

Lower Predation Risk for Migratory Birds at High Latitudes

L. McKinnon,^{1*} P. A. Smith,² E. Nol,³ J. L. Martin,⁴ F. I. Doyle,⁵ K. F. Abraham,⁶ H. G. Gilchrist,⁷ R. I. G. Morrison,² J. Bêty¹

Quantifying the costs and benefits of migration distance is critical to understanding the evolution of long-distance migration. In migratory birds, life history theory predicts that the potential survival costs of migrating longer distances should be balanced by benefits to lifetime reproductive success, yet quantification of these reproductive benefits in a controlled manner along a large geographical gradient is challenging. We measured a controlled effect of predation risk along a 3350-kilometer south-north gradient in the Arctic and found that nest predation risk declined more than twofold along the latitudinal gradient. These results provide evidence that birds migrating farther north may acquire reproductive benefits in the form of lower nest predation risk.

Life history theory predicts that the costs of migration must be compensated for by benefits to lifetime reproductive success (1, 2). Costs of migration include the metabolic and energetic requirements of flight (3), high mortality risk (4, 5), and exposure to extreme weather events (6, 7). Such negative effects are expected to be important for migrant birds that breed in the Arctic, where severe weather events during migration or upon arrival at the breeding grounds can lead to poor body condition, breeding failure, complete reverse migration, and even death (8). Bird migration patterns have been thought to be determined mainly by food availability (9), habitat-related parasite pressures (10), and predation risk during migration (4).

Arctic-nesting birds exhibit some of the most impressive migratory strategies, such as flying from wintering areas at the southern tip of southern America, southern Africa, and Oceania to their breeding grounds in the Arctic (11, 12). The physiological costs of migrating to and breeding at these arctic sites have been well documented for species such as shorebirds (7, 13, 14). Birds could reduce these costs by breeding at more southerly latitudes, thereby decreasing both migration costs and the metabolic costs of breeding in the extreme Arctic environment. However, if competition for food resources, risk of parasite infection, and

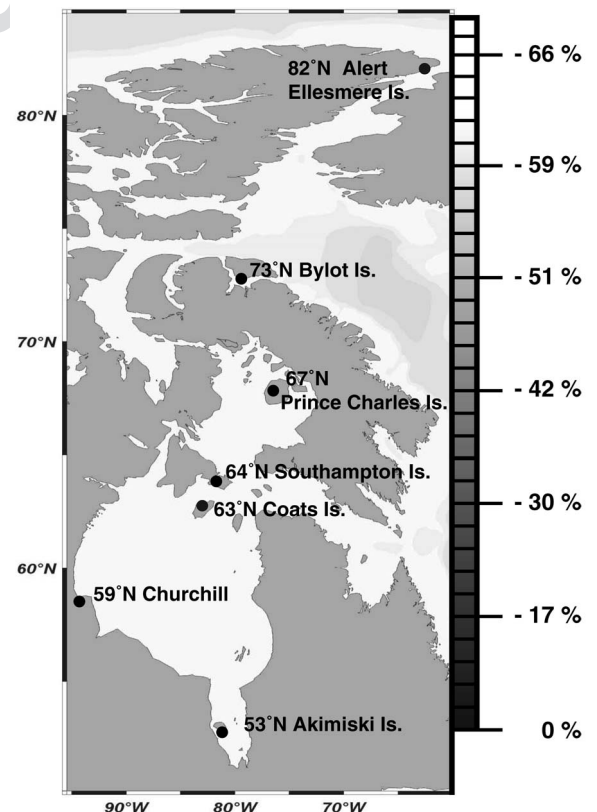
predation at southern sites are high, then increasing migration distance could have reproductive and/or survival benefits. Potential fitness benefits of breeding at higher latitudes have been quantified in terms of reduced parasite loads (15) and greater food availability due to longer daylight hours (16).

