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Review

The emperor penguin - Vulnerable to projected rates of warming and sea ice loss

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ABSTRACT

We argue the need to improve climate change forecasting for ecology, and importantly, how to relate long-term projections to conservation. As an example, we discuss the need for effective management of one species, the emperor penguin, *Aptenodyptes forsteri*. This species is unique amongst birds in that its breeding habit is critically dependent upon seasonal fast ice. Here, we review its vulnerability to ongoing and projected climate change, given that sea ice is susceptible to changes in winds and temperatures. We consider published projections of future emperor penguin population status in response to changing environments. Furthermore, we evaluate the current IUCN Red List status for the species, and recommend that its status be changed to Vulnerable, based on different modelling projections of population decrease of ≥50% over the current century, and the specific traits of the species. We conclude that current conservation measures are inadequate to protect the species under future projected scenarios. Only a reduction in anthropogenic greenhouse gas emissions will reduce threats to the emperor penguin from altered wind regimes, rising temperatures and melting sea ice; until such time, other conservation actions are necessary, including increased spatial protection at breeding sites and foraging locations. The designation of large-scale marine spatial protection across its range would benefit the species, particularly in areas that have a high probability of becoming future climate change refugia. We also recommend that the emperor penguin is listed by the Antarctic Treaty as an Antarctic Specially Protected Species, with development of a species Action Plan.

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1. Introduction

The UN Framework Convention on Climate Change (UNFCCC) first entered into force on 21 March 1994, just over 25 years ago. Since then the UNFCCC has made enormous progress, but world outcomes, in real terms, have been slow to emerge, such that climate action is now more urgent than ever (Espinosa, 2019). Forecasting the future, often with sparse data, remains technically challenging (Dietze, 2017), nevertheless, many atmospheric and oceanic climate processes are already changing and are projected to continue changing (e.g. Vaughan et al., 2013; Larsen et al., 2014), and as physical drivers of ecosystem functioning, will continue to influence seabird demography and population dynamics (Jenouvrier, 2013; Oro, 2014). However, relevant and direct ecological links can be challenging to identify, since a number of confounding factors, such as other anthropogenic impacts, including pollution, habitat loss and interactions with fisheries (Trathan et al., 2015; Ropert-Coudert et al., 2019), may alter associations between climate and seabird demography (Oro, 2014). This is also exacerbated because biological datasets are often short, or do not cover biologically important stages, such as post-breeding dispersion, or other key life history periods (Isles and Jenouvrier, 2019). Furthermore, there is often a mismatch between the spatial scales at which ecological processes occur and at which environmental variables are observed and forecast (Snover et al., 2013; Isles and Jenouvrier, 2019), whilst we also need a better understanding of adaptive capacity (e.g. phenotypic plasticity of behaviours, micro-evolutionary processes) and dispersal capabilities (Jenouvrier and Visser, 2011).

We urgently need to improve forecasting for ecology, and importantly, how to relate long-term projections to conservation. Failure to understand the complexity of global change impacts on ecological processes remains a major issue, and consequently, translation of projected climate change into direct policy and conservation actions has been slow (Trathan and Agnew, 2010).

In this review, we therefore highlight some of the potential outcomes of climate change and suggest possible approaches for the effective management of one species, the emperor penguin, *Aptenodyptes forsteri*. We focus on this iconic species as there is a growing body of evidence highlighting the challenges facing this species, given projected climatic conditions over the coming century (Jenouvrier et al., 2009, 2012, 2014, 2017; Ainley et al., 2010; Trathan et al., 2011). The emperor penguin is one of the few species (possibly the only one) for which we have modelled colony population forecasts for the global population over the entire species range (Jenouvrier et al., 2014). Moreover, given this body of work, it is perhaps surprising that conservation actions have been slow to emerge. For other species, where there is less modelling work to support conservation action, including for species outside the Antarctic, progress is also likely to be slow. Appropriate early recognition of future climate change impacts, would mean that local conservation actions can be empowered.

It is now generally recognised that the Antarctic marine ecosystem is changing (Turner et al., 2009a). Nevertheless, exacerbation of climate change impacts should not be allowed to occur through inappropriate management practices. Thus, as climate change potentially introduces a greater level of ecosystem uncertainty (e.g. changes in species distribution, phenology, behaviour and physiology, or timing of prey match-mismatch), successful ecosystem outcomes potentially mean that management practices may need to be more conservative than presently considered (Trathan and Agnew, 2010).

We argue that the need for enhanced precautionary management is now necessary, particularly given continued increases in greenhouse gas (GHG) emissions (Le Quéré et al., 2018, 2019; Nisbet et al., 2019). We consider the emperor penguin an exemplar for other species, and discuss its life history and ecological background, future climate change and effects on the species, re-analysis of the IUCN Red List threat status, and methods for protecting the emperor penguin, before drawing together our key conclusions.

2. Methods

To select articles for our review, we used The Web of Science Service for UK Education and databases provided by Clarivate Analytics. We conducted the literature review (in October 2018 and then again in May 2019) using a broad range of search terms that represent the variety of ways in which emperor penguin and climate may be included, or emperor penguin and diet. Thus, the terms 'emperor penguin' or '*Aptenodytes forsteri*' were combined with the following terms: 'climate change' [71 papers], 'sea ice' [122 papers], 'fast ice' [34 papers], 'population change' [73 papers], 'diet' [48 papers]. We also searched in the literature-cited sections of all retrieved articles. Many papers appear multiple times across the different searches; a search including all the above terms revealed 187 publications. In many papers, only passing mention of emperor penguins is made. Our review was also informed by expert opinion from all authors, including those authors that have written extensively on the species, in particular about its natural history and projected responses to climate change. We recognise that as for the physical sciences (e.g. Bamber et al., 2019), expert judgement can provide key insights.

To complement these topics, we also considered how protection under the Antarctic Treaty might be conferred on the species. Therefore, we also reviewed documents available through the Antarctic Treaty Secretariat concerning species protection processes such as the designation of Antarctic Specially Protected Species.

Finally, we considered a number of emperor penguin colonies where research has been undertaken, including some of the longest running science in Antarctica. Consideration of these sites is provided in the Supplementary Material, Part 1.

3. Life history and ecological background

3.1. Discovery of the emperor penguin

The first emperor penguin (*Aptenodytes forsteri* Gray, 1844) ever captured was probably taken during the Russian Naval Expedition of 1819–1821, under the command of Fabian Gottlieb von Bellingshausen. However, the expedition did not have a naturalist amongst the crew, and so did not recognise it as a new species, instead concluding that it was the same as one previously seen at South Georgia.

