* 85: 71-72.

Danks, H. V., and D. R. Oliver. 1972. Diel periodicities of emergence of some high arctic Chironomidae (Diptera). *Canadian Entomology* 105: 903-916.

Day, R. H. 1998. Predator populations and predation intensity on tundra-nesting birds in relation to human development. ABR Inc., Fairbanks, AK. 112 pp.

Deeming, D. C. 2001. Behaviour patterns during incubation. In: *Avian Incubation. Behaviour, environment and evolution* (D. C. Deeming, ed.), Oxford, Oxford University Press: pp 63-87.

- Dhondt, A. A. 1987. Cycles of lemmings and Brent Geese *Branta b. bernicla*: a comment on the hypothesis of Roselaar and Summers. *Bird Study* 34: 151–154.
- Dinsmore, S. J. and J. J. Dinsmore. 2007. Modeling avian nest survival in Program Mark. *Studies in Avian Biology* 34: 73-83.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modelling avian nest survival. *Ecology* 83: 3476-3488.
- Drent, R. 1975. Incubation. Pp. 333-420 in: *Avian Biology*, vol. 5 (D. S. Farner and J. R. King, eds.). New York, Academic Press.
- Drent, R. H. 1970. Functional aspects of incubation in the Herring Gull. *Behaviour* S17: 1-132.
- Drury, W. H., Jr. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. *Auk* 78: 176–219.
- Durango, S. 1949. The nesting association of birds with social insects and with birds of different species. *Ibis* 91: 140-143.
- Dyrcz, A., J. Witkowski, and J. Okulewicz. 1981. Nesting of ‘timid’ waders in the vicinity of ‘bold’ ones as an antipredation adaptation. *Ibis* 123: 542-545.

Edlund, S. A. 1990. Bioclimatic zones in the Canadian arctic archipelago; in Canada's missing dimension science and history in the Canadian arctic islands, (ed.) C. R. Harington; v. 1, p. 421-441.

Emery, R. B., D. W. Howerter, L. M. Armstrong, M. G. Anderson, J. H. Devries, and B. L. Joynt. 2005. Seasonal variation in waterfowl nesting success and its relation to cover management in the Canadian Prairies. *Journal of Wildlife Management* 69: 1181-1193.

Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223.

Erckmann, W. J., Jr. 1981. The evolution of sex-role reversal and monogamy in shorebirds. Ph.D. Thesis, University of Washington, 320 pp.

Etterson, M., and R. Bennett. 2005. Including transition probabilities in nest survival estimation: a Mayfield Markov chain. *Ecology* 86: 1414-1421.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? *Condor* 96: 761-768.

Findlay, C. S., and F. Cooke. 1982. Breeding synchrony in the Lesser Snow Goose (*Anser caerulescens caerulescens*). I. Genetic and environmental components of hatch date variability and their effects on hatch synchrony. *Evolution* 36: 342-351.

- Fontaine, J. J., and T. E. Martin. 2006a. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9: 428-434.
- Fontaine, J. J., and T. E. Martin. 2006b. Habitat selection responses of parents to offspring predation risk: an experimental test. *American Naturalist* 168: 811-818.
- Fontaine, J. J., M. Martel, H. M. Markland, A. M. Niklison, K. L. Decker, and T. E. Martin. 2007. Testing ecological and behavioural correlates of nest predation. *Oikos* 116: 1887-1894.
- Forbes, M. R. L., R. G. Clark, P. J. Weatherhead, and T. Armstrong. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defence theory. *Behavioural Ecology and Sociobiology* 34: 79-85.
- Fretwell, S. D., and H. L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds: I. Theoretical development. *Acta Biotheoretica* 19: 16-36.
- Gaston, A. J., R. Decker, F. G. Cooch, and A. Reed. 1986. The distribution of larger species of birds breeding on the coasts of Foxe Basin and Northern Hudson Bay, Canada. *Arctic* 39: 285-296.

Gaston, A. J. and H. Ouellet. 1997. Birds and mammals of Coats Island, N.W.T. *Arctic* 50: 101-118.

Ghalambor, C. K., and T. E. Martin. 2001. Fecundity survival trade-offs and parental risk-taking in birds. *Science* 292: 494-497.

Ghalambor, C. K., and T. E. Martin. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behavioral Ecology* 13: 101-108.

Gochfeld, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds, p. 289-377. In J. Burger and B. Olla [eds.], *Behaviour of marine animals*. Vol. 5, Shorebirds: breeding behavior and populations. Plenum Press, New York.

