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The breeding ecology of ruddy turnstones (*Arenaria interpres*) in the eastern Canadian Arctic

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ABSTRACT. In 2002 and 2003, studies were made of the breeding phenology, nesting success, nesting density, and rates of nest predation of ruddy turnstones (*Arenaria interpres*) at East Bay, Southampton Island, Nunavut, Canada. Previous data from East Bay were used to compare nesting chronology and nest success across years. Bird banding data were used to examine migration routes and rates of return. In all years, ruddy turnstones initiated nests within 7 days of arrival at the study area. The median date of incubation onset was the same in 2002 and 2003, despite different spring snow conditions. Snow remained later in the season in 2003 and the overall range of incubation onset was greater than in 2002. Ruddy turnstones at East Bay nested at high densities and in semi-colonial groups with a significantly aggregated distribution. In both years, nest success was low, predation was high, and lemmings were scarce. These data (and data from earlier East Bay studies) support the ‘alternative prey hypothesis’. Resighting rates of breeding adults between 2002 and 2003 were also low. Individuals banded at East Bay were resighted at Delaware Bay on the Atlantic coast of the United States, the Caribbean Islands, and in southern Brazil. This study increases our knowledge of this understudied species about which there is conservation concern.

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Introduction

Due to dramatic population declines, the ruddy turnstone (*Arenaria interpres*; Fig. 1) has been identified as a species of conservation concern in the United States (Brown and others 2001) and in Canada (Donaldson and others 2000). Its breeding ecology has rarely been studied in North America (Bent 1929; Stout and others 1967; Nettleship 1973; Piersma and Morrison 1994), and many aspects of it remain unknown (Nettleship 2000). For example, few accurate measurements of nest densities have been made, and there is limited information on breeding success and productivity. How these parameters vary annually in relation to weather and other factors has received little attention. The need also exists for more detailed information on many other aspects of basic breeding ecology, including timing of breeding, patterns of dispersion, and rates of site fidelity.

The ruddy turnstone exhibits a holarctic breeding distribution that includes rocky coasts and tundra habitats. Those breeding in the Canadian high Arctic and Greenland (*A. i. interpres*) winter from coastal Britain to southwestern Europe and northwestern Africa. Those breeding in the eastern Canadian Arctic and low Arctic regions (*A. i. morinella*) winter from Long Island, New

York, to southern Brazil, and from central California as far south as Tierra del Fuego (Nettleship 2000). Most (87%) of this latter race migrates along the Atlantic coast (Morrison and others 2001).

Throughout the breeding range, the sexes arrive together in late May or early June and pairing occurs on the territory shortly after the breeding areas are exposed by snowmelt. Egg laying occurs within 7–10 days of arrival (Bergman 1946) and is often highly synchronous in a breeding area (Nettleship 1967). Incubation usually begins with the third egg of a 4 egg clutch (Bergman 1946). After a 21–24 day incubation period, in which both members of a pair share incubation, chicks hatch during the peak of insect emergence (Nettleship 1967, 1973). The hatching of all chicks within a clutch normally takes place within a 24 hour period (Nettleship 2000) and the male provides most or all brood care (Parmelee and MacDonald 1960; Nettleship 1967, 1973).

The dispersion of ruddy turnstone nests is of particular interest because they defend their nests aggressively from predators (Larsen and others 1996), and may engage in group defence (Nettleship 2000). Group defence would be facilitated by a clumped distribution of nests. Similarly, a propensity towards group defence may select for nesting synchrony.

Like other shorebirds, ruddy turnstones are primarily ‘income’ breeders where nutritional resources required for egg formation are acquired locally on the breeding grounds, as opposed to ‘capital’ breeders which use endogenous reserves accumulated elsewhere (Klaassen and others 2001; Morrison and Hobson 2004). The ability to acquire sufficient local nutritional resources in the early season may determine the date of clutch initiation, and may be influenced by factors such as weather and

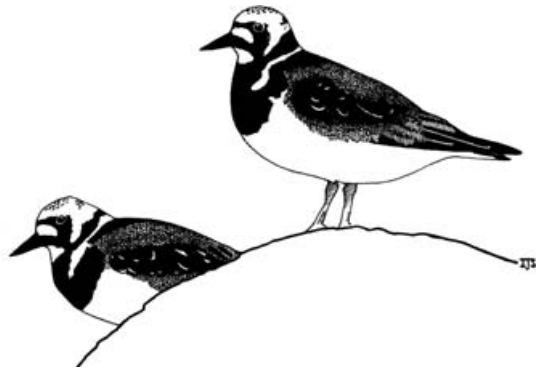


Fig. 1. Ruddy turnstones (*Arenaria interpres*) in breeding plumage. Drawing by Iain J. Stenhouse.

snow cover, both of which determine the availability of invertebrate prey during the prelaying period (Lank and others 1985; Nol and others 1997).

