



The Auk 124(1):276–290, 2007
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Printed in USA.

ANNUAL VARIATION IN THE BENEFITS OF A NESTING ASSOCIATION BETWEEN RED PHALAROPES (*PHALAROPUS FULICARIUS*) AND SABINE'S GULLS (*XEMA SABINI*)

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ABSTRACT.—By nesting near aggressive birds, timid species can reap the benefits of aggressive nest defense while avoiding the costs. Red Phalaropes (*Phalaropus fulicarius*; hereafter “phalaropes”) typically nest in grass-sedge marshes, but nests have also been noted in rocky coastal habitats. We studied the reproductive ecology of phalaropes at East Bay, Southampton Island, Nunavut, to determine whether their use of coastal nesting areas reflected a protective nesting association with an aggressive larid, the Sabine's Gull (*Xema sabini*; hereafter “gull”). From 2000 to 2002, we found and monitored 29 phalarope nests with gull nests nearby (≤ 150 m away) and 26 without gulls nearby. Coastal phalarope nests were nearer to gull nests than expected by chance. No habitat differences were detected between coastal areas with and without gull nests, but only three phalarope nests were found in coastal areas without gull nests. Thermistor probes inserted in phalarope nests revealed that incubators with gulls nearby behaved less cryptically, taking more frequent and longer incubation recesses. In human-approach experiments, phalaropes with gulls nearby flushed earlier than those without gulls. In 2000 and 2001, hatch success was 17–20% higher for phalaropes with gulls nearby, but these nests had lower success rates than those without nearby gulls in 2002. These gulls are able to defend their nests from avian predators only; in 2002, arctic foxes (*Alopex lagopus*) were abundant, and their primary prey, collared lemmings (*Dicrostonyx torquatus*), were scarce. We suggest that phalaropes select coastal areas near gulls, but that this association is beneficial to phalaropes only in years when egg predation by arctic foxes is low. Received 25 January 2005, accepted 26 February 2006.

Key words: nest defense, nest predation, nesting association, *Phalaropus fulicarius*, Red Phalarope, Sabine's Gull, shorebird, *Xema sabini*.

Variation Annuelle des Bénéfices d'une Association pour Nicher entre *Phalaropus fulicarius* et *Xema sabini*

RÉSUMÉ.—En nichant près d'oiseaux agressifs, les espèces plus timides peuvent tirer des bénéfices d'une défense agressive du nid sans en assumer les coûts. Les Phalaropes à bec large (*Phalaropus fulicarius*; ci-après « phalaropes ») nichent typiquement dans des marais, mais des nids ont déjà été trouvés dans des habitats côtiers rocheux. Nous avons étudié l'écologie de reproduction des phalaropes à East Bay, sur l'île Southampton au Nunavut, afin de déterminer si leur utilisation des aires de nidification côtières reflète une association protectrice pour nicher avec un laridé agressif, la Mouette de Sabine (*Xema sabini*; ci-après « mouette »). De 2000 à

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2002, nous avons trouvé et fait un suivi de 29 nids de phalarope à proximité de nids de mouette (à ≤ 150 m de distance) et 26 sans nid de mouette à proximité. Les nids de phalarope côtiers étaient plus près des nids de mouette qu'à la normale. Aucune différence d'habitat n'a été détectée entre les régions côtières avec et sans nids de mouette mais seulement trois nids de phalaropes ont été trouvés dans les régions côtières sans nids de mouette. Des sondes à thermistance insérées dans des nids de phalaropes ont révélé que les individus incubant près des mouettes se comportaient de façon moins cryptique et prenaient des pauses d'incubation plus fréquentes et plus longues. Dans les expériences à approche humaine, les phalaropes nichant près des mouettes fuyaient le nid plus rapidement que ceux sans mouette à proximité. En 2000 et 2001, le succès d'éclosion était 17–20% plus élevé pour les phalaropes nichant près des mouettes mais ces nids avaient un succès plus faible que ceux sans mouette à proximité en 2002. Ces mouettes sont capables de défendre leur nid contre les prédateurs aviens seulement; en 2002, les renards (*Alopex lagopus*) étaient abondants et leur proie principale, le lemming *Dicrostonyx torquatus*, était rare. Nous suggérons que les phalaropes sélectionnent les régions côtières à proximité des mouettes mais que cette association est bénéfique aux phalaropes seulement lors des années où la prédation sur les œufs par les Renards arctiques est faible.

PREDATION IS THE primary cause of reproductive failure in birds (Ricklefs 1969), and selective pressure to mitigate this loss through adaptive nest-site choice should be strong. Studies of the adaptive significance of nest-site selection typically focus on habitat (e.g., Martin 1992, 1998; Clark and Shutler 1999), but success may also depend on the distribution of nests (e.g., McKinney 1965, Tinbergen et al. 1967, Göransson et al. 1975). Spatial patterns of nests are usually described for single species, but interactions between nesting neighbors are not limited to conspecifics. For example, many birds nest with more aggressive species in apparent protective associations (reviewed in Haemig 2001). Such associations are common in Arctic and sub-Arctic regions, with putative protectors ranging from large waders to raptors (e.g., Popham 1897, Koskimies 1957, Paulson and Erckmann 1985, Blomqvist and Elander 1988).

A timid bird nesting in association with a bold species can benefit (1) when the bold species provides early warnings that allow the timid species to react with cryptic behavior ("information parasitism" hypothesis; Nuechterlein 1981) and (2) when the bold species defends an area around its own nest, indirectly protecting all birds nesting nearby ("defense parasitism" hypothesis; Dyrce et al. 1981).

The Red Phalarope (*Phalaropus fulicarius*; hereafter "phalarope") exhibits no nest-defense behavior (e.g., Tracy et al. 2002) and, thus, could

benefit from a protective association. Across the circumpolar Arctic, phalaropes prefer to nest in grassy marshes (e.g., Kistchinski 1975, Mayfield 1979, Ridley 1980) but have also been observed nesting in rocky and exposed habitats within colonies of Arctic Terns (*Sterna paradisaea*; Höhn 1971, Hildén and Vuolanto 1972, Egevang et al. 2004). At East Bay, Southampton Island, phalaropes nest in both sedge marshes and rocky coastal areas. Many nests in coastal areas are in or near a Sabine's Gull (*Xema sabini*; hereafter "gull") colony. By assessing the habitat and distribution of phalarope nests, recording behavior of incubating adults, and comparing the success of nests with and without gulls nearby, we tested whether a protective nesting association exists between phalaropes and gulls.

