

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

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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. We 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, we 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 our sites, and was not well predicted by local conditions such as temperature, wind or snow melt. Timing of breeding was related to 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. We hypothesise that when predation risk is high, the value of potential re-nesting exceeds the energetic risks of early breeding. Synchrony of breeding was significantly higher in late breeding years suggesting a relatively fixed date for the termination of nest initiation, after which nesting is no longer profitable.

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 (Meltofte et al. 2007a). Because shorebirds are 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 and incubation might 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, Nol et al. 1997, Sandercock et al. 1999). Increased

energetic demands of homeothermy during the pre-breeding season also could result in delayed breeding (Morrison et al. 2005).

While total snow cover precludes nesting in some years (Mayfield 1978), partially snow covered ground might 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 *Pluvialis squatarola* (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 (Smith et al. 2007). Populations of jaegers and arctic foxes *Alopex lagopus* 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. (Lack 1954, Angelstam et al. 1984). These cycles in predator abundance could play a role in determining the timing of nest initiation if birds can assess predation risk (Ebbinge and Spaans 2002). Abundant predators might 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 re-nesting 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 population or community (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, *Arenaria interpres*, 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 (Green et al. 1977, Nol et al. 1997, Meltofte 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).

Timing of arrival to the breeding grounds can also constrain the timing of nest initiation. Shorebirds nesting in the Canadian arctic are highly migratory, travelling thousands of kilometres from wintering grounds 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 (Roudybush et al. 1979), the timing of shorebird breeding could be related to the timing of their arrival on the breeding grounds (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, 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 (Meltofte 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, Meltofte et al. 2007a, Meltofte 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, we know of no community level analyses of nesting chronology for Nearctic shorebirds. Here, we present data for the timing of arrival and breeding at 4 sites, for 12 shorebird species and up to 9 years per species. We 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 62°51'N, 82°29'W (Fig. 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. 1). Habitat details and descriptions of the shorebird community at this site appear in Smith (2003) and Smith et al. (2007).

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 24-ha island; only timing of arrival data are therefore available. 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 because of its raised topography and good drainage.

The fourth site was on the northwest side of Prince Charles Island, at 68°11'N, 76°43'W (Fig. 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). As a result of this uplift, the centre of Prince Charles Island is primarily unvegetated, broken shale. Raised beach features are common, and particularly so on its 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 waters of the Foxe Basin; landfast ice persists until July, and coastal areas remain cool throughout the summer.

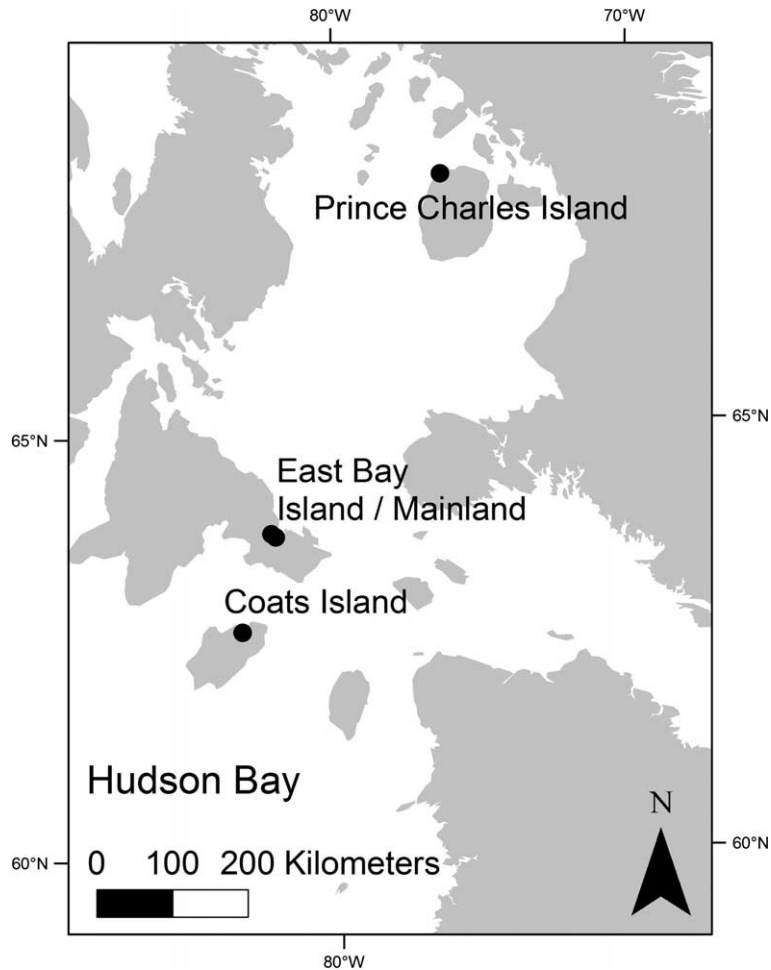


Figure 1. The four study sites in the eastern arctic, Nunavut, Canada. The East Bay Mainland and Island sites are separated by a distance of only 7 km.

