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Global terrestrial distribution of penguins (*Spheniscidae*) and their conservation by protected areas

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Abstract

Establishing protected areas (PAs) ranks among the top priority actions to mitigate the global scale of modern biodiversity declines. However, the distribution of biodiversity is spatially asymmetric among regions and lineages, and the extent to which PAs offer effective protection for species and ecosystems remains uncertain. Penguins, regarded as prime bioindicator birds of the ecological health of their terrestrial and marine habitats, represent priority targets for such quantitative assessments. Of the world's 18 penguin species, eleven are undergoing population declines, for which ten are classified as 'Vulnerable' or 'Endangered'. Here, we employ a global-scale dataset to quantify the extent to which their terrestrial breeding areas are currently protected by PAs. Using quantitative methods for spatial ecology, we compare the global distribution of penguin colonies, including range and population size analyses, with the distribution of terrestrial PAs classified by the International Union for Conservation of Nature, and generate hotspot and endemism maps worldwide. Our assessment quantitatively reveals < 40% of the terrestrial range of eleven penguin species is currently protected, and that range size is the significant factor in determining PA protection. We also show that there are seven global hotspots of penguin biodiversity where four or five penguin species breed. We suggest that future penguin conservation initiatives should be implemented based on more comprehensive, quantitative assessments of the multi-dimensional interactions between areas and species to further the effectiveness of PA networks.

Keywords Biodiversity hotspots · IUCN · Macroecology · Penguins · Protected areas · Species richness

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Introduction

In recent decades, direct anthropogenic threats to terrestrial wildlife, primarily habitat degradation and exploitation of natural resources, and indirect anthropogenic threats, primarily climate change, have become increasingly prevalent, triggering declines and extinctions of biodiversity (Dirzo et al. 2014; Trathan et al. 2014; Newbold et al. 2015; Urban 2015; Ceballos et al. 2015). Concerns over accelerating wildlife loss have importantly been mitigated by the establishment of protected areas (PAs)—geographical space designated and managed with the long-term aim to sustainably conserve biodiversity, ecosystem services, and cultural values (Brooks et al. 2004; Moilanen et al. 2009; Bertzky et al. 2012). They have become the most widely implemented conservation action (Gillingham et al. 2015), and as of 2018, 14.9% of global terrestrial areas (including inland waters) and 7.3% of the ocean are covered by some form of legal protection (UNEP-WCMC, IUCN, NGS 2018). However, one of the central challenges faced by the PA approach is the identification of vulnerable or irreplaceable organisms and geographic regions that take into account the spatial and phylogenetic asymmetry of resident biodiversity (e.g., endemism, species richness, taxonomic uniqueness) and population structure (e.g., range size, population size, conservation status) (Reid 1998; Myers et al. 2000; Orme et al. 2005; Gaston et al. 2008). Here, we implement an exhaustive global-scale approach to assess the overlap between PAs and the terrestrial breeding range (i.e., observed locations of individuals or colonies of penguins on land) of penguins globally as a primary step towards an integrative understanding of the efficiency of the current PA network in mitigating biodiversity declines.

Over the last 6 decades, PAs have generally been considered an effective conservation approach. Their goal is to encourage ecological resilience by buffering against negative pressures such as climate change, sustainably manage resources, and promote mutually beneficial human-ecosystem interactions (refer to Gaston et al. 2008; Secretariat of the Convention on Biological Diversity 2008). They have also been designated for the protection of species and populations in biodiversity hotspots, including areas with high species richness or endemism (Myers et al. 2000; Thiollay 2002; Brooks et al. 2006; Trathan et al. 2014). These biodiversity hotspots represent areas that are environmentally suitable and able to sustain multiple species, making the area valuable and worthy of protection. Protected areas also encompass areas and organisms which have been prioritized for conservation actions based on ecological attributes that affect persistence such as range size, population size, and threats such as habitat degradation (Reid 1998; Boersma and Parrish 1999; Pichegru et al. 2010; Bertzky et al. 2012; Dirzo et al. 2014; Trathan et al. 2014; Meiri et al. 2018). Range size and population size are commonly used to estimate vulnerability, rarity, and extinction risk of a species and thus supports PA designation and threat classification (Ferrière et al. 2004; Höglund 2009; Chevin et al. 2010; Pimm et al. 2014; Venter et al. 2014; Meiri et al. 2018). For example, species with small geographic ranges generally have fewer individuals and lower genetic variation compared to species with larger ranges (e.g., Galapagos penguins, *Spheniscus mendiculus*). As a result, these species might not be able to maintain genetic diversity and spatial persistence if a portion of their range is altered, which would ultimately escalate their priority as targets for conservation (Frankham 1996; Gaston 2003; Höglund 2009; Charlesworth and Charlesworth 2010; Borboroglu and Boersma 2013; Meiri et al. 2018). Effective protection of these restricted populations is likely to have a bigger impact on overall species survival than protecting one population in a wide ranging species (Mace et al. 2008; Pimm et al. 2014).

