King Penguin

(Aptenodytes patagonicus)

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1. SPECIES (COMMON AND SCIENTIFIC NAMES)

King penguin, *Aptenodytes patagonicus*

2. DESCRIPTION OF THE SPECIES

The king penguin is one of two extant species in the genus *Aptenodytes*. Together with its close relative, the emperor, the king differs from other penguins in its large size, long and thin beak, and bright colors. Paleontological evidence suggests that about 3 million years ago, a third *Aptenodytes* species, the Ridgen's penguin (*A. ridgeni*), lived in New Zealand (Fordyce and Jones 1990; Williams 1995). The genus *Aptenodytes* split off around 40 million years ago from the branch that led to all other living penguin species (Jouventin 1982).

The king, the second-largest penguin, differs from the emperor in its thinner appearance and the marked auricular and brighter orange patches that extend as a narrow stripe around the neck (fig. 1). Unlike the emperor penguin, the king has an unfeathered tarsus. The head, chin, and throat are blackish. The lower beak mandibles are orange to bright pink. The eye is brown with a thin, dark iris. The flippers are proportionally larger than the emperor's and ventrally white with blue black at the tip. The dorsal side of the body, ranging from the neck over the back to the tail and the feathered legs, looks bright silver blue after the molt. The dorsal plumage is separated from the white ventral side by a thin black line and becomes a dull gray after the end of summer. The tail is rather short and dark gray. The robust feet are black. Within pairs, the male is most often larger than the female. The crèched chick is feathered with brown down before developing thick brown dunes that are maintained until around 10 months of age (fig. 2). The beak is blackish until the chick molts into immature plumage. The auricular patches of immature birds are much paler (yellow) than those of adults. The king acquires adult plumage at the

FIG. 1. King penguin showing orange-yellow auricular patch on the head and orange on the lower mandible. (P. Ryan)

FIG. 2. Adult king penguin near a king penguin chick. The brown-feathered chicks were thought to be a separate species and were called "oakum boys" because they resembled sailors who became covered in tar and hemp when filling cracks between the boards on ships. (P. D. Boersma)

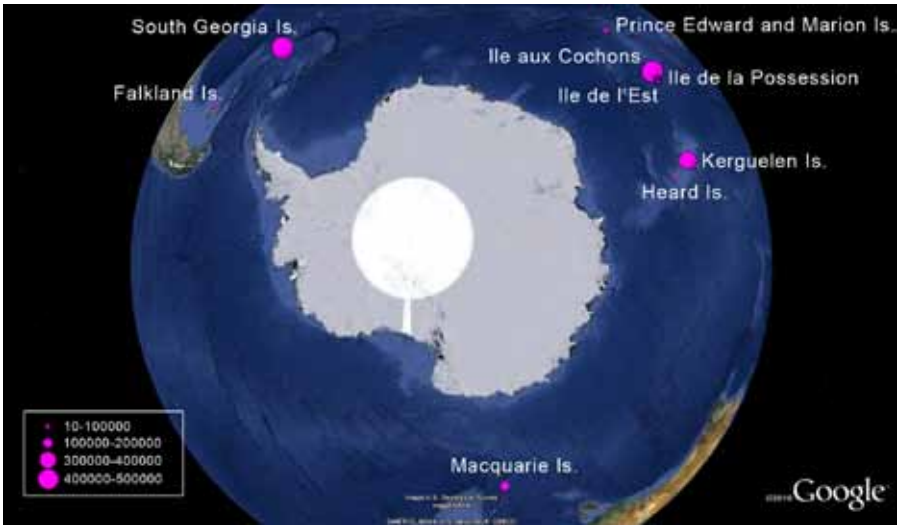

FIG. 3. Distribution and abundance of the king penguin.

age of three years (Williams 1995).

3. TAXONOMIC STATUS

The king penguin, first described in 1778 by the English naturalist John Frederick Miller, was distinguished from the emperor penguin in 1844 by George Robert Gray (Gray 1844). The generic name *Aptenodytes* is derived from the ancient Greek and means "without the capacity to fly," and its specific epithet *patagonicus* is derived from "Patagonia." Several subspecies have been suggested, but two are currently recognized: *A. p. patagonicus* breeds in the South Atlantic Ocean, and *A. p. halli* breeds in the southern Indian and Pacific Oceans. Some distinct variation in size occurs by locality, but accurate and comparable data are lacking. For example, the flipper lengths of kings at the Crozet Islands and Marion Island are about 5% longer than in South Georgia Island. Conversely, flipper lengths of birds from the Kerguelen Islands are about 16% smaller than on Crozet (table 1.1). The Crozet and Kerguelen archipelagoes lie only 1,400 kilometers apart, but penguin populations appear genetically isolated from one another (Viot 1987). Body mass also varies by locality. For example, birds from South Georgia are as much as 25% heavier than the Crozet birds during courtship.

4. RANGE AND DISTRIBUTION

King penguins breed on sub-Antarctic islands between latitude 45° south and 55° south, namely on the Falkland/Malvinas Islands and South Georgia Island in the South Atlantic Ocean, on Prince Edward, Crozet (including Cochons, Possession, and l'Est), Kerguelen, and Heard Islands in the southern Indian Ocean, and on Macquarie Island in the southwestern Pacific Ocean (table 1.2; fig. 3). One breeding pair has been reported from the South Sandwich Islands, but consistent breeding awaits confirmation. All breeding sites are generally located within a distance of 400 kilometers from the Antarctic Polar Front.

The king's foraging ecology, including their range and distribution in relation to marine features, is one of the most extensively studied among marine vertebrates. During summer, irrespective of the location of their breeding site, their at-sea distribution is strongly dependent on frontal zone features, particularly the Antarctic Polar Front. However, the Sub-Antarctic Front is also frequented by birds from some breeding sites (Crozet Islands [Bost et al. 2009], Falklands/Malvinas [Pütz 2002; Pütz and Cherel 2005]).

In autumn and winter, birds caring for chicks forage beyond the Antarctic Polar Front, in Antarctic waters, up to the limit of the pack ice (Moore et al. 1999; Pütz et al. 1999; Bost et al. 2004). Only birds from the small breeding colony of the Falklands/Malvinas make use of the slope of the Patagonian Shelf up to 38° south (Pütz 2002). In general, the kings' winter foraging area is encompassed by the Antarctic Polar Front to the north and the Antarctic Divergence (up to the limit of the sea ice) to the south. Breeding birds foraging very close to the colonies, over slope waters, at the end of their return trips in winter, can return with almost-intact prey in their stomachs (Cherel et al. 1996).

FIG. 4. Adult king penguin with an egg threatens to peck another king penguin. (P. D. Boersma)

Where adult nonbreeders and immature birds disperse is unknown. Juveniles probably disperse off the Polar Frontal Zone as far as 60° south (Ainley et al. 1984), that is, in the same sectors used by juvenile emperor penguins (Kooyman et al. 1996).

