



Sentinels Of the Ocean

The science of the world's penguins

Contents

- 1 Overview
- 1 Status of penguin populations
- 1 Penguin biology
 - Species 3
- 22 The Southern Ocean
- 24 Threats to penguins
 - Fisheries 24
 - Increasing forage fisheries 24
 - Bycatch 24
 - Mismatch 24
 - Climate change 25
 - Habitat degradation and changes in land use 25
 - Petroleum pollution 25
 - Guano harvest 26
 - Erosion and loss of native plants 26
 - Tourism 26
 - Predation 26
 - Invasive predators 26
 - Native predators 27
 - Disease and toxins 27
- 27 Protecting penguins
 - Marine protected areas 27
 - Ecosystem-based management 29
 - Ocean zoning 29
 - Habitat protections on land 30
- 31 Conclusion
- 32 References

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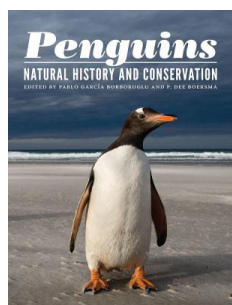
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Overview

Penguins are remarkable creatures. King penguins can hold their breath for 23 minutes and dive over 1,600 feet deep in their search for food. The Magellanic penguin can cover 107 miles in a day and as much as 10,000 miles in a year. The emperor penguin breeds on the Antarctic ice, the egg incubating for up to 55 days on the feet of a fasting male, at temperatures below minus 40 degrees Fahrenheit in winds up to 90 mph.

Because penguins live most of their lives at sea but return to land to breed and molt, they are gauges of marine health that are accessible to researchers and relatively easy to study. Through these ocean sentinels, scientists can learn about the health of marine ecosystems across the Southern Hemisphere and use this knowledge to develop realistic and effective conservation strategies for the world's southern oceans.

Penguins can also teach us about the health of coastal lands. Many penguins breed on islands to avoid mammalian predators, including dogs, cats, and rodents, and declines in these penguin populations can indicate when such predators have invaded these habitats. Many penguin species live in deserts or dry locations where chicks rarely encounter rain before their waterproof feathers grow. Chick mortality can signal an increase in the intensity and frequency of storms.

Despite the often isolated locations, penguin tourism is a locally significant economic driver. Each year, upwards of 500,000 people travel from all over the world just to glimpse a group of little blue penguins coming ashore on Phillip Island, Australia. About 120,000 people visit Punta Tombo, Argentina, each year for a stroll through the bustling Magellanic penguin colony, and almost 200,000 tourists journey to the Galápagos Islands for an opportunity to see the only penguin species that lives near the equator.

This report summarizes current scientific understanding of penguin biology and the place of these important seabirds in the global ecosystem. It also offers some general recommendations for safeguarding penguins, including ocean zoning, ecosystem-based management, and habitat protections.

Status of penguin populations

Of the 18 penguin species, 12 are in decline. On the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, only three penguin species are listed as Least Concern; four are listed as Near Threatened, six as Vulnerable, and five as Endangered. Species with the highest level of concern have restricted distributions and small populations and are threatened by humans directly and indirectly through development within their breeding sites, petroleum pollution, overfishing, climate change, and introduction of invasive species, such as rats and cats. All five endangered penguin species live in temperate regions—generally closer to humans than Antarctic penguins are—and therefore experience greater direct threats.

Penguin biology

Penguins are Southern Hemisphere seabirds that live in diverse habitats, ranging from the volcanic Galápagos Islands on the equator to the frozen sea ice of Antarctica. They nest in deserts and forests, on rocks, sand, and ice, under bushes and trees, in burrows, or in the open (García-Borboroglu and Boersma 2013).

Within the penguin family, appearance, range, and life history vary widely (Williams 1995, García-Borboroglu and Boersma 2013). Some migrate 2,500 miles in a year, while others remain sedentary. Breeding areas range from Antarctic ice to hot, dusty coastal deserts. All penguins molt once a year, except for the Galápagos penguin,

which molts twice a year (Boersma 1978, Boersma et al. 2013b). Penguins are long-lived, with some individuals living more than 30 years in the wild. Many species do not reproduce until ages 3 to 8. Some, like the king penguin, take 18 months to raise a single chick, while others raise two in as little as 60 days.

Raising a penguin chick requires two parents (García-Borboroglu and Boersma 2013). While one parent guards and broods chicks, the other forages at sea for food, which it transports back to the nest in its stomach. Because adult penguins must have a partner to successfully rear their chicks, they are typically faithful throughout the breeding season. Fidelity varies among species, especially between years: One pair of Magellanic penguins bred together for 16 years (Boersma 2008), while 85 percent of emperor penguins find a new partner each breeding season (Wienecke et al. 2013).

Though penguins breed on land, they forage at sea. Some are inshore feeders, such as yellow-eyed and African penguins, while others, like macaroni and king penguins, feed offshore (Davis and Renner 2003). At sea, penguins are vulnerable to predation by killer whales, sea lions, seals, and sharks. On land, eggs and young chicks are targeted by predatory birds, such as petrels, skuas, sheathbills, and gulls, and by such mammals as rats, skunks, foxes, and cats.



In the breeding season, Magellanic penguins gather in large nesting colonies.

Species

The 18 penguin species are classified into six groups: large, brush-tailed, yellow-eyed, crested, banded, and little; and geographically into Antarctic, sub-Antarctic, and temperate.



Yellow-Eyed



Scientific name:

Megadyptes antipodes

Population:

About 1,700 breeding pairs

IUCN status:

Endangered

Threats:

Habitat degradation
and invasive predators

This penguin is the fourth-largest and a major tourist attraction in New Zealand. It breeds on the southeastern coast of New Zealand's South Island and on Auckland, Campbell, Stewart, and adjacent islands. Breeding occurs in mature coastal forests, regenerating coastal scrub, and on partially exposed cliffs (Seddon et al. 2013). As of 2013, only an estimated 1,700 breeding pairs remained across the species' small range. The population declined for a number of reasons, primarily introduced predators such as cats, stoats and other weasels, dogs, rats, and hedgehogs and deterioration of nesting habitats from the cutting of coastal forests. Although ongoing conservation efforts have mitigated habitat degradation, threats at sea remain difficult to evaluate and manage (Seddon et al. 2013). Fur seal and Hooker's sea lion populations, previously hunted by sealers, will take a toll as they recover and prey on penguins. Yellow-eyed penguins also are vulnerable to sporadic outbreaks of disease (Seddon et al. 2013).

Where Yellow-Eyeds Live



Southern Rockhopper



Scientific name:

Eudyptes chrysocome

Population:

1.2 million breeding pairs

IUCN status:

Vulnerable

Threats:

Climate change, pollution,
and habitat degradation

This species, the smallest crested penguin, breeds on sub-Antarctic and temperate islands in the Atlantic Ocean. The number of southern rockhopper penguins has declined 34 percent since the 1970s, and this trend appears to have worsened recently (Pütz et al. 2013). The cumulative effects of climate variation, commercial fishing, and oil pollution are thought to contribute to the southern rockhopper decline, though the magnitude of these threats varies among sites (Pütz et al. 2013, BirdLife International 2010).

Where Southern Rockhoppers Live



Northern Rockhopper



Scientific name:
Eudyptes moseleyi

Population:
265,000 breeding pairs

IUCN status:
Endangered

Threats:
Habitat degradation

This species breeds on islands in the South Atlantic and Indian oceans. The northern rockhopper population has declined by 57 percent since the 1970s (Cuthbert 2013). When the oil tanker M/S Oliva ran aground in 2011 on Nightingale Island, it released 1,500 metric tons of fuel oil into the sea 19 miles from rockhopper colonies on Inaccessible Island and Tristan da Cunha. Of the 3,700 oiled penguins rescued from the affected area, only 381 were successfully rehabilitated (Cuthbert 2013).

