

to demand. CO₂ even controls the density of stomata; as a compensatory mechanism, their numbers increase if the concentration of CO₂ drops. Similar to animals, a major puzzle has been how plants sense CO₂. Hu *et al.* (2) found that the carbonic anhydrases βCA1 and βCA4 in the model plant *Arabidopsis thaliana* function in CO₂ sensing. Plants lacking the two enzymes were greatly impaired in their response to increases in atmospheric CO₂, showing much less stomatal pore closure. In contrast to the extracellular location of the mouse carbonic anhydrase, the plant enzymes are inside the cell, both adjacent to the cell membrane and inside chloroplasts. Thus, although the enzymatic function of the enzymes—as either transponder or sensor—is conserved, the site of action is very different, implying that the sensing mechanism also may be different. Astonishingly, Hu *et al.* (2) found that expressing a structurally unrelated mammalian α-carbonic anhydrase in *Arabidopsis* plants lacking carbonic anhydrases restored CO₂ responsiveness. This supports the transponder hypothesis, as it is

less probable that the downstream signaling machinery in the plant can function with this very different enzyme.

A key element of stomatal closure is the efflux of ions. Hu *et al.* (2) further showed that intracellular bicarbonate released by carbonic anhydrase activates anion channels in guard cells, allowing ions to efflux, thus triggering the closure of stomatal pores (see the figure). Plants overexpressing the β-carbonic anhydrases in guard cells also improved conservation of water, which suggests a possible means to engineer plants that use less water.

Although plants and humans diverged about 1 billion years ago, they use similar mechanisms to detect CO₂ sensing. Two main observations suggest that their common sensing mechanism must have evolved independently. There is a striking difference in the cellular location of the enzymes. Moreover, there are five classes of carbonic anhydrase enzymes that are unrelated in protein sequence and structure; plants and animals express different family members (6).

Why plants evolved this mechanism is obvious—they need to adjust the valves to optimize CO₂ uptake from the atmosphere while minimizing water loss. In humans, one may speculate that this mechanism was retained to help identify rotting food, and now serves mainly to identify carbonated drinks. The observation that carbonic anhydrase is also present in insect gustatory and olfactory cells and may cooperate with ionotropic receptors (ion channels that, when activated by a ligand, open and permit ion flow) may help to identify how insects and mammals use CO₂ sensors to discern food sources (7).

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ECOLOGY

Explaining Bird Migration

Olivier Gilg^{1,2} and Nigel G. Yoccoz³

Arctic shorebirds can travel tens of thousands of kilometers every year as they fly along intercontinental flyways from their southern wintering grounds to their remote, harsh breeding sites. How these birds solve the navigational and physiological constraints has been largely answered, but why they migrate is still a question with many possible answers (1). On page 326 of this issue, McKinnon *et al.* (2) present a continent-wide study that points to predation as a driving mechanism for migration. The study also elucidates the role of predation in shaping Arctic terrestrial biodiversity.

For migration to be sustained in evolutionary terms, the associated costs and benefits must balance. The costs—higher energetic requirements and mortality risk—increase with flyway length and, hence, with latitude. The benefits of Arctic breeding grounds include open landscapes, per-

manent daylight, time-limited but abundant resources, limited competition, lower pathogen loads, and lower predation pressure, but not all these benefits increase with latitude. For example, if Arctic migrants were just looking for rich and open habitats to be exploited under permanent daylight, they would stop in the low-Arctic zone, never reaching the northernmost regions in Greenland and Canada. Although other hypotheses still need to be properly tested (3), McKinnon *et al.* provide convincing evidence of lowered predation pressure the further north one gets. The authors focus on shorebirds, but their results might be relevant for other ground-nesting birds, because all their sites share a key predator in these ecosystems: the Arctic fox.