5. SUMMARY OF POPULATION TRENDS

King populations throughout the Sub-Antarctic have increased since the end of the last century following a drastic decline during the 19th and the beginning of the 20th century (Macquarie Island [Rounsevell and Copson 1982], Heard Island [van den Hoff et al. 1993], Kerguelen Islands [Weimerskirch et al. 1989], Crozet Islands [Delord et al. 2004], Marion Island [Williams et al. 1979], South Georgia Island [Lewis Smith and Tallowin 1979], Falklands/Malvinas [Otley et al. 2007]). The king population declined due to exploitation associated with the sealing industry (Conroy and White 1973; Conroy 1975; Rounsevell and Copson 1982). Most of the colonies grew rapidly between 1970 and 1990, sometimes at a rate especially high for a long-lived seabird (Weimerskirch et al. 1992).

During the past 15 years, population variability was high (table 1.2). Recent surveys indicate that several large colonies appear to have decreased and stabilized at a lower population level. The population has begun to stabilize over the past decade, and we estimate the global population at 1.6 million annual breeding pairs (range 1,584,320–1,728,320). The counts occur in January, at peak or just following peak egg laying (fig. 4). Therefore, the numbers of breeding pairs are underestimates, because they do not include the pairs that failed before the counts or late-nesting pairs that lay eggs until mid-March. The 18-month breeding cycle of this species means the proportion of late breeders is regulated primarily by the breeding success of the preceding year.

6. IUCN STATUS

Since 2004, the International Union for Conservation of Nature (IUCN) has listed the king penguin in the Least Concern category on its Red List of Threatened Species (IUCN 2011). The population size is large, and colonies have recently increased and/or stabilized at all breeding sites throughout its range.

LEGAL STATUS. This species is protected throughout its range, with colonies located either in designated nature reserves or sites of special scientific interest administered by the respective national authorities and regulated by management plans.

7. NATURAL HISTORY

BREEDING BIOLOGY. Kings have a breeding-molt cycle of more than one year, the longest among seabirds because the chicks fast during the winter. The life cycle was studied in detail at South Georgia Island (Stonehouse 1960; Olsson 1996; Olsson and Brodin 1997) and the Crozet Islands (Barrat 1976; Weimerskirch et al. 1992; Gauthier-Clerc et al. 2001; Descamps et al. 2002) and investigated at Marion Island (du Plessis et al. 1994; van Heezik et al. 1994) and the Falklands/Malvinas

FIG. 5. King penguins nesting on Salisbury Plain, South Georgia Island. (P. D. Boersma)

(Otley et al. 2007).

Kings often breed in large, dense colonies (mean density about 2 breeders per square meter, [Barrat 1976]) located on flat, sandy beaches or near-shore valleys (fig. 5). Protection against the dominant wind direction during winter is a determinant of colonization and colony breeding success (Weimerskirch et al. 1992).

The breeding cycle lasts about 14–15 months from courtship to chick fledging (but see Otley et al. 2007). This unusual extended cycle results from the large size of the bird and the halting of chick growth from autumn to early spring. Some chicks fast for up to five months during winter before being fed by their parents and fledging (Cherel et al. 1987). The extended breeding cycle means that colonies are continuously occupied with crèched chicks throughout the year. The reproductive cycle (n) begins at the end of winter and is initiated mostly by failed breeders of the current year (cycle n-1) returning to the colonies for the prenuptial molt (date of first arrival: Crozet, range 22 Sept.–1 Oct., n = 3 years; South Georgia, range 8 Sept.–6 Nov.) (Weimerskirch et al. 1992; Williams 1995). Males and females do not arrive to molt at the same time, which results in a low rate of mate fidelity (28.6 % [Barrat 1976]). After their molt, they forage at sea for more than two weeks (Crozet, 17.1 ± 0.5 days, n = 3 years [Descamps et al. 2002]) before returning to shore between late October and December. Penguins come to the colonies with large body reserves, approximately four kilograms (Weimerskirch et al. 1992; Cherel et al. 1993; Gauthier-Clerc et al. 2001), as they have to fast during the first part of breeding (courtship and early incubation for males), and insufficient body reserves may induce a delay or even complete breeding failure (Gauthier-Clerc et al. 2001).

The laying period is asynchronous and extends over four months, from early November to mid-March, but with considerable variation between breeding sites and years (fig. 6). At Crozet, the mean laying date over three consecutive years ranged from 22 December ± 19.5 days to 14 January ± 15.9 days (Weimerskirch et al. 1992). A marked laying peak usually occurs between the second half of November and the second half of

December, corresponding to the so-called early breeders (Gauthier-Clerc et al. 2001). The king penguin, like its close relative, the emperor penguin, has no nest and incubates its single large egg on its feet (table 1.3), sheltered by a feathered-skin pouch (fig. 7). Incubation lasts around 54 days. Re-laying is rare and occurs only when the egg is lost during incubation (Weimerskirch et al. 1992).

From courtship to hatching, the two parents exchange duties six times, one incubating while the other forages at sea (Descamps et al. 2002). Hatching may take 2–3 days, but the chick can be fed through a hole in the shell. Chicks have a thin covering of down and are brooded while balanced on their parents' feet (fig. 8). From hatching to crèching, both parents alternate brooding duties, each making four to five foraging trips usually 4–12 days in duration. This period lasts about one month before the chicks form crèches, by mid-February (fig. 9). During mid-April (15–26 April [Weimerskirch et al. 1992]), the almost fully grown chicks usually have gained extensive body reserves (Cherel et al. 1993) (fig. 10). At the same time, the adults start to desert the colony for extended periods because of the scarcity of prey (Charrassin and Bost 2001). During the winter period, the chicks lose weight, fast, and get an average of 4.7 feeds from their parents between 1 May and 31 August (Crozet, n = 3 years [Descamps et al. 2002]). Parents return to feed chicks usually by mid-September and continue to feed them until the chicks fledge. The chicks' molt occurs between the second half of November and early January.

Breeders usually lay eggs every year, even when failure is almost certain, late in the season. At best, successful breeding occurs every two years (Olsson 1996; Jiguet and Jouventin 1999). Birds that ended molt early (October) have their eggs between mid-November and early January (early breeders), thereby maximizing the likelihood that their chicks will have sufficient energy reserves to survive the winter fasting period. Conversely, kings that ended their molt later, that is, in December and January (late breeders), do not have eggs until late January to March, and thus their chicks crèched with insufficient energy reserves for the winter fast. The heavier the crèched chick, the higher its probability of fledging (Cherel et al. 1987).