Shorebirds and their predators

Our study includes more than 75% of the shorebird species nesting in the eastern low- and mid-arctic. Those best represented in the samples include the American golden plover *Pluvialis dominica*, black-bellied plover, dunlin *Calidris alpina*, red phalarope *Phalaropus fulicarius*, ruddy turnstone, semipalmated plover *Charadrius semipalmatus*, semipalmated sandpiper *Calidris pusilla*, and white-rumped sandpiper *Calidris fuscicollis*. Our observational data, and in particular our 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 such as mating system, territoriality, nest defence, foraging behaviour and the northern and southern limits of the species' breeding ranges. 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 (i.e. attacks on potential predators) 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 jaegers and arctic foxes. At East Bay and Coats Island, parasitic jaegers *Stercorarius parasiticus* are assumed to be the dominant avian predator. They were at least 15 times more abundant than long-tailed jaegers *Stercorarius longicaudus*, and the latter species is thought to rely primarily on

lemmings as prey (Wiley and Lee 1998). Long-tailed jaegers were the most abundant jaeger species at Prince Charles Island. Pomarine jaegers *Stercorarius pomarinus* were encountered in both years at Prince Charles Island, but this species is rare at the other three sites. Herring gulls *Larus argentatus* were observed regularly, but are believed to eat shorebird eggs infrequently (K. A. pers. obs.). Other potential predators, assumed to be unimportant because of their scarcity, include: peregrine falcons *Falco peregrinus*, glaucous gulls *Larus hyperboreus*, sandhill cranes *Grus canadensis* and common ravens *Corvus corax*.

At East Bay and Coats Island, we recorded the number of arctic foxes and jaegers observed per person \times hour, and used this as an index of relative predator abundance between years. On most days, these observations were made between 7 am and 7 pm. 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). We also recorded the number of lemming (primarily *Dicrostonyx torquatus*) encounters at East Bay, and use this to reflect the abundance of potential alternative prey (Summers 1986, Summers and Underhill 1987, Bêty et al. 2002). No lemmings are present on Coats islands (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 1–3m, and was therefore higher than what would be experienced by shorebirds at ground level. Although a number of weather variables were collected, we selected mean daily temperature from 10–30 June, mean daily wind speeds from 10–30 June, and mean daily wind-chill 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 (Hodkinson 2003), while the wind-chill temperature may more accurately reflect the energetic costs of homeothermy. We 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 (below). Snow-melt was monitored by making daily estimates of the percentage of snow free ground in a fixed area (1.5 \times 1.5 km) within the study sites.

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 or 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, we 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 we believed that these first sightings did not represent the arrival of the species to the area, we 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. 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.

We define the timing of nest initiation as the date upon which the first egg was laid but this date was rarely observed directly. When nests were found with partial clutches, we 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, we 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 or less in most cases.

Statistical analyses

We limited the more detailed analyses to species for which we had a minimum of four nests in each year at a given site, to avoid an undue influence of rare or atypical sightings. Typically however, the samples for common species were much larger (Table 1). We report, for each species and year, the earliest, first quartile, median, third quartile and latest nests. We did this because shorebirds initiating nests at different times within the laying period may be responding to different conditions. We defined the total length of the laying period as the time between the initiation of the earliest and latest nests we observed, but also reported 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.

