Concluding Remarks

It is increasingly recognized that the snowpack is a multiphase reactor in which physical exchange processes, heterogeneous reactions, and photochemical reactions take place. Quantitative understanding is, however, lacking, hampering efforts to simulate snowpack processes. A major problem is that the physical and chemical nature of the surface of snow and ice is not well understood. In particular, it is not clear what effect ionic species contained in snow have on ice surface structure, composition, and chemistry. The composition of most of the snowpack organic carbon has not been determined, and even the inorganic chemistry involving halogen oxidation is ill-defined. The microphysical location of reactive species (particle phase, dissolved in ice, or adsorbed on ice) must also be known if quantitative understanding is to be achieved. Laboratory experiments can help to quantify elementary physical and chemical processes, while model studies can be implemented to assess their global- and regional-scale impacts.

Air-snow interactions may affect the chemical composition of the global atmosphere. The rapid decrease in the global extent of snow cover (58) highlights the need to improve our understanding of this intriguing and highly interdisciplinary area of physical science.

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REVIEW

Environmental Change and Antarctic Seabird Populations

J. P. Croxall,* P. N. Trathan, E. J. Murphy

Recent changes in Antarctic seabird populations may reflect direct and indirect responses to regional climate change. The best long-term data for high-latitude Antarctic seabirds (Adélie and Emperor penguins and snow petrels) indicate that winter sea-ice has a profound influence. However, some effects are inconsistent between species and areas, some in opposite directions at different stages of breeding and life cycles, and others remain paradoxical. The combination of recent harvest driven changes and those caused by global warming may produce rapid shifts rather than gradual changes.

The broad scientific consensus is that the warming of Earth's climate since the 1970s has been at a rate greater than at any time in the last thousand years (1). This has generated concern about the consequential biological and ecological changes, affecting the range and distribution of species; their phenology and physiology; the cycles, composition, and interactions of communities; and the structure and dynamics of ecosystems (2).

There is a widespread belief that Antarctic ecosystems represent more pristine environments than elsewhere on our planet and that the current phase of climate change poses a new challenge to the survival of Antarctic wildlife.

Some of the strongest signals of global climate warming have come from polar regions, especially the Antarctic, where large increases in air temperature and extensive melting of ice shelves have been observed (3–5). It might be supposed, therefore, that concurrent changes in biological responses should be evident, particularly in species at higher levels in food chains, which might integrate and/or amplify effects. However,

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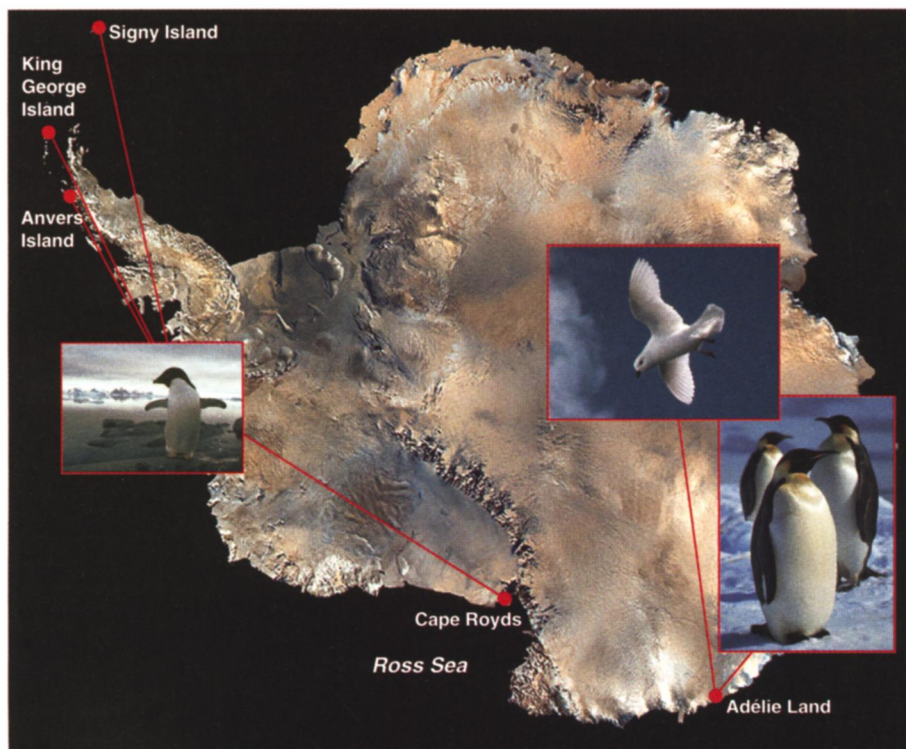
Fig. 1. Topographic map of Antarctica (*34*). Snow petrel: I. Boyd, British Antarctic Survey (BAS); Adélie penguin: P. Bucktrout, BAS; Emperor penguin: P. Cooper, BAS.