PREY AND FORAGING ECOLOGY. With the exception of the

FIG. 6. King penguins are a bill length away from their neighbors as they keep their eggs and young chicks on their feet. (P. Ryan)

FIG. 7. Adult king penguin incubating an egg at South Georgia Island. (P. D. Boersma)

FIG. 8. King penguin with chick between its feet. (P. D. Boersma)

FIG. 9. King penguin chicks fatten up for the winter and enjoy the close contact with other chicks as they wait for their parents. (P. Ryan)

FIG. 10. Adult king penguin is lost in a crowd of chicks that must fast in the winter when adults depart the colony, leaving the chicks without food until they return. (J. Weller)

Falklands/Malvinas, all king breeding sites are located within the vicinity of the Antarctic Polar Front. Many aspects of the kings' foraging ecology have been intensively studied at various breeding sites, including their diving behavior (Kooyman et al. 1992; Pütz et al. 1998; Charrassin et al. 1998, Charrassin et al. 1999; Moore et al. 1999; Charrassin and Bost 2001; Bost et al. 2002; Charrassin et al. 2002; Wienecke and Robertson 2006; Pütz and Cherel 2005; Bost et al. 2007) and diet (Adams and Klages 1987; Hindell 1988; Cherel and Ridoux 1992; Olsson and North 1997; Moore et al. 1999; Cherel et al. 2002). Except for the emperor penguin, no bird is able to dive deeper (up to 440 m [Charrassin et al. 2002]), although mean foraging depths are between 100 and 200 meters, increasing from incubating to crèching (Charrassin et al. 2002) and during winter (Moore et al. 1999). Regardless of the breeding location, kings are specialized predators that target mainly lanternfish (myctophids), that is, small, schooling mesopelagic fish (review in Cherel et al. 2002). These fish constitute the bulk of mesopelagic fish in the Polar Frontal Zone (Sabourenkov 1991) and are caught by pursuit-diving, mostly during daylight hours (Pütz and Bost 1994). King penguins dive synchronously (Pütz and Cherel 2005). During winter, the proportion of squid (e.g., Moore et al. 1998) in the diet increases up to 64% by biomass for breeders feeding their chicks (Cherel et al. 1996). When myctophid availability decreases, kings catch some other pelagic fish such as the ice fish (*Champsocephalus gunnari*) (Bost et al., unpubl. data).

PREDATORS. At some breeding sites, killer whales (*Orcinus orca*) are the major at-sea predator targeting both adults and fledglings during their departure from and arrival on the beach. Vagrant young leopard seals (*Hydrurga leptonyx*) also prey on king penguins during their winter sojourn along sub-Antarctic coasts. Some adult male Kerguelen fur seals (*Arctocephalus gazella*) at Marion Island (Hofmeyr and Bester 1993) and the Crozet Islands (Charbonnier et al. 2010) regularly take king penguins, and South American sea lion (*Otaria flavescens*) bulls prey on kings at the Falklands/Malvinas (Pütz, pers. obs.).

Ashore, the sub-Antarctic and Antarctic giant petrels *Macronectes halli* and *M. giganteus* prey on injured penguins or penguins in poor condition (Hunter 1983). Giant petrels also take chicks, mostly those in poor body condition, but can also catch and kill full-grown, healthy chicks, sometimes at night (Le Bohec et al. 2003). Predation by skuas (*Stercoraria* spp.) is mostly on deserted eggs or eggs robbed from inexperienced breeding birds when mates are exchanging nest duties. The lesser sheathbill (*Chionis minor*) takes mostly deserted eggs and unattended small chicks, but

FIG. 11. A fat juvenile king penguin sleeps with its bill under its wing as it gets ready to molt at Neko Harbor, Antarctic Peninsula. Note the lack of yellow or orange plumage. (P. D. Boersma)

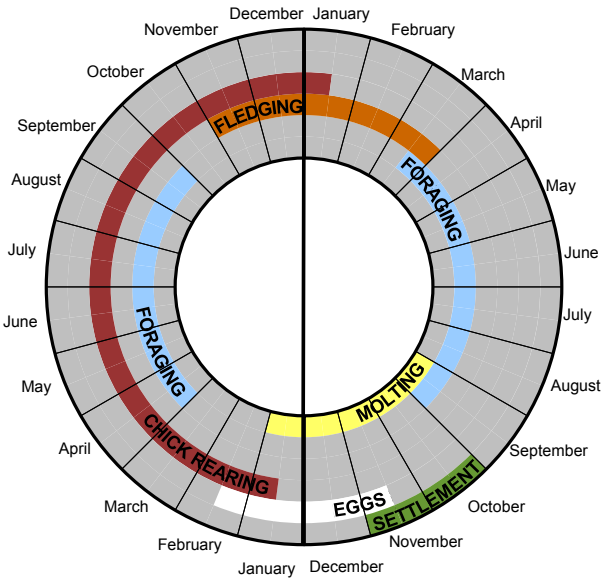

FIG. 12. The annual cycle of the king penguin is about 17 months, the longest of any penguin species.

it also steals food when chicks are fed by their parents during winter and spring (Verheyden and Jouventin 1991). In the Falklands/Malvinas, turkey vultures and crested caracaras prey on abandoned eggs and chicks (Pütz, pers. obs.).

MOLT. The first penguins coming ashore to molt are unsuccessful breeders (fig. 11). The peak of their molt is 17 October ± 4.6 days at Crozet (n = 3 years [Descamps et al. 2002]) and before November at the Falklands/Malvinas (Otley et al. 2007). Molting birds usually congregate along the banks of rivers, which they often use as a freshwater supply. The peak of molt for successful breeders is from late November to early January at both sites. Between fledging and the beginning of the molt, successful parents spend one month at sea. For early molters, molt duration is the same at the northern and southern limits of the range (Crozet, 31.0 + 3.9 days [Weimerskirch et al.1992]; South Georgia, 31.2 days, range 27–36 [Stonehouse 1960]). At Crozet, the molt duration of successful breeders is shorter (22.7 + 1.0 days [Weimerskirch et al. 1992]), indicating that molt duration depends on the outcome of the previous breeding season. During molt on land, the birds replace all their feathers and also their mandible plates. Feather growth begins at sea when penguins build up their energy reserves, including fat, and protein in anticipation of fasting and growing new feathers (Cherel et al. 1993; Cherel et al. 1994). Kings reach their peak body mass at the very beginning of the molting process and suffer their greatest mass loss during the molting fast, corresponding to about 51% and 45% of the initial weight of early and late breeders, respectively (Weimerskirch et al. 1992).

ANNUAL CYCLE. The king has one of the most unusual annual cycles of any of the penguins. It takes eighteen months to rear one chick, which means there is an overlap during the summer months when both eggs and large chicks are present. See figure 12.

8. POPULATION SIZES AND TRENDS

In recent decades, king populations have increased across their range (table 1.2). Exploitation of penguins for their oil associated with the sealing industry in the 19th and early 20th centuries resulted in their population decline. After commercial exploitation ceased, king populations quickly recovered during the second part of the 20th century at all breeding sites (Macquarie Island [Rounsevell and Copson 1982], Heard Island [van den Hoff et al. 1993], Kerguelen Islands [Weimerskirch et al. 1989], Crozet Islands [Delord et al. 2004], Marion Island [Williams et al. 1979], South Georgia Island [Lewis Smith and Tallowin 1979], Falklands/

Malvinas [Otley et al. 2007]). The largest population occurs on the Crozet Islands (at least 612,000 pairs, i.e., about 50% of the global population). However, whereas the breeding colonies on Possession Island are counted annually, no recent data are available for the world's largest king colony at Hogs Island (500,000 pairs in 1988 [Guinet et al. 1995]). Kerguelen and Heard Island colonies were slower to recover and are still increasing. At Macquarie Island, the most recent estimate is of 150,000–170,000 breeding pairs (Parks and Wildlife Service 2006), representing an increase of 4–6% per year since 1984 (D. E. Rounsvell, unpubl. data), with recent recolonization of collapsed colony sites (Van Den Hoff et al. 2009). The South Georgia population is now approximately 450,000 pairs, an increase of 11% per year since 1985–86 (P. N. Trathan, pers. comm.). The Falklands/Malvinas population fledged the first chick in 1965 and is estimated at more than 1,000 pairs (Otley et al. 2007). The breeding pairs in the king colony at the Falklands/Malvinas has increased recently after declining slightly or being stable for a decade (Pütz, unpubl. data).