Where Northern Rockhoppers Live



Erect-Crested



Scientific name:

Eudyptes sclateri

Population:

80,000 breeding pairs

IUCN status:

Endangered

Threats:

Fisheries pressure and overfishing, pollution, and habitat degradation

This is the least studied of all penguin species because of its extremely isolated breeding grounds (Davis 2013). The population breeds on Bounty Islands and Antipodes Islands off the southeastern coast of New Zealand, and the little evidence that exists suggests significant population declines since the 1970s. Very little data are available on erect-crested penguins' population size, breeding success, and diet, making it difficult to determine specific threats to the species. Due to its restricted range, however, any local disturbance may have a disproportionately large impact on the population. The most plausible cause of recent decline is low food availability due to climate change-related fluctuations in ocean circulation and surface temperature (Davis 2013).

Where Erect-Cresteds Live



Fiordland



Scientific name:

Eudyptes pachyrhynchus

Population:

2,500-3,000 breeding pairs

IUCN status:

Vulnerable

Threats:

Introduced predators

This crested penguin breeds on Stewart, Solander, and Codfish islands and on the west coast of New Zealand's South Island. The population, estimated at 2,500 to 3,000 breeding pairs, fell substantially over the past 100 years (Taylor 2000). Although recent surveys found that their numbers are stable or increasing at some sites, the population size and trend remain poorly understood (Mattern 2013a). The general decline is probably due to introduced land predators (Taylor 2000), particularly the stoat, a member of the weasel family.

Where Fiordlands Live



Snares



Scientific name:

Eudyptes robustus

Population:

26,000-31,000 breeding pairs

IUCN status:

Vulnerable

Threats:

Climate change, fisheries pressure and overfishing, and pollution

This crested penguin breeds only on the Snares Archipelago off southern New Zealand. The Snares penguin is of significant cultural importance to the New Zealand Maori, and in 1998, the Snares Islands became part of a UNESCO World Heritage site, the New Zealand Sub-Antarctic Islands. Though the Snares population is thought to be stable, its confined breeding range makes it vulnerable to local disturbances such as oil spills and the introduction of terrestrial predators (Mattern 2013b).

Where Snares Live



African



Scientific name:

Spheniscus demersus

Population:

26,000 breeding pairs

IUCN status:

Endangered

Threats:

Climate change, fisheries pressure and overfishing, and pollution

This is one of four temperate species of banded penguin and breeds along the coast of Namibia and South Africa. During the nonbreeding stage, African penguins may travel up to 62 miles offshore, but most stay within 12 miles of the coast. The population has undergone a large, sustained decrease over the past century; in South Africa, it fell by half in just eight years, from 57,000 breeding pairs in 2001 to 21,000 pairs in 2009. The main threat is lack of food. Their primary prey, sardines and anchovies, have been depleted in penguin foraging waters, probably because of pressure from commercial fishing and climate change-related variation in oceanographic conditions (Crawford et al. 2008, 2013).

Where Africans Live



Magellanic



Scientific name:

Spheniscus magellanicus

Population:

1.3 million breeding pairs

IUCN status:

Near Threatened

Threats:

Climate change, fisheries pressure and overfishing, and pollution

These penguins are highly migratory, spending most of their lives at sea and returning to land only to breed and molt. Magellanic breeding colonies lie on the coast and coastal islands of South America, between 40 and 55 degrees south latitude. The trends in the population differ among colonies: Those in the north of Argentina are growing, but the largest Magellanic breeding colony at Punta Tombo, in the nation's south, is declining (Pozzi et al. 2015). Punta Tombo is a tourist attraction that draws over 120,000 visitors annually (Boersma et al. 2013a). Major threats to Magellanic penguins include climate variation; incidental catch of penguins in fishing gear; competition with fisheries for food; and petroleum pollution, particularly for the Atlantic portion of the population, which spends the winter at sea in a restricted, narrow, offshore area between northern Argentina and southern Brazil (Boersma et al. 2013a).

Where Magellanics Live



Humboldt



Scientific name:

Spheniscus humboldti

Population:

1,520-5,000 breeding pairs

IUCN status:

Vulnerable

Threats:

Fisheries pressure, overfishing, climate change, and habitat degradation

Also known as the Peruvian penguin, this species has at least 60 breeding colonies along coastal Peru and Chile. The population size has varied considerably and declined overall since the 19th century, though recent surveys found that colonies may be rebounding (International Union for Conservation of Nature 2014, de la Puente et al. 2013). Major threats to the species include increased El Niño and other climatic variations, overfishing, incidental catch by fishing trawlers and in the gillnets of small-scale fishers, and habitat degradation (de la Puente et al. 2013).

Where Humboldts Live



Galápagos



Scientific name:

Spheniscus mendiculus

Population:

1,500-4,700 breeding pairs

IUCN status:

Endangered

Threats:

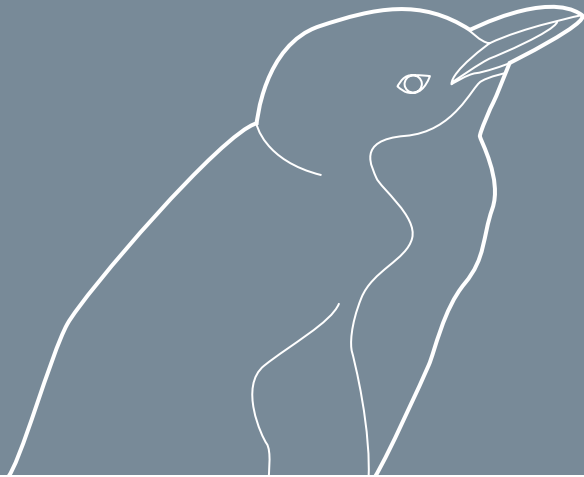
Climate change and introduced predators

This penguin, endemic to the Galápagos Islands, is the northernmost of all penguin species. The population has declined considerably since the 1970s, with decreasing availability of prey and introduced predators being the primary culprits. Food availability fluctuates in the Galápagos between La Niña years when cold, nutrient-rich water upwells to the ocean surface, bringing small fish and crustaceans into penguin foraging waters, and El Niño years when this upwelling is disrupted. Although Galápagos penguins are equipped to cope with these natural fluctuations, the frequency and intensity of El Niños have increased in the last 30 years, putting pressure on the population and causing it to decline (Boersma 1998, Vargas et al. 2007, Boersma et al. 2013b).

Where Galápagos Live



Little



Scientific name:

Eudyptula minor

Population:

300,000 breeding pairs

IUCN status:

Least concern

Threats:

Introduced predators, pollution, and habitat degradation

As its name suggests, this is the smallest living penguin, with a length of about 13 inches. The little penguin, also called the little blue or fairy penguin, breeds in New Zealand and Australia. Some researchers have suggested splitting the species into three: the white-flipped penguin in the Banks Peninsula in New Zealand, the little penguin in New Zealand, and the little penguin in Australia. But so far, DNA evidence does not support this division (Dann 2013). In general, the little penguin population is stable, abundant, and well-dispersed, though populations have declined at several sites, often because of predators and habitat degradation (Dann 2013).

Where Littles Live



King



Scientific name:

Aptenodytes patagonicus

Population:

1.6 million breeding pairs

IUCN status:

Least concern

Threats:

Fisheries pressure

This penguin species is the world's second-largest and is recognized by the bright orange and yellow coloration of its neck and bill. King penguins breed on sub-Antarctic islands in the southern Atlantic, Indian, and Pacific oceans. Colonies throughout its breeding range have stabilized or increased over the past decade (Bost et al. 2013) due in part to the end of nearby sealing and whaling in the 1970s and 1990s and of hunting king penguins for their oil. If a fishery developed for lanternfish, the king penguin's primary prey, it could threaten the population.