interpreting signals of biological response to climate change is complicated by the highly coupled nature of the atmosphere-ice-ocean systems of the Southern Ocean (*4*, *6*).

The bulk of Antarctic wildlife lives in the Southern Ocean that surrounds the continent (Fig. 1). Antarctic marine systems have suffered major perturbation through hunting and fishing over the last two centuries, particularly amongst top predators (*7*). This human harvesting virtually eliminated Antarctic fur seals, penguins at various sites, and most whale species, and it caused overexploitation and collapse of several fish species and stocks. The consequential changes in these ecosystems remain unknown or inferred, but they potentially complicate the detection of changes attributable to climate warming on the marine environments or on the prey on which seabirds rely.

Here we review the evidence from arguably the best studied of vertebrate groups, seabirds. We conclude that many recent changes, particularly in population levels, may plausibly be attributed to climate change but that evidence of clear and consistent patterns, let alone of causal mechanisms, remains equivocal and requires more rigorous and comprehensive study of the processes involved.

Understanding changes in seabird populations requires knowledge of the dynamics of marine ecosystems, which are the most complex, hardest to study, and least understood of Earth's biomes. Studies are

few, time series are short, and quantitative knowledge of the dynamics of interactions between predators, their prey, and environment (including anthropogenic factors) remains very limited.

Nevertheless, some of the most plausible inferences concerning the effects of changes in ice distribution and extent on the distribution and ecology of Antarctic birds have come through studies of three of the most ice-dependent of all species: Adélie penguin (the only one to have been studied in depth at more than one site), Emperor penguin, and snow petrel. Indeed, these studies represent virtually all the long-term data currently available for high-latitude Antarctic seabirds. None of these species suffered exploitation, nor more than minimal anthropogenic effects to their part of the ecosystem, at least until very recently.
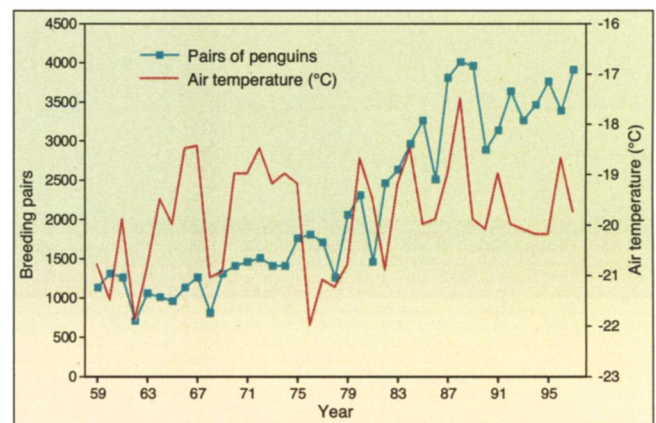
Adélie Penguin

Adélie penguins (*Pygoscelis adeliae*) are found around the entire Antarctic. Despite depending on access to snow-free ground, they breed further south (in summer) than any other penguin. In winter, they appear dependent on the

zone of sea ice within 100 km of the pack-ice edge, known as the marginal ice zone (MIZ), where they forage for Antarctic krill (*Euphausia superba*) and small fish (*8*). In summer, when they depend almost exclusively on krill, the late breakout of ice can prevent them from breeding or seriously affect their breeding success, given the brevity of the Antarctic summer at high latitudes (*7*).

The paleoecological record for Adélie penguins indicates fluctuations in their appearance and disappearance in close conjunction with ice cover. At the last glacial maximum [19,000 years before the present (yr B.P.)], Adélie penguins were virtually if not entirely absent from Antarctica (*9*, *10*). As the Antarctic ice shelves retreated after large-scale warming, Adélie penguin colonies rapidly appeared and extended deep into the Ross Sea, eventually (during a period ~6000 yr B.P. when climate was warmer than nowadays) colonizing areas of east Antarctica from which they are absent today (*3*, *9*, *10*).