Göranson, G., J. Karlson, S. G. Nilsson, and S. Ulfstrand. 1975. Predation on bird's nests in relation to antipredator aggression and nest density: an experimental study. *Oikos* 26: 117-120.

Götmark, F., D. Blomqvist, O. C. Johansson and J. Bergkvist. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? *Journal of Avian Biology* 26: 305-312.

Graham, K. 2004. Semipalmated plover breeding success and adult survival: effects of weather and body condition. M.Sc. Thesis, Trent University, Peterborough, ON, Canada.

Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time specific variation in passerine nest survival: new insights into old questions. *Auk* 122: 661-672.

Gratto-Trevor, C. L. 1992. Semipalmated Sandpiper (*Calidris pusilla*). No. 6 in *The Birds of North America* (A. Poole and F. Gill, Eds.). The Birds of North America Inc., Philadelphia.

Gratto, C. L. and F. Cooke. 1987. Geographic variation in the breeding biology of the Semipalmated Sandpiper. *Ornis Scandinavica* 18: 233-235.

Green, G. H., J. J. D. Greenwood, and C. S. Lloyd. 1977. The influence of snow conditions on the date of breeding of wading birds in north-east Greenland. *Journal of Zoology, London* 183: 311-328.

Gunness, M. A. and P. J. Weatherhead. 2002. Variation in nest defense in ducks: methodological and biological insights. *Journal of Avian Biology* 33: 191-198.

Haemig, P. D. 2001. Symbiotic nesting of birds with formidable animals: a review with application to biodiversity conservation. *Biodiversity and Conservation* 10: 527-540.

Hanski, I., and E. Korpimäki. 1995. Microtine rodent dynamics in northern Europe: parameterized models for the predator-prey interaction. *Ecology* 76: 840-850.

Hegyí, Z., and L. Sasvari. 1998. Parental condition and breeding effort in waders. *Journal of Animal Ecology* 67: 41-53.

Heywood, W. W., and B. V. Sanford. 1976. Geology of Southampton, Coats and Mansel Islands, District of Keewatin, Northwest Territories. Geological Survey of Canada Memoir No. 382. 35p.

Hildén, O. 1979. Nesting of Temminck's Stint *Calidris temminckii* during an arctic snowstorm. *Ornis Fennica* 56: 30-32.

Hill, S. 1983. Incubation capacity as a limiting factor of shorebird clutch size. M.Sc. Thesis, University of Washington.

Hochachka, W. M., K. Martin, F. Doyle, and C. J. Krebs. 2000. Monitoring vertebrate populations using observational data. *Canadian Journal of Zoology* 78: 521-529.

Hodkinson, I. D. 2003. Metabolic cold adaptation in arthropods: smaller-scale perspective. *Functional Ecology* 17: 562-567.

- Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation on the European pine sawfly. *Canadian Entomologist* 91: 293–320.
- Holling, C. S. 1961. Principles of insect predation. *Annual Review of Entomology* 6: 163–182.
- Holmes, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-back Sandpiper (*Calidris alpina*) in Northern Alaska. *Condor* 68: 3–46.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12: 197–229.
- Ims, R. A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *American Naturalist* 136: 485.
- Innes, M. J. G., Goodacre, A. K., Weston, A. A., and J. R. Weber. 1968. Gravity and isostasy in the Hudson Bay region. In: Beals, C. S., ed., *Science, History and Hudson Bay*. Vol. 2. Ottawa: Department of Energy Mines and Resources. 703-728.
- Jaenike, J., and R. D. Holt. 1991. Genetic variation for habitat preference: evidence and explanations. *American Naturalist* 137: S67.

Jehle, G., A. Yackel Adams, J. A. Savidge, and S. K. Skagen. 2004. Nest survival estimation: a review of alternatives to the Mayfield estimator. *Condor* 106: 472-484.

Johnson, D. H. 1979. Estimating nesting success: the Mayfield method and as alternative. *Auk* 96: 651-661.

Johnson, D. H. 2007. Methods of estimating nest success: an historical tour. *Studies in Avian Biology* 34: 1-12.

Johnson, O. W., and P. G. Connors. 1996. American Golden-Plover *Pluvialis dominica*. No. 201 in *The Birds of North America* (A. Poole and F. Gills Eds.). The Academy of Natural Sciences, Pennsylvania; The American Ornithologists Union, Washington.

Jönsson, P. E. and T. Alerstam. 1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. *Biological Journal of the Linnean Society* 41: 301-314.