The species was first described scientifically and distinguished from its closest relative, the king penguin (*A. patagonicus* Miller, 1778), in 1844 by George Robert Gray, head of ornithology at the British Museum. Gray examined and described specimens from the British Naval Expedition of 1839–1843, under the command of James Clarke Ross. Ross appears to have returned several specimens of large penguins, including one from the Falkland Islands (Richardson and Gray, 1865). Gray named the emperor penguin with its specific Latin name in honour of Johann Reinhold Forster, naturalist on James Cook's second voyage of 1772–1775.

Despite the renown of the Cape Crozier colony from the gripping historical account of a visit in 1911, (Cherry-Garrard, 1922), almost all details of emperor penguin ecology remained obscure until 1954. Only five colonies had by then been discovered (Wienecke et al., 2010), and all were logistically difficult to access as breeding only starts in the dead of winter, after fast ice has formed. Stonehouse (1952) was the first to observe parts of the breeding biology at Emperor Island, Dion Islets (67.87°S, 68.72°W), staying for two and a half months (see also Stonehouse, 1953). Further reports of the species' annual cycle then came from Pointe Géologie (Prévost, 1953, 1961). Subsequently, most studies have been undertaken at colonies in East Antarctica and the Ross Sea (see Supplementary Material, Part 1), with the data obtained allowing projections of future trends under various scenarios of ecosystem change. Nevertheless, whilst natural history patterns are well known, much of the species' ecology at sea still remains poorly described, especially in West Antarctica, whilst early life also remains

poorly documented (Labrousse et al., 2019). Probably because of its unique breeding biology, coupled with an ability to endure environments deemed extreme by human standards, the emperor penguin has achieved almost mythical or iconic status in the minds of many.

3.2. Life cycle of the emperor penguin

The emperor penguin has a long breeding cycle, initiating breeding in the Austral winter to complete the rearing of its single chick within a year; it is the only warm-blooded Antarctic species that breeds during the winter and as such is uniquely adapted. Its closest relative, the king penguin, has an extended breeding cycle, taking more than a year to raise its single chick (Bost et al., 2013).

Emperor penguin colonies occur in coastal locations around the continent with almost all on fast ice, which is sea ice held in place by geographic features and grounded icebergs. However, when fast ice is present for an insufficient period (Fretwell et al., 2014), or subjected to sustained winds that cause early ice break up (Zitterbart et al., 2014), colonies can occur on ice shelves or icebergs, or even land. Currently, only one colony is entirely located on land where it has been for at least 70 years (Fretwell et al., 2012; Wienecke et al., 2010), but others have access to small islands or exposed rock areas for part of the season. At present, it is not known whether access to land is important for these latter colonies.

All colonies that have been studied so far have a similar annual schedule (Fig. 1). Prior to breeding, both males and females must forage intensely to build their body reserves, necessary for females to lay their single egg, and for males to fast whilst undertaking the entire egg incubation. Birds gather at their preferred sites from April onwards, upon development of stable fast ice. Courtship, egg laying and incubation occur as winter proceeds. Chicks hatch and are brooded during July and August, the coldest time in Antarctica. Chicks then begin to crèche in September, when left alone in the colony so that both parents can forage simultaneously to satisfy the chick's growing demands. Chicks are provisioned by both parents until they fledge, usually during December, just before the fast ice begins to break out. By this time, chicks must have replaced their natal down with feathers that provide waterproofing and insulation.

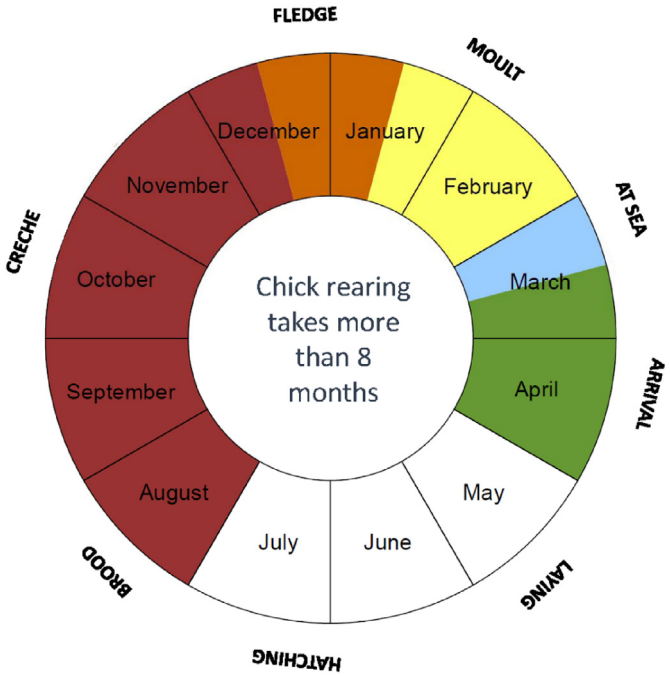

Fig. 1. Emperor penguin breeding cycle. Adapted from Wienecke et al., 2013. Note that timings can vary between sites.

Adults moult between January and March: on accessible islands; on the continental ice cap where it is accessible; on fast ice; or on consolidated pack ice, that is floes that normally drift with the ocean and wind, but which may merge and combine. Unlike all other seabird families, penguins undertake a catastrophic moult, during which they replace their entire plumage within a few weeks; during this time, their plumage no longer provides water-proofing and they cannot enter the sea. Thus, they must have a stable platform and sufficient body reserves to moult successfully.

Emperor penguins depend upon stable fast ice throughout their breeding period. Consequently, late fast ice formation, early break up, or even complete failure of fast ice formation, strongly reduces the chances of successful breeding at any given breeding location (Jouventin, 1975). Emperors spend much of their time frequenting the pack ice covered ocean, both during the breeding season (Wienecke and Robertson, 1997) and post breeding (Kirkwood and Robertson, 1997; Rodary et al., 2000; Kooyman et al., 2004; Goetz et al., 2018).