Where Kings Live



Chinstrap



Scientific name:

Pygoscelis antarctica

Population:

4 million breeding pairs

IUCN status:

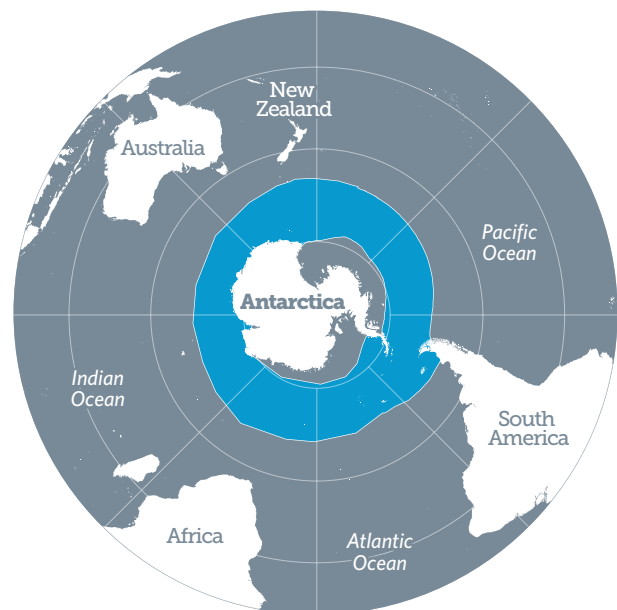
Least concern

Threats:

Climate change

Located primarily on the Antarctic Peninsula and on South Shetland, South Orkney, and South Sandwich islands, these penguins have been tracked by satellite up to 4,000 miles from their colonies when not breeding (Trivelpiece and Trivelpiece 2013). Their diet consists almost entirely of krill, and there is extensive overlap between chinstraps' range and the developing krill industry. Because krill feed on algae associated with sea ice, reduced ice coverage due to climate change may alter their abundance and distribution, also affecting chinstraps. Populations have fallen more than 50 percent during the past 30 years at colonies in the South Shetland Islands, consistent with sea ice declines in the Scotia Sea that may have reduced krill abundance (Trivelpiece et al. 2011). Climate change may also affect chinstraps through increased rainfall, which can wet chicks and cause them to die of hypothermia (Trivelpiece and Trivelpiece 2013).

Where Chinstraps Live



Gentoo



Scientific name:

Pygoscelis papua

Population:

387,000 breeding pairs

IUCN status:

Near threatened

Threats:

Fisheries pressure and overfishing

This is the third-largest penguin species, with adults weighing 11 to 18 pounds. Eighty percent of the world's gentoo population breeds on the Antarctic Peninsula, South Georgia Island, and the Falkland Islands/Malvinas. They are relatively sedentary and often forage close to their breeding colonies. Gentoo penguins demonstrate a high degree of flexibility in breeding and diet, and their range has expanded southward on the Antarctic Peninsula in recent years (Lynch 2013). Although their populations are either stable or increasing, they still can be affected by increases in precipitation. Snow can cover their breeding site and delay egg laying when it does not blow off or melt. Rain can flood nests and wet chicks, causing death from hypothermia.

Where Gentoos Live



Macaroni



Scientific name:

Eudyptes chrysolophus

Population:

6.3 million breeding pairs

IUCN status:

Vulnerable

Threats:

Climate change, introduced predators, and disease

These crested penguins breed on small islands throughout the southern Atlantic and Indian oceans. Though their ranges during the nonbreeding (winter) season are not well known, recent telemetry results from one colony indicated a migration range of more than 1.16 million square miles. The diet of macaroni penguins varies according to location, with Antarctic krill the dominant prey at South Georgia Island and in the southwestern Atlantic. Nearly half of all macaronis used to breed at South Georgia, but that population fell from 5 million breeding pairs in the 1980s to less than 1 million in 2002, and the global population has declined by approximately 30 percent since 1993 (Crossin et al. 2013).

Where Macaronis Live



Royal



Scientific name:
Eudyptes schlegeli

Population:
500,00 breeding pairs

IUCN status:
Vulnerable

Threats:
Climate change, pollution,
and introduced predators

Once thought to be a subspecies of the macaroni penguin, royals are now considered a separate species (Crossin et al. 2013). The most obvious physical difference between the two is the black face of the macaroni penguin and white to gray face of the royal. This species' breeding distribution is restricted, with the majority of the population breeding on Australia's Macquarie Island in the South Pacific. Royal penguins should do well with the recent control and removal of introduced cats, rats, and rabbits from Macquarie Island (Crossin et al. 2013).

Where Royals Live



Emperor



Scientific name:

Aptenodytes forsteri

Population:

238,000 breeding pairs

IUCN status:

Near threatened

Threats:

Climate change and diminished and dispersed prey

These penguins breed in the most extreme conditions of any penguin species. Females lay their egg during the Antarctic winter and then make the long journey back to sea to forage, leaving the adult male to incubate the egg for up to 55 days on the Antarctic ice. The males fast this entire period, enduring minus 40 F temperatures and wind speeds of up to 90 mph. Emperor penguins are the largest of the penguin family and are featured in the popular documentary “March of the Penguins.” The current estimated global population of 238,000 breeding live in 45 known colonies around the Antarctic coast. Their populations are expected to decline as sea ice diminishes with a warming climate (Wienecke et al. 2013). In some areas, rising temperatures may cause total reproductive failure of colonies. The population is projected to decline by 19 percent before 2100, with two-thirds of colonies reducing by half (Jenouvrier et al. 2014). One colony on the Antarctic Peninsula, where warming is most rapid, has already disappeared (Wienecke et al. 2013).

Where Emperors Live



Adélie



Scientific name:

Pygoscelis adeliae

Population:

2.4 - 3.8 million breeding pairs

IUCN status:

Near threatened

Threats:

Climate change

The range of this highly migratory species stretches far across the Southern Ocean. Its population of more than 10 million breeds along the Antarctic coast and, like the emperor penguin's, is expected to decline with the thinning of sea ice and increased rainfall. Like chinstrap populations, Adélie numbers have dropped more than 50 percent during the past 30 years at colonies in the South Shetland Islands, paralleling ice declines throughout the Scotia Sea and the probable decrease in sea ice algae and the krill that feed on them (Trivelpiece et al. 2011). If penguin chicks get wet during a rainstorm before their waterproof feathers grow, they are likely to die of hypothermia (Boersma and Rebstock 2014). These are relatively new problem for Antarctic species that are well-adapted to cold and minimal snow. The Adélie is also likely to be affected by increased fishing pressure on krill in the Southern Ocean.

Where Adélies Live



Threats to penguins

Though direct hunting of penguins and their eggs has largely subsided (García-Borboroglu and Boersma 2013, Trathan et al. 2015), penguins remain vulnerable to a host of threats on land and at sea.



Oiled and starving Magellanic penguin in Punta Tombo, Argentina.

Fisheries

Increasing forage fisheries

Commercial fisheries targeting forage fish, the primary prey of penguins, have serious implications for penguins. When food availability is low, chicks are less likely to survive (Cresswell et al. 2012). Furthermore, adults are more likely to abandon chicks when food availability is low (Ainley et al. 1983, Davis and McCaffrey 1986, Trivelpiece and Trivelpiece 1990, Yorio and Boersma 1992, Cresswell et al. 2012), thus making chicks vulnerable to predation as well as starvation. For Magellanic penguins in Punta Tombo, Argentina, the leading cause of chick death every year is starvation (Boersma and Rebstock 2014). In many years, penguins traveled over 370 miles from Punta Tombo in search of food (Boersma and Rebstock 2009), leaving their mates and chicks at their nests for several weeks. These adults were frequently unable to return to the nest in time, and chicks starved.