METHODS

Study area.—Field work was conducted from late May to early August, 2000–2002, in the East Bay Migratory Bird Sanctuary, Southampton Island, Nunavut (63°59'N, 081°40'W; Fig. 1). The study plot ran 4 km along the coast and 3 km inland. Saline areas near the coast are colonized by few plants, which leaves the sand and rock substrates largely exposed. Inland from the coast, low-lying areas and freshwater ponds are separated by raised gravel beaches 1–3 m high. Ponds are numerous throughout the plot and are brackish ≤ 1 km from the low-tide mark. They range in size from 0.1 ha to 5 ha



FIG. 1. The study area at East Bay, Southampton Island, Nunavut, Canada (63°59'N, 081°40'W).

but are generally <1 m deep. As the nesting season progresses, large ponds decrease in size and shallow ponds (<30 cm) dry completely.

We identified six distinct habitat types based on elevation, vegetation, appearance, and salinity (Table 1). A detailed summary of the groundcover characteristics of these habitats appears in Smith (2003). We divided the study plot into a coastal and an inland portion (Fig. 2). The coastal habitats comprised intertidal areas, moss carpets, and scrub willow, and the inland types comprised sedge meadows, gravel ridge, and dry heath. In all habitats, vegetation is generally ≤5 cm in height.

Nest finding and monitoring.—In 2000 and 2001, we searched 7 km² of tundra, consisting of 4.5 km² of inland habitats and 2.5 km² in coastal areas. In 2002, we expanded the search area to 12 km²: 8.7 km² of inland and 3.3 km² of coastal habitats. Search effort was greatest at the onset

TABLE 1. Features of the habitats of East Bay, Southampton Island, Nunavut.

Habitat type	Distinguishing features
Intertidal zone	Intertidal or within splash range of fall storms Cryptogamic crust occurs Bare substrate dominant, living moss and graminoids sparse and patchy
Moss carpet	Pond edges in coastal areas Living moss covers substrate Sparse to moderate abundance of grasses and sedges Numerous herbs, but patchy and sparse
Scrub willow	Drier areas in central and northern portions of plot (0.5–1.5 km inland) <i>Salix</i> spp. abundant Herbs, grasses, sedges, and lichens common Substrate of bare soil and small rocks
Dry heath	Drier areas >1 km inland Ericaceous shrubs dominant; a dense cover of mountain avens (<i>Dryas integrifolia</i>) is a distinguishing feature Willows and lichens abundant Herbs moderate in richness and abundance Substrate variable: soil, rock, and gravel Relief varies from flat to extremely hummocked
Sedge meadow	Moist areas and pond edges inland Moss covers substrate, few rocks present Sedges–grasses tall (some >50 mm) and dense Herbs abundant and diverse Relief varies from flat to highly hummocked
Gravel ridge	Bare gravel dominant Flora sparse and depauperate Visibly raised from surrounding areas Colonized sparsely by mountain avens at low edges

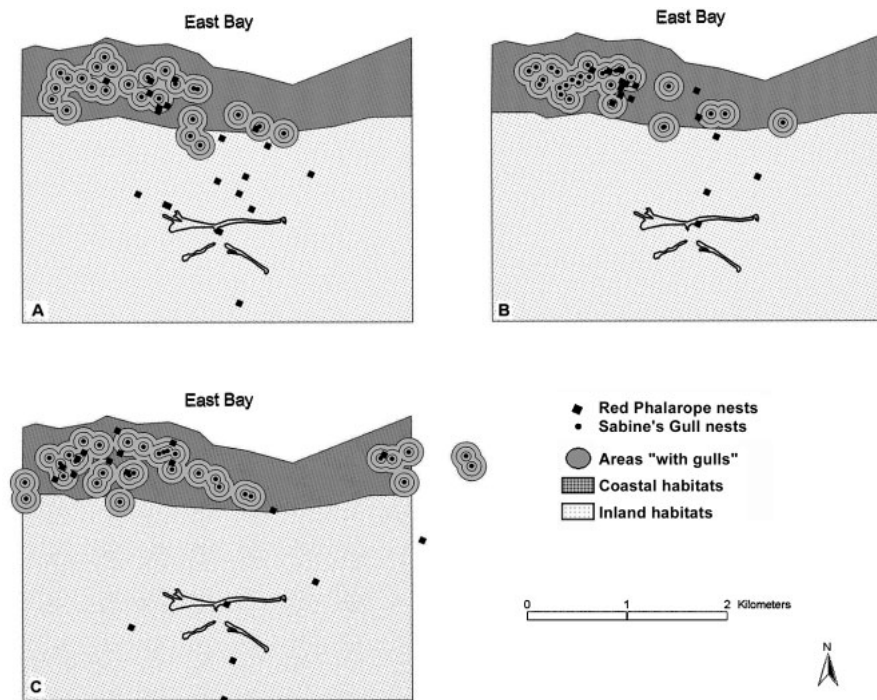


FIG. 2. Distribution of Red Phalarope and Sabine's Gull nests in (A) 2000, (B) 2001, and (C) 2002. Areas within 150 m of Sabine's Gull nests are marked as "with gulls." The northern boundary of the coastal habitats is the approximate high-tide mark of East Bay. Intensive search was limited to the central 7 km² of the 12-km² plot shown in 2000 and 2001.

of the nesting period, from mid- to late June, and was allocated evenly across the study area to avoid bias.

Nests were found through behavioral observation, by flushing birds while walking, and by two people dragging a 30-m length of 5-mm-diameter rope. To mark nests, wooden tongue depressors were placed 10–20 m away at a random bearing (Reynolds 1985). Eggs were checked at regular intervals and floated to estimate developmental stage (van Passen et al. 1984, Liebezeit et al. 2007).

The conspicuous nests of gulls were found primarily during laying and were checked at three-day intervals. At East Bay, gulls nest almost exclusively on mossy pond edges in coastal areas (Stenhouse 2003). They form a loose colony, with most nests <100 m apart (Stenhouse et al. 2001).

To estimate the timing of breeding, laying dates of both phalaropes and gulls were recorded directly or back-calculated from hatch dates. Incubation in gulls lasts 21–22 days

(Stenhouse et al. 2001). In phalaropes, incubation lasts ~19 days (present study; $n = 4$ nests).

Nest site descriptions.—The habitat of phalarope nest sites was described at two spatial scales. First, we quantified groundcover in a 1-m² circle centered on the nest (nest site). Second, in a 75-m² circle surrounding the nest (nest patch), we recorded the percentage of cover for each of the six habitat types. To measure concealment, we used an apparatus constructed of three 12-cm-diameter white plastic discs marked with a black grid. Two disks were fastened at right angles and placed atop a third, providing an identical silhouette from four lateral directions and from overhead. We placed the apparatus in nests and estimated the proportion of markings obscured to the nearest 5%. Estimates of lateral concealment were made from north, south, east, and west, at a distance of 5 m and a height of 40 cm (the approximate height of an arctic fox [*Alopex lagopus*]). Overhead concealment was estimated from eye level, directly above the nest. The height of the rocks or vegetation

directly surrounding the nest (i.e., contacting the bottom disk) was measured to the nearest ± 1 mm at the north, south, east, and west edges. All nest-habitat and concealment data were collected in late July.