Klaassen, M., Å. Lindström, H. Meltofte, and T. Piersma. 2001. Arctic waders are not capital breeders. *Nature* 413: 794.

Klett, A. T., and D. H. Johnson. 1982. Variability in nest survival rates and implications to nest survival studies. *Auk* 99: 77-87.

- Knight, R. L., and S. A. Temple. 1986. Why does intensity of avian nest defense increase during the nesting cycle? *Auk* 103: 318-327.
- Krebs, C. J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959-1962. *Arctic Institute of North America Technical Paper* 15: 1-104.
- Kurki, S., P. Helle, H. Lindén, and A. Nikula. 1997. Breeding success of Black Grouse and Capercaillie in relation to mammalian predator densities on two spatial scales. *Oikos* 83: 12-20.
- Lack, D. 1948. The significance of clutch size. Part 3. Some interspecific comparisons. *Ibis* 90: 25-45.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- Lank, D. B., L. W. Oring, and S. J. Maxson. 1985. Mate and nutrient limitation of egg-laying in a polyandrous shorebird. *Ecology* 66: 1513-1524.
- Lank, D. B., R. W. Butler, J. Ireland, and R. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103: 303-319.
- Lappo, E. G., and P. S. Tomkovich. 2006. Limits and structure of the breeding range of the Curlew Sandpiper *Calidris ferruginea*. *International Wader Studies* 19: 9-18.

Larivière, S., and F. Messier. 1998. Effect of nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? *Oikos* 83: 12-20.

Larsen, T. 1991. Anti-predator behaviour and mating systems in waders: aggressive nest defence selects for monogamy. *Animal Behaviour* 41: 1057-1062.

Larsen, T., T. A. Sordahl, and I. Byrkjedal. 1996. Factors related to aggressive nest protection behaviour: a comparative study of Holarctic waders. *Biological Journal of the Linnean Society* 58: 409-439.

Larson, S. 1960. On the influence of the Arctic Fox *Alopex lagopus* on the distribution of arctic birds. *Oikos* 11: 276-305.

Liebezeit, J. R., P. A. Smith, R. B. Lanctot, H. Schekkerman, I. Tulp, S. J. Kendall, D. Tracy, R. J. Rodrigues, H. Meltofte, J. A. R. Robinson, C. Gratto-Trevor, B. J. McCaffery, J. Morse, and S. W. Zack. 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. *Condor* 109: 32-47.

Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.

Lloyd P., E. Plaganyi, D. Lepage, R. M. Little, and T. M. Crowe. 2000. Nest-site selection, egg pigmentation and clutch predation in the ground-nesting namaqua sandgrouse *Pterocles namaqua*. *Ibis* 142: 123-131.

Lundy, H. 1969. A review of the effects of temperature, humidity, turning and gaseous environment in the incubator on the hatchability of the hen's egg. In: *The fertility and hatchability of the hen's egg* (T. C. Cartar and B. M. Freeman eds.), pp. 143-176. Oliver and Boyd, Edinburgh.

Lyon, B., and R. Montgomerie. 1987. Ecological correlates of incubation feeding: a comparative study of high Arctic finches. *Ecology* 68: 713-722.

Macdonald, S. D., and D. F. Parmelee. 1962. Feeding behaviour of the Turnstone in arctic Canada. *British Birds* 55: 241-243.

Maher, W. J. 1974. Ecology of pomarine, parasitic, and long-tailed jaegers in northern Alaska. *Pacific Coast Avifauna* 37: 1-148.

Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138: 298-307.

- Mallory, M. L., and P. J. Weatherhead. 1993. Incubation rhythms and mass loss of Common Goldeneyes. *Condor* 95: 849-859.
- Manolis, J. C., D. E. Andersen, and F. J. Cuthbert. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117: 615-626.
- Martin, A. P., and D. Baird. 1988. Lemming cycles: which Palearctic migrants are affected. *Bird Study* 35: 143-145.
- Martin, T. E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology* 69: 74-84.
- Martin, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. *Current Ornithology* 9: 163-197.
- Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141: 897-913.
- Martin, T. E. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101-127.
- Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 79: 656-670.

Martin, T. E. and C. K. Ghalambor. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation. *American Naturalist* 153: 131-139.

Martin, T. E. and C. K. Ghalambor. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behavioural Ecology* 13: 101-108.

Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effect. *Proceedings of the Royal Society of London Series B* 267: 2287-2293.

Marzluff, J. M., J. C. Withey, K. A. Whittaker, M. D. Oleyar, T. M. Unfried, S. Rullman, and J. DeLap. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanising landscape. *Condor* 109: 516-534.