We may therefore interpret Adélie population changes of the last few decades in terms of ice distribution caused by climate warming. In the Ross Sea (where 32% of Adélie penguins breed), sea-ice cover was extensive and persistent throughout the 1960s. During this time, Adélie populations remained low but stable. When temperatures rose (Fig. 2) and ice cover decreased in the 1970s, populations increased. Since 1979, population trends have been inversely related to the extent of winter sea-ice (*11*, *12*). No relation was found between population in one year and sea-ice extent in the preceding year. Instead, the best predictor of Adélie penguin population change in this area was maximum winter sea-ice extent 5 years earlier, indicating that juvenile survival, expressed in terms of recruitment to the breeding population at an average age of 4 to 5 years (*11*), was crucial. Independent of sea ice extent, there were also significant correlations with the El

Fig. 2. Trends in breeding population of Adélie penguin in the Ross Sea in relation to air temperature. Penguin data from Cape Royds; air temperature data from Ross Island (*10*, *11*).
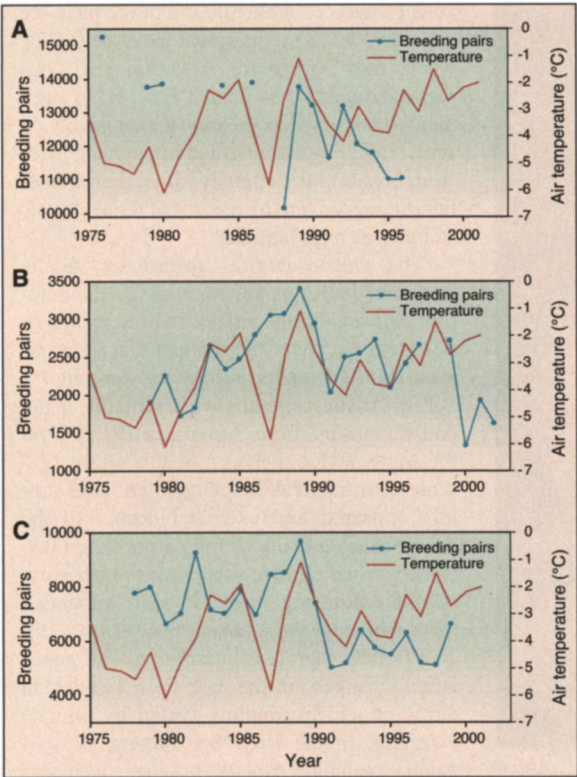
Fig. 3. Trends in Adélie penguins in western Antarctica in relation to air temperature. (**A**) Anvers Island; penguin data from (*18*). (**B**) Signy Island; penguin data from (*19, 35*). (**C**) King George Island; penguin data from (*20*). Air temperature data, from closest source to each site, from (*36*).

Niño-Southern Oscillation (ENSO) index (*11, 12*), suggesting links with the coupled variability in the physical systems influencing the Southern Ocean (*3–6*).

It has been suggested that greater ice extent provides two problems for young, inexperienced Adélie penguins (*11*). First, more extensive and consolidated ice provides fewer areas of open water for feeding. Second, more northerly ice extent may constrain foraging to areas outside the food-rich waters just south of the Antarctic circumpolar cur-

rent. Nevertheless, it remains difficult to understand why it is mostly the juvenile penguins that are affected.

On the western side of Antarctica, on the Antarctic Peninsula and its associated island groups, Adélie penguins face a very different situation (Fig. 3). Here, warming has been more rapid than elsewhere in the region (*5, 13, 14*), resulting in a steady decrease in the extent of the winter and spring sea-ice (*13, 14*) that are essential as wintering habitats for Adélie penguins.

The Adélie penguin populations in this region increased substantially between the 1950s and 1970s. They then stabilized or decreased in the 1980s, and, at some sites, in the 1990s (*15–18*) (Table 1). Data from King George Island, South Shetland Islands, and Signy Island, South Orkney Islands reveal positive correlations between population size and the extent of winter sea-ice (*19, 20*). At King George Island, an additional positive correlation with recruitment (juvenile survival) in the following year was found (*20*) (Table 2).