Emperor penguin diet, with the exception of two studies in the Weddell Sea (Ainley et al., 1992; Pütz, 1995), has mainly been investigated during the chick-provisioning period, when emperor penguins are most accessible by researchers. Their diet during this time is composed of fish (particularly Antarctic silverfish *Pleuragramma antarcticum*), crustaceans (mainly Antarctic krill *Euphausia superba*) and squid (particularly the arrow squid *Psychroteuthis glacialis*, and the Antarctic neosquid *Alluroteuthis antarcticus*). Diet composition varies enormously with time of year and location (Offredo and Ridoux, 1986; Klages, 1989; Ainley et al., 1992; Wienecke and Robertson, 1997; Cherel and Kooyman, 1998; Kooyman et al., 2004; Cherel, 2008; Ratcliffe and Trathan, 2012). For example, at Drescher Inlet (72.83°S 19.33°W) in the Weddell Sea, during October/November, emperors fed mainly on krill, followed by squid and some fish (Klages, 1989), but later, squid dominated their diet, followed by fish (Piatowski and Pütz, 1994). In comparison, at Auster (67.40°S 63.97°E) in East Antarctica, during August/September, emperors caught mainly krill, followed by fish and some squid. However, later (October to December), the percentage of squid increased, comprising up to half the diet. In December, fish was by far the dominant dietary component, with hardly any krill (Kirkwood and Robertson, 1997). Diet composition can also vary at the same site between years; for example, at Auster in 1988 during early chick rearing, diet was almost exclusively fish and squid (Robertson et al., 1994), whilst in 1993, penguins predominantly fed on krill, followed by fish, but with some squid (Kirkwood and Robertson, 1997). In the pack ice of the Scotia-Weddell Confluence, emperor penguins fed largely on squid (*Gailteuthis glacialis*, *P. glacialis*) and with only small amounts of fish (Ainley et al., 1992). Such results indicate that emperor penguins hunt opportunistically for available nektonic prey. They probably also feed opportunistically to take benthic prey (Rodary et al., 2000).

Throughout their annual cycle, emperor penguins rely upon the availability of prey. Almost all colonies occur near polynyas (areas of open water, or persistently loose sea ice) within the larger scale ice field (Massom et al., 1998, 2009), or “flaw leads” that form at the junction of coastal fast ice and offshore pack ice. These areas of open water may provide foraging opportunities during the breeding period. Similar, such habitat requirements are also preferred by the Weddell seal (*Leptonychotes weddellii*) (LaRue et al., 2019). However, whilst adults almost continuously associate with sea ice, fledglings may forage in more northern waters (up to 55°S) just after independence (Kooyman et al., 1996; Kooyman and Ponganis, 2008; Wienecke et al., 2010; Thiebot et al., 2013; Labrousse et al., 2019).

Currently, 54 emperor penguin breeding colonies (Fig. 2) are known (Fretwell and Trathan, 2009; Fretwell et al., 2012, 2014; Wienecke, 2011; Ancel et al., 2014; LaRue et al., 2015), though a few small colonies might still remain to be found (Ancel et al., 2017). One colony, Emperor Island, probably moved due to much reduced fast ice following regional warming (Trathan et al., 2011), whilst others have