While the majority of PAs are nationally designated and categorized using the International Union for Conservation of Nature (IUCN) system based on management objectives and legal status (IUCN 2001; Dudley 2008; see Table 1 in Online Resource), alternative international, regional, and national classifications are also used (e.g., UNESCO World Heritage sites). The purpose of PA category systems is to first acknowledge a PA, its current conservation goals, and its governing organisation and then to provide stakeholders with a framework for delivering, reporting, and monitoring management effectiveness into the future. Different category systems call for different levels of protection, each with different management approaches (e.g., restricted access, public use, resource exploitation). These categories provide a standardized outline for defining PAs, but there is high variability between actual management and the broad category recommendations. The category system and associated data does not indicate if a PA was created to protect a specific species or if that species merely occurs within a PA that was established for other management objectives. The system also does not quantify the effectiveness of the PA designation on a specific species Nevertheless, any organism occupying area within a PA will be subject to the effects of the PAs. Therefore, it is useful as a classification tool to group similar PAs by overall management objective (e.g. protect a specific species, promote sustainable ecosystem use) as a baseline for further studies on efficacy. Furthermore, when assessing the irreplaceability of a species and its vulnerability to population decline, it is important to consider how PA classification affects the overall coverage of the PA (Pressey et al. 1994; Pressey and Taffs 2001; Dudley 2008).

A prime example of taxonomically unique organisms encompassing critical ecological features considered in conservation decisions and PAs are penguins. Penguins, broadly regarded as wildlife and cultural icons, are represented in public climate change and conservation movements as focal targets for protection. These unique birds, comprising of 18 species globally, are primarily restricted to the southern hemisphere (the only exception being *Spheniscus mendiculus* from the Galápagos Archipelago). Approximately two-thirds of penguin species are experiencing major population declines (Borboroglu and Boersma 2013; Boersma and Rebstock 2014; Trathan et al. 2014; Ropert-coudert et al. 2019), which has resulted in ten species (> 55% of their global diversity) currently at risk of extinction, categorised as Vulnerable or Endangered by the IUCN Red List (Ellis 1999; Boersma 2008; IUCN 2018). While some species have widespread distributions and high population densities, others have highly restricted ranges (Fig. 1, Table 1), which likely increases their vulnerability to environmental change.

Penguins are critically dependent on and constrained to limited areas of land for breeding and associated regions of the ocean for foraging (Borboroglu and Boersma 2013). Typically, foraging ranges are influenced by prey availability and other factors, while breeding occurs annually at the same location (Boersma 2008). Both habitats are vital for penguin survival and pose different threats that they must contend with (Ropert-Coudert et al. 2019). Anthropogenic drivers of population declines for penguins include climate change, habitat loss and degradation, commercial fishing and bycatch, oil spills, pollution, and tourism, whereas environmental threats include invasive species competition, El Niño events, and predation (Borboroglu et al. 2008; Gandini et al. 2010; Pichegru et al. 2010; Borboroglu and Boersma 2013; Trathan et al. 2014; Ropert-Coudert et al. 2019). While many threats operate in the marine environment (i.e., overfishing and bycatch), terrestrial threats such as unregulated tourism, over-exploitation, and habitat modification have more direct negative effects on penguin productivity and survival (Trathan et al. 2014).

This paper focuses on the overlap between terrestrial PAs and breeding sites of penguins for several reasons. Firstly, although penguins spend a disproportionate amount of time in

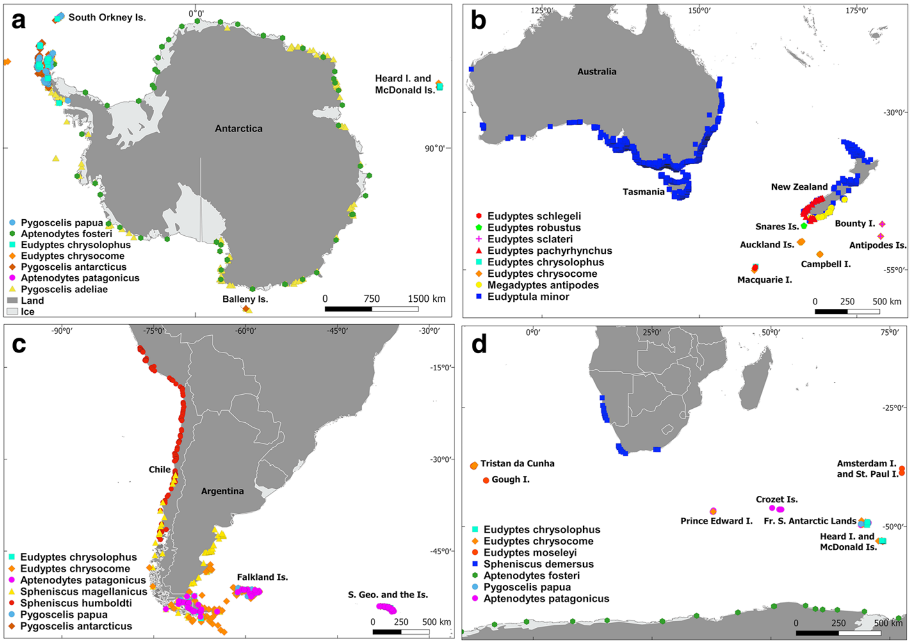

Fig. 1 Map of penguin nest site distribution in **a** Antarctica, **b** Australia, New Zealand, and surrounding sub-Antarctic islands, **c** South America, and **d** South Africa and surrounding sub-Antarctic islands. Not shown are Galapagos penguins nesting only on the Galapagos Islands. **a** is projected using South Pole Lambert Azimuthal Equal Area. **b**, **c**, and **d** are projected using the World Geodetic System 1984. Basemap from Natural Earth (http://www.naturalearthdata.com)

