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Review

# Pollution, Habitat Loss, Fishing, and Climate Change as Critical Threats to Penguins

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**Abstract:** *Cumulative human impacts across the world's oceans are considerable. We therefore examined a single model taxonomic group, the penguins (Spheniscidae), to explore how marine species and communities might be at risk of decline or extinction in the southern hemisphere. We sought to determine the most important threats to penguins and to suggest means to mitigate these threats. Our review has relevance to other taxonomic groups in the southern hemisphere and in northern latitudes, where human impacts are greater. Our review was based on an expert assessment and literature review of all 18 penguin species; 49 scientists contributed to the process. For each penguin species, we considered their range and distribution, population trends, and main anthropogenic threats over the past approximately 250 years. These threats were harvesting adults for oil, skin, and feathers and as bait for crab and rock lobster fisheries; harvesting of eggs; terrestrial habitat degradation; marine pollution; fisheries bycatch and resource competition; environmental variability and climate change; and toxic algal poisoning and disease. Habitat loss, pollution, and fishing, all factors humans can readily mitigate, remain the primary threats for penguin species. Their future resilience to further climate change impacts will almost certainly depend on addressing current threats to existing habitat degradation on land and at sea. We suggest protection of breeding habitat, linked to the designation of appropriately scaled marine reserves, including in the High Seas, will be critical for the future conservation of penguins. However, large-scale conservation zones are not always practical or politically feasible and other ecosystem-based management methods that include spatial zoning, bycatch mitigation, and robust harvest control must be developed to maintain marine biodiversity and ensure that ecosystem functioning is maintained across a variety of scales.*

**Keywords:** bycatch, habitat degradation, marine pollution, overfishing, resource competition, switch

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Contaminación, Pérdida de Hábitat, Pesca y Cambio Climático como Amenazas Críticas para los Pingüinos

**Resumen:** *Los impactos humanos acumulativos a lo largo de los océanos del planeta son considerables. Por eso examinamos un solo modelo de grupo taxonómico, los pingüinos (Spheniscidae), para explorar cómo las especies y las comunidades marinas pueden estar en riesgo de disminuir o de extinguirse en el hemisferio sur. Buscamos determinar la amenaza más importante para los pingüinos y sugerir métodos para mitigar estas amenazas. Nuestra revisión tiene relevancia para otros grupos taxonómicos en el hemisferio sur y en las latitudes norteñas, donde los impactos humanos son mayores. Nuestra revisión se basó en una evaluación experta y una revisión de literaratura de las 18 especies de pingüinos; 49 científicos contribuyeron al proceso. Para cada especie de pingüino, consideramos su rango y distribución, tendencias poblacionales y las principales amenazas antropogénicas en aproximadamente los últimos 250 años. Estas amenazas fueron la captura de adultos para obtener aceite, piel y plumas y el uso como carnada para la pesca de cangrejos y langostas: la recolección de huevos; la degradación del hábitat terrestre; la contaminación marina; la pesca accesoria y la competencia por recursos; la variabilidad ambiental y el cambio climático; y el envenenamiento por algas tóxicas y enfermedades. La pérdida de hábitat, la contaminación y la pesca, todos factores que los humanos pueden mitigar, siguen siendo las amenazas principales para las especies de pingüinos. Su resiliencia futura a más impactos por cambio climático dependerá certeramente de que nos enfoquemos en las amenazas actuales a la degradación de hábitats existentes en tierra y en el mar. Sugerimos que la protección de hábitats de reproducción, en conjunto con la designación de reservas marinas de escala apropiada, incluyendo alta mar, será crítica para la conservación futura de los pingüinos. Sin embargo, las zonas de conservación a gran escala no son siempre prácticas o políticamente viables, y otros métodos de manejo basados en ecosistemas que incluyen la zonificación espacial, la mitigación de captura accesoria, y el control fuerte de captura deben desarrollarse para mantener la biodiversidad marina y asegurar que el funcionamiento de los ecosistemas se mantenga a lo largo de una variedad de escalas.*

**Palabras Clave:** captura accesoria, competencia por recursos, contaminación marina, degradación de hábitat, sobrepesca

## Introduction

Many fisheries across the world's oceans are depleted (e.g., Cury et al. 2011; Pikitch 2012). Other changes in coastal ecosystems have also occurred, brought about by land-based activities that modify or destroy natural habitats, cause runoff of sediments, nutrients, toxins, and pollutants, and even alter the flow of currents and tides. Changes in offshore ecosystems include the extraction of mineral resources, pollution from vessel traffic, and the construction of infrastructure for oil development or offshore wind farms (e.g., Halpern et al. 2008). Across the world's oceans, the regions with the largest cumulative impacts from multiple stressors are generally in the northern hemisphere; however, cumulative impacts in southern latitudes are also substantial but generally lower (Halpern et al. 2008). Southern latitudes are less studied; therefore, we assessed a single widespread taxonomic group, penguins (Spheniscidae), to examine how humans affect marine systems across southern latitudes.