Mayfield, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73: 255-261.

Mayfield, H. F. 1973. Black-bellied Plover incubation and hatching. *Wilson Bulletin* 85: 82-85.

Mayfield, H. F. 1978. Undependable breeding conditions in the Red Phalarope. *Auk* 95: 590-592.

McLean, I. G., J. N. M. Smith, and K. G. Stewart. 1986. Mobbing behaviour, nest exposure, and breeding success in the American robin. *Behaviour* 96: 171-186.

Meltofte, H. 1976. Ornithological observations in Southern Peary Land, North Greenland, 1973. *Meddelelser om Grønland*, 205: 1-57.

Meltofte, H. 1985. Populations and breeding schedules of waders, Charadrii, in High Arctic Greenland. *Meddelelser om Grønland, Bioscience* 16: 43 pp.

Meltofte, H. 2001. Wader population censuses in the Arctic: getting the timing right. *Arctic* 54: 367-376.

Meltofte, H., M. Elander, and C. Hjort. 1981. Ornithological observations in Northeast Greenland between 74° 30' and 76° 00' N. lat. *Meddelelser om Grønland, Bioscience* 3: 52 pp.

Meltofte, H., T. Piersma, H. Boyd, B. McCaffery, B. Gantner, V. Golovnyuk, K. Graham, C. L. Gratto-Trevor, R. I. G. Morrison, E. Nol, H.-U. Rösner, D. Schamel, H. Schekkerman, M. Y. Soloviev, P. S. Tomkovich, D. M. Tracy, I. Tulp and L.

Wennerberg. 2007a. A circumpolar review of the effects of climate variation on the breeding ecology of Arctic shorebirds. *Meddelelser om Grønland, Bioscience* 59: 48pp.

Meltofte., H., T. T. Høye, N. M. Schmidt and M. C. Forchhammer. 2007b. Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders. *Polar Biology* 30: 601-606.

Meltofte, H., T. T. Høye, and N. M. Schmidt. 2008. Effects of food availability, snow and predation on breeding performance of waders at Zackenberg. Pp. 325-343 in Meltofte, H., T.R. Christensen, B. Elberling, M.C. Forchhammer, and M. Rasch (eds): *High-arctic ecosystem dynamics in a changing climate. Ten years of monitoring and research at Zackenberg Research Station, Northeast Greenland. Advances in Ecological Research* 40, Academic Press.

Montevecchi, W. A. 1976. Field experiments on the adaptive significance of avian eggshell pigmentation. *Behaviour* 58: 26–39.

Montgomerie, R. D., and P. J. Weatherhead. 1988. Risks and rewards of nest defence by parent birds. *Quarterly Review in Biology* 63: 167-187.

Morrison, R. I. G., and K. A. Hobson. 2004. Use of body stores in shorebirds after arrival on High Arctic breeding grounds. *Auk* 121: 333-344.

Morrison, R. I. G., Y. Aubry, R. W. Butler, G. W. Beyersbergen, G. M. Donaldson, C. L. Gratto-Trevor, P. W. Hicklin, V. H. Johnston, R. K. Ross. 2001. Declines in North American shorebird populations. Wader Study Group Bulletin 94: 34-38.

Morrison R. I. G., N. C. Davidson, and T. Piersma. 2005. Transformations at high latitudes: why do Red Knots bring body stores to the breeding grounds? *Condor* 107: 449-457.

Nams, V. O. 1997. Density-dependent predation by skunks using olfactory search images. *Oecologia* 110: 440-448.

Nebel, S. and B. J. McCaffery. 2003. Vocalization activity of breeding shorebirds: documentation of its seasonal decline and applications for breeding bird surveys. *Canadian Journal of Zoology* 81: 1702-1708.

Nettleship, D. N. 2000. Ruddy Turnstone (*Arenaria interpres*). No. 537 in *The Birds of North America* (A. Poole and F. Gill, Eds.). The Birds of North America Inc., Philadelphia.

Nice, M. M. 1957. Nesting success in altricial birds. *Auk* 74: 305-321.

Niemuth, N. D., and M. S. Boyce. 1995. Spatial and temporal patterns of predation of simulated Sage Grouse nests at high and low nest densities: an experimental study.

Canadian Journal of Zoology 73: 819-825.

Nol, E., and M. S. Blanken. 1999. Semipalmated Plover (*Charadrius semipalmatus*). No. 444 in The Birds of North America (A. Poole and F. Gill, Eds.). The Birds of North America Inc., Philadelphia.