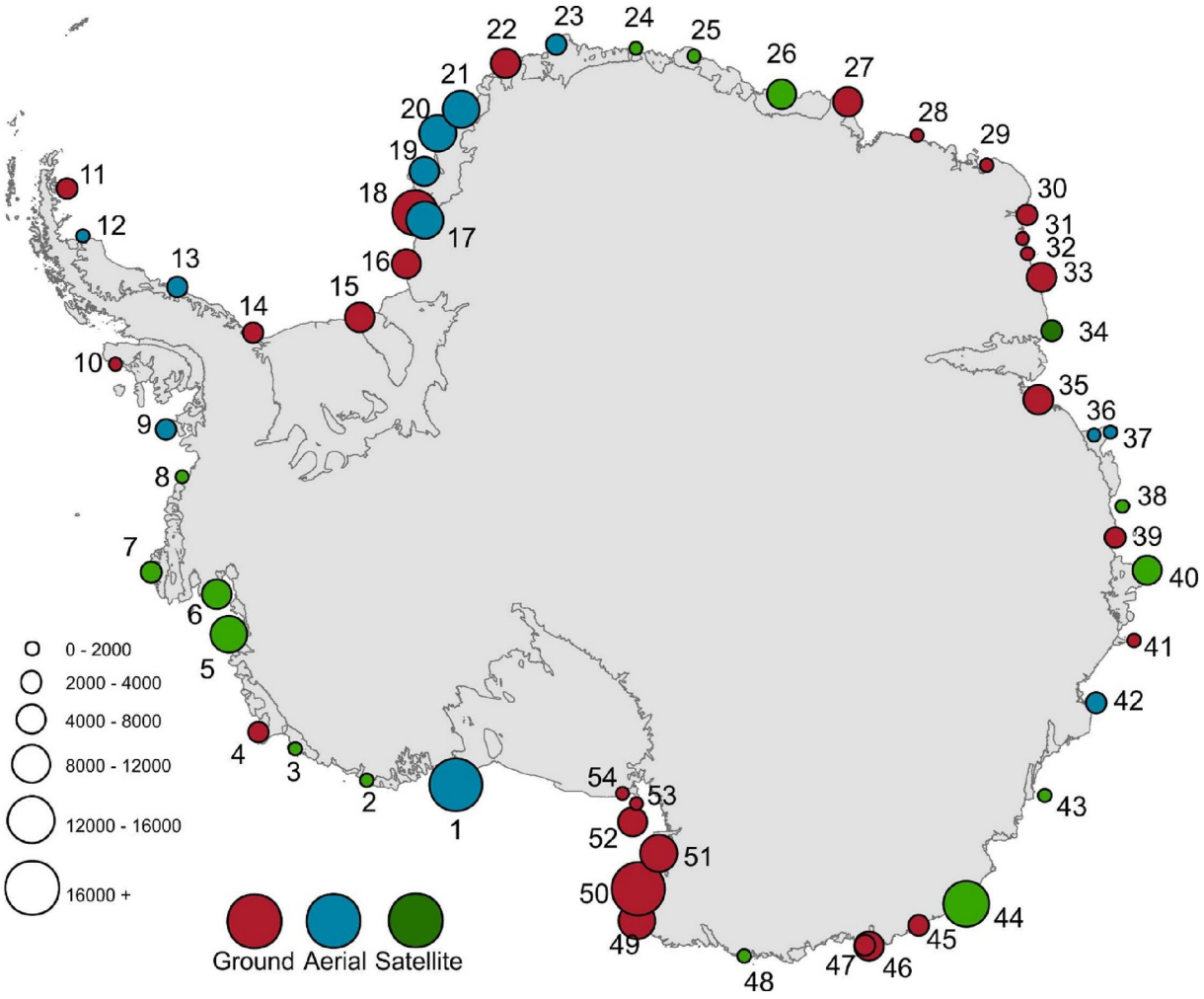

Fig. 2. Distribution of emperor penguin breeding sites. The size of each colony is proportionate to the symbol size. Colonies that have been visited on the ground are shown in red, those that have been overflown are in blue, and those only observed by satellite are in green. Colony names are: 1 - Cape Colbeck, 2 - Rupert Coast, 3 - Ledda Bay, 4 - Thurston Glacier, 5 - Bear Peninsula, 6 - Brownson Islands, 7 - Noville Peninsula, 8 - Bryan Coast, 9 - Smyley Island, 10 - Rothschild Island, 11 - Snow Hill Island, 12 - Larsen Ice Shelf, 13 - Dolleman Island, 14 - Smith Peninsula, 15 - Gould Bay, 16 - Luitpold Coast, 17 - Halley Bay, 18 - Dawson-Lambton Glacier, 19 – Stancomb-Wills Glacier, 20 - Drescher Inlet, 21 - Riiser-Larsen Ice Shelf, 22 - Atka Bay, 23 - Sanae, 24 - Astrid Coast, 25 - Lazarev Ice Shelf, 26 - Ragnhild, 27 - Riiser-Larsen Peninsula/Gunnerus Bank, 28 - Umebosi Rock, 29 - Amundsen Bay, 30 - Kloa Point, 31 - Fold Island, 32 - Taylor Glacier, 33 - Auster, 34 - Cape Darnley, 35 - Amanda Bay, 36 - Barrier Bay, 37 - West Ice Shelf, 38 - Burton Ice Shelf, 39 - Haswell Island, 40 - Shackleton Ice Shelf, 41 - Bowman Island, 42 - Peterson Bank, 43 - Sabrina Coast, 44 - Dibble Glacier, 45 - Pointe Géologie, 46 - Mertz Glacier, 47 - Mertz break off, 48 - Davis Bay, 49 - Cape Roget, 50 - Coulman Island, 51 - Cape Washington, 52 - Franklin Island, 53 - Beaufort Island, 54 - Cape Crozier. Recent movement between Halley Bay and Dawson-Lambton are not accounted for in the figure (Fretwell and Trathan, 2019). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

relocated following changes in ice shelf morphology (e.g. Ancel et al., 2014; LaRue et al., 2015; Fretwell and Trathan, 2019). The use of remote sensing satellite technology and the discovery of new colonies has enabled a revised estimation of total population distribution and size. Currently, approximately 256,500 breeding pairs is considered a plausible breeding population estimate (Fretwell et al., 2012; Ancel et al., 2014), excluding the numbers of juveniles, sub-adults and non-breeders, or the small colonies found since 2014. Although local population estimates based on time series of aerial and ground-based photography (e.g. Kooyman et al., 2007, Barber-Meyer et al., 2008, Kooyman and Ponganis, 2016; Barbraud & Weimerskirch, 2001; Barbraud et al., 2011; Robertson et al., 2014) are available for some sites, movement between colonies potentially makes understanding of population change more complex. As such, remote sensing, despite a number of important caveats (Fretwell et al., 2012), now offers opportunities for monitoring wider population change including at colonies not accessible to standard counting methods.

4. Future climate change and effects on emperor penguins

The current era of rapid environmental change is projected to negatively impact the emperor penguin, particularly by changing the extent, formation and persistence of sea ice, especially fast ice (e.g. Jenouvrier et al., 2009, 2012, 2014, 2017; Ainley et al., 2010; Trathan et al., 2011). Owing to regional differences in climate, different colonies may have dissimilar population trajectories (Barber-Meyer et al., 2008; Kooyman and Ponganis, 2016; Jenouvrier et al., 2014), in some cases related to emigration (LaRue et al., 2015; Jenouvrier et al., 2017). Our understanding of the influence of climate change on emperor penguin populations is not yet fully developed (Ainley et al., 2010; Larsen et al., 2014). At present, individual life histories of emperor penguins are only monitored on an annual basis at Pointe Géologie, and as reviewed in the Supplementary Material, Part 1, only a few other long-term time series of colony size exist at other sites. Accounting for both uncertainties in our understanding of climate and ecological responses of emperor penguins to climate, state-of-the-art demographic models have concluded that negative climate change-related impacts on the emperor

penguin can be considered *likely* (Jenouvrier et al., 2014; Larsen et al., 2014), with *high agreement* amongst experts (Ainley et al., 2010; Larsen et al., 2014).

The vast majority of emperor penguin colonies occur on fast ice, with a few exceptions as noted above; consequently, inter-annual variability in fast ice is a key feature of emperor penguin performance (Massom et al., 1998, 2009). In a future world, without seasonally persistent fast ice, alternate habitat would have to be used. Given that the emperor penguin is an obligate sea ice dependent species, coupled with the documented vulnerability of sea ice to weather and climate change, the potential is great for significant reduction in, and loss of emperor penguin breeding habitat. Sea ice extent is a convenient correlation that is probably a proxy for other, more-difficult-to-quantify factors that actually have bearing on emperor penguins. It is influenced by the interconnected atmosphere-ice-ocean system of the Southern Ocean. Since the start of the modern satellite era in 1979, Antarctic sea ice area has shown considerable inter-annual variability with marked regional variation, and including both increases and decreases (Turner et al., 2009a, b, 2017; Stammerjohn et al., 2008, 2012; Parkinson, 2019). Trends in sea ice extent are potentially independent of what might be happening with coastal fast ice: e.g. altered winds may lead to more extensive large-scale sea ice, but possibly reduced fast ice (Ainley et al., 2010). Nevertheless, in the long-term the loss of large-scale sea ice in general means that ultimately fast ice is likely to be affected. Modelled projections of sea ice remain a key issue, including uncertainty about recent sea ice anomalies, which remain an active topic of discussion (e.g. Fetterer et al., 2016; Turner et al., 2017; Bronselaer et al., 2018; Meehl et al., 2019; Wang et al., 2019).

Most climate models agree that future global climate change will lead to reductions in sea ice area of close to 30% (or 40%) over the 21st century following medium (or high) emissions scenarios (Bracegirdle et al., 2008, 2015; Palerme et al., 2017) and therefore will impact emperor penguins (Ainley et al., 2010; Jenouvrier et al., 2014, 2017). However, it is important to also note that emperors are likely to be affected well before the end of the 21st century as a destabilization of their breeding platforms prior to fledging seriously diminishes their chances of breeding successfully.

A climate-dependent demographic model without emigration, projected that many emperor colonies would decrease by > 50% from their current size by 2100, resulting in a dramatic global population decrease (Jenouvrier et al., 2014). More recently, Jenouvrier et al. (2017) considered whether emigration may reverse the anticipated global population decrease; the study used detailed emigration/immigration processes, including emigration distance, habitat structure, informed emigration behaviours, and density-dependent emigration rates, and highlighted the uncertainty associated with current understanding. Relative to models without emigration/immigration, emigration can either offset or accelerate climate driven population decreases. Importantly, increased emigration, potentially a symptom of increasing colony instability owing to changes in suitable habitat, may decrease the global population by up to 65%, depending upon the rate of emigration and distance individuals relocate. Cristofari et al. (2016) also highlighted that robust estimations of extinction risk are only possible by including emigration rates as colony-scaled population size is more indicative of local stochastic events. Thus, understanding animal emigration/immigration is key to assessing the scenario by which emperors will respond or adapt to changing habitat owing to climate change.