As of 2008, forage fish made up 37 percent of global annual marine fish catch (Alder et al. 2008). Ninety percent of this yield is processed as fish oil and fish meal, which are used as feed for fish, pigs, and chickens (Pikitch et al. 2012, Alder et al. 2008). The demand for farmed carnivorous fish is likely to increase in emerging economies (Pikitch et al. 2012), putting growing pressure on wild forage species populations and affecting large fish, marine mammals, and seabirds alike.

Bycatch

Bycatch—the unintentional harvest of nontarget marine species—poses a threat to penguins, which can become entangled as they dive after prey that is already caught in fishing nets (González-Zevallos and Yorio 2006). When the penguins are unable to free themselves, they drown. Bycatch can be a significant threat, depending on timing and location of fisher and penguin overlap and the type of equipment used (Trathan et al. 2015). Bycatch of penguins is probably underreported and therefore a more substantial threat than currently recognized (Boersma et al. 2013a). Furthermore, many of the penguins that die in nets are adults, which has a disproportionately negative effect on the population (Saether and Bakke 2000), due to reduced reproduction and an increased rate of starvation among chicks. In March 2009, 1,380 dead Magellanic penguins (48 percent adult, 52 percent juvenile) washed ashore in Chile; all were presumed drowned by entanglement in fishing nets while migrating (Schlatter et al. 2009).

Mismatch

Fishing pressure and climate variation both affect where marine species can thrive (Crawford et al. 2013, García-Borboroglu and Boersma 2013), which may result in a mismatched distribution of breeding penguins and their prey. This is particularly problematic for penguins because they are often linked with specific sites and cannot travel as far for food as other species, such as whales and marine turtles (Grémillet et al. 2008). Predator-prey mismatch was observed in the early 2000s off the coast of South Africa when sardine and anchovy populations were depleted in the penguin breeding range by intense fishing and climatic variation that caused fish stocks to move north. This probably contributed to the dramatic collapse of the Western Cape penguin population, which plummeted from 39,000 breeding pairs to 11,000 in five years (Crawford et al. 2013).

Climate change

The effects of climate change on penguin populations are largely unknown but harmful where well-documented (Boersma 1978, Boersma and Rebstock 2014, Trathan et al. 2015). Increased storm frequency and intensity, loss of sea ice, acidification of ocean water, and changes in ocean currents threaten marine wildlife worldwide.

Though penguins spend most of their lives at sea, their chicks hatch with only a layer of downy feathers to keep them warm. Until their juvenile waterproof feathers grow, their down must remain dry to maintain a safe body temperature. Thus, penguins breed in dry climates and during dry times of the year. However, more frequent and intense storms, associated with climate change, increase the likelihood of chicks getting wet before their waterproof feathers grow, resulting in higher rates of chick death from hypothermia (Boersma and Rebstock 2014). Although storms are rare, they can be devastating. Half of Magellanic penguin chicks at Punta Tombo, Argentina, were killed by a storm in 1991, and 43 percent suffered a similar fate in 1999 (Boersma and Rebstock 2014). Chicks face a related threat in Antarctica where a rise in ocean temperature is expected to decrease the extent and duration of sea ice (Wienecke et al. 2013). If land-fast ice breaks up too early in the breeding season, downy chicks that are unfit for life in the sea are likely to die (Boersma 2008).

Climate change will affect food availability for penguins across the Southern Hemisphere. Chinstraps and Adélies on the Antarctic Peninsula depend on krill to feed themselves and their young. Krill spend the winter under the sea ice, hiding from predators and eating algae. Decreasing sea ice inhibits krill survival, reducing the numbers of this critical species that are available to support the marine food web. Ocean acidification could further decrease Antarctic krill abundance by dissolving calcium carbonate that occurs naturally in marine waters (Wienecke et al. 2013). Krill require calcium carbonate in their environment to rebuild their shells after each molt (Nicol et al. 1992).



Galápagos penguins are affected by climate change through increasingly frequent and severe El Niño events.

Pacific Ocean seabirds, including the Galápagos and Humboldt penguins, are affected by climate change through increasingly frequent and severe El Niño events. During these periods, the cold, nutrient-rich upwellings of Peru's Humboldt current and the Crowell current around the Galápagos Islands—which typically push high-quality food into penguin foraging waters—are disrupted, reducing the availability of prey (Boersma 1978). Severe El Niño events, such as occurred in 1982 and 1998, are marked by penguins' reproductive failure and substantial population declines (Boersma 1978, Vargas et al. 2007). The trend of more frequent El Niño events is likely to continue, putting species with small populations, such as the Galápagos penguin, at greater risk (Boersma 1998, Vargas et al. 2007).

Habitat degradation and changes in land use

Habitat degradation is a significant threat to several penguin species and is linked to human land-use activities that increase pollution, exploitation, tourism, predation, disease, and the prevalence of toxins. Although individually, these threats are generally not as severe as those associated with commercial fisheries and climate change, terrestrial threats cumulatively can be major factors in reproductive failure and population decline among penguins.

Petroleum pollution

The number of penguins killed each year by oil pollution is probably higher than currently realized, which would make it one of the most significant anthropogenic threats to penguins (Trathan et al. 2015, García-Borboroglu et al. 2008). Even on the most remote islands, penguins are vulnerable to pollution by oil tankers that operate too close to shore (Cuthbert 2013). When penguins swim through oil, their feathers clump and lose their insulating properties. The water then becomes too cold for them, and they must return to land to maintain their



The cumulative effects of habitat degradation, commercial fishing, and oil pollution are thought to contribute to the northern rockhopper decline.

body temperature. Because they are unable to forage on land, these penguins are likely to starve (Crawford et al. 2013). Other effects of petroleum exposure include suppression of penguins' immune systems, loss of blood from ulcers along the digestive tract, and increased vulnerability to parasites (Gandini et al. 1994, Crawford et al. 2013). Since 1968, 14 major oil spills have been documented off the coast of South Africa. In 2000, the M/V Treasure sank off of western South Africa, killing 2,000 adult and immature penguins and 4,350 chicks in less than two months (Crawford et al. 2000).

Guano harvest

Guano is a valuable organic fertilizer derived from the excrement of birds and bats. The removal of guano from penguin colonies is detrimental. African and Humboldt penguins use guano to sculpt burrows for nesting and raising chicks (Crawford et al. 2013). In Namibia and South Africa, guano removal from coastal islands in the 1800s and 1900s caused penguins to nest on open rock, where eggs and chicks were exposed to predation, heat stress, storms, and flooding (Kemper et al. 2007). In 2000, on Halifax Island, Namibia, 68 chicks in surface nests died in just two hours when the temperature rose to 98.6 F (Kemper et al. 2007).

Erosion and loss of native plants

Introduced grazers such as cattle, sheep, goats, and rabbits have reduced vegetation at some penguin breeding sites, leading to erosion-induced landslides and subsequent burrow collapse (Pütz et al. 2013). Though these events are infrequent, they have been documented in southern rockhopper, northern rockhopper and Magellanic penguin colonies (Pütz et al. 2013, Cuthbert 2013, Croxall et al. 1984). Furthermore, young chicks rely on plants for shelter, and reduced vegetative cover exposes them to adverse weather and predators.

Tourism

The little, yellow-eyed, Magellanic, and Galápagos penguins are major attractions, and the development of tourism on the Antarctic Peninsula and sub-Antarctic islands is increasing. Though tourists usually do not directly harm penguins, infrastructure development and increased human activity may contribute to degradation of the breeding habitat and introduction of diseases and alien species. They can also cause penguins to delay returning to their nests, depriving chicks of food (Seddon and Ellenberg 2008). Generally, penguins appear to tolerate intense tourism, but stress hormones are elevated with human visitation in some species (Walker et al. 2005, Boersma et al. 2013b).