Annual nesting success in Arctic breeding areas may also be highly influenced by variation in predation pressure caused by dynamic predator-prey cycles. An abundance of lemmings (*Lemmus* or *Dicrostonyx* spp.) results in high reproductive output by predators such as the Arctic fox (*Alopex lagopus*) (Wilson and Bromley 2001). However, lemming cycles are relatively short, 3–5 years in most locations studied (Krebs 1964; Summers and others 1998) and when lemming populations crash, predator populations remain high (Elton 1942; Spaans and others 1998). Predators functionally respond to the lack of lemmings by switching to alternative prey, such as bird eggs or young (Roselaar 1979; Summers 1986). Several studies of Arctic-nesting birds support this ‘alternative prey hypothesis’, suggesting an indirect effect of lemming cycles on avian reproductive success (Blomqvist and others 2002; Summers and others 1989; Summers and others 1998; Underhill and others 1989). In ruddy turnstones specifically, Summers and others (1989) observed short-term fluctuations in the number of first-year (non-breeding) birds observed during the winter in South Africa, which the authors attributed to successful breeding during high lemming years in Siberia.

At East Bay, researchers have observed a 3 year cycle of Greenland collared lemmings (*Dicrostonyx groenlandicus*) (Stenhouse 2003; Smith 2003). At this site, primary shorebird egg predators are Arctic foxes and Arctic skuas (parasitic jaegers, *Stercorarius parasiticus*).

In this study, the breeding ecology of ruddy turnstones in the eastern Canadian Arctic in 2002 and 2003 is documented. Specifically, comparisons are made as follows: 1) breeding phenology between years (that is arrival dates, onset of incubation, hatching synchrony and departure for migration), 2) breeding phenology at East Bay with other Arctic regions, and 3) nesting success and nesting densities between years. Where possible, data available from 2000 and 2001 are used to make further comparisons. Data on the abundance of lemmings and foxes between years are employed to examine predator-prey dynamics.

Finally, band resightings are used to estimate return rates between years and to track broad scale movements of ruddy turnstones in the western hemisphere.

Methods

Study area

The East Bay migratory bird sanctuary (64° 01'N, 81° 47'W) encompasses approximately 1200 km² on the eastern side of Southampton Island, which lies at the mouth of Hudson Bay in Nunavut, Canada. Research was carried out within the sanctuary from late May to late July 2002 and 2003 in a study area running along 4.6 km of coastline with a width of 1.4 km. The area consists of low-lying wetland tundra with an extensive mosaic of freshwater and brackish ponds (0.1 ha–5 ha, < 1 m deep). At this site, wetland areas are dominated by mosses, sedges and grasses, while drier areas are dominated by mountain avens (*Dryas integrifolia*) and dwarf shrubs (*Salix* spp.).

Although generally considered low Arctic, the climate at East Bay is influenced by the deep, cold waters of the Foxe Channel, producing an environment more typical of high Arctic locations. Winds are predominantly from the northeast, coming directly off the bay, where land-fast sea ice often remains well into July. Throughout the study period, average wind speed in summer was 18 km/h (ranging from 11–92 km/h), average daily temperature was 6°C (ranging from 0 to 21°C), and mean windchill temperature was –2°C (ranging from –18 to 21°C).

Snow cover and weather

Daily estimates of snow cover (% of land covered by snow) were made from a raised gravel ridge, which provided a complete view of the study area. Weather was recorded twice daily with a DAVIS (Hayward, CA) weather station at 0800h and 2000h.