Current projections have modelled the impact of future climate change on the demographic parameters of adult emperor penguin populations. However, juveniles also play a crucial role in the dynamics of seabird populations, and it has recently been shown that survival of juvenile emperor penguins is affected by climate variability (Abadi et al., 2017). Thus, understanding the influence of climate variations on juvenile survival is also key to assessing the fate of emperor penguins (Labrousse et al., 2019).

Marine predators integrate many factors when choosing where and when to breed or to forage, and emperor penguins are no different. In addition to suitable stable breeding habitat, they must also have predictable and profitable prey resources within a certain distance of their breeding sites, because chicks need regular provisioning (see Prévost, 1961). This places important constraints upon where adults can forage, and upon the size, location and distribution of their breeding sites (Ashmole, 1963; Massom et al., 2009; Ancel et al., 2017; Warwick-Evans et al., 2018; Trathan et al., 2018). Constraints associated with a breeding location will affect a colony's population size if conditions are no longer suitable year on year. Currently occupied sites will almost certainly change as climate alters, and many sites may no longer be sustainable. Therefore, emperor penguins may have to relocate, but areas with reliable fast ice conditions will be more difficult to find (Ainley et al., 2010; Trathan et al., 2011; LaRue et al., 2015; Jenouvrier et al., 2017).

The influence of sea ice will not only be important in terms of a platform for breeding, but projected sea ice loss may also have important consequences for food resources. There is now an extensive literature on the role of sea ice for primary and secondary production, and in turn, prey distribution (e.g. Brierley and Thomas, 2002). Indeed, Meyer et al. (2017) recently questioned a dominant paradigm that suggests that winter sea ice is generally the main feeding ground for larvae of Antarctic krill, reporting instead that the pack ice zone appears to be a food-poor habitat for larval development, and in contrast, the more open marginal ice zone provides a more favourable food environment for high larval krill growth rates. Nevertheless, Meyer et al. (2017) suggest that complex under-ice habitats are vital for larval krill when water column productivity is limited by light, by providing structures that offer protection from predators and to collect organic material released from the ice. With sea ice loss, emperor penguin responses will probably also be strongly dependent on the relationship between sea ice and food resources.

Beside the negative aspects of climate variability and change, other threats to emperors probably remain relatively small if not negligible (Trathan et al., 2015), with a few important exceptions. Following the entry into force of the Protocol on Environmental Protection to the Antarctic Treaty in 1998, threats associated with tourism and scientific endeavours have been regulated by national permitting authorities, whilst collection of eggs or adults for zoos is probably rare. The Association of Zoos and Aquariums (AZA) in the USA report 31 captive emperors, whilst the Japanese Zoo Association (JAZA) reports just 22 (Boersma et al., 2017); no other zoo association reports any holdings of emperor penguins, and though not all zoos are members of such associations, numbers are probably low. Other important threats at local scales will continue to require international oversight through Initial and Comprehensive Environmental Evaluations (IEEs and CEEs) to ensure that colonies are not affected by future developments, such as new aircraft runways, or new or enhanced research facilities, and that appropriate up-to-date biological data are used for management decisions (Lynch et al., 2016). Other threats, such as by-catch in fisheries (e.g. Crawford et al., 2017) and resource competition from fisheries (e.g. Trathan et al., 2018) are apparently currently non-existent. The regional commercial fishery for Antarctic krill operates distant from emperor breeding sites; however, very little is known about the distribution of juveniles and non-breeding birds which sometimes forage far from the continent (Kooyman et al., 1996; Kooyman and Ponganis, 2008; Wienecke et al., 2010; Thiebot et al., 2013; Goetz et al., 2018; Labrousse et al., 2019). Currently, there is no commercial harvest for Antarctic silverfish. Suggestions that exploitation of Antarctic toothfish (*Dissostichus mawsoni*) may allow population increases in prey species for penguins (Pinkerton et al., 2016; Ainley et al., 2017), such as Antarctic silverfish, are currently being tested in areas where toothfish fisheries operate, for example in the Ross Sea. In addition to changing predation pressure, ocean acidification, decreasing sea ice extent and decreasing salinity will all play a part and may affect the availability of

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prey species.

5. Re-analysis of the IUCN Red List threat status

5.1. Population decline and habitat projections

The International Union for Conservation of Nature (IUCN) Red List of threatened species status for the emperor penguin was last assessed in 2018 (BirdLife International, 2018). The species was listed as Near Threatened because it was projected to undergo a moderately rapid population decrease over the next three generations owing to the projected effects of climate change; however, it was noted that there was considerable uncertainty over future climatic changes and how this would impact the species. Now, as understanding about future climate change impacts has increased, including use of several approaches that incorporate the likely population trajectory of the emperor penguin (Ainley et al., 2010; Jenouvrier et al., 2014, 2017; Abadi et al., 2017), a re-assessment of the Red List status of the species is appropriate.

Ainley et al. (2010) considered habitat variability and modelled habitat alterations, qualitative changes to population size and distribution, in response to average tropospheric temperature increases to 2 °C above preindustrial levels (ca. 1860). These authors considered four CMIP3 models that were part of the IPCC AR4 and which provided the best representation of the Southern Ocean: GFDL-CM2.1, GFDL-CM2.0, MIROC3.2(hi-res), and MRI-CGCM2.3.2a, evaluating the composited model ENSEMBLE. The ENSEMBLE projected a marked narrowing of emperor penguin zoogeographic range at 2 °C above pre-industrial levels. Colonies north of 70°S, that is ~50% of emperor colonies (40% of the breeding population), were projected to decrease or disappear, with possible limited growth south of 73°S. Net change would result largely from positive responses to increase in polynya persistence at high latitudes, overcome by decreases in pack ice cover at lower latitudes and ice thickness (Ainley et al., 2010). Under the IUCN criteria (IUCN, 2017), the projected change in the emperor population would meet the Vulnerable threat status under condition A3, that is, population reduction [≥30%] projected, inferred or suspected to be met in the future. This, coupled with reported impacts following extreme events, such as those documented by Barbraud et al. (2015) and Fretwell and Trathan (2019), could be especially important in high-latitude locations that may previously have been considered as climate refugia. Based on that result and possible similar decreases in other Weddell Sea colonies, it appears that only the Ross Sea colonies may be less vulnerable than colonies elsewhere. However, beyond the timespan of current models, with current rates of warming, these too may also decrease.