The number of nest-habitat variables was reduced through principal component analysis (PCA). Separate analyses were conducted for percentage of cover data at 1 m² and 75 m². Variables with low or no correlations in the correlation matrix were removed before analysis. Principal component scores were generated only for readily interpretable components with eigenvalues > 1 (Guttman 1954).

Random site descriptions.—In each year, the study area was divided into a 50 \times 100 m grid. Eighty grid intersections were selected at random. At each location, we tossed a stick backwards over our heads and used the point of the stick as the random site. At these sites, habitat data were collected as for nest sites, at 1-m² and 75-m² scales. Sites falling in ponds were not included in analyses.

Predators and defense.—Potential nest predators are abundant at East Bay. Parasitic Jaegers (*Stercorarius parasiticus*), arctic foxes, and Herring Gulls (*Larus argentatus*) were observed regularly. Peregrine Falcons (*Falco peregrinus*), Long-tailed Jaegers (*S. longicaudus*), Glaucous Gulls (*L. hyperboreus*), Sandhill Cranes (*Grus canadensis*), and Common Ravens (*Corvus corax*) were also observed. The number of these predators observed in the study plot daily (sightings day⁻¹) was used as an index of relative predator abundance between years. Because the influence of generalist predators on avian nesting success may depend on the abundance of alternative prey (e.g., Summers 1986, B  ty et al. 2002), daily observations of collared lemmings (*Dicrostonyx torquatus*; hereafter “lemmings”) were also noted.

The mean flushing distance of gulls in response to the approach of predators is 160 m (Stenhouse et al. 2005). We used ARCVIEW GIS 3.2 (ESRI, Redlands, California) to plot nest locations (± 3 m accuracy), and we defined all areas within 150 m of any gull nests as “with gulls.” Gulls at East Bay nest primarily in coastal habitats, so areas without gulls were further classified as “coastal without gulls” or “inland” on the basis of habitat characteristics.

Indices of density and dispersion.—Using the geographic-information-system map, the

minimum distance to the nest of a conspecific was determined for each phalarope nest using the “nearest feature” extension of ARCVIEW (Jenness 2002). These nearest-neighbor distances were used to investigate spatial patterning among both inland- and coastal-nesting phalaropes, using the Clark and Evans test with Donnelly’s modification (Clark and Evans 1954, Donnelly 1978). The significance of deviations from random patterns was determined with Z-tests (Krebs 1989). To assess whether phalaropes tend to nest near gulls, the distances between coastal phalarope nests and gull nests were compared with the distances between coastal random points and gull nests using Mann-Whitney U-tests. Random points, equal in number to coastal phalarope nests, were generated with the “generate randomly distributed points” extension for ARCVIEW (Lead 2002). We also used U-tests to compare the distance from inland and coastal phalarope nests to the nearest neighbor of any species of shorebird or larid. Both this measure and relative density (nests per square kilometer searched) were used to assess nesting densities around phalarope nests in inland and coastal habitats.

Nesting success.—The Mayfield method was used to estimate hatch success and daily mortality rates for phalarope nests (Mayfield 1961). Nests hatching at least one chick were considered successful. Most hatch events were observed directly, but small eggshell fragments in the nest lining were also accepted as evidence of hatch (Mabee 1997). Both abandoned and depredated nests were considered to have failed. 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). Standard errors were calculated following Johnson (1979). Survival rates were compared using CONTRAST (Hines and Sauer 1989).

To examine factors affecting hatch success, we used Cox’s proportional hazard regression (Manolis et al. 2000). Habitat variables were included in the models by using the first and second principal components of the 1-m² and 75-m² habitat analyses. We also included the proportion of exposure days during which a phalarope nest was within 150 m of an active gull nest (arcsine transformed) as an index of the protection derived from gulls. The distance

between phalarope nests and their nearest neighbors, as well as the number of gulls within 150 m, were tested as covariates. Predictors were assessed individually for significant Wald statistics, and final models were created through a backwards-removal likelihood-ratio analysis with a removal criterion of $\alpha = 0.05$.

Flushing distance experiments.—In 2002, we approached nests on foot to compare responses to an approaching threat by phalaropes with and without gulls nearby. Responses of shorebirds to human intrusion resemble those elicited by other predators (e.g., Armstrong 1956, Gochfeld 1984). We approached nests at a steady pace from a random bearing. The distance at which the bird flushed was recorded (± 1 m) with a handheld rangefinder. Flush distances for phalaropes with and without gulls nearby were compared with a Mann-Whitney *U*-test. We used linear regression to assess the influence of nest concealment and incubation stage on flush distances (e.g., Knight and Temple 1986, Götmark et al. 1995). To minimize disturbance, approach experiments were combined with regular nest-monitoring visits.

Monitoring incubation behavior.—Thermistor probes attached to Hobo Temp-XT data loggers (Onset Instrument Corporation, Pocasset, Massachusetts) were placed in the nests of incubating phalaropes with and without gulls nearby in 2002. The probes consisted of 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. The tip of the probe (2 \times 5 mm) was centered in the nest and was level with the top surface of the eggs. Therefore, it was in contact with the brood patch when the bird was incubating. Readings were taken every 30 s, allowing 66 h 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 <10 min.

Loggers were placed in completed clutches only. Several nests failed before loggers could be deployed. The 10 logger systems were distributed opportunistically between nests with and without gulls. Nests were visited every third day to retrieve data.

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 behavior and that they accurately

captured departures of the incubator to within ± 30 s. Temperatures neared 40°C when the incubating bird was present and dropped sharply to ambient temperature (-2°C to 12°C) when the incubator departed. These temperature traces were used to calculate the proportion of a 24-h period during which nests were incubated (percentage of nest attentiveness), the number of recesses per 24 h, and the mean recess duration per 24 h. Individual nests were monitored for periods ranging from 3 to 18 days. For each nest, we generated a mean value for each of the three behavioral parameters and used these means for subsequent analyses. Incubation behavior was compared for nests with and without nearby gulls using Mann-Whitney *U*-tests. Unless otherwise noted, means are reported as mean \pm SE, and tests were conducted with $\alpha = 0.05$.