Nest monitoring

Ruddy turnstone nests were located on foot by observing pair behaviour on a territory and watching the male or female return to the nest from a distance. Nest locations were recorded (to the nearest ± 3m) with a hand-held Global Positioning System (GPS). In both years, nest searching effort was most intense during mid to late June, the period of nest initiation. Nests were visually inspected (for number of eggs and general condition) every 3–7 days during early and mid-incubation, but more frequently (every 1–2 days) near the expected hatch date, as all eggs usually hatch within 1–2 days and the highly precocial chicks leave the nest within hours of hatching (Nettleship 2000).

During nest checks, the stage of incubation for individual nests was determined by floating 2–4 eggs from each nest in a cup of warm water and assigning them to float categories, defined *a priori* (Perkins 2004). The float category scheme was highly effective for estimating the onset of incubation for failed nests, as the linear models for both years showed a high correlation between the

egg float category and the known day of incubation for successful nests (2002, $R^2 = 0.87$, $P < 0.001$, $n = 9$ nests; 2003, $R^2 = 0.92$, $P < 0.001$, $n = 12$ nests). The day of incubation was calculated with the linear equation and was accurate within ± 1.64 days for 2002 and ± 1.03 days for 2003 nests.

Nest fate was defined as 'successful' if at least one chick hatched, or 'failed' if eggs were depredated or abandoned. Most successful nests were observed at hatching, but those found empty near the estimated hatch date (within 1–2 days) with small eggshell fragments in the nest lining material were assumed to have been successful (Mabee 1997). Based on earlier studies (see Nettleship 2000), an incubation period of 23 days was assumed. Only one nest was found during laying, thus, the onset of incubation was calculated as date of hatch minus 23 days.

Nest locations were mapped using Arcview[®] 3.3 (ESRI, Redlands, CA). Nest density was estimated for each year as the number of nests divided by the size of the study area (6.4 km^2). Although it is more easily compared to literature values, it should be noted that this index of density is inherently biased, as research efforts at East Bay were focused in the area of highest ruddy turnstone densities. For a more objective index of density, a nearest neighbour approach (Clark and Evans 1954) was used. For each nest, the distance to the nearest conspecific nest was determined using the 'nearest feature' extension of Arcview (Jenness 2004). Using these nearest neighbour distances, non-random spatial patterning of nests was calculated using the Clark and Evans test (Clark and Evans 1954). Donnelly's modification was employed to correct for the lack of a buffer strip around the study area (Donnelly 1978).

The presence or absence of foxes and lemmings was recorded daily. Individuals were unmarked, and, therefore, observations indicate only whether a fox or lemming was seen, not necessarily the number of individuals present.

Statistical analyses

Weather conditions between years were compared with two sample *t*-tests. Because only one nest was found during laying, direct evidence of timing of breeding was available only for nests where hatch was observed. Due to differences in the error of float/age regression between years, analytical comparisons in breeding phenology were

limited to successful nests only. The Mann-Whitney *U*-test was used to: 1) investigate differences in the date of incubation onset across years, 2) examine the relationship between the timing of incubation onset (relatively early or late) and fate (failed or successful) for individual nests, and 3) compare nearest neighbour distances across years. A *z*-test was used to assess whether nests were significantly aggregated or dispersed (Krebs 1989). The Mayfield method was used to estimate hatching success and daily survival rates of nests (Mayfield 1961; Bart and Robson 1982). Exposure days were terminated at the last active visit for nests of unknown fate, and halfway between the penultimate and final visit for nests of known fate found empty (Manolis and others 2000). Survival rates were compared with a chi-square analysis using the program CONTRAST (Hines and Sauer 1989). All other statistical analyses were carried out using SYSTAT for Windows version 10.2.01 (SYSTAT Software, Inc, Richmond, CA). All values are reported as means \pm SE, and the critical probability (α) was set at $P \leq 0.05$.

Results

Weather

Weather conditions were similar between the years. There was no statistical difference between years in mean temperatures early in the season (1–30 June; 2002 = $4.7 \pm 0.5^\circ\text{C}$; 2003 = $2.9 \pm 0.3^\circ\text{C}$; $t = 3.2$, $P < 0.01$), or late in the season (15–31 July; 2002 = $9.2 \pm 0.6^\circ\text{C}$; 2003 = $11.7 \pm 1.0^\circ\text{C}$; $t = -2.2$, $P < 0.05$). In both years, there was a bout of heavy rain (including hail and sleet), cold temperatures, and periods of extremely high winds (up to 92 km/h) during the latter half of June (around the time of incubation onset).