Seabird populations integrate spatial and temporal variability in their physical environment and in prey, so they are often considered reasonable proxies of ecosystem status (e.g., Mallory et al. 2010). Penguins and their population processes potentially reflect local or regional oceanic conditions better than any other seabird group. This is because they are highly constrained in their foraging habitat, particularly during their breeding season (Ropert-Coudert et al. 2004). In contrast, volant seabirds, which are able to range beyond their immediate neighborhood, can compensate for deficiencies in local foraging conditions. Penguin populations therefore potentially reflect both natural variability and directional change in oceanographic production within several hundred kilometers of their colonies, including changes induced by human activities. Consequently, penguins have been identified as marine sentinels (Boersma 2008) and have been used as ecosystem monitoring species in long-term ecological research programs (Agnew 1997).

We chose penguins as our model taxonomic group because their ecology and life history is well known. Their conservation status and threats have recently been reviewed (García-Borboroglu & Boersma 2013), and, as charismatic species, they are of considerable public concern. The family has 6 extant genera (Davis & Renner 2003) that include 18 species (Table 1): 2 large *Aptenodytes*, both of which are long-range oceanic foragers that breed in either the Antarctic or Sub-Antarctic; 3 *Pygoscelis* or brush-tailed penguins, also mainly Antarctic or Sub-Antarctic; 7 *Eudyptes* or crested penguins, inhabiting Sub-Antarctic or temperate regions; *Megadyptes* and *Eudyptula* each with a single species, both of which are mainly temperate; and 4 *Spheniscus* or banded penguins, which occupy temperate to tropical areas.

Populations of many penguin species have declined substantially in the past 2 decades. The 1996 International Union for Conservation of Nature Red List reported 5 species as threatened. In 2013, 11 species (60%) were

**Table 1. Estimated values for risk,[a] severity,[b] and impact,[c] respectively, for anthropogenic threat factors for penguins based on expert opinion.**

| *Main center for breeding population* | *Species* | *Harvest of animals* | *Harvest of eggs* | *Habitat degradation* | *Marine pollution* | *Fisheries bycatch* | *Fisheries competition* | *Climate variability* | *Climate change* | *Disease* | *IUCN[d] threat category* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Polar | Emperor Penguin | 000 | 000 | 000 | 000 | 000 | 000 | 111 | 122 | 000 | NT |
| | Adélie Penguin | 000 | 000 | 000 | 000 | 000 | 100 | 212 | 122 | 000 | NT |
| Sub-Antarctic | King Penguin | 000 | 000 | 000 | 000 | 000 | 000 | 111 | 122 | 100 | LC |
| | Chinstrap Penguin | 000 | 000 | 000 | 000 | 000 | 100 | 212 | 122 | 000 | LC |
| | Gentoo Penguin | 000 | 100 | 000 | 000 | 000 | 100 | 200 | 122 | 000 | NT |
| | Macaroni Penguin | 000 | 000 | 000 | 000 | 000 | 100 | 212 | 122 | 111 | VU |
| | Royal Penguin | 000 | 000 | 000 | 000 | 000 | 000 | 000 | 100 | 100 | VU |
| | Southern Rockhopper Penguin | 100 | 000 | 224* | 100 | 000 | 000 | 122 | 100 | 100 | VU |
| | Northern Rockhopper Penguin | 000 | 100 | 212 | 111 | 000 | 000 | 212 | 100 | 000 | EN |
| Oceania | Little Penguin | 000 | 000 | 224* | 100 | 111 | 000 | 111 | 122 | 100 | LC |
| | Fiordland Penguin | 000 | 000 | 326** | 100 | 224* | 000 | 000 | 100 | 000 | VU |
| | Snares Penguin | 000 | 000 | 000 | 000 | 133* | 100 | 000 | 100 | 000 | VU |
| | Erect-crested Penguin | 000 | 000 | 000 | 000 | 000 | 000 | 000 | 100 | 000 | EN |
| | Yellow-eyed Penguin | 000 | 000 | 339*** | 000 | 224* | 000 | 000 | 100 | 224* | EN |
| Africa | African Penguin | 100 | 000 | 224* | 326** | 000 | 339*** | 224* | 122 | 212 | EN |
| South America | Magellanic Penguin | 000 | 100 | 212 | 224* | 326** | 224* | 122 | 122 | 224* | NT |
| | Humboldt Penguin | 100 | 100 | 224* | 100 | 326** | 236** | 224* | 122 | 000 | VU |
| | Galápagos Penguin | 000 | 000 | 326** | 000 | 000 | 000 | 236** | 122 | 212 | EN |