the ocean rather than on land, breeding is only possible on land and during a specific time of year. Penguins are also philopatric, returning to the same nesting areas each year and even to the same nest. Without successful breeding, recruitment of new individuals and population stability is impossible. Having PAs include penguin nesting sites will protect them from the aforementioned terrestrial threats, limiting these pressures and increasing their overall reproductive success. Therefore it is critical to analyse current conservation methods impacting penguin colonies to ensure continued survival. Secondly, differences in PA management, designation categories, conservation objectives, and overall ecosystem structure on land versus in the ocean highlight the necessity of assessing terrestrial PAs and marine PAs (MPAs) separately. Lastly, there are more terrestrial PAs globally than MPAs, and data on penguin range are of higher quality and quantity than marine distribution data.

We provide a global analysis of the patterns of terrestrial penguin biodiversity distribution and their protection under the current PA network. Therefore, we aim to address whether: (i) the terrestrial geographic distribution of global penguin species is sufficiently protected by existing terrestrial PAs or overlaps with biodiversity hotspots classified by Myers et al. (2000) (hereafter called Myers' hotspots), (ii) endangerment, as categorized by the IUCN Red List, is predominant among penguin species for which lower proportions of their ranges are covered by PAs, and (iii) whether terrestrial hotspots of penguin biodiversity (species richness and endemism) fall within existing PAs. Our findings thus focus on quantifying the extent of protection for penguins, which types of PAs occur within terrestrial sites used by penguins, and if factors such as range or population size are correlated to

Table 1 Summary table of all penguin species, including IUCN Red List conservation status, population size from Borboroglu and Boersma (2013), and area of occupancy (range size). Included is percent of occupancy area coverage by IUCN Protected Areas Categories System Ib-VI (IUCN), IUCN "Not Reported" and "Not Categorized" Protected Areas (NC), and Antarctic Specially Protected Areas (ASPA), Myers' biodiversity hotspots percent coverage of each species range, and total protection of those biodiversity areas

Species	Common name	Status[a]	Population size	Occurrence area (km^2)	Protection level (%)				Biodiversity hotspot (%)	
					IUCN	NC[b]	ASPA[b]	Total	Coverage	Protection
Aptenodytes forsteri	Emperor	NT	595,000	135,395.63	0.11	0.00	0.09	0.16	0.00	0.00
Aptenodytes patagonicus	King	LC	3,200,000	12,855.37	27.06	27.95	0.03	30.18	0.69	100
Eudyptes chrysocome	Southern rockhopper	VU	2,460,000	131,371.72	22.83	16.95	0.07	28.01	0.62	100
Eudyptes chrysolophus	Macaroni	VU	12,600,000	92,703.12	8.73	12.48	0.16	18.47	0.10	100
Eudyptes moseleyi	Northern rockhopper	EN	530,000	238.36	25.34	58.75	n/a	58.75	0.00	0.00
Eudyptes pachyrhynchus	Fiordland-crested	VU	6000	782.70	97.21	72.83	n/a	97.21	100	97.21
Eudyptes robustus	Snares	VU	62,000	0.81	100	0.00	n/a	100	0.00	0.00
Eudyptes schlegeli	Royal	NT	1,700,000	123.05	100	0.00	n/a	100	100	100
Eudyptes sclateri	Erect-crested	EN	140,000	21.50	98.23	0.00	n/a	98.23	96.93	100
Eudyptula minor	Little	LC	469,760	12,455.67	36.97	14.96	n/a	39.17	24.49	29.83
Megadyptes antipodes	Yellow-eyed	EN	3400	773.80	33.56	14.21	n/a	33.12	100	100
Pygoscelis adeliae	Adelie	LC	7,580,000	104,087.96	0.06	0.00	0.29	0.30	0.00	0.00
Pygoscelis antarcticus	Chinstrap	LC	8,000,000	33,972.38	3.55	5.10	0.48	4.99	0.26	100
Pygoscelis papua	Gentoo	LC	774,000	9872.58	14.05	16.07	10.90	17.36	0.00	0.00
Spheniscus demersus	African	EN	52,000	10,392.15	21.77	92.16	n/a	80.10	62.92	100
Spheniscus humboldti	Humboldt	VU	32,000	7926.59	9.64	5.13	n/a	11.16	59.45	5.37
Spheniscus magellanicus	Magellanic	NT	2,600,000	75,092.42	19.68	30.61	n/a	36.12	25.93	10.98
Spheniscus mendiculus	Galapagos	EN	1200	1821.34	0.00	100	n/a	100	100	100

[a] *LC* least concern, *NT* near threatened, *VU* vulnerable, *EN* endangered

[b] *NC* not categorized, *ASPA* Antarctic Specially Protected Areas

Refer to Table 3 in Online Resource for complete PA coverage data the level of protection in order to identify species and areas lacking protection and inform the future implementation and management of these PAs.