Breeding phenology

Ruddy turnstones were first observed on the ground within the first 10 days of June in each year, when $>70\%$ of the area was snow-covered (Table 1). Some individuals were observed flying over the study area a few days before these observations. In general, however, ruddy turnstones appeared to settle on their territories as soon as the areas were exposed, and flocking along the coast or other areas of early snow clearance was not observed.

The tundra was snow-free (0% snow cover) five days earlier in 2002 (17 June) than in 2003 (22 June), but the median start of incubation was the same in both years (20 June; Fig. 2). Overall, the dates of incubation onset

Table 1. Breeding phenology of Ruddy Turnstones at East Bay 2000–2003. The dates for first completed clutch in 2002–2003 were determined by back-calculating from hatch date to incubation onset and adding one day, as incubation begins after the third egg is laid (Bergman 1946). Data for 2000 and 2001 from Smith (2003).

Year	First ruddy turnstone observed	90% of tundra exposed	First complete clutch found	First chicks observed	Dates of hatching (range)
2000	10 June	23 June	21 June	14 July	5–22 July
2001	3 June	7 June	12 June	5 July	12–27 July
2002	10 June	15 June	16 June	8 July	8–17 July
2003	8 June	20 June	14 June	10 July	6–26 July

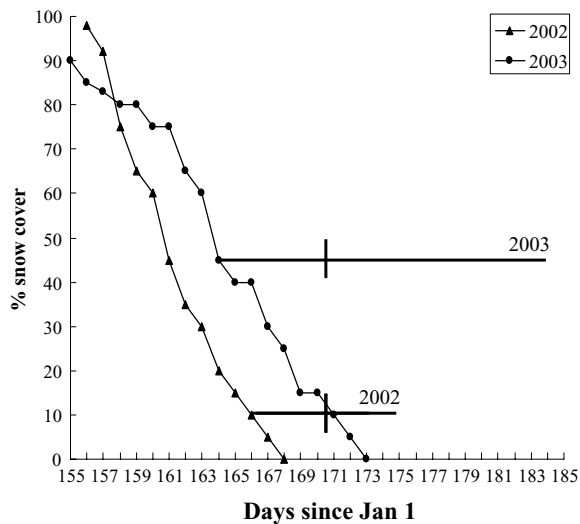


Fig. 2. Rate of snowmelt (percentage snow cover) and onset of incubation for successful nests in 2002 and 2003. Horizontal bars represent the range of incubation onset (2002 $n = 18$ nests; 2003 $n = 16$ nests); vertical bars indicate median.

were not significantly different between years (Mann-Whitney, $U = 131.0$, $P = 0.65$, successful nests only). In 2002, 90% of the tundra was exposed on the median date of incubation onset, while only 55% was exposed on this same median date in 2003. However, the overall range in incubation onset of successful nests was smaller in 2002, than in 2003, the year of later snow melt (nine days in 2002 versus 20 days in 2003; Fig. 2).

The latest hatched nest was nine days later in 2003, compared with 2002 (26 July and 17 July, respectively; Table 1). In 2002, hatching was relatively synchronous: over 90% of successful nests ($n = 18$) hatched within a 7-day period (8–15 July). Hatching was less synchronous in 2003: 69% of successful nests ($n = 16$) hatched within a 7-day period (10–17 July). These analyses for successful nests probably reflect the trends for all nests, as we identified no difference in the estimated date of incubation onset for successful and failed nests (Mann-Whitney, $U = 552.5$, $P = 0.92$).

Family groups with 1–2 day old chicks moved to the shoreline, as observed in other studies (Nettleship 2000). The number of females in the study area declined steadily from mid to late July, and by the end of July, few ruddy turnstones were observed greater than 500 m from the

shore. Aggregations of males and chicks were regularly observed in the coastal areas in mid to late July.

Nesting densities

Over the course of this study, a substantially greater number of nests ($n = 74$; 41 in 2002 and 33 in 2003) was found than previously reported in other North American studies, a maximum of 15 nests found in one breeding season on Ellesmere Island (Nettleship 1967, 1973). For nests with a known clutch size ($n = 71$), the mean number of eggs was 3.97 ± 0.04 .