RESULTS

Principal component analysis of nest habitat.—Through principal component analyses, we reduced the number of nest-habitat variables to two for the 1-m² data and two for the 5-m² data. At the 1-m² scale, the final matrix included eight variables (Table 2), and the first two components (PC1 and PC2) captured 26% and 18% of the variability in the original data, respectively. Principal component 1 loads highly negatively on moss, sedge, and grass (hydrophytic) and positively on lichen and ravens (xerophytic). We interpret PC1 as a measure of moisture, with low scores representing moist sites. Principal component 2 loads negatively on rock and dirt and positively on willow, lichen, and organic crust. This component captures the amount of exposed substrate; willow, lichen, and cryptogamic crust are found in habitats with little exposed substrate.

At the 75-m² scale, PC1 and PC2 explained 21% and 19% of the variation, respectively (Table 2). Principal component 1 loads positively on pond-margin habitats and negatively on dry-heath and sedge-meadow habitats. We interpret PC1 at this scale as a measure of patch size and habitat homogeneity; pond margins are edge habitats, whereas dry-heath and sedge-meadow habitats consist of large patches. Principal component 2 loads positively on moss carpet and scrub willow and negatively on the intertidal-zone habitat type and reflects position within the study area. A high PC2 score

TABLE 2. Component loadings for principal component analyses of Red Phalarope nest-site and nest-patch characteristics. At the site level, original variables are estimated covers (%) in a 1-m² circle centered on the nest. "Crust" refers to an organic crust of lichen and dead moss (cryptogamic crust). At the patch level, original variables are estimated covers (%) of habitat types in a 75-m² circle around the nest.

Nest site			Nest patch		
	Component			Component	
	1	2		1	2
Rock	0.51	-0.68	Gravel ridge	-0.26	-0.06
Crust	0.43	0.41	Dry heath	-0.56	0.05
Lichen	0.53	0.36	Scrub willow	0.11	0.72
Moss	-0.82	0.24	Sedge meadow	-0.51	-0.25
Dirt	-0.22	-0.44	Moss carpet	0.55	0.44
Avens	0.53	0.29	Intertidal	0.49	-0.72
Willow	0.01	0.58	Water	0.55	-0.16
Sedge-grass	-0.61	0.13			

indicates a central location, where moss carpet and scrub willow are common.

Nest abundance and distribution.—Over three years, phalaropes arrived at the study area between 8 and 12 June, several days later than most other shorebirds nesting at East Bay. Snow cover at the time of their arrival was 95% in 2000, 10% in 2001, and 45% in 2002. Gulls arrived between 3 and 11 June, before the arrival of phalaropes in each year. The number of phalaropes present in the study area at late courtship and early incubation (~1 week after arrival) differed between years, with 26.6 birds per square kilometer in 2000, 23.1 birds per square kilometer in 2001, and only 6.8 birds per square kilometer in 2002.

Over three years, we found 55 phalarope nests: 25 inland and 30 near the coast (Fig. 2A–C). For all years, the density of phalarope nests was higher in coastal areas (coastal: 2.9 ± 0.7 nests per square kilometer; inland: 1.6 ± 0.6 nests per square kilometer). Coastal phalarope nests were significantly clumped in all years. By contrast, distribution of inland phalarope nests was random in all years (Table 3).

Of the 30 coastal phalarope nests, 27 were within 150 m of the nearest gull nest. These nests are referred to as "with gulls." Two inland nests were also near gulls, for a total of 29 nests with gulls and 26 without. The mean distance of coastal nests to the nearest gull nest for all years was 92 ± 11 m, compared with 787 ± 106 m for inland nests. Coastal phalaropes selected sites significantly nearer to gulls than expected from a random

distribution within coastal areas (92 ± 11 m vs. 259 ± 49 m; $U = 270$, $df = 30$ and 30 , $P = 0.003$). We detected no habitat differences between random coastal sites with and without gulls (t -tests of 1-m² and 75-m² PC scores; all $P > 0.35$).

Phalaropes nesting near gulls tended to initiate clutches after the latter did. Of 15 phalarope clutches where lay date of both the phalarope and the nearest gull was known, 10 were initiated after the first gull egg was laid. This measure of relative timing is conservative, given that gulls establish territories upon arrival at the breeding grounds (Stenhouse et al. 2001), whereas phalaropes do not defend nesting territories (Tracy et al. 2002). Thus, most gulls had established territories and begun laying when phalaropes selected their nest sites.

Predators and prey.—The frequency of predator and lemming sightings differed substantially between years (Table 4). Lemmings were abundant in 2000 and 2001, but none was seen in 43 days of observation in 2002. Predators were present in all years, but sightings did not co-vary closely across species. Foxes were more abundant in 2001 and 2002 than in 2000. Jaegers, primarily Parasitic Jaegers, were much more abundant in 2002 than in the two other years.

Nesting success.—Nesting success of gulls varied strongly across years. In 2000, 19 of the 25 (76%) nests hatched at least one chick. In 2001, 16 of 25 (64%) nests hatched young. In 2002, only 1 of 35 nests hatched young (3%). Twenty-nine clutches were taken by predators,

TABLE 3. Observed and expected nearest-conspecific-neighbor distances (m; means \pm SE) and indices of aggregation (R) for nest distributions of Red Phalaropes in inland and coastal habitats, 2000–2002. Coastal Red Phalarope nests were significantly clumped in all years.

Year	Nest location	<i>n</i>	Observed	Expected	R^a	z	P
2000	Inland	13	287 \pm 56	337 \pm 55	0.85	−0.92	0.36
	Coast	7	163 \pm 56	365 \pm 82	0.45	−2.46	0.01
2001	Inland	5	353 \pm 50	599 \pm 159	0.59	−1.55	0.12
	Coast	11	142 \pm 49	364 \pm 50	0.39	−4.46	<0.01
2002	Inland	7	738 \pm 96	675 \pm 151	1.09	0.42	0.67
	Coast	12	159 \pm 15	329 \pm 59	0.48	−2.87	<0.01

^a Observed/Expected.

and five were abandoned. Locations of nests appear in Fig. 2A–C.

Mayfield estimates of phalarope hatch success were low in all years, varying from 31% in 2000 and 35% in 2001 to 5% in 2002. In both 2000 and 2001, nests without gulls had daily mortality rates that were $\sim 2\times$ those of nests with gulls. In neither year, however, was this effect significant. In 2002, this trend was reversed, and nests with gulls suffered substantially higher mortality than nests without gulls (Fig. 3). Mayfield estimates for hatch success over a 19-day incubation period showed >17% differences between nests with and without gulls in each year (Table 5), but statistical power to identify significant differences was low, owing to small samples.

The survival of all phalarope nests over all years was best predicted by habitat (75-m² PC2; Table 6). Nests with high PC2 scores had longer survival times and better hatch success. Nests with high scores for PC2 occurred in scrub-willow and moss-carpet habitats in the southern reaches of the coastal areas (refer to Table 2 for loadings). Similarly, 75-m² PC2 was a significant predictor of survival for all nests in 2000.