Jenouvrier et al. (2014) projected large-scale sea ice concentration for each emperor penguin colony for the four seasons of the breeding cycle, using a multi-model ensemble of 20 CMIP3 models. They accounted for uncertainties in climate model selection by performing three different analyses. First, they selected climate models that best reproduced sea ice conditions around each colony at a local spatial scale. For each colony, Jenouvrier et al. (2014) employed a subset of models for which the climatology of the simulated sea ice concentration agreed well with the observed climatology in the vicinity of that colony. Second, they also considered a pan-Antarctic selection, using the same models selected by Ainley et al. (2010), applied to each colony. Finally, they undertook an analysis using all models without any regard to their agreement with observations. The models were forced with a middle range emissions scenario (SRES A1B), which assumed a future socio-economic development depending on fossil and non-fossil energy sources in balanced proportions. Under this scenario, the CO_2 level would double by 2100, from 360 ppm to 720 ppm. Under these model conditions, Jenouvrier et al. (2014) reported that by 2100 the median growth rate (−3.2% per year) projected a population decrease of 78% over three generations, far exceeding the IUCN threshold for Endangered threat status [≥50%] under condition A3. Jenouvrier et al. (2014) further noted that the IUCN projected decrease criteria may not be optimally formulated to capture threats from long-term, directional trends such as global warming. Interestingly, the clusters from the classification in Supplementary Material, Part 1, SM Fig. 1 show important similarities to the projections for the end of the century made by Jenouvrier et al. (2014), highlighting that current regional environmental properties condition robust future projections.

Jenouvrier et al. (2017) enhanced model projections for emperor penguin persistence under future climate change by including emigration/immigration in their population model. This revealed that emigration processes may accelerate, slow down, or reverse the anticipated global population decrease over the short term, when compared with a model without emigration. These authors noted that the response of the global population was complex and depended upon the time-period considered, as the sea ice changes at different rates over time, as well as the interaction amongst emigration processes, including the proportion of emigrants, the emigration distance, and habitat selection behaviours employed. Jenouvrier et al. (2017) reported that informed emigration decisions might act as an ecological rescue for a short time, but at the end of the century the global population will be declining regardless of the emigration scenario; thus, there is a projected global population decrease of between 40% and 99% over three generations. As a result, the projected decrease means that emperors should be listed either as Vulnerable or Endangered, under condition A3.

A key element of population decrease is likely to be related to the survival of immature individuals, as this is a critical component of population dynamics and recruitment. Abadi et al. (2017) therefore analysed the number of emperor penguin fledgling at Pointe Géologie, considering how the Southern Annual Mode (SAM) and sea ice concentration affected juvenile survival. They showed that there was indeed a strong positive effect of SAM on juvenile body condition and survival through its influence on wind patterns, fast ice extent, and distance to open water, highlighting how future climate change scenarios are also likely to affect population recruitment. In modelling first year survival, inclusion of sea ice effects on early life history processes is likely to make forecasts of survival even more pessimistic.

In considering the links between sea ice and emperor penguin population processes, we recognise that drawing ecologically meaningful conclusions can be problematic (Cavanagh et al., 2017). Indeed, Cavanagh et al. (2017) note that the expertise required to access and interpret output from climate and earth system models is hampering progress in utilizing them most effectively when determining the wider implications of climate change. However, the studies by Ainley et al. (2010) and Jenouvrier et al. (2014, 2017) were informed by individuals with expertise in both climate sciences and ecology (cf. Cavanagh et al., 2017). As such, this careful multidisciplinary development provides reassurance when considering the model output.

5.2. Trait-based approaches

In addition to the existing threat criteria (IUCN, 2017), IUCN is developing a 'trait-based' approach for assessing a species vulnerability to climate change (www.iucn.org/theme/species/our-work/species-and-climate-change); we recognise that this approach has considerable value, in addition to the robust demographic modelling analyses already undertaken for emperor penguins (Ainley et al., 2010; Jenouvrier et al., 2014, 2017).

Indeed, Trull et al. (2018) stress that in order to complement existing processes of estimating IUCN Red List status, climate change-specific assessments are needed and that these could be developed using a number of different approaches, ranging from mechanistic models to trait-based assessments, and that trait-based climate change vulnerability assessments have been recognised by the IUCN (Foden et al., 2013). These approaches use species-specific trait data to infer high or low vulnerability to climate change. Traits used in these analyses generally pertain to climate change sensitivity and low

adaptability of species and are coupled with measures of climate change exposure (Foden et al., 2013).

Recent work has suggested that there are three dimensions of climate change vulnerability: sensitivity, exposure and low adaptive capacity, creating four distinct classes of climate change vulnerable species, each with particular implications for conservation (Dawson et al., 2011; Foden et al., 2013). Species that are 'highly climate change vulnerable', are those that are sensitive, exposed and have low adaptive capacity; these are of greatest concern and should be the priority for monitoring and for assessment of interventions to support them. Species that might be 'potential adapters' are sensitive and exposed, but have high adaptive capacity; these may be able to mitigate negative climate change impacts by dispersal or micro-evolution, although close monitoring is still needed. Species that are 'potential persisters' are those that have low adaptive capacity and are exposed, but are not sensitive; these may be able to withstand climate change in situ by themselves, but again, monitoring is needed. Finally, species that are of 'high latent risk' are those that have low adaptive capacity and are sensitive, but are not exposed; these are thought not to be of immediate concern if climate change projections and emissions scenarios are accurate, but could become climate change vulnerable if exposed.

In this context, we note that the emperor penguin has unique traits associated with its breeding behaviour with almost total reliance upon sea ice as a specialised habitat. Hence, the loss or degradation of important habitats and micro-habitats will be vital for emperor penguins, including changing environmental thresholds, such as fast ice availability and quality. Based on the four categories identified by Dawson et al. (2011) and Foden et al. (2013), emperor penguins are both sensitive and exposed, and have so far shown little evidence of adaptive capacity. Therefore, given future sea ice projections based on CMIP models, we consider that emperor penguins are highly climate change vulnerable.

In summary, the outcomes of the three population modelling assessments indicate that under Criterion A3 of the Red List Threat Status Assessment Criteria, the emperor penguin should be considered for reclassification as Vulnerable, or perhaps, Endangered. The traits-based approach further supports a re-examination of the species status. We suggest that the emperor penguin should now become emblematic of a new global conservation paradigm for species threatened by ongoing climate change.