Magellanic penguin breeding colonies are a popular attraction. Managing the effects of tourism is essential.

Predation

Invasive predators

Invasive predators such as cats, dogs, weasels, and rodents kill adult penguins or eat their eggs and young, decreasing reproductive success (Boersma et al. 2013a). The introduction of nonnative predators to penguin habitat is largely connected with the arrival of humans. The impact on a penguin colony can be catastrophic, as demonstrated at Caleta Iguana in the Galápagos Islands in 2005 when one cat increased adult penguin mortality by 49 percent (Steinfurth and Merlen 2005 as cited in Boersma et al. 2013b). Introduced predators in New Zealand are perhaps the most significant threat to penguin populations (Taylor 2000). Ferrets and stoats have had detrimental effects on Fiordland, yellow-eyed, and little penguins (Taylor 2000).

Native predators

Terrestrial predators vary among penguin populations. Seabirds such as petrels, skuas, and gulls take chicks and eggs opportunistically but in low numbers (Williams 1995 and references therein). In some areas, human land-use activities lead to local extinctions of larger land predators, such as foxes and pumas in South America, allowing penguin populations to swell (Boersma et al. 2013a). With decreased hunting, some native predators including sea lions, fur seals, and terrestrial mammals have recolonized breeding sites, putting penguins at risk.



Ferrets and stoats have had detrimental effects on New Zealand's yellow-eyed penguins.

Disease and toxins

Disease and toxins are thought to be minor to moderate threats to most penguin species, but the data are very limited. Because many penguins live in remote areas, exposure to disease has been low historically. Incidents of exposure are likely to increase with globalization, and penguins may be particularly vulnerable to outbreaks. Observers have reported recognized diseases, such as malaria and salmonella, in penguins and emerging ones about which little is known:

- In 1992 and 1993, an unknown disease killed 250 to 300 king penguins and 5,000 to 10,000 macaroni penguins on South Africa's Marion Island without researchers ever identifying its source (Cooper et al. 2009).
- A feather-loss disorder was first observed in 2006 in captive African penguins in South Africa. While affected, chicks lose all of their downy feathers, exposing their bare skin and leaving them featherless for weeks until juvenile or adult plumage grows. It was recorded in Argentina a year later in a Magellanic chick and again in South Africa in wild African penguin chicks. Though not always fatal, the disorder leads to slower growth and smaller size at fledging, increasing the likelihood of mortality (Kane et al. 2010).
- Avian pox has been recorded in at least four species: Magellanic, Humboldt, African, and gentoo (Kane et al. 2012). Avian pox is caused by a virus and typically results in external wartlike growths around the eyes, beak, feet, and cloaca, a part of the penguin's digestive tract and reproductive system. The virus is often fatal in chicks and leads to additional infections in adults that may result in death (Kane et al. 2012). Little is known about its origins.
- The frequency of toxic algal blooms is increasing globally (Howarth 2008). Although not directly lethal, these blooms make individuals more vulnerable to other stressors, contributing to reproductive failure and death (Shumway et al. 2003) and present a particular danger to penguins because of the birds' habitual fasting and long migrations. Just a small dose of the toxin can be enough to harm an emaciated penguin that has traveled long distances with little to eat.

The Southern Ocean

Extending northward from the coast of Antarctica to 60 degrees south latitude, the Southern Ocean is home to a range of aquatic life, from microscopic bacteria and phytoplankton to massive baleen whales, all of which are linked through an intricate food web. A critical piece of this Southern Ocean food web is forage fish, an umbrella term that refers to small and medium-size open-ocean fish as well as squid, krill, and other crustaceans. They are the primary source of food for large fish, mammals, and birds. Forage fish consume plankton, acting as a conduit to transfer energy from the bottom of the food web to larger-bodied predators. Antarctic krill (*Euphausia superba*) is the most prevalent forage fish by abundance and biomass in the Southern Ocean.

Several species of penguin migrate through the Southern Ocean, relying on forage fish for the nutrients they need to survive and reproduce. Antarctic krill constitute up to 75 percent, by number, of the diet of chinstrap, macaroni, Adélie and emperor penguins (Wieneke et al. 2013), and up to 98 percent, by mass, of the diet of chinstrap, Adélie and gentoo penguins (Hinke et al. 2007). In fact, penguins of the Southern Ocean are so dependent on Antarctic krill that their biology is modified to accommodate seasonal fluctuations in its availability (Trivelpiece and Trivelpiece 2013). Antarctic krill are most plentiful in the Southern Ocean in summer, when ample light allows for abundant phytoplankton. Conversely, food is limited in the winter, when there is little light and low productivity. Emperor, Adélie, and chinstrap penguin chicks fledge in the summer during the height of krill productivity.

Recent interest in fishing for forage fish in the Southern Ocean has severe implications for marine wildlife all the way up the food chain. Though forage fish, particularly krill, are seldom eaten by humans, they are processed into fish oil and fish meal, which are used as feed in agriculture and aquaculture (Pikitch et al. 2012). Antarctic krill are also made into omega-3 supplements for human consumption.

The Commission for the Conservation of Antarctic Marine Living Resources

Recent development of the krill fishery and the expanding market for products manufactured from krill indicate that fishing in the Southern Ocean is likely to increase (Nicol and Foster 2003). In response to commercial interest in krill, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) was established in 1982 to protect marine life in Antarctic waters. CCAMLR aims to set catch limits for krill that consider the effects of fishing on marine ecosystems and reduce the impact on krill-dependent predators (Commission for the Conservation of Antarctic Marine Living Resources 2014). Though CCAMLR's member countries have been working to agree on a management protocol for more than 30 years, no formal agreement has been established (Trathan and Ballard 2013).

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Recommendations

To conserve the Southern Ocean food web and maintain healthy penguin populations, a combination of conservation tools is recommended. Penguins and other seabirds require at least one-third of forage fish biomass to remain in the ocean to sustain healthy populations (Cury et al. 2011, Pikitch et al. 2012). No-fishing zones could be set up around seabird breeding colonies, though this would not be possible in many areas (Trathan et al. 2015). Another tool is ecosystem-based fisheries management, which is grounded in the interconnectedness of species in the ecosystem rather than focused on single-species catch limits. In ecosystem-based fisheries management, catch limits are calculated to account for predator needs and potential bycatch. CCAMLR, along with an increasing number of scientists and policymakers, strives to protect the biodiversity of the Southern Ocean through this system.



Protecting penguins

Although climate change is a global challenge requiring global action, specific steps can reduce penguin mortality in some places by alleviating food depletion, bycatch, pollution, and habitat degradation. Marine protected areas (MPAs), ocean zoning, and ecosystem-based management around breeding grounds and migration routes would probably benefit penguins, though few such areas have been designed and implemented effectively.

Marine protected areas

When properly designed and managed, MPAs can be an effective way to maintain biodiversity because they preserve the integrity of the food web, reduce bycatch of penguins, foster healthy fish populations that then “spill over” into fishing areas, and open doors for ecotourism and increased scientific research (Edgar et al. 2014 and references therein, Pichegru et al. 2012, Pichegru et al. 2010). In a 2014 review, established MPAs were found to be most effective when they:

1. Prohibited fishing within their boundaries.
2. Had well-enforced rules.
3. Were over 10 years old.
4. Exceeded 62 square miles.
5. Were isolated by deep water or sand.

MPAs that met at least four of these standards had twice as many large fish species and five times as much large fish biomass as fished areas (Edgar et al. 2014), but these features are difficult to attain. As of 2014, more than 59 percent of MPAs had only two of the five characteristics (Edgar et al. 2014).



The emperor penguin endures minus 40 F temperatures and wind speeds of up to 90 mph. Yet they are vulnerable to climate change as sea ice diminishes.