TABLE 4. Number of sightings per day of arctic foxes, Parasitic Jaegers, Long-tailed Jaegers, and collared lemmings, May–August, 2000–2002, at East Bay, Nunavut, Canada.

Species	Year		
	2000	2001	2002
Arctic Fox	0.04	0.19	0.19
Parasitic Jaeger	0.93	0.81	3.37
Long-tailed Jaeger	0.30	0.08	0.88
Collared lemming	0.56	0.69	0.00

In 2001, survival was best predicted by the height of rocks and vegetation surrounding nests; successful nests had less cover than failed nests (successful: 38 \pm 5 mm; failed: 54 \pm 7 mm). For all years, inland nests surrounded by lower vegetation or rocks had better survival (successful: 44 \pm 3 mm; failed: 63 \pm 6 mm). However, in both cases, the height of cover around the successful nests was intermediate. Random sites ($n = 183$) at East Bay are surrounded by rocks or vegetation 18 \pm 1 mm high.

For coastal nests, the proportion of days that a phalarope was <150 m away from an active gull nest did not predict phalarope nest survival. However, there was a significant interaction effect between gull presence and year: high gull presence increased coastal nest survival in 2000 and 2001 and decreased survival in 2002. Nest survival was also predicted by 75-m² PC1,

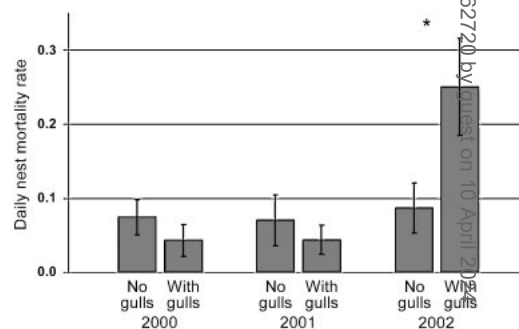


FIG. 3. Daily rate of nest mortality (\pm SE) for Red Phalaropes >150 m away (no gulls) and <150 m away (with gulls) from Sabine's Gulls in 2000–2002. *The difference in mortality between “no gulls” and “with gulls” was significant only in 2002.

TABLE 5. Mayfield estimates of nest survival over a 19-day incubation period for Red Phalaropes nesting >150 m away (no gulls) and <150 m away (with gulls) from Sabine's Gulls in 2000–2002.

Year		Nests	
		No gulls	With gulls
2000	Period survival	0.23	0.43
	95% CI	0.09–0.58	0.19–0.97
	<i>n</i>	12	8
2001	Period survival	0.25	0.42
	95% CI	0.06–0.93	0.19–0.88
	<i>n</i>	6	10
2002	Period survival	0.18	0.00
	95% CI	0.04–0.68	0.00–0.08
	<i>n</i>	8	11

a measure of habitat heterogeneity. Nest sites occurring in habitats with a high PC1 score (fine-grained habitats such as mossy pond margins or narrow land bridges) showed reduced survival.

Flushing distance experiments.—Flush distances were recorded for five phalarope nests with and eight nests without gulls ($n = 29$ flushes). Because flush distance was not related to incubation stage ($r^2 = 0.01$, $P = 0.60$), means for individuals were used in all analyses. Incubators with gulls flushed at significantly greater distances than those without gulls (with: 38 ± 8 m, median = 48 m; without: 10 ± 5 m, median = 5 m; $U = 3.0$, $n_1 = 5$ and $n_2 = 8$, $P = 0.01$). However, mean flush distance was also significantly correlated with percentage of overhead nest concealment ($r^2 = 0.42$, $P = 0.02$), and concealment differed almost threefold between treatments (with: $3.5 \pm 1.9\%$; without: $9.4 \pm 2.2\%$; $U = 8.5$, $n_1 = 5$ and $n_2 = 8$, $P = 0.08$). To control for this difference, we generated residuals from a regression of flush distance on overhead concealment. The residuals for incubators with gulls were larger than for birds without gulls ($U = 6.0$, $n_1 = 5$ and $n_2 = 8$, $P = 0.04$), which suggests that flush distances for phalaropes nesting near gulls were greater than predicted by the differences in nest concealment alone.

Incubation behavior.—Incubation behavior was recorded at nine nests for 42 complete 24-h periods. Four of the nests (15 nest days) were within 150 m of gulls, and five nests (27 nest days) were without gulls. Mean nest attentiveness was significantly higher for phalaropes without gulls

(without: $88.6 \pm 0.0\%$; with: $80.8 \pm 0.0\%$; $U = 0.0$, $n_1 = 4$ and $n_2 = 5$, $P = 0.014$). This significant difference in attentiveness was the product of non-significant differences in both recess frequency (mean number of recesses per 24 h, without gulls: 22.8 ± 2.2 ; with gulls: 29.5 ± 2.7 ; $U = 3.0$, $n_1 = 4$ and $n_2 = 5$, $P = 0.086$) and recess duration (mean recess duration [min], without gulls: 7.6 ± 0.4 ; with gulls: 9.9 ± 1.5 ; $U = 5.0$, $n_1 = 4$ and $n_2 = 5$, $P = 0.221$).

Weather can influence incubation scheduling, and recordings were not made simultaneously on all nests. To control for effects of weather, we examined three independent pairs of nests (12 days total paired observations). Mean nest attendance was consistently higher for incubators without gulls (without: $88.3 \pm 0.9\%$; with: $81.7 \pm 4.4\%$). Incubators without gulls achieved this higher nest attendance by taking fewer recesses (without: 23.0 ± 4.7 recesses per 24 h; with: 29.6 ± 3.9 recesses per 24 h) and recesses of shorter duration (without: 7.9 ± 1.3 min per recess; with: 9.5 ± 2.2 min per recess). Because of small samples, no statistical analyses were done on these paired observations.

DISCUSSION

Demonstrating a nesting association.—In all years, phalarope nest densities were highest in coastal areas with gulls, but the reproductive benefit of coastal nesting to phalaropes varied between years. If this nesting strategy is a protective association, phalaropes must (1) be able to recognize potential protectors, (2) actively select nest sites near gulls and not merely in similar habitat, and (3) derive benefits that exceed the effects of predator swamping.