Methods

Species occurrence data

We compiled a global-scale dataset of the terrestrial geographic distribution of all 18 known penguin species (family Spheniscidae). We first downloaded coordinate data points for all Spheniscidae species from the open-access database Global Biodiversity Information Facility (GBIF 2018). This data was filtered to exclude any points without a record date or dates prior to 1969 (points included last 50 years only to minimize inaccuracies). Data for each species were assessed and compiled individually to limit exclusion errors. We excluded records with duplicate and incorrectly formatted coordinates, records north of the Equator (except for *Spheniscus mendiculus*, whose breeding sites extend slightly over the Equator), records without a valid country code, and records classified as fossil/dead specimens or vagrants (only those recorded as human observation were included). We also excluded spatial records whose locality description was blank, included the keywords "pelagic", "offshore", "at sea", "no information", "marine", "sea", "ocean", or contained ocean names only (such as "Southern Ocean"). The majority of the records in this dataset are colony/breeding site coordinates. However, it does include observations of vagrant penguins sited outside of breeding areas, because there is no systematic way to limit these observations further. The GBIF database does not distinguish between vagrants and breeding sites; therefore, we included colony data points from Borboroglu and Boersma (2013), the most recent published compilation of colony records. The GBIF points were checked against Borboroglu and Boersma (2013) range maps to identify incorrect or impossible records, which were then excluded from the analysis. Finally, a mask was applied to crop all points to global land surfaces. Therefore, our newly curated dataset of global penguins will, additionally, contribute a new resource for future penguin and bird research.

Data on penguin population size and IUCN Red List conservation status (hereafter conservation status) were obtained from Borboroglu and Boersma (2013) and the IUCN Red List (2014, 2018) as a compilation of published and unpublished data from many sources. While population sizes are naturally variable, these population estimates are the most reliable to date based on satellite imaging and/or long-term data collection.

Protected areas data

We collated the spatial data for PAs from the World Database on Protected Areas (WDPA; www.protectedplanet.com). This dataset includes PAs classified by the IUCN Protected Areas Categories System (henceforth referred to as IUCN PAs), the world's most inclusive and globally accepted prioritization scheme for nationally managed PAs (see Dudley (2008) for category descriptions). Due to the variability of protection within and between each IUCN category, we grouped all categories as "IUCN PAs", as the intent was to quantify protection as a whole. Category-specific examination of protection was out of the scope of this analysis. In addition to IUCN PAs, the dataset differentiates PAs that are nationally protected but not categorized ("Not Reported", NR) and international PAs categorised as

“Not Applicable” (NA). Not reported and not applicable PAs were grouped as “Not Categorized” (NC) in our analyses.

The PA distribution map was derived using the 2018 WDPA shapefiles and corresponding attribute tables. Due to the ambiguity of particular records, all point records, those with null latitude and longitude, those listed as “marine”, polygon records with no area information, and those north of the Equator were excluded from these analyses. Some areas are classified using both IUCN and other category systems simultaneously, so overlap between different designation types was removed when determining the total protection for each species.

In addition to the above protected areas, we included Antarctic Specially Protected Areas (ASPA) in our analyses (Terauds 2017, 2018). Similar to IUCN Ia or II PAs, ASPAs protect mammals and seabirds (and other associated ecosystem values) by primarily limiting human interference (Southwell et al. 2017). These areas are recognized by the Protocol on Environmental Protection to the Antarctic Treaty (United Nations 1991) and managed by respective international governments depending on location. Antarctica SPAs are the only set of PAs in Antarctica that can be considered equivalent to IUCN PAs in terms of classification requirements and management objectives (Coetzee et al. 2017). The ASPAs were grouped as “ASPAs” in our analyses.

Species distribution analyses

In order to determine spatial overlap between penguin ranges and PAs, we first calculated range size for each individual species. Due to the fragmented distribution of penguin breeding sites, the area that penguins occupy (‘area of occupancy’, AOO) was calculated. The circular buffer method presented in Hernández and Navarro (2007), Rivers et al. (2010), and Breiner and Bergamini (2018) was modified to create ranges based upon the distance between points for each species. A distance matrix between all points determined the mean value of the minimum distance between points. Using this mean value as the radius, each point was buffered by this distance. Overlapping circles were merged. Although these AOO ranges can include areas not currently occupied by breeding penguins (e.g., area between colonies, geographic features), this method best represents unrecorded colonies, potential future colonies, and areas used by penguins for non-breeding purposes.