In particular, no-take areas—where all fishing is off-limits—can be politically challenging to implement. As of early 2015, only 0.94 percent of the world’s oceans were designated as no-take (MPAtlas 2015). These areas are likely to become increasingly difficult to establish as the global human population increases, making no-fishing zones less economically feasible. Furthermore, for species that make lengthy migrations or have large foraging

ranges, MPAs are too small to encompass the necessary area (Boersma et al. 2015). It is possible, however, to combine MPAs with other management tools to maintain the integrity of the food web and allow penguins to migrate, forage, and reproduce successfully.

Ecosystem-based management

A shift in fisheries management from single-species management to ecosystem-based management is likely to benefit forage species, penguins, and other marine predators. Populations of forage fish can fluctuate dramatically, but once overfished they can take a long time to recover, if at all (Chavez et al. 2003, Pikitch et al. 2012, Essington et al. 2015). And the fluctuations can be difficult to detect because forage fish school together in groups of thousands, yielding a productive catch even in times of population decline (Mullon et al. 2005, Pikitch et al. 2012).

Forage fish in the ocean that serve as prey for large predatory fish such as salmon and tuna are worth twice as much as forage fish caught in commercial fisheries (Pikitch et al. 2012). For example, one study found that when the catch of forage species was decreased by 20 percent in an area, the reproductive success of marine predators in that area nearly doubled, further illustrating the economic and environmental trade-off in exploiting forage fish (Richerson et al. 2009). This trade-off should be considered as part of the management of forage and predator species fisheries (Pikitch et al. 2014).

Ecosystem-based management may use a variety of determinants to set sustainable catch limits—such as prey age, size, biomass and reproductive output, predator condition and reproductive success, and amount of bycatch (Pikitch et al. 2012). When considered together, these points of reference provide a much more comprehensive and practical lens through which to manage fisheries. Measures needed to successfully implement ecosystem-based management include further research to quantify forage fish abundance and bycatch and increased enforcement to eliminate illegal and unregulated fishing in protected waters.

Ocean zoning

For animals such as penguins that have separate wintering and breeding grounds, often with long migration routes in between, management of breeding and molting grounds addresses only part of the issue (Boersma and Parrish 1999, Martin et al. 2007). Ocean zoning, which divides stretches of ocean into designated areas, may be an effective strategy for protecting penguins not only in their coastal breeding waters, but also during migration. Such zoning could accommodate migratory behavior and appropriate human activities (Stokes et al. 2014) by creating management areas with seasonal regulations on fisheries and shipping lanes for petroleum extraction, for example (García-Borboroglu et al. 2008), timed to correspond to the use of the areas by penguin. Fishing, resource extraction, and transport could be regulated spatially and temporally within each zone, and regulations could be seasonal.

Bycatch and incidental mortality of penguins associated with fishing vessels occur mostly in areas close to breeding colonies, indicating the potential of this management system to reduce the impact of fisheries on breeding populations (Boersma and Parrish 1999, Yorio et al. 2010). For example, one zone could be open to fishing except when used by penguins during breeding. This ocean zoning is a flexible system that can adapt to fluctuations in marine wildlife populations and climate variation. When applied and enforced appropriately, it can accommodate penguins, human activities, changes in fish abundance, and climate variation. For ocean zoning to be effective, it must be based on science and have proper enforcement to reduce illegal fishing and other activities.

Habitat protections on land

For some species, managing introduced predators is the single most important terrestrial management solution (Dann 2013). As of 2010, effective predator control was in place in 22 of 38 mainland nesting sites of yellow-eyed penguins, a management strategy that could lead to improvement in the status of the species (Seddon et al. 2013).

Where direct contact with humans is on the rise, several strategies are available to governments to help mitigate the spread of disease and other tourism-associated problems while still benefiting from the worldwide interest in penguins. Governments can designate trails, erect signage and viewing hides, and create programs that educate tourists and local communities. In New Zealand, for example, a volunteer game warden program educates and monitors visitors to help ease the impact of tourism (Stein et al. 2010 as cited in Seddon et al. 2013). Other options include capping tourist numbers, limiting flash photography, and restricting the hours that tourists may visit (Dann 2013, Boersma et al. 2013a).

Conclusion

Penguins are ocean sentinels. They are accessible and appreciated by the public, and they herald changes to coastal and marine habitat, helping to focus conservation efforts. Two-thirds of penguin species are in decline due to intense fishing pressure on forage species, pollution of the oceans, degradation of breeding grounds, and climate change. Though addressing the causes of climate change requires global action, several regional and local management tools, including establishment of marine protected areas, ecosystem-based fisheries management, and ocean zoning, can alleviate stress on penguins and preserve these charismatic seabirds for generations to come.

References

- Ainley, D. G., R. E. LeResch, and W. J. L. Sladen. 1983. *Breeding Biology of the Adélie Penguin*. Berkeley and Los Angeles: University of California Press.
- Alder, J., B. Campbell, V. Karpouzi, K. Kaschner, and D. Pauly. 2008. "Forage Fish: From Ecosystems to Markets." *Annual Review of Environment and Resources* 33: 153-66.
- BirdLife International. 2010. *Rockhopper Penguins: A Plan for Research and Conservation Action to Investigate and Address Population Changes*. Proceedings of an International Workshop, Edinburgh, Scotland, June 2-5, 2008.
- Boersma, P. D., and G. A. Rebstock. 2009. "Foraging Distance Affects Reproductive Success in Magellanic Penguins." *Marine Ecology Progress Series* 375: 263-75.
- Boersma, P. D., E. Frere, O. Kane, L. M. Pozzi, K. Pütz, A. Raya Rey, G. A. Rebstock, A. Simeone, J. Smith, A. Van Buren, P. Yorio, and P. Garcia Borgoroglu. 2013a. "Magellanic Penguin (*Spheniscus magellanicus*)," edited by P. Garcia Borgoroglu and P. D. Boersma, 232-263. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Boersma, P.D., A. Steinfurth, G. Merlen, G. Jimenez-Uzategui, F. H. Vargas, and P. G. Parker. 2013b. "Galápagos Penguin (*Spheniscus mendiculus*)." In *Penguins: Natural History and Conservation*. 294-302. Seattle and London: University of Washington Press.
- Boersma, P. D. 1978. "Breeding Patterns of Galápagos Penguins as an Indicator of Oceanographic Conditions." *Science* 200: 1481-3.
- Boersma, P. D. 1998. "Population Trends of the Galápagos Penguin: Impacts of El Niño and La Niña." *The Condor* 100: 245-253.
- Boersma, P. D. 2008. "Penguins as Marine Sentinels." *BioScience* 58: 597.
- Boersma, P. D., and G. A. Rebstock. 2014. "Climate Change Increases Reproductive Failure in Magellanic Penguins." *PLOS ONE* 9:e85602.
- Boersma, P. D., G. A. Rebstock, and P. Garcia Borgoroglu. 2015. "Marine Protection Is Needed for Magellanic Penguins in Argentina Based on Long-Term Data." *Biological Conservation* 182: 197-204.