Many birds recognize their predators and respond appropriately (e.g., Simmons 1952). Further, some species can discriminate between predators that pose different levels of threat (Walters 1990, Larsen et al. 1996, Stenhouse et al. 2005). Direct tests of the ability of birds to identify potential protectors, however, remain rare. Snowy Owls (*Bubo scandiacus*) can defend their nests from all egg predators (including arctic foxes), but will prey on waterfowl when lemmings are scarce (Ebbinge and Spaans 2002). Some waterfowl (Dark-bellied Brant [*Branta bernicla bernicla*], King Eiders [*Somateria spectabilis*], Greater Snow Geese [*Anser caerulescens atlanticus*]) nest near Snowy Owls in

TABLE 6. Cox's proportional-hazard regression models of nest survival for the Red Phalaropes of East Bay. Final models were created through backwards removal using likelihood ratios (criterion: $\alpha = 0.05$). Only covariates with significant Wald statistics for ≥ 1 group of nests are displayed. Variables assessed but not found significant for any groups of nests include with–without gulls, overhead concealment (%), lateral concealment (%), PC1 (1-m²), PC2 (1-m²), nearest Sabine's Gull nest, nearest Red Phalarope nest, and number of Sabine's Gull nests within 150 m.

	Nests	Protected days / survival days		Average height of vegetation (mm)		PC1 (75-m ²)		PC2 (75-m ²)		Full model		Variables included in final model	
		* Year											
		Wald	P	Wald	P	Wald	P	Wald	P	χ^2	df	P	
All nests, all years	54	3.13	0.07	0.36	0.55	1.54	0.22	4.09	0.04*	4.19	1, 54	0.04*	PC2 (75-m ²)
All nests, 2000	20	–	–	0.16	0.69	1.95	0.16	5.24	0.02*	5.80	1, 20	0.02*	PC2 (75-m ²)
All nests, 2001	15	–	–	5.28	0.02*	0.07	0.80	1.17	0.28	6.23	1, 15	0.01*	Average height of surrounding vegetation
All nests, 2002	19	–	–	0.35	0.55	2.96	0.09	0.38	0.54				
Inland nests, all years	25	1.36	0.24	5.34	0.02*	0.11	0.74	0.99	0.32	5.68	1, 25	0.02*	Average height of surrounding vegetation
Coastal nests, all years	29	7.08	0.03*	2.51	0.11	4.88	0.03*	3.09	0.08	12.56	3, 29	0.01*	PC1 (75-m ²) Prot./Surv. Days*Year

* $P < 0.05$.

years when the owls' preferred prey, lemmings, are abundant (Summers et al. 1994, Bêty et al. 2001), which suggests that they can assess the risks and benefits of nesting near these effective protectors that are also potential predators.

Although we did not directly test whether phalaropes can differentiate between potential protectors and predators, their nesting preferences and behavior suggest that they can. Sabine's Gulls are common at East Bay, and they successfully expel most avian predators, including jaegers, ravens, and larger gulls. Despite extensive behavioral study, they have never been observed depredating the eggs of any other bird species at East Bay (Stenhouse 2003). We found that phalaropes prefer to nest near Sabine's Gulls, but we did not find aggregations near the nests of other aggressive but potentially dangerous species such as Parasitic Jaegers or Herring Gulls. Further, nesting and feeding phalaropes at East Bay reacted to alarm calls of gulls with vigilance ($n = 16$). By contrast, they cowered at the sight of Parasitic Jaegers ($n = 5$) (Smith 2003). Similarly, phalaropes on the Taimyr Peninsula nest near potential protector species such as Black-bellied Plover (*Pluvialis squatarola*) and Long-tailed Jaeger (Larsen and Grunnetjern 1997). Therefore, it seems likely that phalaropes can discriminate between threatening and harmless species and that they identify Sabine's Gulls as potential protectors.

There was strong evidence that phalaropes nesting in coastal habitats selected sites near gulls. The clutches of phalaropes in "with gulls" habitats tended to be laid after the gulls had initiated their clutches. Their nests were also significantly closer to nesting gulls than predicted by random settling; this resulted in a significantly clumped distribution in "with gulls" areas. It is unlikely that this clumping was the result of individual phalaropes returning to coastal sites where they had previously bred successfully, because the few existing data suggest that site fidelity in phalaropes is extremely low (Tracy et al. 2002). Site choice by phalaropes was not constrained by snow cover at the time of nest initiation, because snow cover was <5% in 2001. There was no detectable difference between the available coastal habitat and the "with gulls" habitat preferred by phalaropes.

Thus, the first two conditions for documenting a nesting association appear to be met; phalaropes likely identify gulls as potential

protectors, and a portion of the phalarope population actively selects nest sites near them. However, the benefit of this putative protective association to phalaropes varied between years.

Incubation behavior and nesting associations.—For cryptic species, activity near the nest increases the risk of predation. Reducing the number of incubation recesses decreases detectability by predators in a variety of birds (e.g., Martin et al. 2000, Ghalambor and Martin 2002). Increases in nest attentiveness may also decrease risk of predation by shortening the total incubation period (Martin 1995). Increased nest attentiveness has costs, however, because incubators' body condition may depend on the amount of time budgeted for foraging (Carey 1980, Hegyi and Sasvári 1998). Although recordings were made only in a single year and variability between nests was high, phalaropes nesting in areas without nearby gulls exhibited more cryptic incubation behavior.

By reducing the rate and duration of incubation recesses, phalaropes without gulls nearby spent 7% more time on the nest, which may be sufficient to affect incubator body condition. Phalaropes nesting at Barrow, Alaska (71°N), exhibited 85% nest attendance and lost an average of 14% of their body weight over a 195-day incubation period (Schamel and Tracy 1987). Similarly, incubators at the Arctic National Wildlife Refuge (71°N) exhibited 83% attentiveness and lost 14% of their mass (Erckmann 1981). By contrast, incubators at Wales, Alaska (66°N), spent 70% of their time on the nest and maintained or gained mass over a 225-day incubation period (Erckmann 1981). Thus, the more cryptic behavior exhibited by phalaropes without gulls nearby may compromise body condition, with potential effects on adult survival, parental care duration, or chick survival (Hegyi and Sasvári 1998).

Phalaropes in sedge marsh habitats also rely on cryptic behavior when faced with an immediate threat of predation (e.g., Mayfield 1979, Ridley 1980). There are reports of humans touching incubating males without causing them to flush (Tracy et al. 2002, P. Smith pers. obs.). Both eggs and adults are vulnerable to the common predators at East Bay: arctic foxes and Parasitic Jaegers (Wiley and Lee 1999, Tracy et al. 2002). Consequently, remaining on the nest as predators approach represents a tradeoff between adult survival and clutch loss (e.g.,

Montgomerie and Weatherhead 1988, Götmark et al. 1995, Larsen et al. 1996). Incubators with and without gulls nearby differed markedly in the distance at which they flushed when nests were approached (median with gulls: 48 m; without: 5 m). This difference was greater than could be explained by differences in visibility or concealment. If coastal phalaropes rely on the aggressive defense of nearby gulls, the benefit of remaining on the nest as predators approach may be reduced.