Nol, E., Blanken, M. S., and L. Flynn. 1997. Sources of variation in clutch size, egg size and clutch completion dates of Semipalmated Plovers in Churchill, Manitoba. Condor 99: 389-396.

Norton, D. W. 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. Condor 74: 164-176.

O'Rielly, P. and S. J. Hannon. 1989. Predation of simulated willow ptarmigan nests: the influence of density and cover on spatial and temporal patterns of predation. Canadian Journal of Zoology 67: 1263-1267.

Page, G. W., L. E. Stenzel, D. W. Winkler, and C. W. Swarth. 1983. Spacing out at Mono Lake: breeding success, nest density and predation in the snowy plover. Auk 100: 13-24.

Parmelee, D. F. 1992. White-rumped sandpiper, *Calidris fuscicollis*. No. 29 in The Birds of North America (A. Poole and F. Gills Eds.). The Academy of Natural Sciences, Pennsylvania; The American Ornithologists Union, Washington.

Parmelee, D. F., H. A. Stephens, and R. H. Schmidt. 1967. The birds of southeastern Victoria Island and adjacent small islands. National Museum of Canada Bulletin 222: 1-229.

Parmelee, D. F., W. D. Grenier, and D. W. Graul. 1968. Summer schedule and breeding biology of the White-rumped Sandpiper in the central Canadian Arctic. Wilson Bulletin 80: 5-29.

Paulson, D. R. 1995. Black-bellied Plover (*Pluvialis squatarola*). In A. Poole and F. Gill [eds.], The birds of North America, No. 186. The Academy of Natural Sciences, Pennsylvania, PA, and The American Ornithologists' Union, Washington, DC.

Paulson, D. R., and W. J. Erckmann. 1985. Buff-breasted sandpipers nesting in association with Black-bellies Plovers. Condor 87: 429-430.

Perkins, D. E. 2004. The breeding ecology and behavioral endocrinology of Ruddy Turnstones (*Arenaria interpres*) in the eastern Canadian Arctic. M.Sc. thesis, University of Maine, Orono, Maine.

Piersma, T., and R. I. G. Morrison. 1994. Energy expenditure and water turnover of incubating Ruddy Turnstones: high costs under high arctic conditions. *Auk* 111: 366-376.

Piersma, T., and Å. Lindström. 2004. Migrating shorebirds as integrative sentinels of global environmental change. *Ibis* 146 (Suppl. 1): 61-69.

Piersma, T., M. Klassen, J. H. Bruggemann, A.-M. Blomert, A. Gueye, Y. Ntiamoa-Baidu, N. E. Van Brederode. 1990. Seasonal timing of the spring departure of waders from the Banc d'Arguin, Mauritania. *Ardea* 78: 123-134.

Piersma, T., Å. Lindström, R. H. Drent, I. Tulp, J. Jukema, R. I. G. Morrison, J. Reneerkens, H. Schekkerman, G. H. Visser. 2003. High daily energy expenditure of incubating shorebirds on High Arctic tundra: a circumpolar study. *Functional Ecology* 17: 356-362.

Pitelka, F. A., R. T. Holmes, and S. T. MacLean. 1974. Ecology and evolution of social organisation in arctic sandpipers. *American Zoologist* 14: 185-204.

Rehfish, M. M., and H. Q. P. Crick. 2003. Predicting the impact of climate change on Arctic-breeding waders. *Wader Study Group Bulletin* 100: 86-95.

Reid, J. M., W. Cresswell, S. Holt, R. J. Møller, D. P. Whitfield, and G. D. Ruxton.

2002a. Nest scrape design and clutch heat loss in Pectoral Sandpipers. *Functional Ecology* 16: 305-312.

Reid, J. M., P. Monaghan, G. D. Ruxton. 2002b. Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*). *Behavioural Ecology and Sociobiology* 51: 255-261.

Reynolds, J. D. 1987. Mating system and nesting biology of the red-necked phalarope *Phalaropus lobatus*: what constrains polyandry? *Ibis* 129: 225-242.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions in Zoology* 9: 1-48.

Ricklefs, R. E. 1984. Egg dimensions and neonatal mass of shorebirds. *Condor* 86: 7-11.

Ridley, M. W. 1980. The breeding behaviour and feeding ecology of Grey Phalaropes *Phalaropus fulicarius* in Svalbard. *Ibis* 122: 210-226.

Rockwell, R. F., and L. J. Gormezano. *In press*. The early bear gets the goose: climate change, polar bears and lesser snow geese in western Hudson Bay. *Polar Biology*.