Next, we masked and clipped the PAs using each species’ AOO to quantify the overlap of each PA type (IUCN, NC, and ASPA) within all species ranges. Each type of PA was classified and area was calculated and summed. Overlap between PA type was determined by dissolving all PAs and calculating the difference. We performed all analyses using QGIS 3.2.1 Bonn (QGIS 2018).

Species richness and endemism analyses

After creating a GIS grid shapefile of global penguin distribution with the southern hemisphere (3°N to 90°S) as a mask and a cell size of 1° (~111.12 km at the Equator) projected using South Pole Lambert Azimuthal Equal Area, we constructed the global distribution of species richness of penguins (i.e., number of penguin species contained per single grid cell) using Spatial Analysis in Macroecology (SAM) software, available at http://www.ecoevol.ufg.br/sam (Rangel et al. 2010). We considered as hotspots of penguins those grid cells in which at least four breeding species have been recorded, which represents the richest 2.5% cells (Orme et al. 2005). We then determined the overlap between worldwide biodiversity hotspots, as established by Myers et al. (2000), and AOO to quantify the extent to which a species range within a Myers' biodiversity hotspot is protected by IUCN or NC PAs. Myers et al. (2000) terrestrial biodiversity hotspots (1) "contain at least 0.5% or 1500 of the world's 300,000 plant species as endemics", (2) contain a high percentage of endemic vertebrate species (mammals, birds, reptiles, and amphibians), and/or (3) have lost 70% or more of its primary vegetation (Myers et al. 2000). We performed all biodiversity hotspot analyses using QGIS 3.2.1 Bonn (QGIS 2018).

Additionally, we investigated whether hotspots of penguin endemism are associated with PAs. A species is endemic if it occurs only in a defined area (for penguins, endemic species are usually range restricted to one island or one country). An area has high endemism if it contains many range-restricted species. To determine global endemism, we first calculated the Corrected Weighted Endemism (CWE) for each grid cell. CWE represents the weighted endemism (for each grid cell, the sum of the reciprocal of the total number of grid cells that each species occurs in) divided by species richness (the total number of species in that cell) to correct for species richness correlation. In other words, CWE emphasizes areas that have species with restricted distribution rather than areas with high species richness (Crisp et al. 2001). This index ranges from 0.0 to 1.0, corresponding to having 0–100% of the species occurring within that cell having a restricted range to that cell (Laffan and Crisp 2003). We performed all CWE analyses using the Analysis and Spatial Statistics tools and SDMToolbox (CWE) of ArcGIS 10.6.1 (Brown 2014; ESRI 2018).

Quantitative analyses

To address whether existing PAs are related to specific biodiversity factors, we first employed Spearman Rank Correlation tests to quantify the relationship between population and range size between different types of PAs. Kruskal–Wallis Rank Sum tests were performed to determine whether protection levels (percentage of area covered by an IUCN, NC, of ASPA PA for each species) differed among conservation statuses. We also used a Kruskal–Wallis test to evaluate whether there is an association between range size/population size and conservation status. All statistics were implemented in R version 3.1.2 (R Development Core Team 2019).

Results

Global species distributions

Penguin species are widely distributed across four continents and occupy a global terrestrial area of 629,887 km^2 (Fig. 1, Table 1). Geographic range and population sizes vary considerably across species but are not normally distributed (Kolmogorov–Smirnov $p < 0.01$; Table 2, Online Resource Fig. 1). There is a skewed tendency for range sizes to be small (Online Resource Fig. 1), with the smallest range being 0.81 km^2 (*Eudyptes robustus*) and the largest being 135,395 km^2 (*Aptenodytes forsteri*). Thirteen species have ranges between 0.81 and 40,000 km^2. Individual species ranges can span a large portion of the Antarctic coast (*Pygoscelis adeliae*) while others are restricted to a small island (*E. robustus*).

Table 2 Summary of population and range size Spearman Rank tests and IUCN Red List conservation status Kruskal–Wallis test (df = 3, denoted with †) for protected area coverage by IUCN Protected Areas Categories System Ib-VI (IUCN), IUCN "Not Reported" and "Not Categorized" Protected Areas (NC), and Antarctic Specially Protected Areas (ASPA). Same tests done for Myer's biodiversity hotspots. Coverage represents the percent of penguin ranges covered by a biodiversity hotspot, and Protection represents the total percent protection of these hotspots

	Predictor	Response	r_s	*p*
Protected Area Coverage	Range size	Total	0.65	**0.004***
		IUCN	0.62	**0.007***
		NC	0.46	0.05
		ASPA	0.67	**0.002***
	Population	Total	0.30	0.22
		IUCN	0.46	0.05
		NC	0.21	0.40
		ASPA	0.71	**0.001***
	Conservation status†	Total	$\chi^2 = 1.19$	0.76
		IUCN	$\chi^2 = 3.46$	0.33
		NC	$\chi^2 = 0.91$	0.52
		ASPA	$\chi^2 = 7.09$	0.07
Biodiversity Hotspots	Range size	Coverage	0.09	0.73
		Protection	0.08	0.74
	Population	Coverage	−0.30	0.22
		Protection	−0.32	0.19
	Conservation status†	Coverage	$\chi^2 = 1.10$	0.78
		Protection	$\chi^2 = 1.34$	0.72