These results are almost the converse of those in the Ross Sea. It has been suggested that in western Antarctica, sea-ice extent has reduced beyond the optimum for Adélie penguins and that good conditions for them are attained only in years of large, northward extent of ice (*11*). The quite substantial differences in population patterns between sites (especially the more systematic decrease at Anvers Island) are usually explained by invoking discrete wintering areas for the differ-

ent populations (*18*). This remains to be tested by critical study of winter habitats and ranges, for example with satellite tracking.

The positive correlation between sea-ice extent and successful reproduction and recruitment of krill (*3, 21*) may reflect greater availability of food to krill in years when ice cover is more extensive. In western Antarctica, some additional support for such linkages between population processes and ice cover comes from population changes in Chinstrap penguins (*Pygoscelis antarctica*), which are the closest relatives of the Adélie penguins but are confined to habitats lacking ice-cover, where they also feed on krill. Both species showed sustained population increases in the 1950s through 1970s, but those of the Chinstrap penguins persisted longer; at some sites their population is still increasing (*15–18*). Chinstrap populations at King George Island and Signy Island are inversely correlated with sea-ice extent in winter (*19, 20*) (Table 2), fulfilling predictions that Chinstrap and Adélie penguins may show reciprocal responses to the extent of ice cover.

These hypotheses remain tentative, especially for the Ross Sea, where differences in adult and juvenile survival need further critical study. However, except in the Ross Sea, the continuing loss of sea-ice habitat is likely to lead to further population reductions for Adélie penguins.

Emperor Penguin

Emperor penguins (*Aptenodytes forsteri*) are justly celebrated for their unique adaptations for survival under the most demanding conditions of any polar bird. They breed throughout the Antarctic winter (mainly feeding on small fish but also squid and krill) so that their chicks can fledge before the ice on which their colonies are situated breaks up and the food supplies increase (*22*).

The only long-term data set for this species, from Adélie Land, shows that populations were essentially stable from the 1950s

Table 1. Decadal trends in breeding populations of Antarctic penguins [sources referenced in (*15, 17*)].

	Decade				
Location	1951–1960	1961–1970	1971–1980	1981–1990	1991–2000
Emperor penguin					
Adélie Land	Stable	Stable	Decrease	Stable	Stable
Adélie penguin					
Ross Sea		Stable	Increase	Increase/decrease	Fluctuate
East Antarctica		Increase		Increase	Increase
King George Island	Increase	Increase	Stable	Stable/decrease	Stable
Signy Island	Increase	Increase	Stable	Increase/decrease	Fluctuate
Anvers Island	Increase	Increase	Decrease	Stable	Decrease
Chinstrap penguin					
King George Island	Increase	Increase	Stable	Decrease	Decrease
Signy Island	Increase	Increase	Increase	Fluctuate	Decrease
Anvers Island			Increase	Increase	Increase

Table 2. Relations between population variables and sea-ice extent (Rel. with SIE). t, year; Y, annual index; W, winter; +, positive; −, negative; n.s., not significant, ref., corresponding reference number from which data is derived.

Variable	Rel. with SIE	Ref.
Emperor penguin		
Adélie Land		
Adult survival	Y+*	23
Breeding success	n.s.	23
Hatching success	W−†	23
Adélie penguin		
Ross Sea		
Population size (t + 5)	W−†	10
King George Island		
Population size (t + 1)	W+	20
Recruitment (t + 1)	W+	
Adult survival	n.s.	
Signy Island		
Population size (t + 1)	W+	19
Chinstrap penguin		
Signy Island		
Population size (t + 1)	W−	19
Snow petrel		
Adélie Land		
Proportion breeding	W−	30
Breeding success	S+‡	30
Hatching or fledging success	n.s.	30
Fledging condition	W+	30
Adult survival	W−§	31

*Also negative correlation with sea surface temperature. †Also negative correlation with Southern Oscillation Index. ‡Also negative correlation with local snowfall in spring (*29*). §Negative relation to sea surface temperature but n.s.

to the mid-1970s, followed by a rapid decline until about 1982. Since then, populations have fluctuated around a level about half of that in the 1960s (*24*) (Fig. 4). This decrease was apparently caused by a significant reduction (about 10% per annum, corresponding to halving life expectancy) in adult survival from 1973 to 1979. Breeding success was unaffected, suggesting that the decrease was caused by environmental effects distant from the breeding colonies (*23*). Adult survival was strongly positively correlated with years of extensive sea-ice and strongly negatively correlated with years of warm sea surface temperatures (*23*) (Fig. 4).