More king penguins are visiting the coasts of Tierra del Fuego to molt, and breeding is anticipated. The total breeding population is currently estimated at approximately 1.6 million pairs (table 1.2), and the population is expected to increase in at least some localities (e.g., Kerguelen Island, the Falklands/Malvinas). Recent surveys also indicate that several large colonies have stabilized or decreased compared to the beginning of the 21st century.

9. MAIN THREATS

Human exploitation probably caused the collapse of king populations during the 19th and early 20th centuries when penguins were killed for their oil by the sealing industry. At some breeding sites, populations were either exterminated (e.g., Heard Island) or at least substantially reduced. The cessation of sealing likely explains the exponential increase of subsisting populations and the recolonization of former breeding sites (Conroy and White 1973; Rounsevell and Copson 1982). Demographic studies at two breeding localities indicate very high adult survival at least since the mid-1970s (Crozet, 1975–90, 90.7–95.2% [Weimerskirch et al. 1992]; Crozet, 1998–2003, 90.6% [Le Bohec et al. 2007]; South Georgia, 1992–96, 83.0–97.7% [Olsson and van der Jeugd 2002]) (table 1.4). Juvenile and immature survival also appears to be relatively high (Olsson and van der Jeugd 2002; Gauthier-Clerc et al. 2004). Breeding success is highly variable (Crozet, 1986–88, 30.6%, range 0.7–53.2% [Weimerskirch et al. 1992]; Crozet, 1997–2001, range 20–34% [Descamps et al. 2002]; Gauthier-Clerc et al. 2004) and comparatively low, which is a direct consequence of the mix of early and late breeders; this in turn is affected by each individual's breeding success in the previous year. Breeding success of birds that did not breed or failed in a previous breeding attempt is much higher (51–60%) than for birds that previously bred successfully (5% [Le Bohec et al. 2007]). Thus, the increase in size of the king population was probably caused by a combination of high survival rates for adults, juveniles, and immatures and the relatively high breeding frequency. Furthermore, an increased food supply (myctophid fish) made available by the reduction of whale stocks may have had a positive impact on king penguins (Laws 1977; Rounsevell and Copson 1982).

Some populations have stabilized since the mid-1990s (e.g., Crozet Islands). These populations were approaching carrying capacity during the early 1990s, and climatic factors, such as the Southern Oscillation Index, may have modified their population dynamics (Delord et al. 2004). The warm phase of the Southern Oscillation and warm sea surface temperatures in foraging areas may negatively affect kings' breeding success and adult survival (Le Bohec et al. 2008).

POTENTIAL THREATS. The king is one of the most fortunate species in term of conservation status, with either increasing or stable populations throughout its breeding range. In contrast to the majority of southern seabirds, introduced predators such as cats and rats have had no proven impact on the species.

Increasing tourism within the sub-Antarctic regions could induce disease outbreaks among king colonies. For example, unknown diseases killed at least 250 to 300 kings in 1992–93 at Marion Island (Cooper et al. 2009).

The most important potential threats may be a change in the availability of their main prey. Myctophid fish were commercially exploited by the end of the 1970s and the beginning of the 1990s, with more than 200,000 tons harvested in the South Georgia sec-

tor (Collins et al. 2008). Several attempts to develop new commercial fisheries on a limited scale within the Southern Ocean are ongoing. A large, uncontrolled development of myctophid fisheries close to key foraging areas, especially in the southern Indian Ocean sector (Kerguelen) or in the Scotia Sea (South Georgia) may have deleterious effects on the foraging success and populations of the king.

In the long term, projected temperature increase in the Southern Ocean may also drastically modify king colony distribution and populations (Peron et al. 2012). For example, Intergovernmental Panel on Climate Change (IPCC) models predict a linear increase of 2°C in sea surface temperature in the southern Indian Ocean by the end of the 21st century. The Crozet population of kings is of concern for the following reasons: (1) it depends on distant, dynamic frontal zones, (2) it holds more than half of the world's population (Delord et al. 2004), and (3) demographic parameters might be negatively affected by warm sea surface temperatures within the foraging areas (Le Bohec et al. 2008). Such an increase in sea surface temperature should lead to a decrease in sea-ice extent and a significant southward shift (around 2.5° in latitude) of the position of the Antarctic Polar Front, the key king foraging area (Bost et al. 1997, 2009; Peron et al. 2012). As a consequence, the minimal distance from the colony to the limit of the front is predicted to double by 2099 during the incubation and brood, with a mean distance of approximately 800 kilometers during summer.

Long-term tracking data for foraging king penguins breeding at Crozet indicate that during "warm" years, the predicted foraging zones are much farther south and hence penguins increase their foraging range (Bost et al., in prep.). A maximal foraging range of 750 kilometers during brooding increases the trip duration to more than three weeks. Breeding and foraging data indicate that the probability of partner desertion drastically increases after a threshold of 22 days without relief. Thus, given the energetic constraints of the chick during brooding, the projected increase in traveling distance in the southern Indian Ocean will prevent successful chick rearing (Peron et al. 2012) and hence negatively affect demographic parameters and population sizes (Le Bohec et al. 2008). The projected situation appears similar for kings on Marion Island, and it remains to be seen whether they can adapt to these changing scenarios. Satellite-tracked Magellanic penguins (*Spheniscus magellanicus*) that made trips farther from the nest had lower reproductive success (Boersma and Rebstock 2009). Thus, the warming of the Southern Ocean represents a major threat for king penguins, especially in the southern Indian Ocean, without major adaptations in foraging strategies or timing of reproduction. These environmental changes may occur at time scales too short to allow rapid adaptation of this long-lived species.

10. RECOMMENDED PRIORITY RESEARCH ACTIONS FOR CONSERVATION

The following research actions are a priority for conservation:

1. Determine the marine habitats used, especially during winter, in the first years of life and for nonbreeding adults. Extensive short- and long-term data sets on the foraging ecology and habitat use of breeding birds are already available during the summer months for some key localities (Crozet, Marion, Kerguelen, and South Georgia). More information is needed on breeding birds during the austral winter, when they disperse widely (Pütz 2002; Bost et al. 2004). Finally, place special emphasis on determining the trophic niche of nonbreeding birds. This group includes not only nonbreeding adults and failed breeders but also juveniles (during their first year at sea) and immature birds (three to four years old).
2. Model the foraging habitat to determine the most relevant physical and biotic parameters determining the foraging distribution. Pay special attention to the southernmost breeding locations, because of predicted rise in water temperature in the Southern Ocean.
3. Project foraging responses in marine habitats in light of future changes in sea surface temperature. Analysis of contrasted foraging responses during warm and cold years could inform a modeling approach for projecting penguins' at-sea distribution given variation in sea surface temperature.
4. Complete a census of all breeding populations at regular intervals in order (STET) to detect temporal trends and potential interactions with environmental changes.