*Significant *p* value

†Kruskal–Wallis test

Protected area coverage

All penguin species are protected to some degree (Table 1, Fig. 2; see Figs. 2 and 3 in Online Resource for maps of PAs) by at least one PA (Online Resource Table 2). Total protection based on species range covered by any type of PA varies from 0.16% (*Aptenodytes forsteri*) to 100% of a species range. For seven species, total protection is greater than 50%, and three of these seven species are fully protected by IUCN and NC PAs (*E. robustus, Eudyptes schlegeli,* and *S. mendiculus*; Table 1). For 14 species, IUCN protection is less than 40%, while NC PAs cover 14 species by less than 31% (Table 1, Fig. 2). All Antarctic species are covered to some degree by an ASPA PA, albeit a very small percentage of their range. Additionally, some areas are protected simultaneously by IUCN and NC (Online Resource Table 3). For example, *Eudyptes chrysocome* range is 22.83, 16.95, and 0.07% protected by the IUCN, NC, and ASPA, respectively. However, the total combined protection is 28.01%, indicating an overlap of 15.54%.

Protected area coverage is non-normally distributed across species. Spearman's rank tests revealed that there is a slightly significant relationship between total, IUCN, and ASPA PA coverage and range size (Table 2). Population size and conservation status have non-significant relationships with PA coverage, except for a significant correlation between ASPA protection and population (Table 2).

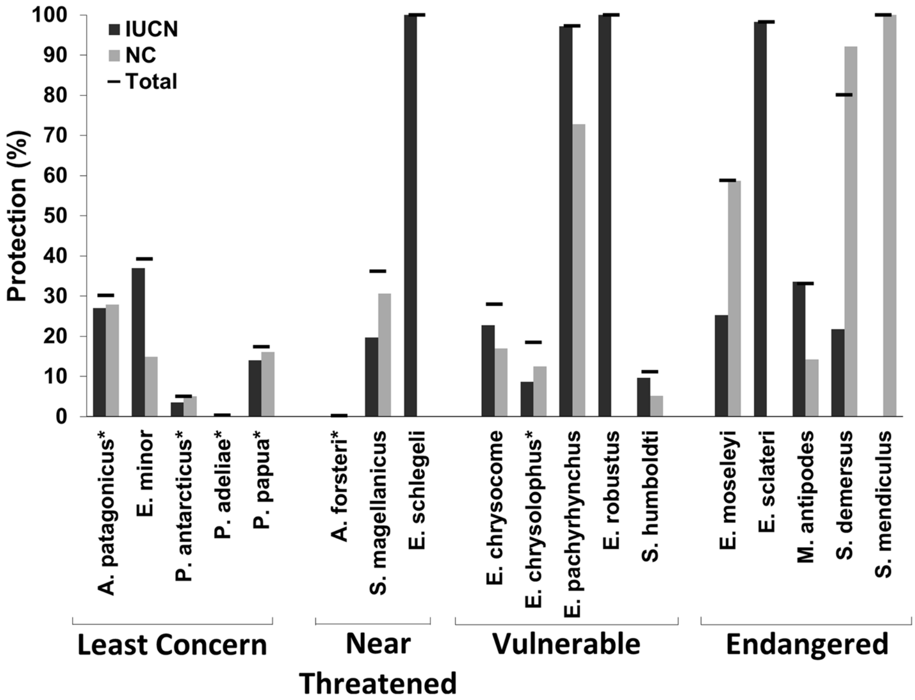

Fig. 2 Percent of occupancy area coverage by IUCN Protected Areas Categories System Ib-VI (IUCN, black bar) and IUCN "Not Reported" and "Not Categorized" (NC, grey bar) protected areas for all penguin species. Total, non-overlapping protected area percent coverage is indicated by the black horizontal line. Antarctic and sub-Antarctic species indicated by *. Species are categorized by IUCN Red List conservation status

Additionally, conservation status is not significantly influenced by range size (Kruskal–Wallis Chi squared = 4.44, df = 3, p value = 0.22) or population (Kruskal–Wallis Chi squared = 7.29, df = 3, p value = 0.06). However, Endangered penguins have smaller range sizes and population sizes (Online Resource Fig. 4). Vulnerable and Endangered species are, in total, more protected than Least Concern and Near Threatened species. Vulnerable species are most protected by IUCN PAs compared with all other conservation statuses, while NC protection remains similar between status levels. Compared with IUCN PAs, NC PAs cover slightly more of total global penguin range.