These results are almost exactly the converse of those for Adélie penguins in the nearby Ross Sea, although in both cases sea-ice extent and processes relating to the Southern Oscillation appear to influence seabird population dynamics. These influences are presumably mediated through the availability or abundance of prey, but the mechanisms are unknown.

The reduction in adult survival, associated with environmental changes, may explain the decrease in Emperor penguin populations, but does not explain why the population did not recover once adult survival recovered in 1981 to the levels prevailing before 1973. Possible explanations may involve habitat features affected by climate warming. First, many Emperor penguin colonies are close to polynyas (permanent open water areas surrounded by ice), which may allow Emperors to forage efficiently in winter (*24, 25*). However, recent data on the location of winter-persistent polynyas (*26, 27*) suggest that the match with Emperor penguin colonies is less close than previously recognized, as several major colonies have no polynyas nearby. Second, after breeding, Emperor penguins must haul out onto pack-ice to molt. They require ice that will not break up during the 3 to 4 week molting period, as birds will perish if they have to swim any distance (*28*). Pack-ice is at its annual minimum in January and February, when Emperors molt (*28*) and has been steadily receding in several, if not most, Antarctic sectors where Emperors occur. This may be another decisive influence on the survival of both adult and juvenile Emperor penguins.

The interactions of Emperor penguins with sea-ice are thus particularly complex. During the winter breeding season, reduced pack-ice extent may depress adult survival but increase hatching success, resulting in an overall decreased breeding population. Climate warming may maintain more and larger polynya close to colonies, which could improve both breeding success and adult survival at this time. But after breeding, reduced access to ice suitable for molting may adversely affect survival of adults, fledglings, and juveniles. Current data on environment-prey-population interactions are insufficient for deriving a single coherent model that explains these observations.
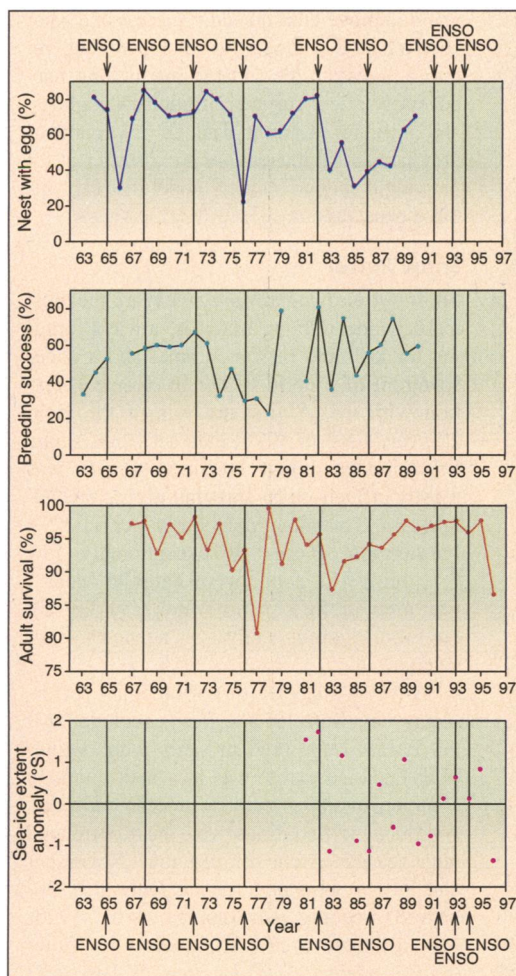
Snow Petrel

Snow petrels (*Pagodroma nivea*) are the most ice-dependent flying seabirds, always foraging for krill and fish in summer and a wider spectrum of prey in winter in close association with ice. A first analysis of the main 27-year (1963 to 1990) data set from Adélie Land indicated that breeding success was mostly influenced by snowfall during the October to November incubation period (*29*). Furthermore, years of exceptionally low breeding performance were stated to occur 1 year after strong El Niño events (*29*) (Fig. 5), but more rigorous analysis is needed to substantiate this.