Reduced predation at higher-latitude sites has yet to be quantified. Predation risk has emerged as a dominant force in the evolution of avian life history, influencing the selection of nest sites and underlying latitudinal clines in the clutch size of passerines (17). We thus predicted that the risk of nest predation could also play a key role in

balancing the costs of long-distance migration. If so, we would expect a negative relationship between nest predation risk and latitude in Arctic ground-nesting shorebirds. To test for this relationship, we systematically measured predation risk by monitoring predation on eggs placed in 1555 artificial nests for a minimum of two summers at seven shorebird breeding sites (table S1) (18) over a latitudinal gradient of 29° (~3350 km) from sub-Arctic to high-Arctic regions of Canada (Fig. 1). By monitoring artificial nests, we controlled for the heterogeneity in survival associated with real nests [temporal, spatial, interspecific, and intra-specific behavioral differences (19)] to yield a controlled effect of predation risk. We monitored artificial nests during early and late shorebird incubation periods. We then tested for the effect of latitude on predation risk, using Cox proportional hazards regression (18, 20).

As predicted, nest predation risk was negatively correlated with latitude. For an increase in 1° of latitude, the relative risk of predation declined by 3.6% (coefficient -0.0360, SE 0.0045, $\chi^2_1 = 63.77$, $P < 0.0001$; Figs. 1 to 3). This equates to a decrease in predation risk of 65% over the studied latitudinal transect of 29°. Previous studies investigating latitudinal trends in predation risk on the nests of temperate-breeding neotropical migrants failed to detect any clear south-north gradient (21). These differences in results could be attributed to differences in real patterns of predation risk between temperate versus Arctic environments, or they could be due to differences in

Fig. 1. Average latitudinal decrease in predation risk and map of the shorebird breeding sites where artificial nests were monitored. The decrease in predation risk (3.6% per degree relative to the southernmost site, Akimiski Island) is indicated at 5° intervals on the latitudinal scale at right.



¹Département de Biologie, Université du Québec à Rimouski and Centre d'Études Nordiques, Rimouski, Québec, G5L3A1, Canada. ²Environment Canada, National Wildlife Research Centre, Ottawa, Ontario, K1A0H3, Canada. ³Ecology and Conservation Group, Environment and Life Sciences Graduate Program and Biology Department, Trent University, Peterborough, Ontario, K9J7B8, Canada. ⁴Département Dynamique des Systèmes Écologiques, Centre d'Écologie Fonctionnelle et Évolutive, Centre National de la Recherche Scientifique, Montpellier, France. ⁵Wildlife Dynamics Consulting, Telkwa, British Columbia, V0J2X0, Canada. ⁶Wildlife Research & Development Section, Ontario Ministry of Natural Resources, Peterborough, Ontario, K9J7B8, Canada. ⁷Environment Canada, National Wildlife Research Centre and Department of Biology, Carleton University, Ottawa, Ontario, K1S5B6, Canada.