Hotspots of species richness and endemism

Our analyses identify seven global hotspots of penguin biodiversity where four or five penguin species breed, concentrated on the sub-Antarctic islands, southern tip of South America, and Antarctic Peninsula (Fig. 3a–c, Online Resource Table 4). All hotspots are protected to some degree, and three are fully protected by IUCN and NC PAs. Furthermore, Macquarie Island is the only penguin hotspot that is simultaneously a Myers' hotspot. Approximately 6.1% of total penguin range falls within a Myers' hotspot, and 10.4% of that area is protected. Out of the 13 species whose ranges fall within a Myers' hotspot, six overlap with a hotspot by more than 60%. The remaining five species ranges do not

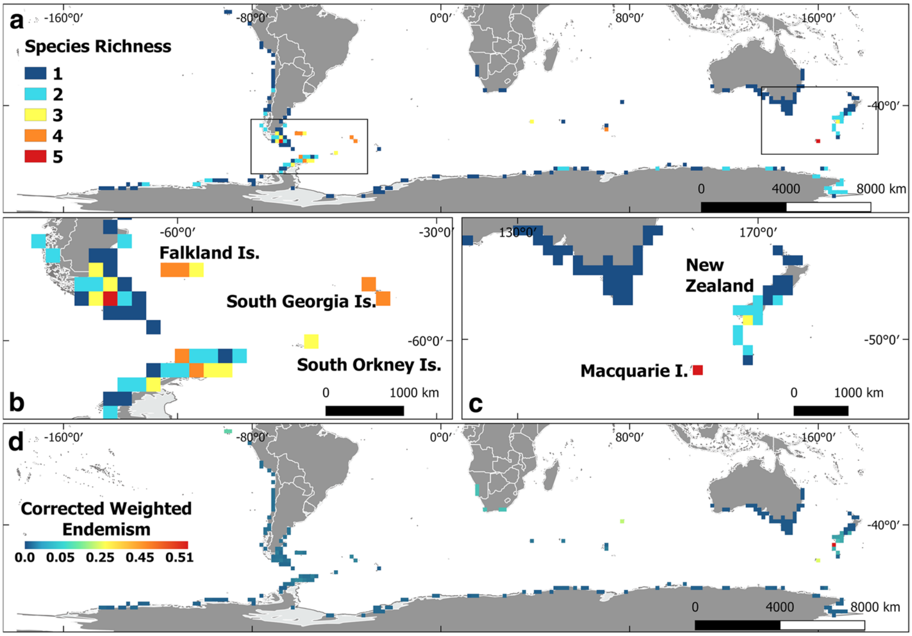

Fig. 3 Map of **a** global penguin species richness, sub-sectioned by regions including **b** southern South America and the Antarctic Peninsula and **c** Australia and New Zealand. Species richness legend applicable for panels **a**–**c**, and colours represent the number of species per 1° grid cell. Map of **d** global penguin corrected weighted endemism ranges from 0 to 0.51 (1 being the highest possible) per 1 degree grid cell. All maps are projected using the World Geodetic System 1984. Basemap from Natural Earth (http://www.naturalearthdata.com)

overlap with a Myers' hotspot. Overall, range size and population size are not significantly related with Myers' hotspot overlap and protection (Table 2).

Globally, CWE ranges from 0.0 to 0.51 (Fig. 3d). Snares Island has the highest CWE of 0.51. Macquarie, Amsterdam, and St. Paul Island have a CWE greater than 0.20, while South Africa, Galapagos Islands, and parts of New Zealand have CWE values ranging from 0.08 to 0.11 (Fig. 3d).In general, penguins have a relatively low CWE.

Discussion

Our study provides the first comprehensive global assessment investigating the relationships between the terrestrial distribution of the world's penguin species and existing PAs. Only 16.80% of the total global penguin range is protected by IUCN, NC, and ASPA PAs combined, and coverage is extremely variable and unpredictable among species, with no standardisation based on conservation status or population size. In addition, penguins generally breed in isolated and endemic populations (Borboroglu and Boersma 2013), resulting in few hotspot areas. It is more common for PAs to be implemented to protect hotspots of biodiversity than to protect isolated populations of one species. Lack of protection is likely to increase species risk of decline under environmental or population changes (Isik 2011; Pimm et al. 2014). Previous analyses of the irreplaceability and vulnerability of penguins (Borboroglu and Boersma 2013; Trathan et al. 2014; Ropert-coudert et al. 2019), combined with our findings, highlight our concerns about the generality and inadequate coverage of global PAs for penguins and support our advocacy for improved prioritization of sites and species. In a rapidly changing world, the identification of such biodiversity patterns will allow evidence-based predictions about the magnitude and impact of anthropogenic threats on species, to potentially influence decisions about environmental management. Therefore, our study closes a major gap in the knowledge of these global interactions experienced by penguins, one of the most charismatic groups of vertebrates on Earth.

Protection efficiency: PAs, hotspots, and 'coldspots'

PAs ensure the persistence of nature by primarily limiting the effects of humans on species and habitats. However, simultaneous management by more than one organization or categorization as different types of PAs highlights the overall mismanagement and non-collaborative designation processes. For example, the Galápagos Islands are classified as a UNESCO World Heritage site, a UNESCO-MAB Biosphere Reserve, a Ramsar site, and an IUCN national park, each of which has different prioritization strategies, goals, and management objectives, resulting in conflicting category rankings and overall protection methods. In theory, a site with multiple protection designations (typically representing additional organizations and stakeholders) could be beneficial for increasing effort, sharing responsibility, or multiplying the types of conservation efforts or organisms protected. It is typical for overlap to occur between national designations and international designations, as seen on the Galápagos Islands. This multiple classification emphasizes the ecological importance of these type of sites on a more local and global scale simultaneously (Deguignet et al. 2017). However, conflicts such as uneven and ineffective use of resources or logistical problems can arise that detracts from the effectiveness of management efforts (Iojă et al. 2010; Deguignet et al. 2017). Understanding the overall coverage of PAs and the overlap between classifications can be used to assess PA effectiveness and the disparity (both positive and negative) between classification and management now and in the future.