Protective association and variation in predator abundance.—Although phalaropes preferred coastal areas with gulls, the reproductive consequences of this preference varied strongly between years. Mean hatch success of phalaropes at East Bay over three years was 22%, within the range of success found in other studies (18–77%; Tracy et al. 2002 and references therein). Hatch success differed between years, from 31–35% in 2000 and 2001 to only 5% in 2002. Breeding success of the gulls was also highly variable, with >60% success in 2000 and 2001 and only 3% success in 2002 (Stenhouse et al. 2005). The low hatch success of all birds at East Bay in 2002 coincided with an absence of lemmings and many sightings of arctic foxes and Parasitic Jaegers (Table 4). Similar correlations between lemming abundance, predation, and nest success are well documented for other birds throughout the circumpolar Arctic (e.g., Summers et al. 1998; Bêty et al. 2001, 2002; and references therein).

Parasitic Jaegers, the most common jaeger species at East Bay, are not dependent on lemmings as prey (Wiley and Lee 1999). However, rodents are the primary prey of arctic foxes across much of the Arctic (Stickney 1991, Van Impe 1996). Arctic foxes show numerical and functional responses to changes in lemming abundance (e.g., Wilson and Bromley 2001) and typically prey on eggs and birds when lemmings are scarce (Larson 1960, Summers 1986). At East Bay, arctic foxes were scarce in 2000 but more abundant in 2001, after a high lemming year in 2000. When lemmings were extremely scarce in 2002, arctic fox predation on birds' eggs, an alternative prey, was high (Smith 2003, present study).

Gulls cannot expel arctic foxes from their breeding territories, nor stop them from eating their eggs (Stenhouse et al. 2005). If gulls offer protection from avian predators only, phalaropes would benefit from nesting near them

only in years of low arctic fox predation. In years when foxes seek out eggs, the higher densities of nests in coastal areas and the activity of the colonial birds may in fact attract foxes (Rodgers 1987, Hogstad 1995). Hatch success of phalaropes nesting in areas with gulls was nearly twice that of phalaropes that nested solitarily inland in 2000 and 2001, when arctic fox predation was low. In 2002, when lemmings were scarce and arctic fox predation was high, phalaropes with gulls nearby had lower hatch success than those without.

Across the North, the duration of lemming cycles typically varies from three to five years (Hanski and Korpimäki 1995). If phalaropes benefit from nesting near gulls in all years except those that follow a lemming decline, this trait would be adaptive over an average lemming cycle and over the life of an individual. However, our results do not unequivocally link the differences in phalarope nest success to the presence of gulls. Habitat factors predicted nest survival over all years, whereas the presence of gulls did not. Nests in scrub-willow and moss-carpet habitats survived better, as did nests with intermediate concealment. These nest habitat features, however, predict increased survival in the habitats where gulls nested. Further, phalaropes did not use coastal habitats without gulls, though we detected no habitat differences between coastal areas with and without the latter.

Although the results are not unequivocal, it seems likely that phalaropes nest in a protective association with gulls but that the benefits of this association are influenced by fluctuations in arctic fox predation. Because few birds can defend their nests from foxes, cycles of lemming abundance and arctic fox predation of eggs are likely to have similar effects on other protective nesting associations among tundra birds.

ACKNOWLEDGMENTS

We are grateful to those who contributed in the field, especially R. Bryant, E. Davies, A. Hargreaves, D. Perkins, C. Saunders, I. Stenhouse, and K. Truman. Funding for the study was provided by the Canadian Wildlife Service, Prairie and Northern Region; the Polar Continental Shelf Project; the Natural Sciences and Engineering Research Council; and the Northern Scientific Training Program.

LITERATURE CITED

- ARMSTRONG, E. A. 1956. Distraction display and the human predator. *Ibis* 98:641–654.
- 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.
- 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.
- BLOMQUIST, S., AND M. ELANDER. 1988. King Eider (*Somateria spectabilis*) nesting in association with Long-tailed Skua (*Stercorarius longicaudus*). *Arctic* 41:138–142.
- CAREY, C. 1980. The ecology of avian incubation. *BioScience* 30:819–824.
- CLARK, P. J., AND F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.
- CLARK, R. G., AND D. SHUTLER. 1999. Avian habitat selection: Pattern from process in nest-site use by ducks? *Ecology* 80:272–287.
- DONNELLY, K. 1978. Simulations to determine the variance and edge-effect of total nearest neighbour distance. Pages 91–95 in *Simulation Models in Archaeology* (I. Hodder, Ed.). Cambridge University Press, London.
- DYRCZ, A., J. WITKOWSKI, AND J. OKULEWICZ. 1981. Nesting of 'timid' waders in the vicinity of 'bold' ones as an antipredator adaptation. *Ibis* 123:542–545.
- EBBINGE, B. S., AND B. SPAANS. 2002. How do Brent Geese (*Branta b. bernicla*) cope with evil? Complex relationships between predators and prey. *Journal für Ornithologie* 143:33–42.
- EGEVANG, C., K. KAMPP, AND D. BOERTMANN. 2004. The breeding association of Red Phalaropes with Arctic Terns: Response to a redistribution of terns in a major Greenland colony. *Waterbirds* 27:406–410.
- ERCKMANN, W. J., JR. 1981. The evolution of sex-role reversal and monogamy in shorebirds. Ph.D. dissertation, University of Washington, Seattle.
- 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. Pages 289–377 in *Behavior of Marine Animals*, vol. 5 (J. Burger and B. Olla, Eds.). Plenum Press, New York.
- GÖRANSON, G., J. KARLSON, S. G. NILSSON, AND S. ULFSTRAND. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: An experimental study. *Oikos* 26:117–120.
- GÖTMARK, F., D. BLOMQUIST, 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.
- GUTTMANN, L. 1954. Some necessary conditions for common-factor analysis. *Psychometrika* 19:149–161.
- HAEMIG, P. D. 2001. Symbiotic nesting of birds with formidable animals: A review with applications to biodiversity conservation. *Biodiversity and Conservation* 10:527–540.
- HANSKI, I., AND E. KORPIMÄKI. 1995. Micotine rodent dynamics in northern Europe: Parameterized models for the predator-prey interaction. *Ecology* 76:840–850.
- HEGYI, Z., AND L. SASVÁRI. 1998. Parental condition and breeding effort in waders. *Journal of Animal Ecology* 67:41–53.
- HILDÉN, O., AND S. VUOLANTO. 1972. Breeding biology of the Red-necked Phalarope *Phalaropus lobatus* in Finland. *Ornis Fennica* 49:57–85.
- HINES, J. E., AND J. R. SAUER. 1989. Program CONTRAST: A general program for the analysis of several survival or recovery rate estimates. U.S. Department of the Interior, Fish and Wildlife Service Technical Report, no. 24.
- HOGSTAD, O. 1995. Do avian and mammalian nest predators select for different nest dispersion patterns of Fieldfares *Turdus phaeo*? A 15-year study. *Ibis* 137:484–489.
- HÖHN, E. O. 1971. Observations on the breeding behaviour of Grey and Red-necked Phalaropes. *Ibis* 113:335–348.
- JENNESS, J. 2002. Nearest features, with distances and bearings, version 3.6d. ARCVIEW extension, ESRI, Redlands, California. [Online.] Available at arcscrips.esri.com.
- JOHNSON, D. H. 1979. Estimating nesting success: The Mayfield method and an alternative. *Auk* 96:651–661.