[a] *Risk values: 0, currently does not occur; 1, currently occurs at some locations; 2, currently occurs periodically across multiple sites; 3, currently a chronic problem across the species range.*
[b] *Severity values: 0, no effects on population processes; 1, some effects on population processes; 2, repeated effects on population processes; 3, widespread effects on population processes.*
[c] *Impact is risk × severity (e.g., 3 [risk] × 2 [severity] = 6 [impact]). Asterisks indicate impact values that have substantial negative effects (the more asterisks, the higher the effect).*
[d] *Current International Union for Conservation of Nature threat status: LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered.*

listed as threatened (5 endangered and 6 vulnerable), 2 as near threatened, and 5 as of least concern (Table 1). Seabirds, in general, are the most threatened bird group (Croxall et al. 2012), and after the albatrosses (Diomedeidae), the penguins are the most threatened seabird taxon.

Species classified as endangered or vulnerable occur mainly in South America (Galápagos [*Spheniscus mendiculus*] and Humboldt [*Spheniscus humboldti*]), Africa (African [*Spheniscus demersus*]), New Zealand (Yellow-eyed [*Megadyptes antipodes*], Snares [*Eudyptes robustus*], Fiordland [*Eudyptes pachyrhynchus*], and Erect-crested [*Eudyptes sclateri*]) or in the Sub-Antarctic (Southern Rockhopper [*Eudyptes chrysocome*], Northern Rockhopper [*Eudyptes moseleyi*], Macaroni [*Eudyptes chrysolophus*], and Royal [*Eudyptes schlegeli*]) (Table 1). A number of these species have small populations or a limited geographic range. Rates of population decline for some species have been considerable, but the causes are often unknown.

Based on the species assessments in García-Borboroglu and Boersma (2013), we determined the main anthropogenic threats to penguins and devised recommendations for the short- and long-term conservation of penguin populations.

## Methods

The comprehensive species-specific literature reviews for each of the 18 penguin species contained in García-Borboroglu and Boersma (2013) included contributions from 49 specialists. Each assessment was subjected to independent peer review and thus represents the best available information for each species. We used these assessments to summarize species-specific information on, in particular, the main anthropogenic factors threatening each species over the past approximately 250 years. We categorized these threats into 9 general themes: harvesting of adults for oil, skin, and feathers and as bait for crab and rock lobster fisheries; harvesting of eggs (hereafter, egging); terrestrial habitat degradation; marine pollution; fisheries bycatch and resource competition; environmental variability and climate change; and toxic algal poisoning and disease.

For each threat factor, we produced 3 indexes, based on expert opinion and agreed upon through consensus (Table 1). Because we were not equally familiar with all species, a consensus approach was favored.

We developed a scale for estimating the risk of whether a given threat factor was thought: not to occur for a given species (0); to occur only at some locations (1); to occur periodically across multiple sites (2); or to be a chronic problem across the species range (3). In addition, we produced a scale of threat severity for whether a given threat factor was thought: not to have any effects on penguin population processes (0); to have some effects on population processes (1); to have repeated effects on population processes (2); or to have widespread effects on population processes (3). We also estimated impacts based on the interaction of risk and severity of the threat (risk × severity).

Threats, such as harvesting and egging, are largely of historical significance; nevertheless, knowledge of these activities can facilitate interpretations of current population processes. In contrast, habitat degradation, pollution, and fisheries interactions reflect current anthropogenic pressures on penguin habitats, both at sea and on land. Climate change and disease may play a relatively minor role now but are likely to become increasingly important over time.

## Results

### Harvest for Oil, Skin, and Feathers and as Bait

In the past, several species of penguin were harvested for oil, skin, and feathers and as bait in commercial fisheries across numerous sites, particularly where they were abundant, generally leading to population declines, sometimes to a very great extent. However, the use of penguins generally declined alongside the decline of other species (seals and whales) targeted throughout much of the 18th, 19th, and early 20th centuries. Such practices are now rare, either because penguin harvesting became uneconomical or because more enlightened management practices prevailed.

### Egging

Historically, egging was common practice for Northern Rockhopper, Yellow-eyed, African, Magellanic (*Spheniscus magellanicus*), and Humboldt penguins in temperate and mid-latitude areas. The effects of egging on these populations may have been substantial and sufficient to cause large population decreases in some species (e.g., Shannon & Crawford 1999); however, in general, the impacts remain unquantified (e.g., Bonner 1984).