- Rodrigues, R. 1994. Microhabitat variables affecting nest-site selection by tundra birds. *Ecological Applications* 4: 110-116.
- Romanoff, A. L. and A. J. Romanoff. 1950. Some physical aspects of the amnion and allantois of the developing chick embryo. *Journal of Experimental Zoology* 114: 87-101.
- Roper, R. J., and R. R. Goldstein. 1997. A test of the Skutch hypothesis: does activity at nests increase nest predation risk? *Journal of Avian Biology* 28: 111-116.
- Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27: 187-205.
- Roudybush, T. E., C. R. Grau, M. R. Peterson, D. G. Ainley, K. V. Hirsch, A. P. Gilman, and S. M. Patten. 1979. Yolk formation in some charadriiform birds. *Condor* 81: 293-298.
- Ruthrauff, D. R. and B. J. McCaffery. 2005. Survival of western sandpiper broods on the Yukon-Kuskokwim Delta, Alaska. *Condor* 107: 597-604.
- Safriel, U. N. 1980. The semipalmated sandpiper: reproductive strategies and tactics. *Ibis* 122: 425.

Samelius, G., and R. T. Alisauskas. 2000. Foraging patterns of arctic foxes at a large arctic goose colony. *Arctic* 53: 279-288.

Sandercock, B. 1997. Incubation capacity and clutch size determination in two calidridine sandpipers: a test of the four-egg threshold. *Oecologia* 110: 50-59.

Sandercock, B. K. 1998. Chronology of nesting events in Western and Semipalmated Sandpipers near the arctic circle. *Journal of Field Ornithology* 69: 235-243.

Sandercock, B. K., D. B. Lank and F. Cooke. 1999. Seasonal declines in the fecundity of Arctic-breeding sandpipers: different tactics in two species with an invariant clutch size. *Journal of Avian Biology* 30: 460-468.

SAS 9.1.3. 2003. SAS Institute Inc., Cary, NC, USA.

Sasvari, L., and Z. Hegyi. 2000. Avian predators influence the daily time budget of lapwings *Vanellus vanellus*. *Folia Zoologica* 49: 211-219.

Schamel, D. 2000. Female and male reproductive strategies in the red-necked phalarope, a polyandrous shorebird. Ph.D. Thesis, Simon Fraser University, Burnaby, Canada.

Schamel, D. and D. M. Tracy. 1987. Latitudinal trends in breeding Red Phalaropes. *Journal of Field Ornithology* 58: 126-134.

Schamel, J. T., D. M. Tracy, and Schamel, D. 2002. The effect of a late spring on nesting Dunlins at Cape Espenberg, Alaska. Abstract, Proceedings of the 9th Alaska Bird Conference, Fairbanks, Alaska.

Schekkerman, H., M. J. W. van Roomen, and L. G. Underhill. 1998. Growth, behaviour of broods and weather-related variation in breeding productivity of curlew sandpipers *Calidris ferruginea*. *Ardea* 86: 153-168.

Schekkerman, H., I. Tulp, T. Piersma, and G. H. Visser. 2003. Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. *Oecologia* 134: 332-342.

Schekkerman, H., I. Tulp, K. M. Calf, and J. J. de Leeuw. 2004. Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2002. Alterra Report 922. Wageningen, Netherlands. 101pp.

Schieck, J. O., and S. J. Hannon. 1993. Clutch predation, cover, and the overdispersion of nests of the Willow Ptarmigan. *Ecology* 74: 743-750.

Schmidt, K. A. 2003. Linking frequencies of acorn masting in temperate forests to long-term population growth rates in a songbird: the veery (*Catharus fuscescens*). *Oikos* 103: 548-558.

- Schmidt, K. A., and R. S. Ostfeld. 2003. Songbird populations in fluctuating environments: predator responses to pulsed resources. *Ecology* 84: 406-415.
- Schmidt, K. A., J. R. Goheen, and R. Naumann. 2001a. Incidental nest predation in songbirds: behavioral indicators detect ecological scales and processes. *Ecology* 82: 2937-2947.
- Schmidt, K. A., J. R. Goheen, R. Naumann, R. S. Ostfeld, E. M. Schaubert, and A. Berkowitz. 2001b. Experimental removal of strong and weak predators: mice and chipmunks preying on songbird nests. *Ecology* 82: 2927-2936.
- Schmidt, K. A., R. S. Ostfeld, and K. N. Smyth. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest site selection in two forest thrushes. *Oecologia* 148: 22-29.
- Schneider, D. C., and B. A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98: 801-811.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121: 526-540.
- Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430-455.