*To whom correspondence should be addressed. E-mail: laura.mckinnon3@gmail.com

EMBARGOED UNTIL 2:00 PM US EASTERN TIME THURSDAY, 14 JANUARY 2010

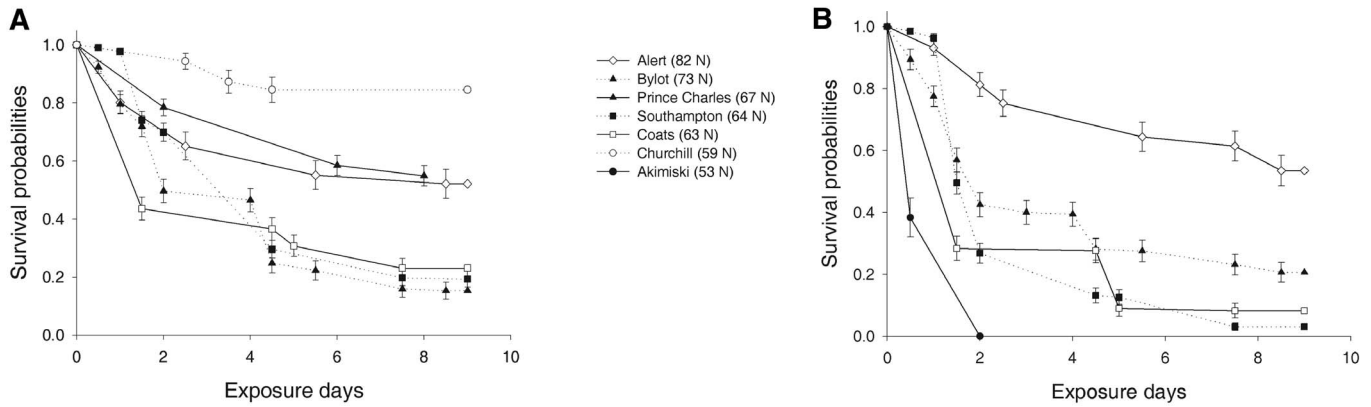
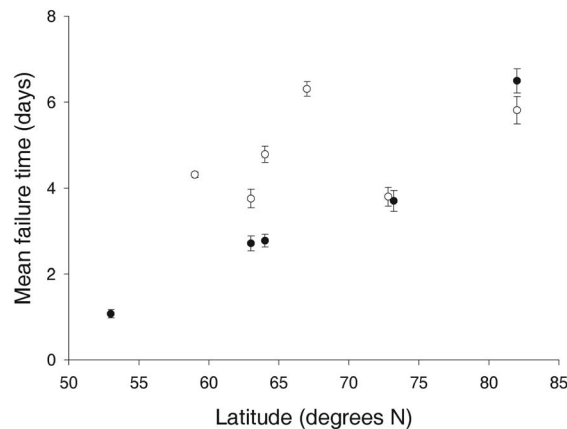


Fig. 2. Kaplan-Meier survival probabilities over 9 exposure days for artificial nests by site for all years during early (A) and late (B) shorebird incubation periods. Each data point on the curve represents the Kaplan-Meier survival

estimate at time t (\pm SEM), which provides the probability that eggs in a nest will survive past time t . Survival probabilities are based on 2 to 4 years of data per site [see table S1 for details (18)]

Fig. 3. Mean failure time in days (\pm SEM) for depredated artificial nests by latitude for all years during early (open circles) and late (solid circles) shorebird incubation periods. Low mean failure times indicate rapid nest loss (high predation risk). Each data point is based on 2 to 4 years of data per site [see table S1 for details (18)]. Overlapping data points for Bylot Island (73° N) have been offset by $\pm 0.2^\circ$.



methodological approaches. In our study, artificial nests enabled us to measure a standardized predation risk, as opposed to the nest success of real nests, which is affected by several factors other than predation pressure (for example, parent birds can compensate for an increased risk of predation by increasing the defense of their nest (22)).

These results provide evidence that the costs of migrating farther north could be compensated for by decreases in predation risk at higher latitudes. However, can lower predation risk at higher latitudes really compensate for the increased migration distances and increased metabolic harshness experienced by high-Arctic-nesting species? Though we may have good estimates of the energetic costs of flying (23) and how standard metabolic rates change with latitude (they increase by 1% per degree of latitude) (24), we still lack the basic understanding of how these variables affect adult survival. The apparent cost associated with migrating to Arctic breeding areas is indicated by the reduced survival of adults that fail to achieve adequate condition before leaving the last spring staging area (7, 13); however, it is not known whether the increased mortality is associated with migration, breeding, or both. To explore these trade-

offs, we require better estimates of demographic parameters for birds breeding at various latitudes, so that we can model the contrasting effects of adult survival versus reproductive components. By combining studies on marked individuals with systematic sampling of ecological conditions experienced on the breeding grounds, we will better be able to link individual itineraries with life history events, thus improving our theoretical understanding of the ecology and evolution of long-distance migration.