In the Antarctic and Sub-Antarctic, eggs of the 3 brush-tailed penguin species were harvested by sealers and whalers until well into the 1950s (Bonner 1984). Egging in northern Gentoo Penguin (*Pygoscelis papua*) populations continues today with legally and strictly controlled collections in the Falkland Islands (Malvinas) (Clausen & Pütz 2002).

Egging may be considered an outdated practice, particularly if not closely supervised and especially where there are no robust analyses of local population size and trend to quantify a sustainable harvest. The impacts of disturbance associated with modern egging practices also remain unknown, but they may be considerable.

**Terrestrial Habitat Degradation**

Habitat degradation is a major threat to most Sub-Antarctic, temperate, and tropical penguin species. At some breeding sites, introduced grazing animals have substantially reduced vegetation cover, which has affected penguin populations. For example, on the Falkland Islands (Malvinas), domestic livestock destroyed the tussock fringe that provided cover for Northern Rockhopper chicks, which increased their mortality during heavy rainfall (Demongin et al. 2010b). Consequently, any further loss of the tussock fringe on the Falkland Islands (Malvinas), Staten Island, and some islands in the Indian Ocean should be halted. In breeding areas of Southern Rockhopper Penguins, habitat destruction, particularly the burning of lowland tussock areas to create agricultural land, is likely to have been a major factor in the past, especially with the settlement of Amsterdam Island and Tristan da Cunha.

Grazing by rabbits (*Oryctolagus cuniculus*) at Macquarie Island has caused landslides that killed penguins and destroyed nesting habitat. However, an eradication program for introduced species appears to have successfully eliminated all rodents from the island (Tasmania Parks and Wildlife Services 2013), and the vegetation is now recovering (D. Bergstrom, personal communication). At Kerguelen grazing by rabbits has also contributed to the progressive destruction of penguin breeding habitats. Small landslides following heavy rains also occur at Gough and Tristan da Cunha (Cuthbert et al. 2009) and have killed breeding penguins. However, such events are infrequent and on a small spatial scale and are currently unlikely to be a major issue.

Introduced predators kill adult penguins or eat their eggs and young, which substantially decreases adult survival or reproductive success. Predator introductions particularly affect temperate and tropical penguin species. For example, pirates, whalers, and fur sealers introduced black rats (*Rattus rattus*) and house mice (*Mus musculus*) to the Galápagos Islands during the 1600s–1800s, and they have had substantial effects on Galápagos Penguin and other seabird populations (Vargas 2009). In 1832, when Ecuador officially claimed the islands and human colonization increased, domestic pigs (*Sus scrofa*), goats (*Capra hircus*), dogs (*Canis lupus familiaris*), and cats (*Felis catus*), and non-native plants were introduced (MacFarland & Cifuentes 1996; Snell et al. 2002). A single cat at Caleta Iguana, Isabela Island, was estimated to increase adult penguin mortality by 49% per year (Steinfurth 2007). Galápagos Penguins are a major tourist attraction (Vargas 2009). Tourists per se might not cause damage to the islands; however, the associated infrastructure facilitates the introduction of diseases, non-native species, and other vectors of habitat degradation. Although there are some illegal operators, tourist sites are generally well controlled, and defined paths and boardwalks are present. Waste management and growing infrastructure problems associated particularly with land-based tourism have put considerable pressure on the managers of the Galápagos National Park (Boersma et al. 2005). More than 200,000 tourists visited the islands in 2013, and as land-based tourism increases, visitor impacts will become more difficult to control.

Disturbance by tourists can pose threats to some penguin species (e.g., Ellenberg et al. 2006, 2007); however, impacts may be more difficult to detect for other species (e.g., Trathan et al. 2008). In general, the magnitude of the effects of tourism on breeding penguins remains unknown. This lack of consensus is potentially due to the wide variety of species studied, the different locations where studies on tourism have taken place, and the assorted levels and types of human activity to which penguins are exposed (Trathan et al. 2008). The impacts of human disturbance should be easily minimized by developing appropriate and anticipatory site- and species-specific visitor management guidelines.