Smith, P. A. 2003. Factors affecting nest site selection and reproductive success of tundra nesting shorebirds. M.Sc. thesis, University of British Columbia, Vancouver, Canada.

Smith, P. A., H. G. Gilchrist, and J. N. M. Smith. 2007a. Effects of nest habitat, food, and parental behaviour on shorebird nest success. *Condor* 109: 15-31.

Smith, P. A., H. G. Gilchrist, J. N. M. Smith, and E. Nol. 2007b. Annual variation in the benefits of a nesting association between Red Phalaropes (*Phalaropus fulicarius*) and Sabine's Gulls (*Xema sabini*). *Auk* 124: 276-290.

Smith, P. A., J. Bart, R. B. Lanctot, B. J. McCaffery, and S. Brown. *In Press*. Detection probability of nests and implications for survey design. *Condor*.

Solís, J. C., and F. de Lope. 1995. Nest and egg crypsis in the ground nesting stone curlew *Burhinus oedicephalus*. *Journal of Avian Biology* 26: 135–138.

Stearns, S. 1992. The evolution of life histories. Oxford University Press, Oxford.

Stickney, A. 1991. Seasonal patterns of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. *Canadian Journal of Zoology* 69: 2853-2859.

Sugden, L. G., and G. W. Beyersbergen. 1986. Effect of density and concealment on American Crow predation of simulated duck nests. *Journal of Wildlife Management* 50: 9-14.

Sullivan-Blanken, M., and E. Nol. 1998. Factors affecting parental behavior in Semipalmated Plovers. *Auk* 115: 166-174.

Summers, R. W. 1986. Breeding production of Dark-bellied Brent Geese (*Branta b. bernicla*) in relation to lemming cycles. *Bird Study* 33: 105-108.

Summers, R. W., and L. G. Underhill. 1987. Factors related to breeding production of Brent Geese (*Branta b. bernicla*) and waders (*Charadrii*). *Bird Study* 37: 161-171.

Summers, R. W., L. G. Underhill, E. E. Syroechkovski Jr., H. G. Lappo, R. P. Prÿs-Jones, and V. Karpov. 1994. The breeding biology of Dark-bellied Brent Geese *Branta b. bernicla* and King eiders *Somateria spectabilis* on the northeastern Taimyr Peninsula, especially in relation to Snowy Owl *Nyctea scandiaca* nests. *Wildfowl* 45:110-118.

Székely, T., and J. D. Reynolds. 1995. Evolutionary transitions in parental care in shorebirds. *Proceedings of the Royal Society of London, Series B* 262: 57-64.

Székely, T., I. Karsai, and T. D. Williams. 1994. Determination of clutch-size in the Kentish Plover *Charadrius alexandrinus*. *Ibis* 136: 341-348.

- Taylor, J. 1976. The advantage of spacing out. *Journal of Theoretical Biology* 59: 485-490.
- Thomas, G. H., R. B. Lanctot and T. Székely. 2006. Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. *Animal Conservation* 9: 252-258.
- Thompson, F. R., III. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* 149: 98-109.
- Tinbergen, N., G. J. Broekhuysen, F. Feekes, J. C. W. Houghton, H. Kruuk, and E. Szulc. 1962. Egg shell removal by the black-headed gull, *Larus ridibundus* L.: a behaviour component of camouflage. *Behaviour* 19: 74-117.
- Tinbergen, N., M. Impekoven, and D. Franck. 1967. An experiment on spacing-out as a defence against predation. *Behaviour* 28: 307-321.
- Tomkovich, P. S. 1988. Breeding schedule and primary moult in Dunlins of the Far East. *Wader Study Group Bulletin* 85: 29-34.
- Tracy, D. M., D. Schamel, and J. Dale. 2002. Red Phalarope (*Phalaropus fulicarius*). No. 698 in *The Birds of North America* (A. Poole and F. Gill, Eds.). The Birds of North America Inc., Philadelphia.

Traylor, J. J., R. T. Alisauskas, and F. P. Kehoe. 2004. Nesting ecology of White-winged Scoters (*Melanitta fusca deglandi*) at Redberry Lake, Saskatchewan. *Auk* 121: 950-962.

Tulp, I. 2007. The arctic pulse: timing of breeding in long-distance migrant shorebirds. Ph.D. Thesis, Rijksuniversiteit Groningen, Netherlands. 259pp.

Tulp, I., and H. Schekkerman. 2001. Studies on shorebirds at Medusa Bay, Taimyr, in summer 2001. Alterra Report 451. Wageningen, Netherlands. 110pp.