5. Reconsider the taxonomic status of the different populations through genetic analysis. The results of combined genetic, morphological, and behavioral analysis may help clarify the taxonomic status of the different populations.

11. CURRENT CONSERVATION EFFORTS

Access to all king breeding sites is restricted, and permits from the respective national authorities are required for research and conservation purposes. Ecotourism, where it occurs, is strictly regulated. Procedures for preventing the outbreak of diseases at sub-Antarctic islands (Kerry et al. 1999) are generally applied. At Crozet and Kerguelen Islands, all the king colonies are under protection and included in the Réserve Naturelle Nationale des Terres Australes et Antarctiques Françaises, a natural reserve. At Macquarie Island, the colonies are included in the World Network of Biosphere Reserves under UNESCO's Man and the Biosphere Programme. The colonies of Marion Island and Prince Edward Island are part of a Special Nature Reserve under the South African Environmental Management: Protected Areas Act. South Georgia penguins live in a special protected area within the Environmental Management Plan for South Georgia. In the Falklands/Malvinas, all wildlife is protected under the Conservation of Wildlife and Nature Bill 1999.

12. RECOMMENDED PRIORITY CONSERVATION ACTIONS FOR INCREASING POPULATION RESILIENCE AND MINIMIZING THREATS AND IMPACTS

1. Implement marine protected areas (MPAs): Because of the imminent risk of the development of a commercial fishing industry targeting myctophid fish (the main king penguin prey), conservation efforts should focus on the development of marine sanctuaries or other MPA regimes in waters surrounding the respective breeding sites. Management of potential myctophid fisheries should take into account the periods when penguins' energy requirements are highest in order (STET) to limit any impact of prey depletion on the foraging range, namely the post-molt (November) and the brooding and early crèche (i.e., mid-January to mid-March) stages. At present, three king breeding sites are included in two recently established MPAs: Macquarie Island and Heard Island. Three other MPAs are planned around Marion and Prince Edward Islands, the Crozet and Kerguelen archipelagoes, and South Georgia Island.
2. Establish high-seas MPAs: Existing and planned MPAs encompass only part of the kings' oceanic habitat and do not include the main feeding areas. Establishing high-seas MPAs in key feeding areas outside national jurisdiction is key to protecting oceanic predators such as king penguins.
3. Restrict access to colonies: Ecotourism activities and access to the colonies must be controlled, especially within the context of possible disease outbreaks in sub-Antarctic localities.

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TABLE 1.1 Biometry of adult King penguins according to sex and locality

	MALES	FEMALES	UNSEXED	REFERENCES
Flipper length				
Crozet	360 (23)			Barrat 1976
South Georgia	343 (70)			Stonehouse 1960
Bill length				
Crozet	125[α] (23)			Barrat 1976
South Georgia	137 (70)			Stonehouse 1960
Macquarie	114.9[α] ±3.4 (5)			Marchant and Higgins 1990
Foot length				
South Georgia	185 (70)			Stonehouse 1960
Body mass				
Crozet	12.8		10.5–15.7	Barrat 1976
start of courtship[1]	13.9		11.9–15.6	Gauthier-Clerc et al. 2001
start of courtship[2]	11.6	0.2	9.3–13.1	Gauthier-Clerc et al. 2001
start of courtship[3]	16.0	0.7	13.8–17.3	Stonehouse 1960
start of courtship[1]	10.8	1.1	7.8–12.8	
chick rearing *	11.1	0.6	9.9–12.5	
chick rearing *				
flipper length	353		335–378	
	331		310–355	
bill length	119[α]		109–127	
	129[α]		116–142	
	114.1[α]	2.9	109.6–118.5	
Foot length	178		160–202	
Body mass				
start of courtship[1]	11.5		9.3–12.5	
start of courtship[1]	14.3		13.2–6.2	
chick rearing*	9.9	0.8	8.4–11.6	
chick rearing*	10.3	0.6	9.3–11	
Flipper length	337	12		
	325	10		
	378	3		
Bill length	92.3[β]	6.7		
	87.6[β]	4.9		

The measurements are in mm and the body mass in kg. Flippers were measured from the axilla to the body side; bill length from tip to mandibular plate excepted for mensurations indicated as α (from the base of mandibular plate to the tip) and β (culmen length). 1: unknown breeding success; 2: males successfully relieved during incubation; 3: males deserted during incubation; *: brooding period, relieved breeders (February-early March, 1 year).

TABLE 1.2 Estimated numbers of King penguin incubating and status of colonies monitored

AREA	LOCATION	ANNUAL BREEDING PAIRS	YEAR	STUDY PERIOD	LONG TERM TREND	POPULATION STATUS	SOURCES
Atlantic Ocean	South Georgia	c. 450 000	2002	1986–2002	Increasing	Increasing	Saudner 2006 Woehler and Croxall 1997 P.A. Prince and S. Poncet u/p
	Fakland Is.	c.1 000	2010	1980–2010	Increasing	Increasing	Clausen and Huin 2003 Pütz, unpubl. data
	South Sandwich Is.	1	1995	_	Unknown	Unknown	P. Harrison in Prince and Croxall (1996)
Indian Ocean	Prince Edward & Marion Is.	6 7 000					
	Prince Edward Is.	2 000	2008	1952–2009	Increasing	Stable	Crawford et al. 2003 Crawford et al. 2009
	Marion Is.	65 000	2008	1952–2009	Increasing	Stable	Crawford et al. 2003 Crawford et al. 2009
	Crozet Is.	611 700–735 700					
	Île de la Possession	79,700	2009	1962–2003	Increasing	Increasing	Weimerskirch et al. 1992 Delord et al. 2004, Weimerskirch et al. unpublished data
	Île de l'Est	100,000	1984	1970, 1984	Stable	Unknown	Despin et al. 1972 Jouventin et al. 1984
	Île aux Cochons	432,000–556,000	1988	1962–1998	Increasing	Unknown	Guinet et al. 1995
	Kerguelen Is.	342 000*	1999			Unknown	See Chamaillé-James et al. 2000
	1. Courbet Peninsula (East)						
	Ratmanoff	52 000	2008	1963–2008	Increasing	Declining	Chamaillé-James et al. 2000 Weimerskirch et al. 1989 Weimerskirch et al. unpublished data
	Cap Digby	72 600	1999	1963–1999	Increasing	Unknown	Chamaillé-James et al. 2000
	2. Rallier du Baty Peninsula (South)						
	Baie Larose	21 400	1985	1973–1985	Increasing	Unknown	Chamaillé-James et al. 2000
	Feu de Joie	40 000	1987		Unknown	Unknown	Chamaillé-James et al. 2000
	Tellurometre	20 000	1982		Unknown	Unknown	Chamaillé-James et al. 2000
	Heard Is.	80 000	2003/04	1963–1993	Increasing	Increasing	Woehler 2006
	Macquarie Is.	150 000–170 000	2000	1930–2000	Increasing	Increasing	Parks and Wildlife Service 2006 Van Den Hoff et al. 2009