Disturbance by scientists may affect penguins, particularly when new research programs are initiated without input from experienced scientists. For example, external marking of King (*Aptenodytes patagonicus*) and Adélie (*Pygoscelis adeliae*) penguins with flipper bands has reduced survival and breeding success (e.g., Saraux et al. 2011). Similarly, in Little Penguins (*Eudyptula minor*) banding reduced adult survival by 4%/year (Dann et al. 2014). However, in a 15-year study, well-fitted stainless-steel bands did not alter survival in Magellanic Penguins that were double-banded, compared with penguins marked with web tags (Boersma & Rebstock 2010). Operational activities can also have a negative impact on penguins. For example, about 7000 King Penguins died from asphyxiation probably after a training flight by a Hercules aircraft over Macquarie Island in 1990 (Rounsevell & Binns 1991).

**Marine Pollution**

Oil pollution through shipwrecks and oil spills is possibly the major anthropogenic-induced cause of death among penguins worldwide (García-Borboroglu et al. 2008). Penguins are extremely susceptible to oil because of their adaptations to life at sea and their extreme need to maintain their plumage in good condition. Furthermore, during the breeding season, penguins are central-place foragers and as such may walk or swim repeatedly through a contaminated site to access their foraging grounds. At present, the majority of the world's shipping remains distant from areas where penguins breed (NCEAS 2008). However, oil spills continue to occur near penguin colonies, particularly off South America and southern Africa.

Marine pollution events can have large local effects, especially for small island populations. Localized pollution can arise after vessels illegally wash out oil tanks while at sea. Consequently, oiled penguins have historically been seen ashore across many parts of the Southern Ocean. The actual number of affected penguins is unknown, but it is likely to be substantially higher than actually observed given the wide distribution of penguins, especially during winter. Many oiled penguins probably die at sea and thus remain undetected.

Marine debris is another potential threat to penguins. For example, in the 1980s, it was relatively common to find Little Penguins entangled in plastic 6-pack beverage yokes. After conservation lobbying, a biodegradable product was introduced in Australia, and the problem quickly disappeared. Even in remote locations, such as the Antarctic Peninsula, Falkland Islands (Malvinas), and at South Georgia, beach surveys reveal substantial amounts of debris, much of which has been discarded from ships, including from fishing vessels (Otley & Ingham 2003). Some penguins are killed at South Georgia when they become entangled in plastic debris or swallow small plastic items, but long-term monitoring data suggest that only a relatively small proportion of the breeding population is affected (B.A.S., unpublished data). The effects of microplastics are unknown. In fishing areas managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), international restrictions on dumping waste at sea have been agreed by the Contracting Parties to the convention. However, elsewhere, local legislation seldom enshrines such specific high standards of waste management.

Marine pollution also originates from other sources. For example, coastal and inshore mining operations along Namibia's southern coast threaten foraging habitats of African Penguins through the large-scale release of sediment into coastal waters. Water turbidity may reduce prey availability and is likely to affect foraging behavior. Sediment movement also contributes to the formation of temporary land bridges to some islands, which allows access by land predators (Kemper 2006).

Organochlorine and heavy metal accumulations, such as mercury, are an increasingly prevalent environmental contaminant, even for remote and isolated seabird communities (e.g., Blévin et al. 2013). However, mercury concentrations reported in penguins are currently below the threshold for adverse impacts, particularly in the Antarctic (Brasso et al. 2012).

### Fisheries Bycatch and Incidental Mortality

Fisheries are a major threat to penguins primarily because of associated incidental mortality and resource competition where fishers and penguins target the same species. Bycatch is comparatively easy to document, but the effects of competition are more difficult to substantiate because long-term monitoring information and prey stock assessments are required, neither of which are available for many species. Other impacts of fisheries are also feasible, including ecological perturbation followed by cascading effects that may alter penguin behavior and their population dynamics (e.g., Mattern et al. 2013).

Fishing nets are a major threat to all penguin species (e.g., González-Zevallos & Yorio 2006), but the severity of the threat depends upon how, where, when, and what nets are used. Exclusion devices that stop penguins entering trawl nets, or allow them to escape unharmed, should be developed and used; however, such devices are not always successful. Mitigation measures should also include separating fishers from penguins, either by spatial or temporal means (Yorio et al. 2010). Without some separation, interactions between penguins and gill nets are inevitable.

### Resource Competition

Many penguins consume so-called forage species, such as fish or krill that may also be taken by commercial fisheries (Cury et al. 2011; Pikitch 2012). Though these fisheries are assumed to compete with penguins for food, in many instances, direct evidence is sparse. However, there is strong evidence that competition for food exists between commercial fisheries and African Penguins. A combination of competition with the fishing industry and environmental variability probably led to a lack of food for all 3 regional African Penguin populations. Numbers of breeding birds in each of the 3 regions have been significantly correlated with estimates of prey biomass (Crawford 2007; Crawford et al. 2011). Off the coast of Namibia, energy-poor pelagic gobies (*Sufflogobius bibarbatus*) have replaced energy-rich sardines (*Sardinops sagax*) as the main penguin prey following the collapse of sardine populations in the late 1960s (Ludynia et al. 2010).