Tulp, I., and H. Schekkerman. 2006. Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule. *Journal of Avian Biology* 37: 207-218.

Tulp, I., and H. Schekkerman. 2008. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic* 61: 48-60.

Tulp, I., H. Schekkerman, and R. Klaassen. 2000. Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2000. Wageningen, Alterra, Green World Research. Alterra Report 219. 87pp.

- Tulp, I., H. Schekkerman, P. Chylarecki, P. Tomkovich, M. Soloviev, L. Bruinzeel, K. Van Dijk, O. Hilden, H. Hotker, W. Kania, M. Van Roomen, A. Sikora, and R. Summers. 2002. Body mass patterns of little stints at different latitudes during incubation and chick-rearing. *Ibis* 144: 122-134.
- Tulp, I., H. Schekkerman, R. Klassen, B. Ens and G. H. Visser. 2009. Body condition of shorebirds upon arrival at their Siberian breeding grounds. *Polar Biology* 32: 481-491.
- Underhill, L. G., R. P. Prÿs-Jones, E. E. Syroechkovski Jr., N. M. Groen, V. Karpov, H. G. Lappo, M. W. J. van Roomen, A. Rybkin, H. Schekkerman, H. Spiekman, and R. W. Summers. 1993. Breeding of waders (Charadrii) and Brent Geese *Branta bernicla bernicla* at Pronchishcheva lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135: 277-292.
- Väisänen, R. A. 1977. Geographic variation in timing of breeding and egg size in eight European species of waders. *Annales Zoologica Fennici* 14: 1-25.
- Vickery, P. D., M. L. Hunter, and J. V. Wells. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* 63: 281-288.
- Walker, J., M. S. Lindberg, M. C. MacCluskie, M. J. Petrula, and J. S. Sedinger. 2005. Nest survival of scaup and other ducks in the boreal forest of Alaska. *Journal of Wildlife Management* 69: 582-591.

Warnock, N. D., and R. E. Gill. 1996. Dunlin *Calidris alpina*. No. 203 in The Birds of North America (A. Poole and F. Gills Eds.). The Academy of Natural Sciences, Pennsylvania; The American Ornithologists Union, Washington.

Webb, D. R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89: 874-898.

White, G. C. 2007. Program Mark, version 5.1, build 2600. Colorado State University, Fort Collins, CO.

White, F. N. and J. L. Kinney. 1974. Avian incubation. *Science* 186: 107-115.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46: S120-S139.

Whittingham, M. J., S. M. Percival, and A. F. Brown. 2002. Nest-site selection by golden-plover: why do shorebirds avoid nesting on slopes. *Journal of Avian Biology* 33: 184-190.

Wiebe, K. L., and K. Martin. 1997. Effects of predation, body condition and temperature on incubation rythms of White-tailed Ptarmigan. *Wildlife Biology* 3: 143-151.

- Wiebe, K. L., and K. Martin. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Animal Behaviour* 56: 1137-1144.
- Wiley, R. H., and D. S. Lee. 1998. Long-tailed Jaeger (*Stercorarius longicaudus*). No. 365 in *The Birds of North America* (A. Poole, Ed.). The Birds of North America Inc., Philadelphia.
- Wiley, R. H., and D. S. Lee. 1999. Parasitic Jaeger (*Stercorarius parasiticus*). No. 445 in *The Birds of North America* (A. Poole and F. Gill, Eds.). The Birds of North America Inc., Philadelphia.
- Williams, J. B. 1996. Energetics of avian incubation. In: *Avian energetics and nutritional ecology* (Ed. By C. Carey), pp. 375-415. London: Chapman and Hall.
- Wilson, D. J. 1997. Predation and animal populations: lessons from lemmings and geese. *Arctic* 50: 377-380.
- Wilson, D. J., and R. G. Bromley. 2001. Functional and numerical responses of predators to cyclic lemming abundance: effects on loss of goose nests. *Canadian Journal of Zoology* 79: 525-532.

Wilson, S., K. Martin, and S. J. Hannon. 2007. Nest survival patterns in Willow Ptarmigan: influence of time, nesting stage and female characteristics. *Condor* 109: 377-388.

Yahner, R. H., and C. G. Mahan. 1996. Effects of egg type on depredation of artificial ground nests. *Wilson Bull* 108: 129-136.

Zumbo, B. D., and D. W. Zimmerman. 1993. Is the selection of statistical methods governed by level of measurement? *Canadian Psychology* 34: 390-400.