TABLE 1.3 King penguin egg size measurements according to the breeding locality

LOCALITY	EGG LENGTH	EGG BREADTH	EGG MASS	REFERENCES
South Georgia Is.	104.8(86–117) (75)	76.0(64–86) (291)	319 (205–440) (n=?)	Stonehouse 1960, Murphy 1936, Williams 1995
Crozet Is.	104.1(92.9–124.0)(291)	73.9 (61.2–87.0) (291)	302 (235–380) (186)	Barrat 1976
Marion Is.	105.8 (93.8–112.5) (35)	74.0 (65.2–79.0)(35)	304 (243–351)(16)	From Rand, 1954; Barrat 1976
Macquarie Is.	109.7 (91–106)(15)	73.9 (69.5–78)(15)	-	From Barrat 1976

Sample size is the last value on the right side inside each block

TABLE 1.4 Main breeding and demographic parameters of King penguin

PARAMETERS	POSSESSION IS. (CROZET)	SOUTH GEORGIA	REFERENCE
Incubation (d)	53.8 +1.5	54–55	Barrat 1976; Stonehehouse 1960; Williams 1995
Chick rearing (d)	1971 : 350 (n=3) 1997–2000: 324 ± 5d n=24)	300–390; 313	Barrat 1976; Stonehehouse 1960; Croxall and Prince 1987; Descamps et al. 2002
Average reproductive success	1986–1988: 30.6% 1997–2001: 20–34%,	84 % (n=1 year)	Stonehehouse 1960; Weimerskirch et al. 1992; Descamps et al. 2002, Gauthier-Clerc et al. 2004
Age of first breeding (yr)	3	-	

REFERENCES

Adams, N. J., and N. T. Klages. 1987. Seasonal variation in the diet of the king penguin (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. *Journal of Zoology* (London) 212:303–24.

Ainley, D. G., E. F. O'Connor, and R. J. Boekelheide. 1984. *The Marine Ecology of Birds in the Ross Sea, Antarctic.* Ornithological Monograph No. 32. 109 pp.

Barrat, A. 1976. Quelques aspects de la biologie et de l'écologie du manchot royal (*Aptenodytes patagonicus*) des îles Crozet. *Comité National Français de la Recherche Antarctique* 40:9–51.

Boersma, P. D., and G. A. Rebstock. 2009. Foraging distance affects reproductive success in Magellanic penguins. *Marine Ecology Progress Series* 375:263–75.

Bost, C. A., J. B. Charrassin, Y. Clerquin, Y. Ropert-Coudert, Y. Le Maho. 2004. Exploitation of the marginal ice zone by king penguins during winter. *Marine Ecology Progress Series* 283:293–97.

Bost, C. A., C. Cotté, F. Bailleul, Y. Cherel, J. B. Charrassin, C. Guinet, D. G. Ainley, and H. Weimerskirch. 2009. Importance of Southern Ocean fronts for seabird and marine mammals. J. Marine Systems. Special Issue on Processes at Oceanic Fronts of the *Journal of Marine Systems* (JMS-SIOF) 79:363–76.

Bost, C.A., C. Cotté, P. Terray, C. Barbraud, K. Delord, C. Guinet, J. B. Charrassin, H. Weimerskirch. In prep. Tracking penguins reveals impacts of large-scale climate variability on food webs.

Bost, C. A., J. Y. Georges, C. Guinet, Y. Cherel, K. Pütz, J. B. Charrassin, Y. Handrich, T. Zorn, J. Lage, and Y. Le Maho. 1997. Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet archipelago. *Marine Ecology Progress Series* 150:21–33.

Bost, C. A., T. Zorn, Y. Le Maho, and G. Duhamel. 2002. Feeding of diving predators and diel vertical migration of prey: King penguins' diet versus trawl sampling at Kerguelen Islands. *Marine Ecology Progress Series* 227:51–62.

Chamaillé-James, S., C. Guinet, F. Nicoleau, and M. Argentier. 2000. A method to assess population changes in king penguins: The use of a Geographical Information System to estimate area-population relationships. *Polar Biology* 23:545–49.

Charbonnier, Y., K. Delord, and J. B. Thiebot. 2010. King-size fast food for Antarctic fur seals. *Polar Biology* 33:721–24.

Charrassin, J. B., and C. A. Bost. 2001. Utilisation of the oceanic habitat by king penguins over the annual cycle. *Marine Ecology Progress Series* 22:285–97.

Charrassin, J. B., C. A. Bost, K. Pütz, J. Lage, T. Dahier, and Y. Le Maho. 1999. Changes in depth utilisation in relation to the breeding stage: A case study with the king penguin *Aptenodytes patagonicus*. *Marine Ornithology* 27:43–47.

Charrassin, J. B., C. A. Bost, K. Pütz, J. Lage, T. Dahier, T. Zorn, and Y. Le Maho. 1998. Foraging strategies of incubating and brooding king penguins *Aptenodytes patagonicus*. *Oecologia* 114:194–201.

Charrassin, J. B., Y. Le Maho, and C. A. Bost. 2002. Seasonal changes in the diving parameters of king penguins. *Marine Biology* 141:581–89.

Cherel, Y., J. B. Charrassin, and E. Challet. 1994. Energy and protein requirements for molt in the king penguin *Aptenodytes patagonicus*. *American Journal of Physiology* 266:R1182–88.

Cherel, Y., J. B. Charrassin, and Y. Handrich. 1993. Comparison of body reserve buildup in prefasting chicks and adults of king penguins (*Aptenodytes patagonicus*). *Physiological Zoology* 66:750–70.

Cherel, Y., K. Pütz, and K. A. Hobson. 2002. Summer diet of king penguins (*Aptenodytes patagonicus*) at the Falkland Islands, southern Atlantic Ocean. *Polar Biology* 25:898–906.

Cherel, Y., and V. Ridoux. 1992. Prey species and nutritive value of food fed during summer to king penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis* 134:118–27.

Cherel, Y., J. C. Stahl, and Y. Le Maho. 1987. Ecology and physiology of fasting in king penguin chicks. *The Auk* 104:254–62.

Clausen, A. P., and N. Huin. 2003. Status and numerical trends of king, gentoo and rockhopper penguins breeding in the Falkland Islands. *Waterbirds* 26(4):389–402.

Collins, M. A., J. C. Xavier, N. M. Johnston, A. W. North, P. Enderlein, G. A. Tarling, C. M. Waluda, E. J. Hawker, N. J. Cunningham. 2008. Patterns

in the distribution of myctophid fish in the northern Scotia Sea ecosystem. *Polar Biology* 31:837–51.

Conroy, J. W. H. 1975. Recent increases in penguin populations in the Antarctic and the Sub-Antarctic. In *The Biology of Penguins*, ed. B. Stonehouse, 321–36. London: Macmillan.