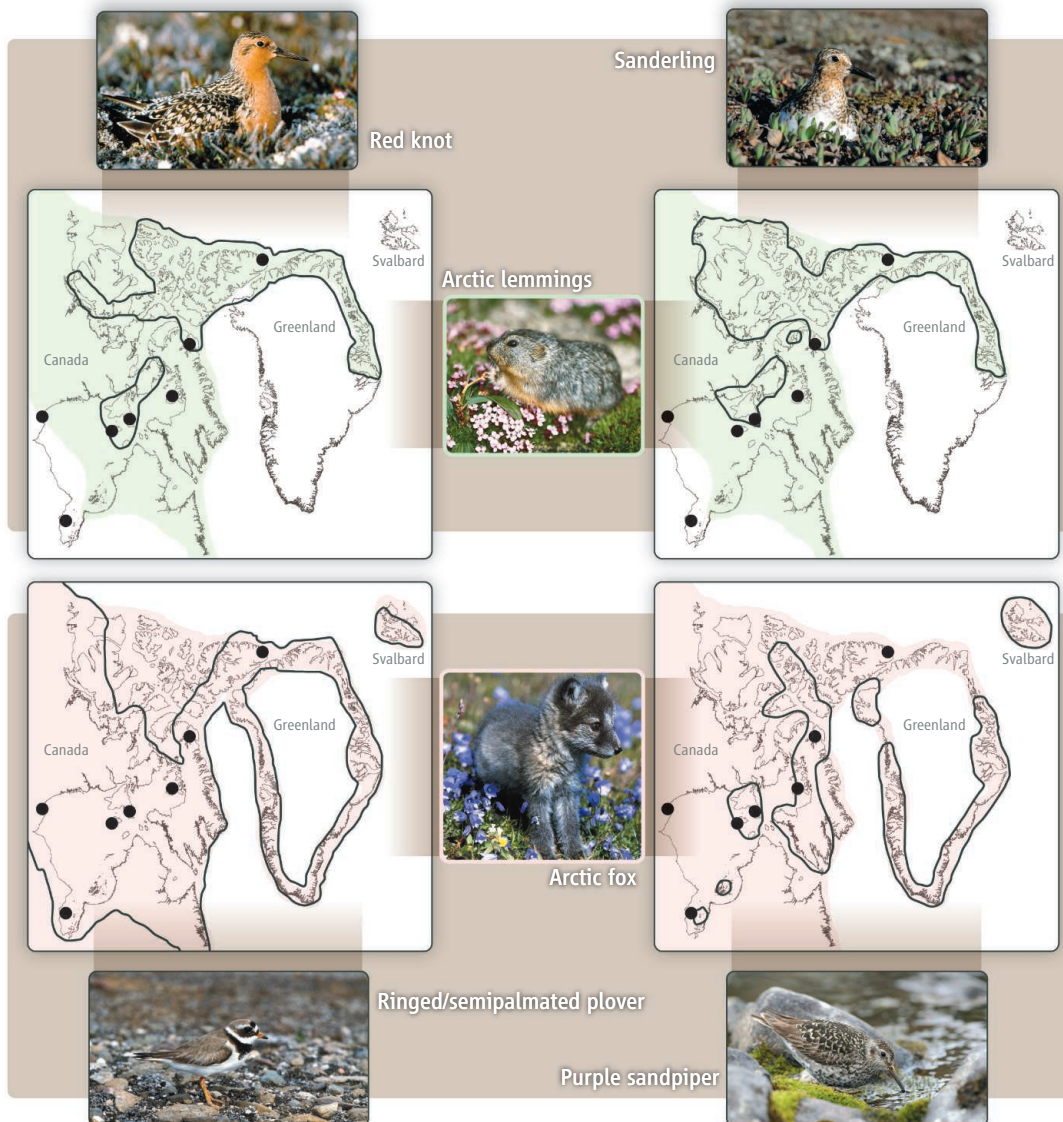
The results also shed light on the dominant role played by predation in the functioning and structuring of Arctic terrestrial vertebrate communities. In this region more than anywhere else, populations are strongly impacted, and sometimes driven, by predator-prey interactions. The key pieces of this puzzle are several species of Arctic lemmings, whose dynamics are typically cyclic. Lem-

Predation pressure falls with increasing latitude, helping to explain why many birds migrate as far north as the high Arctic.

ming densities depend on, but also determine, the functional and numerical responses of predator species (mainly Arctic fox, snowy owl, jaegers, and small mustelids) (4). In turn, the 3- to 4-year lemming cycles strongly affect the dynamics of alternate prey, such as shorebirds and wildfowl, through indirect predator-prey interactions (5–7): In the low phase of the lemming cycle, the fraction of these alternate prey increases in the predators' diets; in the peak phase, predators specialize on lemmings and release their predation pressure on alternate prey. Surprisingly, the mechanisms behind latitudinal trends in predation pressure and the impact of lemming cyclic phases are not discussed by McKinnon *et al.*

In this cat-and-mouse game, shorebirds are both impacting (by contributing to increase predators' survival rates) and impacted by lemming-predator interactions. For the shorebird species that are most sensitive to predation, high predation pressure by the Arctic fox cannot be compensated by reproduction or survival. Viable populations of these species may hence occur only within the lemming distribution range, where the pressure imposed by the Arctic fox is regu-

¹Department of Biological and Environmental Sciences, 00014 University of Helsinki, Finland. ²Lab Biogéosciences, University of Burgundy, 21000 Dijon, France. ³Department of Arctic and Marine Biology, University of Tromsø, 9037 Tromsø, Norway. E-mail: olivier.gilg@gmail.com



Follow the lemmings. Using artificial nests at several field sites in the Canadian Arctic (black dots), McKinnon *et al.* show that Arctic shorebirds face declining predation pressure toward the north (2), an important benefit for long-distance migrants whose biogeography should hence partly be driven by predator-prey interactions. The distribution ranges of several species support the latter hypothesis. In Svalbard and South and West Greenland, lemmings (light green) are absent and terrestrial predators like the Arctic fox (light pink) impose a higher predation pressure on birds. The perfect mismatch between these lemming-free areas and the ranges of some high-Arctic shorebirds (**upper panels**) supports such a predation-driven pattern and suggests that these species are more sensitive to predation than are species that can breed further south or within the entire distribution range of the Arctic fox (**lower panels**). Data are from (14–16) and additional regional sources (17–23).

larly released when lemmings are plentiful (8). Empirical data support this assumption: The highest diversity of *Calidris* species is found within the lemming distribution range (9), and some species (such as Sanderling and Knot) are absent outside of this range (see the figure). Using molecular tools to test for spatial and temporal synchrony in the postglacial expansion of lemmings, fox, and shorebirds, and measuring predation pressures on natural nests from different species and in different communities, should provide additional evidence for the hypothesis, overlooked in previous research [such as (10)], that shorebird biogeography can be explained by predator-prey interactions.

During the 2007–2008 International Polar Year, many large-scale initiatives (11) studied the importance of top-down processes such as changes in predation pressure versus bottom-up processes such as greening of vegetation. The growing evidence that predation is a driving force in structuring Arctic eco-

systems, and the quality of these programs' results, call for the continuation and extension of such circumpolar networks.

Climate change already affects many Arctic species (12). Because these ecosystems are structured by only a handful of species, these changes immediately diffuse to lower and upper trophic levels through strong direct or indirect predator-prey interactions. Scientists in the Arctic must therefore increase their efforts in documenting and modeling changes in predator behavior and dynamics, including the species currently invading from the south (13).

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