In South Africa, purse-seine fisheries compete with African Penguins for their 2 main prey items, anchovies (*Engraulis encrasicolus*) and sardines. Off South Africa, sardine stocks collapsed in the 1960s (Crawford 2007). This was accompanied by an increase in anchovies, which largely replaced sardines (Crawford 1998). In the early 1980s, South Africa's sardine stock recovered, and in the late 1990s and early 2000s, sardine and anchovies were both abundant off South Africa. In the early 2000s, a shift of South Africa's anchovy and sardine stocks to the south and east caused a mismatch in the distribution of penguins and their prey at breeding localities in the Western Cape (Crawford et al. 2008*b*), and because fish processing plants were mainly in the west, this probably also intensified fishing around penguin colonies. These factors, and another collapse of the sardine stock in the mid- 2000s (Coetzee et al. 2008), caused the penguin population in the Western Cape to collapse from 38,000 pairs in 2004 to 11,000 pairs in 2009, equivalent to a loss of >70% of the population (Crawford et al. 2011). A high rate of exploitation of sardines near Dyer Island in the early 2000s (Coetzee et al. 2008) may have reduced penguin food availability and caused penguin numbers to decrease (Crawford et al. 2011). At Robben Island, estimates of survival of adult African Penguins decreased sharply when the biomass of sardines off western South Africa fell below 25% of its maximum observed value (Robinson & Butterworth 2012).

For most other penguin species, data remain inadequate to link penguin population processes statistically with resource competition due to commercial harvesting. However, the pertinent ecological links are generally clear (Cury et al. 2011; Pikitch 2012). Reducing the harvest of forage species is key to maintaining predator population processes (Pikitch 2012). Substantial decreases in penguin populations can occur rapidly, as the case of the African Penguin illustrates, and once a population crashes, recovery is uncertain. Currently, the only large-scale fisheries management authority employing an ecosystem approach is CCAMLR, which is responsible for Southern Ocean fisheries, including the fishery for Antarctic krill (*Euphausia superba*). In setting catch limits, CCAMLR considers the needs of krill-dependent predators as set out in Article II of the Convention (CCAMLR 1980). However, with a human population already exceeding 7 billion, Antarctic krill potentially offers one of only a few remaining major sources of unexploited marine protein. New extraction technologies and markets make it probable that krill fishing will expand. If this occurs, care must be taken to protect krill-eating species because historically, industrialized fisheries typically reduce community biomass by 80% within 15 years of exploitation (Worm et al. 2009). Krill fishing could negatively impact Adélie, Chinstrap (*Pygoscelis antarctica*), Gentoo, and Macaroni penguins if catches increase beyond their current levels. If ecosystem impacts do occur, rebuilding ecological communities (and fisheries) will be challenging, if not impossible, even over long periods (Worm et al. 2009).

Precautionary action by ecosystem and fishery managers needs to be the norm. The onus should be on fisheries managers to demonstrate that fisheries are not having a negative impact on penguins. Peru's action to preserve a fixed escapement of 5 million tons of spawning biomass of Peruvian anchoveta (*Engraulis ringens*) demonstrates a clear commitment to a precautionary approach (P. Majluf, personal communication), similar to that adopted by CCAMLR many decades ago, that should be emulated elsewhere.

## Environmental Variability and Climate Change

Environmental variability affects population processes among penguins, usually through the distribution or availability of their mid-trophic-level prey (e.g., Trathan et al. 2006, 2007; Murphy et al. 2007). Penguins appear to respond to changing environmental conditions in the short term through modifications in breeding parameters and in the long term by altering their distribution and abundance (Boersma & Stokes 1995; Forcada & Trathan 2009).

Direct evidence that climate change affects penguins is scarce. This is mostly because biological monitoring data are relatively short term (the World Meteorological Organization often uses a climatological baseline of 30 years), and it remains difficult to ascertain the causes of recently observed changes in penguin populations. Large-scale changes in marine ecosystems also confound interpretations (Hilton et al. 2006). For example, the historical removal of large fish, seals, and whales has altered marine food webs, making it difficult to differentiate climate-induced population signals for mesopredators from signals from other drivers that also lead to ecosystem alteration. Thus, ascertaining whether changes in penguin populations are the product of current interactions between physical and biological processes remains difficult (Croxall et al. 2002).