Areas and species can also be protected at national scale but not be considered within the WDPA database. For example, the Falkland Islands are governmentally protected but according to Protected Planet, only 61 km^2 of land area is IUCN protected (IUCN and UNEP 2018). A subsequent analysis including and differentiating areas that are locally or nationally protected under different schemes (along with an analysis of effectiveness) will support the global-scale overview presented here.

Conservation focuses on protecting areas that support the largest number of species with the smallest, most threatened populations (Eken et al. 2004; Brooks et al. 2006; Akçakaya et al. 2007; Dirzo et al. 2014). This is especially true for penguins—their populations are generally small with relatively small breeding areas confined to coastal zones. We identified areas of high penguin endemism (CWE, Fig. 3d) that contain species of small ranges which inhabit few other areas. This measure also quantifies areas that have both high endemism and species richness. Loss of even a few populations could be potentially detrimental to entire species as a whole. Additionally, the abundance of areas supporting single species of penguins (as opposed to only seven hotspots of four or five species) and the protection of these 'coldspots' may be preferable if that species is endemic (Orme et al. 2005) or declining in population (Geldmann et al. 2013). For penguins, rarity is a critical parameter to take into account when developing conservation planning. Rarity frequently translates into not only naturally small populations or range sizes (Lennon et al. 2003) but a combination of both (Mace et al. 2008). Any significant population loss could result in the eventual extinction of the whole species (Borboroglu and Boersma 2013; Ropert-coudert et al. 2019). The contradiction between species richness and endemism makes it difficult to determine which penguin species and areas to protect in order to simultaneously maintain genetic, species, and ecosystem diversity.

Future protection of penguins

The geographic data for penguin terrestrial areas used within this study is comprehensive and inclusive of known breeding areas. However, due to the limitations of using the GBIF database (including the ambiguity of local, vagrant, or unusual occurrences), areas may have been included in these analyses that are outside of normal breeding areas. Arguably, while this may inflate the geographic range for some species, the fact that their population persistence depends on these areas is a critical feature that should not be ignored. As a result of progressing and increasingly destructive anthropogenic environmental change, these areas may prove key for the occupation of penguins, which may lead them to be considered for protection in the near future.

As a whole, sites for conservation should be prioritized following the identification of vulnerable and irreplaceable ecosystems and species. However, in practice, prioritization tends to be (primarily) geographically or taxonomically designated, with no clear systematic connection (Rodrigues et al. 2004; Bertzky et al. 2012). Furthermore, protection is focused either proactively or reactively, depending on management objectives (Ropert-coudert et al. 2019). An area can be prioritized in order to prevent future biodiversity loss or repair loss that has already occurred. This is the case for penguins. Existing PAs often do not include species for which conservation is needed the most (Eken et al. 2004). Due to the majority of penguin species being highly threatened, having small ranges and population sizes, or being endemic to small regions, we propose a combination of both proactive and reactive conservation strategies (similarly suggested in Ropert-coudert et al. (2019)). Additionally, the effectiveness of protection should be considered for species experiencing threats or large population declines, in addition to biodiversity hotspots where multiple penguin species breed (specifically the Falkland Islands, Tierra del Fuego, and Southern New Zealand).

Finally, additional assessments of the effectiveness of marine PAs at protecting penguin marine foraging areas and prey are required for the global conservation of all areas vital to penguin survival. Penguins are primarily marine animals and spend most of their time at sea. There is currently no assessment of global-scale marine protection for penguins, although there is ongoing research regarding the threats faced while foraging (Ropert-coudert et al. 2019). This critical habitat should be equally, if not more, protected than their breeding sites.

Conclusion

Over the past three decades, the increasing global biodiversity crises arising as a result of human activities has promoted exponential growth in the development of ecologically- and evolutionary-based conservation approaches (Ferrière et al. 2004; Höglund 2009). These methods rely primarily on PAs to maintain and increase biodiversity and population by promoting processes such as migration and proliferation (e.g., improving habitat connectivity, reducing fragmentation, limiting poaching) (Thomas and Gillingham 2015). However, they are generally failing to protect key species (Gaston 2003). From our findings, we suggest future research should focus on determining those key penguin species that require more protection based upon their rarity. We also suggest protection requirements and conservation needs for each individual species and population sustainability within each PA should be determined. Management and policy should be assessed to distinguish between effective and non-effective PAs, so that future evidence-based policy, including the global promotion of the IUCN category system, can be implemented.

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