In 2002, the nest density within the entire study area was 6.16 nests/km² ($n = 40$) compared to 5.09 nests/km² in 2003 ($n = 33$); mean nest density over the course of this two-year study was 5.63 nests/km² ($n = 73$). The distance of nests to the shoreline ranged from 0.4 km to 1.9 km. The mean distance to the nearest conspecific neighbour was 137 ± 11 m (range 42–321 m, $n = 40$) in 2002 and 167 ± 14 m (range 59–315 m, $n = 33$) in 2003. Nearest-neighbour distances were not significantly different between years (Mann-Whitney, $U = 497.0$, $P = 0.07$). Nests were significantly clustered in both years (in 2002 $z = 4.1$, $P < 0.001$; in 2003 $z = 3.1$, $P < 0.001$); random settling in the study area would have resulted in mean nearest neighbour distances > 220 m.

Nest success and predation rates

Mayfield estimates of nest success were relatively low in 2002 and 2003 (25% and 33%, respectively), in comparison with 2000 and 2001 (100% and 83%, respectively, Table 2). Nest success was lowest in 2002 ($n = 41$) including 20 depredated nests and three abandoned nests. Slightly lower predation was observed in 2003 ($n = 33$), with 14 depredated nests, one abandoned nest, one nest trampled by caribou, and one nest which was inadvertently damaged by a researcher (Table 2). Nest survival rates were not significantly different between 2002 and 2003, chi-square (1, $n = 74$) = 0.37, $P > 0.05$.

No lemmings were observed in 2002 (43 observation days), and only two were seen in 2003 (51 observation days: 0.04/day; Fig. 3). Foxes were sighted at a rate of 0.19/day in 2002, and 0.10/day in 2003 (Fig. 3). Overall, a high number of nests were lost to predators during these lemming scarce years (49% in 2002; 42% in 2003; Table 2). In other years, when lemming numbers were high, ruddy turnstones experienced much higher reproductive success (Fig. 3).

Table 2. Nest survival and predation of ruddy turnstone nests at East Bay, 2000–2003. Mayfield nest success was estimated assuming a 23 d incubation period. See text for an explanation of the calculation of exposure days. Data for 2000–2001 from Smith (2003).

Year	N	Exposure days	N abandoned	N predated	Daily survival rate (95% CI)		Nest success (95% CI)	
2000	6	87	0	0	1	(–)	1	(–)
2001	17	245.5	1	1	0.99	(0.98–1.00)	0.83	(0.64–1.00)
2002	41	392	3	20	0.94	(0.92–0.96)	0.25	(0.14–0.44)
2003	33	321	1	14	0.95	(0.93–0.98)	0.33	(0.19–0.55)

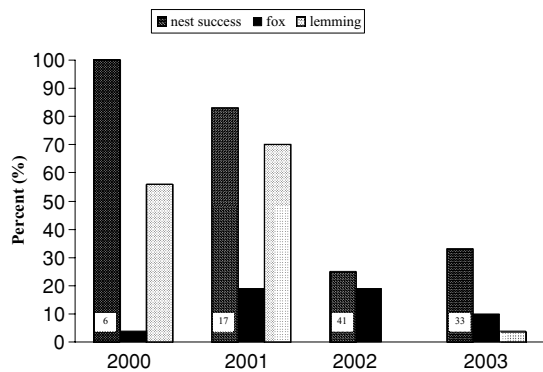


Fig. 3. Nest success (using Mayfield estimation) in 2000–2003 in relation to the percent of observation days foxes and lemmings were observed. Sample sizes (number of nests) are noted within the histogram of nest success.

Clutches that were laid early were not more successful than clutches laid later in the season (no significant difference was observed between the date of incubation onset for hatched nests versus failed nests; Mann-Whitney, $U = 552.5$, $P = 0.92$). However, median onset of incubation (28 June) was later for all four abandoned nests than for successful nests (20 June).

Band resightings

Over the course of this study, 49 adults and 50 chicks were banded. In 2003, 4 of 17 (24%) adult birds captured at East Bay in 2002 were resighted. A nesting pair was observed on the same breeding territory in consecutive years. One female was resighted with a new mate approximately 2 km from her nesting site in 2002. In 2003, one male nested 114 m from his 2002 nest site.