Despite the difficulty in determining the direct impacts of climate change on penguin populations, some evidence is compelling. Increased snowfall resulting from increased warm, wet conditions may have contributed to Adélie Penguin population declines close to Palmer Station, Antarctic Peninsula (Ducklow et al. 2007). These colonies have decreased more rapidly than colonies where wind scour abates snow accumulation. Similarly, more frequent and intense storms due to climate change result in greater reproductive failure of Magellanic Penguins at Punta Tombo, Argentina (Boersma & Rebstock 2014) because more chicks die when rainfall is higher and air temperatures are lower than normal. Decreases in hatching success and in survival of chicks of Southern Rockhopper Penguins at Marion Island have recently been attributed to the increasingly poor condition of parents as they arrive to breed, probably because environmental change has led to poorer feeding opportunities at overwintering grounds (Crawford et al. 2008*a*). Modeling studies have explored the probability of survival of Emperor (*Aptenodytes forsteri*) (e.g., Jenouvrier et al. 2009) and King (e.g., Le Bohec et al. 2008) penguin populations in relation to climate change (based on IPCC scenarios), predicting that warm events will negatively affect both breeding success and adult survival.

Less frequently, climate change appears to benefit some penguin populations. Gentoo Penguins have expanded their range in step with a southward retraction of heavy spring sea ice at the western Antarctic Peninsula (Lynch et al. 2012), and receding ice fields have been associated with colony expansion for Adélie Penguins breeding on Beaufort Island in the Ross Sea (La Rue et al. 2013).

Nonetheless, making future predictions may be more complex than previously envisaged. For example, the foraging efficiency of Adélie Penguins breeding in the Ross Sea can be affected by extreme climatic events disrupting response plasticity in penguin populations (Lescroël et al. 2014). This suggests that the predictive power of relationships built on past observations (when not only the average climatic conditions are changing but also the frequency of extreme climatic anomalies) may not be a good predictor of a species' future response to climate change.

### Toxic Algal Poisoning and Disease

Currently, little is known about toxic algal poisoning of penguins. The only documented instance of poisoning occurred in the Falkland Islands (Malvinas) in November 2002, when a harmful algal bloom caused paralytic shellfish poisoning and the subsequent death of a large number of Southern Rockhopper Penguins and other seabirds (Uhart et al. 2004). Further instances possibly occurred in Chubut, Argentina, in 2000 and 2002, when toxic algal blooms may have killed 13,000 Magellanic Penguins (Shumway et al. 2003). Given that such events can kill large numbers of seabirds, they will probably become a greater problem for penguins and other seabirds in the future if the frequency of harmful algal blooms increases as a result of regional warming and altered ecosystem properties (Shumway et al. 2003).

Knowledge about disease outbreaks in wild populations of penguins is limited, but the greater accessibility to wild places for increasing numbers of tourists raises the potential for pathogen introductions. Also, climate change alters ecosystem properties allowing disease-carrying vectors to establish where historically the climate was unsuitable. Microorganisms are common in wild animals, but little is known about their natural occurrence compared with their introduction by humans. It is often unknown whether they are pathogenic or virulent. In many cases where disease outbreaks have occurred, identifying the active agent has proved difficult (Kerry & Riddle 2009).

Due to their evolution in a relatively pathogen-scarce environment, the naive nature of most Antarctic, Sub-Antarctic, and island penguins is expected to make them more susceptible to introduced exotic diseases and parasites and thus prone to colony or population extirpation (Wikelski et al. 2004). Although disease is a potential risk for all penguins, small global populations (e.g., Galápagos and Yellow-eyed) are in particular danger because they may be compromised by any loss of genetic diversity (Lyles & Dobson 1993), which can result in a reduced ability to react to new pathogens. Galápagos Penguins have extremely low estimates of nuclear genetic diversity (Nims et al. 2008) and extremely low major histocompatibility complex diversity (Bollmer et al. 2007), leaving them potentially more susceptible to new pathogens than are other penguin species. Introduced pathogens are already occurring and spreading among penguin populations (Kane et al. 2010).

Additional information for each of the threats described above is reported in García-Borboroglu and Boersma (2013).

## Discussion

Many populations of penguins appear to be resilient, and given adequate protection, including sufficient habitat and food, populations can recover from relatively low numbers once threats, such as harvesting and egging, are removed. Whether this remains the case in the future as climate change continues to affect ecosystems has yet to be determined. The development of species-specific conservation action plans will be critical where these are not already available.