We assessed patterns in weather variables over the years of the study with linear regression. The relationship

Table 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 \pm SD. *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 \pm SD | First nest \pm SD | Median nest initiation \pm SD | n | First sighting \pm SD | First nest \pm SD | Median nest initiation \pm SD |
| Semipalmated plover | 56 | 8 June \pm 3.5 | 15 June \pm 3.1 | 19 June \pm 6.0 | 0 | 7 June \pm 4.2 | . | . |
| Black-bellied plover | 69 | 5 June \pm 2.6 | 16 June \pm 5.1 | 21 June \pm 5.2 | 9 | 6 June \pm 1.5 | 16 June \pm 8.0 | 22 June \pm 1.1 |
| Red phalarope | 90 | 8 June \pm 3.1 | 19 June \pm 4.0 | 29 June \pm 6.3 | 31 | 7 June \pm 1.2 | 12 June \pm 7.6 | 18 June \pm 4.2 |
| Ruddy turnstone | 178 | 6 June \pm 2.4 | 11 June \pm 3.2 | 17 June \pm 6.1 | 0 | 7 June \pm 3.8 | . | . |
| Red knot | 2 | 6 June \pm 3.1 | 15 June \pm 7.1 | . | 0 | 12 June \pm 3.5 | . | . |
| White-rumped sandpiper | 51 | 4 June \pm 3.2 | 15 June \pm 5.0 | 23 June \pm 7.2 | 14 | 6 June \pm 3.6 | 14 June \pm 8.9 | 10 June \pm 3.8 |
| Semipalmated sandpiper | 2 | 7 June \pm 4.3 | 22 June | . | 144 | 7 June \pm 6.4 | 12 June \pm 6.7 | 18 June \pm 4.0 |
| American golden plover | 8 | 6 June \pm 3.9 | 17 June \pm 1.5 | 21 June \pm 4.8 | 19 | 2 June \pm 2.6 | 14 June \pm 6.9 | 17 June \pm 4.1 |
| Sanderling | 4 | 7 June \pm 2.8 | 22 June | 25 June \pm 3.3 | 0 | 9 June \pm 2.5 | . | . |
| Dunlin | 13 | 6 June \pm 2.4 | 25 June \pm 9.9 | 19 June \pm 4.5 | 62 | 2 June \pm 2.6 | 10 June \pm 7.9 | 16 June \pm 5.8 |
| Purple sandpiper | 0 | 6 June \pm 2.6 | . | . | 0 | 6 June \pm 3.1 | . | . |
| Pectoral sandpiper | 0 | 9 June \pm 3.5 | . | . | 3 | 10 June \pm 2.1 | 13 June | 13 June \pm 0.6 |
| Baird's sandpiper | 0 | 8 June \pm 2.5 | . | . | 0 | . | . | . |
| All species | 473 | 7 June \pm 2.2 | 18 June \pm 3.3 | 22 June \pm 5.3 | 282 | 7 June | 13 June \pm 7.3 | 16 June \pm 3.5 |

| Species | East Bay Island (1999–2007) | | | Prince Charles Island (1996*–1997) | | | | |
|------------------------|-----------------------------|-------------------------|---------------------|------------------------------------|----|-------------------------|---------------------|---------------------------------|
| | n | First sighting \pm SD | First nest \pm SD | Median nest initiation \pm SD | n | First sighting \pm SD | First nest \pm SD | Median nest initiation \pm SD |
| Semipalmated plover | 0 | 4 June \pm 2.6 | . | . | . | . | . | . |
| Black-bellied plover | 0 | 4 June \pm 2.0 | . | . | 6 | . | 11 June | 15 June \pm 3.0 |
| Red phalarope | 0 | 5 June \pm 3.6 | . | . | 29 | . | 9 June | 16 June \pm 3.8 |
| Ruddy turnstone | 0 | 1 June \pm 4.2 | . | . | 12 | . | 11 June | 15 June \pm 2.9 |
| Red knot | 0 | 5 June \pm 2.1 | . | . | . | . | . | . |
| White-rumped sandpiper | 0 | 31 May \pm 2.5 | . | . | 11 | . | 11 June | 15 June \pm 4.1 |
| Semipalmated sandpiper | 0 | 30 May \pm 2.7 | . | . | 2 | . | 16 June | . |
| American golden plover | 0 | 30 May \pm 2.9 | . | . | 4 | . | 14 June | 16 June \pm 1.6 |
| Sanderling | 0 | 2 June | . | . | . | . | . | . |
| Dunlin | 0 | 1 June \pm 2.6 | . | . | 2 | . | 14 June | . |
| Purple sandpiper | 0 | 3 June \pm 5.2 | . | . | . | . | . | . |
| Pectoral sandpiper | 0 | 3 June | . | . | . | . | . | . |
| Baird's sandpiper | 0 | 3 June \pm 2.6 | . | . | . | . | . | . |
| All species | 0 | 2 June \pm 2.0 | . | . | 66 | . | 12 June | 15 June \pm 2.3 |

Table 2. Selected weather parameters for the four study sites in the eastern arctic, Nunavut.