- KISTCHINSKI, A. A. 1975. Breeding biology and behaviour of the Grey Phalarope *Phalaropus fulicarius* in East Siberia. *Ibis* 117:285–301.
- KNIGHT, R. L., AND S. A. TEMPLE. 1986. Why does intensity of avian nest defense increase during the nesting cycle? *Auk* 103:318–327.
- KOSKIMIES, J. 1957. Terns and gulls as features of habitat recognition for birds nesting in their colonies. *Ornis Fennica* 34:1–6.
- KREBS, C. J. 1989. *Ecological Methodology*. Harper Collins, New York.
- LARSEN, T., AND S. GRUNDETJERN. 1997. Optimal choice of neighbour: Predator protection among tundra birds. *Journal of Avian Biology* 28:303–308.
- 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.
- LEAD, S. 2002. Generate randomly distributed points. Arcview extension, ESRI, Redlands, California. [Online.] Available at arcscrips.esri.com.
- 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, AND OTHERS. 2007. Assessing the development of shorebird eggs using the flotation method: Species-specific and generalized regression models. *Condor*. In press.
- MABEE, T. J. 1997. Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bulletin* 109:307–313.
- 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, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455–473 in *Ecology and Conservation of Neotropical Migrant Landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- 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., J. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proceedings of the Royal Society of London, Series B* 267:2287–2293.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MAYFIELD, H. F. 1979. Red Phalaropes breeding on Bathurst Island. *Living Bird* 17:7–39.
- McKINNEY, F. 1965. Spacing and chasing in breeding ducks. *Wildfowl* 16:92–106.
- MONTGOMERIE, R. D., AND P. J. WEATHERHEAD. 1988. Risks and rewards of nest defence by parent birds. *Quarterly Review of Biology* 63:167–187.
- NUECHTERLEIN, G. L. 1981. 'Information parasitism' in mixed colonies of Western Grebes and Forster's Terns. *Animal Behaviour* 29:985–989.
- PAULSON, D. R., AND W. J. ERCKMANN. 1985. Buff-breasted Sandpipers nesting in association with Black-bellied Plovers. *Condor* 87:429–430.
- POPHAM, H. L. 1897. Notes on birds observed on the Yenisei river, Siberia, in 1895. *Ibis* 3:89–108.
- REYNOLDS, J. D. 1985. Sandhill Crane use of nest markers as cues for predation. *Wilson Bulletin* 97:106–108.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions in Zoology*, no. 9.
- RIDLEY, M. W. 1980. The breeding behavior and feeding ecology of Grey Phalaropes *Phalaropus fulicarius* in Svalbard. *Ibis* 122:210–226.
- RODGERS, J. A., JR. 1987. On the antipredator advantages of coloniality: A word of caution. *Wilson Bulletin* 99:269–271.
- SCHAMEL, D., AND D. M. TRACY. 1987. Latitudinal trends in breeding Red Phalaropes. *Journal of Field Ornithology* 58:126–134.
- SIMMONS, K. E. L. 1952. The nature of the predator-reactions of breeding birds. *Behaviour* 4:161–171.
- SMITH, P. A. 2003. Factors affecting nest site selection and reproductive success of tundra nesting shorebirds. M.Sc. thesis, University of British Columbia, Vancouver.

- STENHOUSE, I. J. 2003. The reproductive behaviour and ecology of Sabine's Gulls (*Xema sabini*) in the eastern Canadian Arctic. Ph.D. dissertation, Memorial University, St. John's, Newfoundland.
- STENHOUSE, I. J., H. G. GILCHRIST, AND W. A. MONTEVECCHI. 2001. Reproductive biology of Sabine's Gull in the Eastern Canadian Arctic. *Condor* 103:98–107.
- STENHOUSE, I. J., H. G. GILCHRIST, AND W. A. MONTEVECCHI. 2005. An experimental study examining the anti-predator behavior of Sabine's Gulls (*Xema sabini*) during breeding. *Journal of Ethology* 23:103–108.
- STICKNEY, A. 1991. Seasonal patterns of prey availability and the foraging behaviour of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. *Canadian Journal of Zoology* 69:2853–2859.
- 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., L. G. UNDERHILL, AND E. E. SYROECHKOVSKI, JR. 1998. The breeding productivity of Dark-bellied Brent Geese and Curlew Sandpipers in relation to changes in the numbers of arctic foxes and lemmings on the Taimyr Peninsula, Siberia. *Ecography* 21:573–580.
- SUMMERS, R. W., L. G. UNDERHILL, E. E. SYROECHKOVSKI, JR., H. G. LAPPO, R. P. PRYSGONES, 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.
- TINBERGEN, N., M. IMPEKOVEN, AND D. FRANCK. 1967. An experiment on spacing-out as a defence against predation. *Behaviour* 28:307–321.
- TRACY, D. M., D. SCHAMEL, AND J. DALE. 2002. Red Phalarope (*Phalaropus fulicarius*). In *The Birds of North America*, no. 698 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- VAN IMPE, J. 1996. Long-term reproductive performance in White-fronted Geese *Anser a. albifrons* and Tundra Bean Geese *A. fabalis rossicus* wintering in Zeeland (the Netherlands). *Bird Study* 43:280–289.
- VAN PASSEN, A. G., D. H. VELDMAN, AND A. J. BEINTEMA. 1984. A simple device for determination of incubation stages in eggs. *Wildfowl* 35:173–178.
- WALTERS, J. R. 1990. Anti-predatory behavior of Lapwings: Field evidence of discriminative abilities. *Wilson Bulletin* 102:49–70.
- WILEY, R. H., AND D. S. LEE. 1999. Parasitic Jaeger (*Stercorarius parasiticus*). In *The Birds of North America*, no. 445 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- 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.

Associate Editor: D. B. Lank