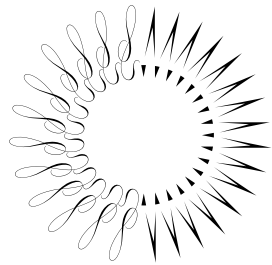
- Boersma, P. D., and J. K. Parrish. 1999. "Limiting Abuse: Marine Protected Areas, a Limited Solution." *Ecological Economics* 31: 287–304.
- Bost, C., K. Delord, C. Barbraud, Y. Cherel, K. Pütz, C. Cotté, C. Perón, and H. Weimerskirch. 2013. "King Penguin (*Apenodytes patagonicus*)."
6–21. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and M. Niquen C. 2003. "From Anchovies to Sardines and Back: Multidecadal Change in the Pacific Ocean." *Science* 299: 217–21.
- Commission for the Conservation of Antarctic Marine Living Resources. 2014. CCAMLR Convention. <https://www.ccamlr.org/en/organisation/camlr-convention> (accessed 30 July 2014).
- Cooper, J., R. J. M. Crawford, M. S. D. E. Villiers, B. M. Dyer, G. J. G. Hofmeyr, and A. Jonker. 2009. "Disease Outbreaks Among Penguins at Sub-Antarctic Marion Island: A Conservation Concern." *Marine Ornithology* 37: 193–6.
- Crawford, R. J. M., S. A. Davis, R. T. Harding, L. F. Jackson, T. M. Leshoro, M. A. Mejer, R. M. Randall, L. G. Underhill, L. Upfold, A. P. van Dalsen, E. van der Merwe, P. A. Whittington, A. J. Williams, and A. C. Wolfaardt. 2000. "Initial Impact of the Treasure Oil Spill on Seabirds off Western South Africa." *South African Journal of Marine Science* 22: 157–76.
- Crawford, R., L. Underhill, J. Coetzee, T. Fairweather, L. Shannon, and A. Wolfaardt. 2008. "Influences of the Abundance and Distribution of Prey on African Penguins *Spheniscus demersus* off Western South Africa." *African Journal of Marine Science* 30: 167–175.
- Crawford, R. J. M., J. Kemper, and L. G. Underhill. 2013. "African Penguin (*Spheniscus demersus*)."
210–31. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Cresswell, K. A., J. R. Wiedenmann, and M. Mangel. 2012. "A Model of Parental Conflict: Predicting Provisioning Behavior of Penguin Partners in Response to Local Changes in Krill." *Ecological Modelling* 246: 68–78.
- Crossin, G. T., P. N. Trathan, and R. J. M. Crawford. 2013. "Macaroni Penguin (*Eudyptes chrysolophus*) and Royal Penguin (*Eudyptes schlegeli*)."
184–208. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Croxall, J. P., S. J. McInnes, and P. A. Prince. 1984. "The Status and Conservation of Seabirds at the Falkland Islands." 271–91. In *Status and Conservation of the World's Seabirds*, ICBP Technical Publication No. 2. Cambridge: ICBP.
- Cury, P. M., I. L. Boyd, S. Bonhommeau, T. Anker-Nilssen, R. J. M. Crawford, R. W. Furness, J. A. Mills, E. J. Murphy, H. Osterblom, M. Paleczny, J. F. Piatt, J.-P. Roux, L. Shannon, and W. J. Sydeman. 2011. "Global Seabird Response to Forage Fish Depletion—One-Third for the Birds." *Science* 334: 1703–6.
- Cuthbert, R. J. 2013. "Northern Rockhopper Penguin (*Eudyptes moseleyi*)."
130–143. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Dann, P. 2013. "Little Penguin (*Eudyptula minor*)."
231–263. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Davis, L. S. 2013. "Erect-Crested Penguin (*Eudyptes sclateri*)."
144–51. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Davis, L. S., and F. T. McCaffrey. 1986. "Survival Analysis of Eggs and Chicks of Adélie Penguins (*Pygoscelis adeliae*)."
The Auk 103: 379–88.
- Davis, L. S., and M. Renner. 2003. *The Penguins*. London: T. & A. D. Poyser.
- de la Puente, S., A. Bussalleu, M. Cardena, A. Valdes-Velasquez, P. Majluf, and A. Simeone. 2013. "Humboldt Penguin (*Spheniscus humboldti*)."
264–83. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Edgar, G. J., R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S. Barrett, M. a Becerro, A. T. F. Bernard, J. Berkhout, C. D. Buxton, S. J. Campbell, A. T. Cooper, M. Davey, S. C. Edgar, G. Försterra, D. E. Galván, A. J. Irigoyen, D. J. Kushner, R. Moura, P. E. Parnell, N. T. Shears, G. Soler, E. M. a Strain, and R. J. Thomson. 2014. "Global Conservation Outcomes Depend on Marine Protected Areas With Five Key Features." *Nature* 506: 216–20.
- Essington, T. E., P. E. Moriarty, H. E. Froehlich, E. E. Hodgson, L. E. Koehn, K. L. Oken, M. C. Siple, and C. C. Stawitz. 2015. "Fishing Amplifies Forage Fish Population Collapses." *Proceedings of the National Academy of Sciences* doi:10.1073/pnas.1422020112.
- Gandini, P., P. D. Boersma, E. Frere, M. Gandini, T. Holik, S. T. Auk, and N. Jan. 1994. "Magellanic Penguins (*Spheniscus magellanicus*) Affected by Chronic Petroleum Pollution Along Coast of Chubut, Argentina." *The Auk* 111: 20–7.
- García-Borboroglu, P., and P. D. Boersma, eds. 2013. *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- García-Borboroglu, P., P. D. Boersma, L. M. Reyes, and V. Ruoppolo. 2008. "Contaminación Por Hidrocarburos Y Su Efecto Sobre El Pingüino De Magallanes Pablo." *Estado de Conservación del Mar Patagónico, versión electrónica*.
- González-Zevallos, D., and P. Yorio. 2006. "Seabird Use of Discards and Incidental Captures at the Argentine Hake Trawl Fishery in the Golfo San Jorge, Argentina." *Marine Ecology Progress Series* 316: 175–83.