| Year | Prince Charles Island | | East Bay Mainland | |
|------|--------------------------------|-------------------------------|--------------------------------|-------------------------------|
| | Mean temp. (°C, 25–30 June) | Date of 50% snow clearance | Mean temp. (°C, 10–30 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 |
| Year | East Bay Island | | Coats Island | |
| | Mean temp. (°C, 10–30 June) | Date of 50% snow clearance | Mean temp. (°C, 10–30 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 | . | . |

between weather and timing of arrival for each species was also investigated with linear regression models, and results for these numerous tests were interpreted recognising the possibility for type I error (Moran 2003). The five metrics of timing of breeding (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 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 wind-chill 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, we 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). 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. S. pers. obs.).

The Coats Island site had heavy snow cover in the spring of 2004, as did much of the eastern arctic in that year (Melfo et al. 2007a). The date of 50% snow cover was 18 days later in 2004 than in 2006, and the mean temperature 10–30 June was correspondingly lower (Table 2). Prince Charles Island had exceptionally late snowmelt in 1996, with a date of 50% snow clearance of 30 June.

We 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 (10–30 June, all $R^2 < 0.03$, $P > 0.05$). However, the average daily wind-chill low from 10–30 June, an index of the energetic cost of thermo-regulation, showed a pronounced warming between 1999–2007 ($R^2 = 0.85$, $P < 0.001$). 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). 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 the 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 numbers of predators encountered by field staff was relatively stable between years, and lemmings were absent in all years. Both foxes and jaegers were most abundant in 2006. On Coats Island, long-tailed jaegers, a putative lemming specialist, were seen only 8 times in 3 years. At Prince Charles Island, lemming abundance was high in 1996 (with 3 to 12 fresh, active burrows per hectare

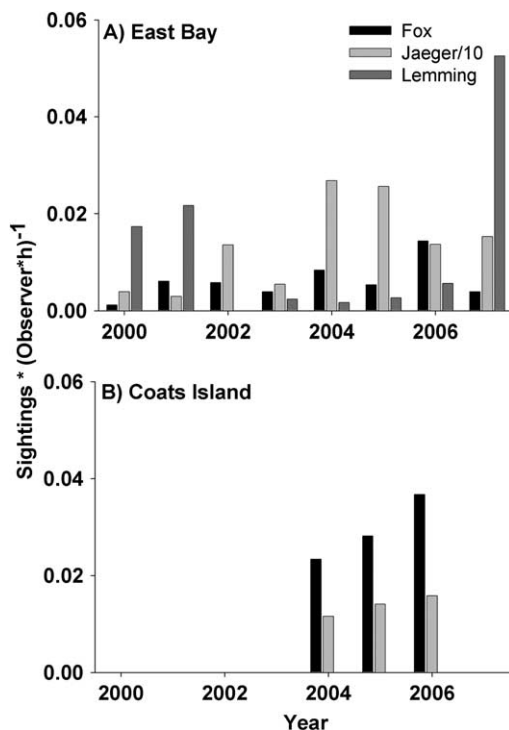


Figure 2. The number of predators and lemmings encountered in each year (sightings per observer hour) at the East Bay (a) and Coats Island (b) sites. Note that jaegers were the most abundant predator in all years; the encounter rate displayed in the figure is divided by 10 to equalize the scale among species.

in the most favourable habitats) and moderate in 1997 (0.5 to 4 fresh, active burrows per hectare 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 km^2 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 wind-chill 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 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). For individual species, no weather variables were significant predictors (at $\alpha = 0.05$) of timing of arrival to the East Bay Island site. At East Bay Mainland, the date of snow cover and to a lesser extent temperature in June were related to timing of arrival for semipalmated plovers (snow cover $P = 0.006$, temperature $P = 0.02$) and ruddy turnstones (snow cover $P = 0.003$, temperature $P = 0.02$). Due to the numerous tests, and the lack of a consistent effect across species and sites, these results may be spurious.

Because we 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 commonly 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 3–11 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 1).

Timing of nest initiation

We 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 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 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 1).

The climate variable demonstrating the largest influence was the timing of snow clearance (Table 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 10–30 June, nor the daily wind-chill lows during this period were significant predictors of timing of breeding (Table 3).

For nests initiated as late as the median initiation date, the number of predator sightings had a significant effect on initiation date (Table 3). While snow cover had a strong overarching effect on timing of breeding, abundant predators corresponded to earlier dates of nesting than would be predicted by snow cover alone (parameter estimate = -12.6 ± 5.4 d (SE)).