6. Methods for protecting the emperor penguin

Out of the water, emperor penguins are not agile and cannot easily negotiate rough terrain, or even rough sea ice; they are certainly unable to leap or scramble to ascend steep terrain, as can many other penguin species. They require relatively flat, gradual access either to sea ice or beaches. Loss of suitable breeding habitat is therefore one of the most important challenges that emperor penguins face, one also encountered by many other species. In the recent past, some colonies have successfully relocated from the sea ice onto ice shelves (Fretwell et al., 2014). However, this is only possible where the ablation of shelf fronts or the presence of snow bridges enables access, which varies between years (Zitterbart et al., 2014). In a warming environment that will potentially result in increased calving of ice shelves, opportunities for this might change. Furthermore, if the rates of flow of ice shelves alter, surfaces may be more highly crevassed. Also, the lack of shelter exposes colonies to strong winds, though most CMIP models also project wind changes, with weakening coastal easterlies (Bracegirdle et al., 2008; Bintanja et al., 2014). Ice-free ground is rare in Antarctica (< 1% of Antarctica; Burton-Johnson et al., 2016) and the chances that suitable rock areas will emerge is difficult to predict, especially given substantial uncertainty brought by a range of factors including solid earth change effects on the Antarctic cryosphere and the future behaviour of the Greenland ice sheet (e.g. Whitehouse et al., 2019). Under the strongest forcing scenario, ice-free areas could expand by around 25% (Lee et al., 2017), but with most of this inland in the Antarctic Peninsula, in areas where emperor colonies cannot relocate. Moreover, should emperors move to any newly available suitable ice-free areas, there is the potential for increased competition for food resources (e.g. LaRue et al., 2019), or interactions with other seabirds and marine mammals, which may lead to disturbance or increased predation of chicks (Trathan et al., 2011). Extensive sea ice currently provides a barrier to the arrival of most other such species, particularly in winter; however, with future reductions in sea ice, the potential for increased interactions is likely, leading to additional stressors on emperor populations. Thus, until Governments implement the principal objective of the UNFCCC — to stabilize GHG concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system — the emperor penguin will continue to be threatened. Where feasible, responsible regional management authorities must consider how to preserve biodiversity and reduce other risks, whilst GHG emissions are stabilized or reduced. This is now essential as global emissions of CO_2 from fossil fuels and industry have increased by > 1.5% per year on average between 2008 and 2017 (Le Quéré et al., 2018), despite reductions in some developing countries (Le Quéré et al., 2019). Similarly, atmospheric methane has grown very rapidly each year between 2014 and 2017, and as such the climate warming impact of methane, if continued at > 5 ppb per year in the coming decades, will be sufficient to challenge the Paris Agreement (Nisbet et al., 2019).

Protecting the emperor penguin, and other Antarctic and Southern Ocean biota, requires that choices about GHG must now be made (Rintoul et al., 2018), especially as even at 2 °C above preindustrial levels, major changes in emperor penguin distribution will occur (Ainley et al., 2010). The symbolic 'guardrail' of 2 °C introduced in international climate agreements after the UNFCCC meeting in Copenhagen in 2009 and reaffirmed at Paris in 2015, must be maintained and GHG emissions must start decreasing in the coming decade (Rockström et al., 2017). Inevitably, there will be inertia in both social and physical systems, such that the climate will continue to change, even after aggressive global action to reduce GHG emissions (Mastrandrea et al., 2010). Therefore, at the global scale, particularly given current rates of GHG emissions (Le Quéré et al., 2018; Nisbet et al., 2019), we must do better than the Paris Agreement, as reaching the guardrail will only be the first key step. At the regional Antarctic scale, other tools are now needed until GHG emissions stabilize and reduce, and the climate recovers.

Three management tools are available in the Antarctic that may help reduce or eliminate other stressors that could otherwise add to the burden that the emperor penguin faces from climate change. South of 60° S, environmental regulation is undertaken through the Antarctic Treaty System (Berkman et al., 2011). Particularly relevant to conservation of the emperor penguin is the Protocol on Environmental Protection to the Antarctic Treaty (hereafter the Protocol) and the Convention on the Conservation of Antarctic Marine Living Resources, which together enable spatial protection on land and at sea and the designation of a species as specially protected.

Annex V of the Protocol enables the Antarctic Treaty Parties to designate Antarctic Specially Protected Areas (ASPAs) to protect environmental values, including areas with important or unusual assemblages of species, including major colonies of breeding native birds or mammals. These ASPAs can be on land or at sea (in the form of Marine Protected Areas (MPAs)), although in the latter case the designation of large MPAs has largely been left to the Commission for the Convention of Antarctic Marine Living Resources, CCAMLR (Brooks et al., 2016; Chown et al., 2017). In protecting areas of ocean, MPA boundaries may also include ice shelves, adjacent fast ice and pack ice, and so potentially afford more complete protection for emperors at their breeding site and whilst feeding or moulting at sea. Furthermore, MPAs may also protect areas of high productivity necessary for the support of various mobile marine populations, including penguins, marine mammals and fish, and that is part of the reason why large-scale MPAs are preferred

for conservation. However, in considering the designation of MPAs, CCAMLR also evaluates many factors in addition to the protection and conservation of species, habitats, communities and ecological processes (CCAMLR, 2011); such considerations include the harvesting of living marine resources and as such, MPAs are unlikely to be designated purely for the protection of a single species such as the emperor penguin.

To date, eight ASPAs have been designated by the Antarctic Treaty Consultative Parties that include protection for emperor penguins at their breeding sites, but these offer only limited protection whilst birds are at sea, even though some include a small marine component. The designated ASPAs are:

(1) ASPA No. 101, Taylor Rookery, Mac. Robertson Land, protects an area covering the whole of the northernmost rock exposure on the east side of Taylor Glacier, Mac. Robertson Land. It is the only known site where the emperor penguin breeds entirely on land. It is also important because of long-term monitoring.
(2) ASPA No. 105, Beaufort Island, McMurdo Sound, Ross Sea, protects the whole of Beaufort Island above the mean high water mark, and includes the adjacent fast ice occupied by breeding emperor penguins.
(3) ASPA No. 107, Emperor Island, Dion Islands, Marguerite Bay, Antarctic Peninsula, protects the Dion Islands, a small archipelago comprising several islands, rocks and reefs, situated near to Adelaide Island in Marguerite Bay. The colony was one where breeding also occurred on land, but it now appears that emperors no longer breed at the site (Trathan et al., 2011), or only breed there in small numbers (Hart, 2016).
(4) ASPA No. 120, Pointe Géologie Archipelago, Terre Adélie, protects four islands: Rostand, Le Mauguen, Lamarck and Claude Bernard; a nunatak, and a breeding ground for emperor penguins located in the heart of the Pointe Géologie Archipelago in the coastal area of Terre Adélie. The site is an important site for scientific research for Antarctic seabirds and seals where long-term studies of the population dynamics and social behaviour of emperors are undertaken.
(5) ASPA No. 124, Cape Crozier, Ross Island. Cape Crozier is at the eastern extremity of Ross Island, where an ice-free area comprises the lower eastern slopes of Mount Terror. Large cracks in the ice shelf are covered by fast ice that is occupied annually by breeding emperor penguins. Annual counts of emperors have been undertaken.
(6) ASPA No. 127, Haswell Island, protects Haswell Island (the largest island in the archipelago), its littoral zone, and the adjacent section of fast ice in the Davis Sea. The site is used for the study of emperors and their habitat.
(7) ASPA No. 169, Amanda Bay, Ingrid Christensen Coast, Princess Elizabeth Land, East Antarctica, protects several thousand pairs of emperor penguins in the south-west corner of Amanda Bay, whilst providing for continued collection of valuable long-term research and monitoring data and comparative studies with colonies elsewhere in East Antarctica.
(8) ASPA No. 173, Cape Washington and Silverfish Bay, Victoria Land, northern Ross Sea. This is the most recently designated protected area; it was established specifically to protect both one of the largest emperor penguin colonies in existence, as well as an important nursery area for Antarctic silverfish. With an area of 279 km^2, it is one of the largest protected areas. This colony has been part of a long-term population study of emperor penguins in the Ross Sea, including a series of physiological and behavioural studies.