A recent analysis (*30*) of breeding performance data from 1973 to 1999 concluded that the fewest birds bred in years when winter (July) sea-ice extent was at a maximum. In contrast, overall breeding success and body condition of fledglings were best correlated with sea-ice extent the previous November and July to September, respectively (*30*). Improved breeding performance in the 1990s was attributed to overall increase in winter sea-ice extent (*30*). Data from 1981 to 1997 indicated that adult survival was inversely related to winter sea-ice extent (*31*). This unexpected result (*31*) might be related to a concurrent reduction in polynya, a habitat much favored by snow petrels. Nevertheless, it is difficult to reconcile all these interpretations on the basis of essentially the same data set, though it is not impossible that both local snowfall and regional sea-ice extent are expressions of the same physical processes.
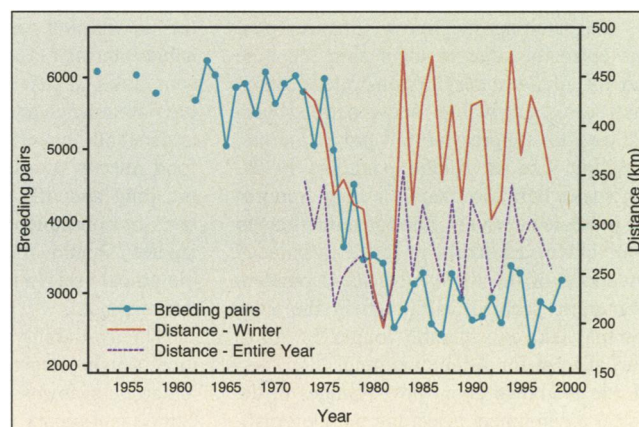
Fig. 4. Trends in breeding population of Emperor penguins at Pointe Geologie, Adélie Land, in relation to distance between colony and northern limit of pack ice. Data from (*23*).

Fig. 5. Trends in snow petrel breeding population (nest with egg), breeding success, and adult survival in relation to years of strong ENSO events (vertical lines) and sea-ice extent anomaly. Data from (29, 30).

Future Prospects and Perspectives

Sea-ice extent in winter has a profound influence on all three species of seabirds discussed here, at least at some stage of their breeding and life cycle. Usually the relation is a positive one—more ice means greater survival or breeding success (Table 2). The main exceptions are hatching success in Emperor penguins (probably due to increasing the time taken for adults to reach open-water feeding areas), adult survival in snow petrels (perhaps due to suppression of polynya), and population size of Adélie penguins in the Ross Sea (where too much ice may compromise juvenile survival). Further reductions in sea-ice extent are likely to result in reduced populations of the three most ice-dependent of Antarctic seabirds, although in the Ross Sea it may take considerably longer for this to occur, at least for Adélie penguins.

Little is known about how changes in the physical environment affect the marine organisms on which seabirds feed. Some plausible hypotheses are emerging for Antarctic krill (3, 21), but these are not the main prey for Emperor

penguins or snow petrels. The nature of their prey suggests that direct effects of ice-cover on prey abundance and availability may only be part of the picture, even for the high-latitude Southern Ocean. Knowledge of the interactions between processes originating in the Southern Ocean and those originating outside the system (such as the ENSO) will be crucial to understanding the dynamics of the nekton (such as fish and squid) and zooplankton prey of seabirds. At lower latitudes in the Southern Ocean, there is evidence of potential large-scale regime shifts over the last 20 years with major consequences for krill-dependent species (32). These consequences not only include reductions in penguin and albatross populations but also massive increases in Antarctic fur seals (33). Other changes have involved copepods, squid, and myctophid fish, including the steady increase in King penguins, which feed on myctophids, over the last 50 years (17).

It remains unknown whether these changes were stimulated by previous removals from the Antarctic system of seals and whales or are the product of interactions between physical and biological processes. However, the combination of historical harvest-driven changes to Southern Ocean ecosystem dynamics with the changes engendered by global warming may produce not just gradual changes in oceanographic and food chain dynamics but more rapid shifts between alternative trophic pathways.

To resolve these questions, we must understand quantitatively the climatic and environmental processes and their seasonal interactions with biological environments and population processes. The few long-term demographic studies of vertebrates must be analyzed in conjunction with accurate data on the distribution, extent, and nature of their habitat during breeding and nonbreeding seasons alike, together with at least indices of prey abundance and availability. We need to understand the effects of environment and food supply at different stages of seabird breeding and life cycles in order to predict rates or consequences of change. Long-term studies should focus on sites chosen for biological relevance, rather than logistic convenience.

The availability of novel tracking and remote-sensing technology and the ability of Antarctic seabirds—especially penguins—to carry instruments for monitoring activity as well as physical and biological environmental conditions (and even provide estimates of encounter rate with prey) have great potential

for exciting advances in understanding how polar seabirds will respond to environmental change.

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