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.

Table 3. Results of an analysis of timing of breeding for shorebirds at East Bay Mainland and Coats Island, Nunavut. Separate general linear models (GLMs) 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 ($^{\circ}\text{C}$, 10–30 June), mean daily windchill low ($^{\circ}\text{C}$, 10–30 June) and mean wind speed (km h^{-1} , 10–30 June).

| Predictor | Earliest nests | | 1st quartile | | Median | | 3rd quartile | | Latest nests | | Synchrony (SD) | |
|--|----------------|-------|--------------|-------|--------|-------|--------------|-------|--------------|-------|--------------------------|-------|
| | F | P | F | P | F | P | F | P | F | P | F | P |
| Site | 11.73 | 0.002 | 11.05 | 0.002 | 18.28 | 0.000 | 16.53 | 0.000 | 19.93 | 0.000 | 16.74 | 0.000 |
| Species | 6.83 | 0.000 | 3.84 | 0.002 | 6.83 | 0.000 | 3.59 | 0.003 | . | . | 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^{-1} | 5.42 | 0.025 | 4.27 | 0.046 | 5.02 | 0.031 | . | . | . | . | . | . |
| | | | | | | | | | | | Site | |
| | | | | | | | | | | | Earliest nest initiation | |

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 (5 ± 4 d) and 2006 (4 ± 1 d).

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, $F_{1,29} = 6.4$, $P = 0.02$). We observed no significant inter-specific differences in synchrony of breeding (7 species, 31 species \times 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 (Meltofte 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 we 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 two of five species, and no correlation was found between temperatures at European staging grounds and arrival of the birds in Greenland (Meltofte 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 (Meltofte 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, Meltofte 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. S. and K. A. 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 (Meltote 1976, 1985, Green et al. 1977, but see Meltote 2007b). These results demonstrate that timing of nest initiation differed between species and sites, but was also 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, which was relatively invariant. Instead, the interval between arrival and laying varied among species. For some species, this interval was shorter than the physiological threshold for egg production proposed by Roudybush et al. (1979, approximately 1 week), suggesting that individuals are foraging actively immediately upon arrival or even before arrival to the breeding grounds. Differences in timing of laying therefore could reflect differences in the ability of shorebirds to gather sufficient food resources for egg formation.

In high arctic Greenland, Meltote 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 (Meltote 1985, Meltote 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 (Nettleship 2000). While this behaviour is not entirely confined to this species (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. We 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.

We 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 we 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 (Green et al. 1977, Meltote 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 typically 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. Furthermore, 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 (Green et al. 1977, Meltote 1985, Meltote et al. 2007a). In some years, complete snow cover well into the breeding season can preclude nesting altogether (Mayfield 1978), or even result in the death of adult birds (as observed by JLM at Prince Charles Island in 1996). A heavy snow cover limits the availability of nest sites and delays the emergence of surface active arthropods. In our 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, Meltote et al. 1981). If predators employ this strategy successfully, shorebirds may choose to nest later if there is a high presence of predators. We documented large inter-annual 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. We also found strong evidence for an increased rate of nest survival early in the breeding season at these sites (Smith and Wilson in press), 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 re-nesting should the need arise.

Re-nesting in the event of predation is common for shorebirds (Nol et al. 1997, Tulp et al. 2000, Meltofte et al. 2007a), 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, 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 the potential for adverse effects on nest success (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 (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, snow-melt 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 we are confident in our interpretation that synchrony is influenced by this relatively fixed cut-off date, we should note the important influence of re-nesting on the apparent synchrony of breeding. Second breeding

attempts are necessarily initiated later than first nests. Thus, synchrony as measured by us decreases in years of high re-nesting, which complicates interpretation of these results. Years of early breeding afford the greatest opportunity for re-nesting, and this may in part account for the apparent low synchrony in early-breeding years. Further, re-nesting 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 (data available on request).

Regardless, nest synchrony relates to the proportion of late nests in the population of breeding birds. In order for individuals to breed successfully, their eggs must not only hatch, but their chicks must also develop, fledge and successfully make the long migration south before freezing temperatures reduce the availability of arthropods. We found that nest initiation ceases at the end of June or early July; a finding corroborated by other studies (Meltofte et al. 2007a, 2007b). Chick growth is highest when nests hatch around the peak of arthropod abundance (Schekkerman et al. 2003) and chick survival declines in nests where 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 (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 re-nesting 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 because offspring from later nests would have insufficient time to hatch, fledge and prepare for southward migration.

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