Threats exerting pressure on penguin habitats (habitat degradation, pollution, and fisheries interactions) are major conservation issues today and require concerted action to mitigate future population declines for many species. These are among the most important threats to penguins, so conservation action will be particularly important given future threats due to climate change and increased levels of disease. The impacts of increasing temperatures are now altering the state of the world's oceans (Solomon et al. 2007), while ocean acidification is predicted to have a substantial impact on marine systems over the coming decades (e.g., Kawaguchi et al. 2013). Climate change will undoubtedly have profound long-term effects on penguins, not only through impacts on productivity regimes and food webs, but also through the spread and introduction of new diseases and toxic poisoning (Shumway et al. 2003) to hitherto naive penguin populations with probably low resistance (Bollmer et al. 2007; Nims et al. 2008).

There is now growing indirect evidence that climate change negatively affects penguins. The current challenge is to disentangle these effects from other anthropogenic impacts and natural variation because these drivers often interact and lead to direct and indirect effects. This does not mean climate change is currently a minor threat to penguins; rather, it means we cannot accurately quantify its importance.

Realistically, humankind can do little to mitigate the impacts of climate change in the short term. However, habitat degradation, pollution, and fishing can all be managed at appropriate spatial and temporal scales. A risk averse or precautionary approach to the conservation of penguins would thus take immediate action to offset these impacts. Toward that end, we scored these and other anthropogenic threats (Table 1). Although penguins everywhere are at different degrees of risk, the species breeding in South America, Africa, and Oceania are most at risk. Conservation actions in these temperate regions, where contact with human populations is more common, should be of the highest priority (Table 1).

Many penguin species face a common set of anthropogenic threats that also affect other seabird species, marine mammals, and taxa across a variety of trophic levels. We therefore conclude that there is an urgent need to establish marine-protected areas (MPAs) as an effective means for protecting penguins. MPAs are an important management tool for conserving marine biodiversity because they allow for the sustainable and rational use of marine resources and potentially enhance fisheries management (Gell & Roberts 2003). An increasing number of intergovernmental meetings, agreements, and conventions have endorsed their use and committed to the development of MPAs, including the United Nations World Summit on Sustainable Development (UN WSSD), the IUCN World Parks Congress, the Convention for the Protection of the Marine Environment of the North-East Atlantic, and CCAMLR. In 2002, the UN WSSD set a target for governments to protect 20–30% of all marine habitats under their jurisdiction.

Determining the appropriate size of an MPA is important in the planning process. For penguins, an MPA must encompass areas they use in each of their life stages, including central-place breeding adults, free-ranging juveniles, and nonbreeding adults. At present, the size of most existing MPAs (Supporting Information) is inadequate to protect the life processes of penguins (Boersma & Parrish 1999).

Protecting species requires cooperation at local, national, and international levels. For penguins and many other species dependent on oceans with intact ecosystem services, the future looks uncertain. As human pressures mount on marine resources, the designation of effective MPAs is likely to be harder to achieve and ocean zoning more challenging, especially in the High Seas and areas beyond national jurisdiction (Trathan 2012). Large-scale conservation zones are not always practical or politically feasible to implement, consequently other spatial management approaches, including spatial zoning with multiple-use areas, fisheries access areas, and strictly protected areas, must be developed to maintain marine biodiversity and ensure ecosystem functioning.

With increasing human populations, pressures on ocean resources will continue to grow and innovative and flexible conservation tools are needed. MPAs can be effective in achieving multiple goals (Kelleher 1999). They can have many forms and uses (Dudley 2008), and ocean planners will need to be creative in the future if they want to balance rational use and sustainable exploitation against the conservation of important habitats and species, biodiversity and communities, and ecological processes.

Other management techniques utilizing ecosystem-based management frameworks should also be developed (e.g., identification of thresholds of forage fish abundance below which ecosystem functioning may be impaired, and harvesting reduced or stopped [e.g., Cury et al. 2011]). Similarly, coastal habitats must be rigorously protected to ensure that traditional breeding sites are maintained because penguins are generally highly philopatric. Strict controls on introduced species must also be maintained. At sea, rigorous zoning of shipping lanes is necessary to keep ships away from important bird areas, including resting, transit, and foraging areas. Ecosystem managers must also introduce precautionary management actions in the face of climate change, acting in a defensive manner to build ecosystem resilience (Trathan & Agnew 2010).

Based on our single model taxonomic group, we conclude that despite the lower cumulative impacts of human activities in the southern hemisphere (Halpern et al. 2008), the world's marine communities, and penguins in particular, are now at considerable risk. The simultaneous occurrence of multiple high-intensity stressors has been a prerequisite for major extinction events in the past (Barnosky et al. 2011), so concerted action to conserve penguin populations today will be essential to facilitate populations that are robust and resilient to climate change impacts in the future.

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## Supporting Information

A list of spatial protection measures for each penguin species (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Table SI. Existing protected areas for each of the 18 penguin species.

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