In 2004, 16% of the adults banded over the course of this study were resighted at East Bay (8 of 49; A. Hargreaves, personal communication, 27 July 2004). One of these was a female originally banded as an adult in 2002, while the rest were returns of adults originally

banded in 2003. Four of these individuals (50% of resighted birds) had new mates, and their previous mates were not observed in the area. In 2005, three males that were banded (and radio-tagged) in 2003 were resighted at East Bay. One of these males was observed with a new mate 155 m from the site of his nest in 2003. Though 50 chicks were banded at East Bay in 2002–2003, none were resighted in the study area in subsequent years (2003–2005).

Ruddy turnstones banded at East Bay in 2002 and 2003 were observed elsewhere (6% of all birds banded; Table 3). Conversely, birds banded elsewhere were observed at East Bay. From 2000–2005, at least 14 individual ruddy turnstones at East Bay were observed with green leg-flags, indicating that these birds were banded in the United States, presumably during migration through Delaware Bay.

Discussion

Prior to this study at East Bay, many aspects of ruddy turnstone breeding biology had not been examined. This study not only contributes to our overall knowledge of an understudied species, but also provides information that may be critical to the management and conservation of this declining species. Major findings include: 1) timing of breeding was influenced by factors other than early season temperature and snow conditions, 2) breeding was synchronous, 3) birds nested semi-colonally, 4) nesting densities were high, 5) nest success was low, 6) predation was high, 7) fluctuations in nest success were synchronous with small mammal populations, and 8) individuals from this breeding population migrate along the North American flyway and winter as far away as southern Brazil.

Factors influencing the timing of breeding

Reproductive success is influenced by many factors, and one of the most critical may be arrival date (Drent and

Table 3. Ruddy turnstones banded at East Bay in 2002 and 2003 that were resighted elsewhere.

Year	No. of birds banded at East Bay Migratory Bird Sanctuary (64° N, 81° W)		No. of birds resighted	Location of Resighting	Date	Notes
2002	Adult M	9	1	Delaware Bay, USA (39° N, 75° W)	28 May 03	On spring migration
	Adult F	8	0	—	—	—
	Chicks	21	1	Mostardas, Brazil (31° S, 50° W)	25 Apr 03	Killed by a hawk
2003	Adult M	17	3	Guadeloupe, Caribbean (16° N, 61° W)	30 Aug 03	last obs. 27 Jul 03 with 4 2d old chicks
				Delaware Bay, USA	11 May 04	On spring migration
				Delaware Bay, USA	30 May 04	On spring migration
	Adult F	15	1	Delaware Bay, USA	29 May 04	On spring migration
	Chicks	29	0	—	—	—

others 2003). Shorebirds are known to adjust breeding schedules according to snow conditions encountered upon arrival (Green and others 1977; Tulp and Schekkerman 2001; Schekkerman and others 2004), or even forego breeding in unusually late or harsh years (Mayfield 1978). In the Arctic, however, where the time window for reproduction is limited by the short summer, time constraints may require individuals to commence breeding while the tundra is still largely snow-covered (Chernov 1985).

The timing of breeding in ruddy turnstones at East Bay is similar to records from other parts of their breeding range (Schekkerman and others 2004; Nettleship 1967). However, the range of dates in 2003 was relatively large (16 days) as compared to other studies in which 5–10 days were cited (Schekkerman and others 2004; Nettleship 1967). The tundra was exposed later and early season temperatures were cooler in 2003 than in 2002, but the median onset of incubation remained the same in both years. This suggests that the timing of breeding is influenced by factors other than early season temperature and snow conditions.

The median date for incubation onset was the same between years, but the range of individual dates in 2003, a relatively late snow melt year, was much greater. Site fidelity may interact with snow melt on territories and influence the timing of breeding of individual pairs. Pairs may wait until suitable snow-free patches are exposed on their territories before initiating a clutch. The timing of nest initiation is likely also affected by the condition of females upon arrival.