Conroy, J. W. H., and M. G. White. 1973. The breeding status of the king penguin. *British Antarctic Survey Bulletin*. 32:31–40.

Cooper, J., R. J. M. Crawford, M. S. De 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* 37:193–96.

Crawford, R. J. M., J. Cooper, B. M. Dyer, M. D. Greyling, N. T. W. Klages, P. G. Ryan, S. L. Petersen, L. G. Underhill, L. Upfold, W. Wilkinson, M. S. De Villiers, S. Du Plessis, M. Du Toit, T. M. Leshoro, A. B. Makhado, M. S. Mason, D. Merkle, D. Tshingana, V. L. Ward, and P. A. Whittington. 2003. Populations of surface-nesting seabirds at Marion Island, 1994/95–2002/03. *African Journal of Marine Science* 25:427–40.

Crawford, R. J. M., P. A. Whittington, L. Upfold, P. G. Ryan, S. L. Petersen, B. M. Dyer, and J. Cooper. 2009. Recent trends in numbers of four species of penguins at the Prince Edward Islands. *African Journal of Marine Science* 31(3):419–26.

Croxall, J. P., and P. A. Prince. 1987. Seabirds as predators on marine resources, especially krill, at South Georgia. In *Seabirds: Feeding Ecology and Role in Marine Ecosystems*, ed. J. P. Croxall, 347–68. Cambridge: Cambridge University Press.

Delord, K., C. Barbraud, and H. Weimerskirch. 2004. Long-term trends in the population size of king penguins at Crozet archipelago: Environmental variability and density dependence? *Polar Biology* 27:793–800.

Descamps, S., M. Gauthier-Clerc, J. P. Gendner and Y. Le Maho. 2002. The annual breeding cycle of unbanded king penguins *Aptenodytes patagonicus* on Possession Island (Crozet). *Avian Science* 2:87–98.

Despin, B., J. L. Mougin, and M. Segonzac. 1972. Oiseaux et mammifères de l'Île de l'Est. *Comité National Français de la Recherche Antarctique* 31:1–106.

Du Plessis, C. J., Y. M. van Heezik, and P. J. Seddon. 1994. Timing of king penguin breeding at Marion Island. *Emu* 94:216–19.

Fordyce, R. C., and C. M. Jones. 1990. Penguin history and new fossil material from New Zealand. In *Penguin Biology*, ed. L. S. Davis and J. T. Darby, 551–648. San Diego, CA: Academic Press.

Gauthier-Clerc, M., J. P. Gendner, C. A. Ribic, W. R. Fraser, E. J. Woehler, S. Descamps, C. Gilly, C. Le Bohec and Y. Le Maho. 2004. Long-term effects of flipper bands on penguins. *Proceedings of the Royal Society B* 271:423–26.

Gauthier-Clerc, M., Y. Le Maho, J. P. Gendner, J. Durant and Y. Handrich. 2001. State-dependent decisions in long-term fasting king penguins, Aptenodytes patagonicus, during courtship and incubation. *Animal Behaviour* 62:661–69.

Gray, G. R. 1844. Aptenodytes. *Annals and Magazine for Natural History* 13:315.

Guinet, C., P. Jouventin, and J. Malacamp. 1995. Satellite remote sensing in monitoring change of seabirds: Use of Spot Image in king penguin population increase at Ile aux Cochons, Crozet Archipelago. *Polar Biology* 15:511–15.

Guinet, C., M. Koudil, C. A. Bost, J. P. Durbec, J. Y. Georges, M. C. Mouchot, and P. Jouventin. 1997. Foraging behaviour of satellite-tracked king penguins in relation to sea-surface temperatures obtained by satellite telemetry at Crozet Islands: A study during three austral summers. *Marine Ecology Progress Series* 150:11–20.

Hindell, M. A. 1988. The diet of the king penguin *Aptenodytes patagonicus* at Macquarie Island. *Ibis* 130:193–203.

Hofmeyr, G. J. G., and M. M. Bester. 1993. Predation on king penguins by Antarctic fur seals. *South African Journal of Antarctic Research* 23:71–74.

Hunter, S. 1983. The food and feeding ecology of the giant petrels Macronectes halli and M. giganteus at South Georgia. *Journal of Zoology* 200(4):521–38.

IUCN (International Union for Conservation of Nature) 2011. IUCN Red List of Threatened Species. Version 2011.2. www.iucnredlist.org (accessed 15 March 2012).

Jiguet, F., and P. Jouventin. 1999. Individual breeding decisions and long-term reproductive strategy in the king penguin *Aptenodytes patagonicus*. *Ibis* 141 (3):428–33.

Jouventin, P. 1982. *Visual and Vocal Signals in Penguins: Their Evolution and Adaptative Characters.* Berlin: Paul Parey.

Jouventin, P., D. Capdeville, F. Cuenot-Chaillet, and C. Boiteau. 1994. Exploitation of pelagic resources by a non-flying seabird-satellite tracking of the king penguin throughout the breeding cycle. *Marine Ecology Progress Series* 106:11–19.

Jouventin, P., J. C. Stahl, H. Weimerskirch, and J. L. Mougin. 1984. The seabirds of the French subantarctic islands and Adélie Land, their status and conservation. In *Status and Conservation of the World's Seabirds*, ed. J. P. Croxall, P. G. H. Evans, and R. W. Schreiber, 609–25. ICBP Technical Publication No. 2. Cambridge: International Council for Bird Preservation.

Kerry, K., M. Riddle, and J. Clarke. 1999. Diseases of Antarctic wildlife. Scientific Committee on Antarctic Research (SCAR) and the Council of Managers of National Antarctic Programs (COMNAP). Kingston: Australian Antarctic Division.

Kooyman, G. L., Y. Cherel, Y. Le Maho, J. P. Croxall, P. H. Thorson, V. Ridoux, and C. A. Kooyman. 1992. Diving behavior and energetics during foraging cycles in king penguins. *Ecological Monographs* 62:143–63.

Kooyman, G. L, T. G. Kooyman, M. Horning, and C. A. Kooyman. 1996. Penguin dispersal after fledging. *Nature* 383:397.

Laws, R. J. 1977. Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society B* 279 London B: 81–96.

Le Bohec, C., J. Durant, M. Gauthier-Clerc, N. C. Stenseth, Y. H. Park, R. Pradel, D. Grémillet, J. P. Gendner, and Y. Le Maho. 2008. King penguin population threatened by Southern Ocean warming. *Proceedings of the National Academy Sciences of the United States of America* 105: 2493–97. [[AUS: Title as at PNAS website.]]

Le Bohec, C., M. Gauthier-Clerc, J. P. Gendner, N. Chatelain, and Y. Le Maho. 2003. Nocturnal predation of king penguins by giant petrels on the Crozet Islands. *Polar Biology* 26(9):587–90.

Le Bohec, C., M. Gauthier-Clerc, D. Grémillet, R. Pradel, A. Béchet, J. P. Gendner, Y. Le Maho. 2007. Population dynamics in a long-lived seabird: 1. Impact of breeding activity on survival and breeding probability in unbanded king penguins. *Journal of Animal Ecology* 76:1149–60.