In contrast, only the Ross Sea Region (RSR) MPA has been designated by CCAMLR (CCAMLR, 2016) to include some consideration of protection for emperor penguins. The RSR MPA encompasses emperor penguin breeding sites at Cape Roget, Coulman Island, Cape Washington, Franklin Island, Beaufort Island, Cape Crozier and Cape Colbeck. It also includes protection for important feeding areas, as well as moult areas in the eastern Ross Sea, though these latter sites may be close to the MPA Special Research Zone that allows harvesting. Currently, the RSR MPA protects only one of the emperor penguin meta-populations proposed by Younger et al. (2015, 2017). Protection of all genetically distinct meta-populations might be important for future resilience to environmental change; certainly protection of the climate change refugial meta-populations is likely to be vital. CCAMLR is actively considering other MPAs in the west Antarctic Peninsula, the Weddell Sea, and in East Antarctica. Cumulatively, if adopted, these would help protect a further 25 breeding sites and some offshore foraging areas, providing protection for other meta-populations (Younger et al., 2015, 2017), as well as for other species (e.g. Ropert-Coudert et al., 2018).

Thus, to date, seven active breeding sites are protected by ASPAs and seven by the RSR MPA (of which three are also protected by ASPAs); more colonies may eventually become protected. The RSR MPA and the proposed MPAs elsewhere in Antarctica should also afford protection for other life history processes, including potentially foraging and moulting. MPAs may provide for more comprehensive protection of emperor penguins (and other species), but the numerous considerations necessary during their initial, sometimes lengthy, planning stages mean that they are more difficult to agree and become designated by CCAMLR.

Given the potential for severe impacts of climate change in the Antarctic on emperor penguins (Ainley et al., 2010; Jenouvrier et al., 2014, 2017), and the relatively limited utility offered by ASPAs for protecting areas of ocean, it would be prudent to consider other means of protection. Annex II to the Protocol enables any species to be designated an Antarctic Specially Protected Species (SPS). Designating the emperor penguin as an Antarctic SPS could confer comprehensive protection across all life history stages and processes, and would ensure protection of all genetically distinct meta-populations. Such a designation would be complementary to the existing area-based methods of protection.

In assessing the case for designation, several considerations are required:

(1) Any Antarctic Treaty Party, the Committee for Environmental Protection (CEP) established by the Protocol, or the Scientific Committee on Antarctic Research (SCAR) may propose a species for special protection. Such a proposal should set out a general description of the species, including details of its distribution, including both breeding and foraging ranges, information on its populations and their trends, and details of any national or international protection already being accorded outside the Antarctic Treaty System. The proposal must also include a draft Action Plan (Supplementary Material, Part 2) to address threats to the species, and which includes arrangements to monitor progress against the plan.
(2) On the basis of the proposal, SCAR is required to assess the species against the IUCN Red List criteria. If the species falls in the Vulnerable or higher threat category, SCAR then recommends listing as an Antarctic SPS to the CEP, which in turn makes a recommendation to the Antarctic Treaty Consultative Parties.
(3) The emperor penguin is currently listed by the IUCN as Near Threatened; it is the only Antarctic penguin species listed with a threat status more serious than Least Concern. For designation as an Antarctic SPS, the species would require an IUCN designation of at least Vulnerable, which more properly reflects the species' status.
(4) If a listing is agreed, the preparation of an Action Plan would be required. This would allow all Parties to agree the actions necessary to conserve the species and assist in the recovery or maintenance of its populations.
(5) Periodic reports on the emperor penguin as an Antarctic SPS would enable the CEP and the Antarctic Treaty Parties to assess the success

of the Action Plan. Such reports could be prepared by SCAR, potentially in collaboration with the IUCN Species Survival Commission's Penguin Specialist Group, BirdLife International, or by other groups of interested scientists from within the Treaty Parties.

Designation as an Antarctic SPS has the potential to ensure that regional management actions would take into consideration any activity that might impact upon emperor penguins, including consideration of breeding sites and prey availability during critical life history periods. Regional management would be obligated to consider the species' requirements when supporting other management objectives. As an Antarctic SPS, even if colonies move or relocate, individual birds (including adults and juveniles) would still receive consideration, no matter what the boundaries might be of any particular ASPA or MPA.

It is apparent that large changes are projected to take place in Antarctica and across the Southern Ocean, with wider impacts worldwide (Bronselaer et al., 2018; Rintoul et al., 2018). The fate of the emperor penguin can help us understand some of the consequences of change in the high latitudes, especially given the close connection between the species and physical forcing. As an Antarctic SPS, a coordinated Action Plan will be necessary; this should include suggestions for conservation plans and action, ongoing decision-making, periodic population assessments, increased research on the ecology of the species and the development of monitoring priorities, including to better understand the relationship between demography, climate change and other threats. Importantly, such an Action Plan should also include priorities for telemetry work to help determine where and when, and which demographic categories of emperors are at greatest risk in relation to threats at sea.

7. Conclusion

(1) Based on the current literature, and the projected level of climate change associated with increasing GHG emissions, we conclude that the emperor penguin is vulnerable to altered wind regimes, rising temperatures, changes to fast ice extent and duration, and melting sea ice and should therefore be accorded an IUCN Red List threat status of Vulnerable at the very least.
(2) Only a reduction in anthropogenic GHG emissions will reduce the environmental threats to the emperor penguin; but until such time, other conservation actions are necessary, including increased spatial protection at breeding sites and foraging locations.
(3) We recommend that, as a priority, the species continues to be the focus of collaborative international research, and that special conservation activities, including designation of large-scale MPAs should be pursued as this should afford protection for all life history processes. Further, complementary protection through designation as an Antarctic SPS should be followed.
(4) The emperor penguin has the potential to be seen as an exemplar for how species might be protected under future climate change scenarios.

Declaration of competing interest

The authors are not aware of any actual or potential conflicts of interest.

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Appendix A. Supplementary data

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