Semi-colonial nesting

Nests were significantly aggregated in both years of this study and synchrony of breeding was high (particularly in 2002 when weather was more favourable). Nesting semi-colonially may enhance predator deterrence through communal defence. In a comparative study of 111 species of shorebirds, Larsen and others (1996) found colonial species to be more aggressive in nest defence than solitary breeders. At East Bay, ruddy turnstones were observed engaging in group defence, and aerial pursuits and scolding of predators by more than one individual appeared to be more effective at deterring aerial and terrestrial predators from nesting areas.

Surveys conducted at East Bay in 2000–2002 showed the highest breeding density of ruddy turnstones reported to date (7–9 pairs/km²), although few accurate measurements have been made (Nettleship 2000). Other breeding density estimates range from 0.93 pairs/km² (North Greenland; Meltofte 1976, 1985, Underhill and others 1993) to 6.6 pairs/km² (Gulf of Bothnia, Finland; Vuolanto 1968). Nesting density estimates from 2002 and 2003 were also high (5–6 nests/km²). Factors contributing to nesting densities at East Bay or elsewhere are unknown.

Factors influencing nest success

Nest success was relatively low in both years (Table 2), while lemmings were scarce (Fig. 3) and predation was high. Predation rates at East Bay (49% and 42%) were

higher than estimates from other breeding sites in North America at 18–27% (Nettleship 1967; Parmelee and MacDonald 1960), but lower than reported for Siberia at 67% (Schekkerman and others 2004).

Previous Arctic studies have reported relatively high nest success in ruddy turnstones during years when lemmings are abundant and low nest success during periods of lemming scarcity and provide strong support for the ‘alternative prey hypothesis’ (Underhill and others 1993; Tulp and others 1998; Tulp and Schekkerman 2001; Schekkerman and others 2004). Similarly, large-scale fluctuations in predation pressure at East Bay appear to be linked to the numerical and functional responses of Arctic foxes to lemming cycles (Fig. 3).

Higher breeding synchrony in 2002 may have contributed to higher predation rates via mechanisms associated with density dependent predation, specifically attributed to ‘area-restricted searching’ behaviour in which a predator (in this case, foxes) intensively searches a small area following an encounter with a nest (Tinbergen and others 1967).

Although many studies of reproductive success in birds have shown that it is generally better to lay early (Perrins 1970; Daan and others 1989), this was not the case in this study. Pairs that initiated nests earlier were not more successful than those that nested later in the season. However, the severe predation pressure at East Bay over the course of this study likely confounds any potential influence of lay date on reproductive success because most nests failed.

Migration and rates of return

The band resighting data in this study indicate that this population of ruddy turnstones migrates along the North American flyway (Delaware Bay) and winters in the Caribbean and Brazil. The apparent return rate of ruddy turnstones was low (24% and 16%) when compared to return rates in Finland at 78% (Bergman 1946) and in Fennoscandia at 66% (Boyd 1962). The low return rates at East Bay may reflect the apparently poor breeding conditions there in 2002 and 2003. There was some evidence of adult mortality or divorce between years (42% of resighted individuals had new mates).

Conclusion

Although early season conditions did not appear to be the driving factor affecting overall breeding phenology of this population, focal research of individual pairs in the early season is needed to better understand how site fidelity, early season conditions, female arrival condition, and other variables interact and affect the timing of individual nest initiation.

The apparent need for our study birds to commence breeding activities within a few days of arrival may emphasize the importance of arrival condition of ruddy turnstones to their reproductive success. Although shorebirds are primarily income breeders (Klaassen and others 2001), females arriving with greater nutritional resources

(body stores) may be more physiologically capable of initiating clutches earlier, as the ability to utilise energy immediately upon arrival could accelerate the onset of egg production (Morrison and Hobson 2004; Morrison and others 2005). Further research is needed throughout the annual cycle to identify factors influencing the arrival condition of both sexes. Additional breeding studies of this ruddy turnstone population should be conducted during years when predation pressure is less severe to examine the influence of arrival condition and lay date on reproductive success.

This study documented the highest breeding density of ruddy turnstones reported to date. Although the potential adaptive value of high breeding densities remains unclear, semi-colonial nesting may be a response to high predation pressure. Future studies should compare the breeding success of populations at different densities and investigate the potential factors driving nest dispersion in ruddy turnstones, for example predation rates, food availability, and site quality.

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