- Grémillet, D., S. Lewis, L. Drapeau, C. D. Van Der Lingen, A. Jenny, J. C. Coetzee, H. M. Verheye, F. Daunt, S. Wanless, P. G. Ryan, and J. A. Huggett. 2008. "Spatial Match-Mismatch in the Benguela Upwelling Zone: Should We Expect Chlorophyll and Sea-Surface Temperature to Predict Marine Predator Distributions?" *Journal of Applied Ecology* 45: 610–21.
- Hinke, Jefferson T., Kasia Salwicka, Susan G. Trivelpiece, George M. Watters, and Wayne Z. Trivelpiece. 2007. "Divergent Responses of Pygoscelis Penguins Reveal a Common Environmental Driver." *Oecologia* 153: 845–55.
- Howarth, R. W. 2008. "Coastal Nitrogen Pollution: A Review of Sources and Trends Globally and Regionally." *Harmful Algae* 8: 14–20.
- International Union for Conservation of Nature. 2014. IUCN Red List of Threatened Species. <http://www.iucnredlist.org> (accessed 29 July 2014).
- Jenouvrier, S., M. Holland, J. Stroeve, M. Serreze, C. Barbraud, H. Weimerskirch, and H. Caswell. 2014. "Projected Continent-Wide Declines of the Emperor Penguin Under Climate Change." *Nature Climate Change* 4: 715–8.
- Kane, O. J., J. R. Smith, P. D. Boersma, N. J. Parsons, V. Strauss, P. Garcia-Borboroglu, and C. Villanueva. 2010. "Feather-Loss Disorder in African and Magellanic Penguins." *Waterbirds* 33: 415–21.
- Kane, O. J., M. M. Uhart, V. Rago, A. J. Pereda, J. R. Smith, A. Van Buren, J. A. Clark, and P. D. Boersma. 2012. "Avian Pox in Magellanic Penguins (*Spheniscus magellanicus*)." *Journal of Wildlife Diseases* 48: 790–4.
- Kemper, J., Underhill, L. G. and Roux, J.-P. 2007. "Artificial Burrows for African Penguins on Halifax Island, Namibia: Do They Improve Breeding Success?," in: Kirkman, S.P.(ed), *Final report of the BCLME (Benguela Current Large Marine Ecosystem) project on top predators as biological indicators of ecosystem change in the BCLME*. Avian Demography Unit, Cape Town, South Africa, 101–6.
- Lynch, H. 2013. "Gentoo Penguin (*Pygoscelis papua*)." 72–88. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- "Marine Protected Areas," Marine Conservation Institute. <http://www.mpatlas.org/explore>.
- Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris. 2007. "Optimal Conservation of Migratory Species." *PLOS ONE* 2: e751.
- Mattern, T. 2013a. "Fiorland Penguin (*Eudyptes pachyrhynchus*)." 152–67. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Mattern, T. 2013b. "Snares Penguin (*Eudyptes robustus*)." 168–83. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Mullon, C., P. Fre, and P. Cury. 2005. "The Dynamics of Collapse in World Fisheries." *Fish and Fisheries* 6: 111–20.
- Nicol, S., M. Stolp, and O. Nordstrom. 1992. "Change in the Gross Biochemistry and Mineral Content Accompanying the Moulting Cycle in the Antarctic Krill *Euphausia superba*." *Marine Biology* 113: 201–9.
- Nicol, S., and J. Foster. 2003. "Recent Trends in the Fishery for Antarctic Krill." *Aquatic Living Resources* 16: 42–5.
- Pichegru, L., D. Grémillet, R. J. M. Crawford, and P. G. Ryan. 2010. "Marine No-Take Zone Rapidly Benefits Endangered Penguin." *Biology Letters* 6: 498–501.
- Pichegru, L., P. G. Ryan, R. Van Eeden, T. Reid, D. Grémillet, and R. Wanless. 2012. "Industrial Fishing, No-Take Zones and Endangered Penguins." *Biological Conservation* 156: 117–25.
- Pikitch, E., P. D. Boersma, I. L. Boyd, D. O. Conover, P. Cury, T. Essington, S. S. Heppell, E. D. Houde, M. Mangel, D. Pauly, É. Plagányi, A. Sainsbury, K., and R. S. Steneck. 2012. "Little Fish Big Impact: Managing a Crucial Link in Ocean Food Webs." *Lenfest Forage Fish Task Force*. 1–108.
- Pikitch, E. K., K. J. Rountos, T. E. Essington, C. Santora, D. Pauly, R. Watson, U. R. Sumaila, P. D. Boersma, I. L. Boyd, D. O. Conover, P. Cury, S. S. Heppell, E. D. Houde, M. Mangel, É. Plagányi, K. Sainsbury, R. S. Steneck, T. M. Geers, N. Gownaris, and S. B. Munch. 2014. "The Global Contribution of Forage Fish to Marine Fisheries and Ecosystems." *Fish and Fisheries* 15: 43–64.
- Pozzi, L. M., P. García Borboroglu, P. D. Boersma, and M. A. Pascual. 2015. "Population Regulation in Magellanic Penguins: What Determines Changes in Colony Size?" *PLOS ONE* 10: e0119002.
- Pütz, K., A. R. Rey, and H. Otley. 2013. "Southern Rockhopper Penguin (*Eudyptes chrysocome*)." 112–29. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Richerson, K. et al. 2009. "Accounting for Indirect Effects and Non-Commensurate Values in Ecosystem Based Fishery Management (EBFM)." *Marine Policy* 34: 114–9.
- Saether, B., and O. Bakke. 2000. "Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate." *Ecology* 81: 642–53.
- Schlatter, R. P., R. D. E. L. A. Araucanía, R. Omero, J. O. V. Asquez, A. L. L. Izama, C. A. H. Hernández, and A. Lejandro. 2009. "Mortandad de Pingüino de Magallanes." *Boletín Chileno de Ornitología* 15: 78–86.

- Seddon, P.J., and U. Ellenberg. 2008. "Effects of Human Disturbance on Penguins." 163-80. In *Marine Wildlife and Tourism Management*. Oxford: CABI Publishing.
- Seddon, P. J., U. Ellenberg, and Y. van Heezik. 2013. "Yellow-Eyed Penguin (*Megadyptes antipodes*)." 90-110. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Shumway, S. E., S. M. Allen, and P. D. Boersma. 2003. "Marine Birds and Harmful Algal Blooms: Sporadic Victims or Under-Reported Events?" *Harmful Algae* 2: 1-17.
- Stein, A., K. Beer, and P.J. Seddon. 2010. "Sandfly Bay Revisited: A Report on Visitor Attitudes, Awareness, and Activities at the Sandfly Bay Wildlife Refuge, Otagos Peninsula." *Wildlife Management Report* no. 237.
- Steinfurth, A., and G. Merlen. 2005. "Predación de Gatos Salvajes (*Felis catus*) Sobre el Pinguino de Galápagos (*Spheniscus mendiculus*) el Caleta Iguana, Isla Isabela." Unpublished report to the Galápagos National Park Service and the Charles Darwin Foundation, Puerto Ayora.
- Stokes, D. L., P. D. Boersma, J. Lopez de Casenave, and P. García-Borboroglu. 2014. "Conservation of Migratory Magellanic Penguins Requires Marine Zoning." *Biological Conservation* 170: 151-61.
- Taylor, G. A. 2000. *Action Plan for Seabird Conservation in New Zealand*. Department of Conservation, Biodiversity Recovery Unit, Wellington, New Zealand.
- Trathan, P. N., and G. Ballard. 2013. "Adelie Penguin (*Pygoscelis adeliae*)." 36-57. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Trathan, P. N., García-Borboroglu, P., Boersma, D., Bost, C.-A., Crawford, R. J. M., Crossin, G. T., Cuthbert, R. J., Dann, P., Davis, L. S., De La Puente, S., Ellenberg, U., Lynch, H. J., Mattern, T., Pütz, K., Seddon, P. J., Trivelpiece, W. and Wienecke, B. 2015. "Pollution, habitat loss, fishing, and climate change as critical threats to penguins." *Conservation Biology* 29: 31-41.
- Trivelpiece, W. Z., and S. G. Trivelpiece. 1990. "Courtship Period of Adelie, Chinstrap, and Gentoo Penguins." 113-27. In *Penguin Biology*. San Diego: Academic Press.
- Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. "Variability in Krill Biomass Links Harvesting and Climate Warming to Penguin Population Changes in Antarctica." *Proceedings of the National Academy of Sciences* 108: 7625-8.
- Trivelpiece, W. Z., and S. Trivelpiece. 2013. "Chinstrap Penguin (*Pygoscelis antarctica*)." 58-71. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Vargas, F. H., R. C. Lacy, P. J. Johnson, A. Steinfurth, R. J. M. Crawford, P. D. Boersma, and D. W. Macdonald. 2007. "Modelling the Effect of El Niño on the Persistence of Small Populations: The Galápagos Penguin as a Case Study." *Biological Conservation* 137: 138-48.
- Walker, B. G., P. D. Boersma, and J. C. Wingfield. 2005. "Physiological and Behavioral Differences in Magellanic Penguin Chicks in Undisturbed and Tourist-Visited Locations of a Colony." *Conservation Biology* 19: 1571-7.
- Wienecke, B., G. Kooyman, and Y. Le Maho. 2013. "Emperor Penguin (*Aptenodytes forsteri*)." 22-34. In *Penguins: Natural History and Conservation*. Seattle and London: University of Washington Press.
- Williams, T.D. 1995. *Bird Families of the World: The Penguins*. Oxford: Oxford University Press.
- Yorio, P., F. Quintana, P. Dell'Arciprete, and D. González-Zevallos. 2010. "Spatial Overlap Between Foraging Seabirds and Trawl Fisheries: Implications for the Effectiveness of a Marine Protected Area at Golfo San Jorge, Argentina." *Bird Conservation International* 20: 320-34.
- Yorio, P., and P. D. Boersma. 1992. "The Effects of Human Disturbance on Magellanic Penguin (*Spheniscus magellanicus*) Behaviour and Breeding Success." *Bird Conservation International* 2: 161-73.



Emperors are the largest of the penguins, standing up to 4 feet tall.



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