References and Notes

1. S. C. Stearns, *Q. Rev. Biol.* **51**, 3 (1976).
2. T. Alerstam, A. Hedenstrom, S. Åkesson, *Oikos* **103**, 247 (2003).
3. M. Wikelski *et al.*, *Nature* **423**, 704 (2003).
4. R. C. Ydenberg, R. W. Butler, D. B. Lank, B. D. Smith, J. Ireland, *Proc. Biol. Sci.* **271**, 1263 (2004).
5. A. J. Baker *et al.*, *Proc. Biol. Sci.* **271**, 875 (2004).
6. R. W. Butler, *Auk* **117**, 518 (2000).
7. R. I. G. Morrison, N. C. Davidson, J. R. Wilson, *J. Avian Biol.* **38**, 479 (2007).
8. B. Ganter, H. Boyd, *Arctic* **53**, 289 (2000).
9. D. J. Levey, F. G. Stiles, *Am. Nat.* **140**, 447 (1992).
10. T. Piersma, *Oikos* **80**, 623 (1997).
11. J. M. Boland, *Condor* **92**, 284 (1990).
12. J. van de Kam, P. J. de Goeij, T. Piersma, L. I. Zwarts, *Shorebirds: An Illustrated Behavioural Ecology* (KNNV Publishers, Utrecht, Netherlands, 2004).

13. R. I. G. Morrison, *Ardea* **94**, 607 (2006).
14. T. Piersma *et al.*, *Funct. Ecol.* **17**, 356 (2003).
15. M. Laird, *C. J. Zool.* **39**, 209 (1961).
16. H. Schekkerman, I. Tulp, T. Piersma, G. H. Visser, *Oecologia* **134**, 332 (2003).
17. T. E. Martin, P. R. Martin, C. R. Olson, B. J. Heidinger, J. J. Fontaine, *Science* **287**, 1482 (2000).
18. See supporting material on Science Online.
19. T. E. Martin, J. Scott, C. Menge, *Proc. Biol. Sci.* **267**, 2287 (2000).
20. D. R. Cox, *J. Royal Stat. Soc. Series B Methodol.* **34**, 187 (1972).
21. T. E. Martin, *Ecol. Monogr.* **65**, 101 (1995).
22. J. Kis, A. Liker, T. Székely, *Ardea* **88**, 155 (2000).
23. A. Kvist, A. Lindström, M. Green, T. Piersma, G. H. Visser, *Nature* **413**, 730 (2001).
24. W. W. Weathers, *Oecologia* **42**, 81 (1979).
25. Funded by ArcticNet, Environment Canada, Fonds Québécois de Recherche sur la Nature et les Technologies, a Garfield Weston Foundation Award for Northern Research, Institut Paul Emile Victor (formerly Institut Français de Recherches et Technologies Polaires), International Polar Year (IPY) Project ArcticWOLVES, Natural Sciences and Engineering Research Council of Canada (Northern Internship Program and Discovery Grant), Northern Ecosystem Initiatives, Northern Scientific Training Program, and the Ontario Ministry of Natural Resources. Logistical support was provided by the Ontario Ministry of Natural Resources, the Polar Continental Shelf Project, Parks Canada, and D. Leclerc. We also thank the Department of National Defense and staff of the Environment Canada weather station for logistic support at Alert; Vicky Johnston and crew for support on Prince Charles Island; the many field assistants that monitored artificial nests: A. Blachford, A. Béchet, J. Carrier, M. Cloutier, A.-M. d'Aoust-Messier, E. d'Astous, T. Daufresne, S. Gan, D. Hogan, L. Jolicoeur, C. Juillet, J.-R. Julien, B. Laliberté, P. Y. l'Hérault, R. Lopez, P. Meister, M. Nelligan, D. Ootoova, L. Qangu, D., C. Rabouam, G. Reid, N. Ward, and S. Williams; G. Gauthier and D. Berteaux, leaders of the IPY ArcticWOLVES project, for fostering collaboration between the authors; and O. Gilg, C. Juillet, L. P. Nguyen, T. Piersma, D. Reid, and two anonymous reviewers for helpful discussions or comments on early versions of the manuscript.

Supporting Online Material

www.sciencemag.org/cgi/content/full/[vol]/[issue no.]/[page]/DC1
Materials and Methods
SOM Text
Table S1
References

7 October 2009; accepted 1 December 2009
10.1126/science.1183010