Lewis Smith, R. I., and J. R. B. Tallowin. 1979. The distribution and size of king penguin rookeries on South Georgia. *British Antarctic Survey Bulletin* 49:259–76.

Marchant, S., and P. J. Higgins. 1990. *Handbook of Australian, New Zealand and Antarctic Birds.* Melbourne, Australia: Oxford University Press.

Moore, G. J., B. Wienecke, and G. Robertson. 1998. Food requirements of breeding king penguins at Heard Island and potential overlap with commercial fisheries. *Polar Biology* 20:393–402.

———. 1999. Seasonal change in foraging areas and dive depths of breeding king penguins at Heard Island. *Polar Biology* 21:376–84.

Murphy, R. C. 1936. *Oceanic Birds of South America*. Vol. 1. New York: American Museum of Natural History.

Olsson, O. 1996. Seasonal effect of timing and reproduction in the king penguin: A unique breeding cycle. *Journal of Avian Biology* 27:7–14.

Olsson, O., and A. Brodin. 1997. Changes in king penguin breeding cycle in response to food availability. *Condor* 99:994–97.

Olsson, O., and H. P. van der Jeugd. 2002. Survival in king penguins *Apten-*

odytes patagonicus: Temporal and sex-specific effects of environmental variability. *Oecologia* 132(4):509–16.

Olsson, O., and A. W. North. 1997. Diet of the king penguin *Aptenodytes patagonicus* during three austral summers at South Georgia. *Ibis* 139:504<-13.

Otley, H., A. Clausen, D. Christie, N. Huin, and K. Pütz. 2007. Breeding patterns of king penguins on the Falkland Islands. *Emu* 107:156–64

Parks and Wildlife Service. 2006. Macquarie Island Nature Reserve and World Heritage Area Management Plan. Hobart, Tasmania: Parks and Wildlife Service. 189 pp.

Peron, C., H. Weimerskirch, and C. A. Bost. 2012. Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proceedings of the Royal Society B*.

Prince, P. A., and J. P. Croxall. 1996. The birds of South Georgia. *Bulletin of the British Ornithologists' Club* 116:81–104.

Pütz, K. 2002. Spatial and temporal variability in the foraging areas of breeding king penguins. *Condor* 104(3):528–38.

Pütz, K., and C. A. Bost. 1994. Feeding behavior of free-ranging king penguins (*Aptenodytes patagonicus*). *Ecology* 75 (2):489–97.

Pütz, K., and Y. Cherel. 2005. The diving behaviour of brooding king penguins (*Aptenodytes patagonicus*) from the Falkland Islands: Variation in dive profiles and synchronous underwater swimming provide new insights into their foraging strategies. *Marine Biology* 147:281–90.

Pütz, K., Y. Ropert-Coudert, J. B. Charrassin, and R. P. Wilson. 1999. Foraging areas of king penguins (*Aptenodytes patagonicus*) breeding at Possession Island, southern Indian Ocean. *Marine Ornithology* 27:77–84.

Pütz, K., R. P. Wilson, J. B. Charrassin., T. Raclot, J. Lage, Y. Le Maho, M. A. M. Kierspel, B. Culik, and D. Adelung. 1998. Foraging strategy of king penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. *Ecology* 79(6):1905–21.

Rand, R. W. 1954. Notes on the birds of Marion island. *Ostrich* 26(2):57–69.

Rounsevell, D. E., and G. R. Copson. 1982. Growth rate and recovery of a king penguin, *Aptenodytes patagonicus*, population after exploitation. *Australian Wildlife Research* 9:519–25.

Sabourenkov, E. N. 1991. Mesopelagic fish of the southern ocean—summary results of recent Soviet studies. Commission for the Conservation of Antarctic Marine Living Resources, Hobart, Australia, SC-CAMLR-SSP/7: 433–57.

Sanders, S. 2006. *Important Bird Areas in the United Kingdom Overseas Territories: Priority Sites for Conservation.* Sandy, Bedfordshire, England: Royal Society for the Protection of Birds.

Stonehouse, B. 1960. The king penguin *Aptenodytes patagonicus* at South Georgia. 1: Breeding behaviour and development. *Scientific Report of the Falkland Islands Dependent Survey* 23:1–81.

Trathan, P. N., C. Bishop, G. Maclean, P. Brown, A. Fleming, M. A. Collins. 2008. Linear tracks and restricted temperature ranges characterise penguin foraging pathways. *Marine Ecology Progress Series* 370:285–94.

Van Den Hoff, J., R. J. Kirkwood, and P. B. Copley. 1993. Aspects of the breeding cycle of king penguins *Aptenodytes patagonicus* at Heard Island. *Marine Ornithology* 21:49–55.

Van den Hoff, J., C. R. McMahon, and I. Field. 2009. Tipping back the balance: Recolonization of the Macquarie Island isthmus by king penguins (*Aptenodytes patagonicus*) following extermination for human gain. *Antarctic Science* 21 (3):237–41.

Van Heezig, Y., P. J. Seddon, J. Cooper, and A. L. Plös. 1994. Interrelationships between breeding frequency, timing and outcome in king penguins *Aptenodytes patagonicus:* Are king penguins biennial breeders? *Ibis* 136(3):279–84.

Verheyden, C., and P. Jouventin. 1991. Over-wintering strategies of the Lesser Sheathbill *Chionis minor* in an impoverished and insular environment. *Oecologia* 86:132–39.

Viot, C. R. 1987. Différenciation et isolement entre populations chez le manchot royal (*Aptenodytes patagonicus*) et le manchot papou (*Pygoscelis papua*). *L'Oiseau et la Revue Française d'Ornithologie* 57:251–59.

Weimerskirch, H., J. C. Stahl, and P. Jouventin. 1992. The breeding biology and population dynamics of king penguins *Aptenodytes patagonicus* on the Crozet Islands. *Ibis* 134:107–17.

Weimerskirch, H., R. Zotier, and P. Jouventin. 1989. The avifauna of the Kerguelen Islands. *Emu* 89:15–29.

Wienecke, B., and G. Robertson. 2006. Comparison of foraging strategies of incubating king penguins *Aptenodytes patagonicus* from Macquarie and Heard Islands. *Polar Biology* 29:424–38.

Williams, A. J., W. R. Siegfried, A. E. Burger, and A. Berruti. 1979. The Prince Edward Islands: A sanctuary for seabirds in the Southern Ocean. *Biological Conservation* 15:59–71.

Williams, T. D. 1995. *The Penguins.* Oxford: Oxford University Press.

Woehler, E. J. 2006. Status and conservation of the seabirds of Heard Island. In *Heard Island–Southern Ocean Sentinel*, ed. K. Green and E. J. Woehler, 128–65. Chipping Norton, NSW, Australia: Surrey Beatty & Sons.

Woehler, E. J., and J. P. Croxall. 1997. The status and trends of Antarctic and Subantarctic seabirds. *Marine Ornithology* 25:43–66.