



Do ocean currents shape patterns of penguin hybridization?

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Abstract

Asymmetrical hybridization and gene flow can result from biotic factors, such as demographic shifts, behavioral differences, or genetic incompatibilities, as well as abiotic factors, such as prevailing winds or oceans currents. Although birds generally circumvent these abiotic influences due to their high mobility, penguins may represent an exception, as ocean currents can constrain their dispersal. In this study, I investigated whether ocean currents indeed lead to asymmetrical hybridization patterns in penguins. I compiled an overview of known penguin hybrids and examined whether these hybridization events aligned with the prevailing ocean currents. Most instances of penguin hybridization were linked to numerical imbalances at the breeding colonies—often involving vagrant individuals—suggesting that limited mate choice is the primary driver of hybridization between penguin species. Assessing the role of ocean currents in these events was challenging due to uncertainties about the origin of vagrant individuals or cases where the hybridizing species shared the same breeding location. Nevertheless, ocean currents do appear to play an important role in penguin hybridization dynamics. In four instances, I was able to infer the most probable origin of vagrant individuals, showing that hybridization patterns were generally consistent with the prevailing ocean currents. Overall, hybridization in penguins is thus shaped by a combination of abiotic (ocean currents) and biotic factors (numerical imbalances at breeding colonies).

Keywords Genetics · Interbreeding · Introgression · Hubb’s principle · Mate choice · Sphenisciformes

Introduction

Between 10 and 20% of bird species have been reported to have hybridized in the wild (Ottenburghs 2023). When hybrid offspring are fertile and backcross with one of the parental species, genetic material can introgress from one species into the other (Rheindt and Edwards 2011; Ottenburghs et al. 2017). Introgression is often biased toward one of the hybridizing species due to demographic factors (e.g., numerical imbalance in potential partners; Baker 1996; McCracken et al. 2013), behavioral differences (e.g., female choice; Peters et al. 2017; Lamichhaney et al. 2020), or genetic constraints (e.g., Haldane’s Rule; Ottenburghs 2022). However, abiotic factors can also play a role in the asymmetrical flow of genetic material. For example, wind

patterns have been shown to influence the direction of gene flow between certain tree species (Kling and Ackerly 2021) and ocean currents have shaped population genetic patterns in some aquatic organisms (White et al. 2010). Asymmetrical hybridization and introgression can thus be the outcome of the interplay between biotic and abiotic factors.

In general, abiotic factors do not markedly influence hybridization and introgression in birds, because most avian species are highly mobile and can actively avoid adverse weather conditions. A notable exception might concern penguins because the movement patterns of these flightless birds are partly shaped by ocean currents. Indeed, genomic analyses of extant as well as recently extinct penguin taxa revealed that their diversification was strongly influenced by the onset of the Antarctic Circumpolar Current (Cole et al. 2022). Moreover, patterns of past introgression between different penguin species are closely aligned with the prevailing ocean currents around Antarctica (Vianna et al. 2020; Cole et al. 2022). For example, gene flow between crested penguins (genus *Eudyptes*) followed the clockwise direction of the Antarctic Circumpolar Current (Vianna et al. 2020). Given that most hybridization events in penguins seem to

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involve vagrant individuals ending up in colonies of another species (Morrison and Sagar 2014), it is likely that ocean currents impact hybridization patterns in penguins.

In this study, I assessed whether oceanic currents do indeed result in asymmetrical hybridization patterns across penguin genera. First, I made an overview of known records of penguin hybridization, taking into account the type of supporting evidence (i.e., observations, morphological descriptions, or genetic analyses; following Ottenburghs 2021) and making a distinction between reports of putative hybrid individuals and observations of mixed pairs at breeding colonies (Ottenburghs and Nisbet 2025). For the sake of completeness, I have also included captive penguin hybrids in this overview. When possible, I deduced the most likely origin of the vagrant individuals and checked whether their arrival aligns with ocean currents.

Reliable records of penguin hybrids

Extant penguin species (order Sphenisciformes) are divided over six genera, of which two are monotypic (*Megadyptes* and *Eudyptula*). No wild hybrids have been reported in the genera *Aptenodytes*, *Megadyptes*, *Pygoscelis*, and *Eudyptula*. Most hybrid records in penguins have occurred in the genus *Eudyptes*, and one hybrid combination has been documented in the genus *Spheniscus* (Fig. 1, Table 1). Detailed descriptions of these hybrid records will be provided in the following sections.

Captive hybrids between Adelie Penguin (*Pygoscelis adeliae*) and Gentoo Penguin (*Pygoscelis papua*) were housed in St. Louis Zoo, USA (International Zoo Yearbook 1968). In addition, several studies have reported gene

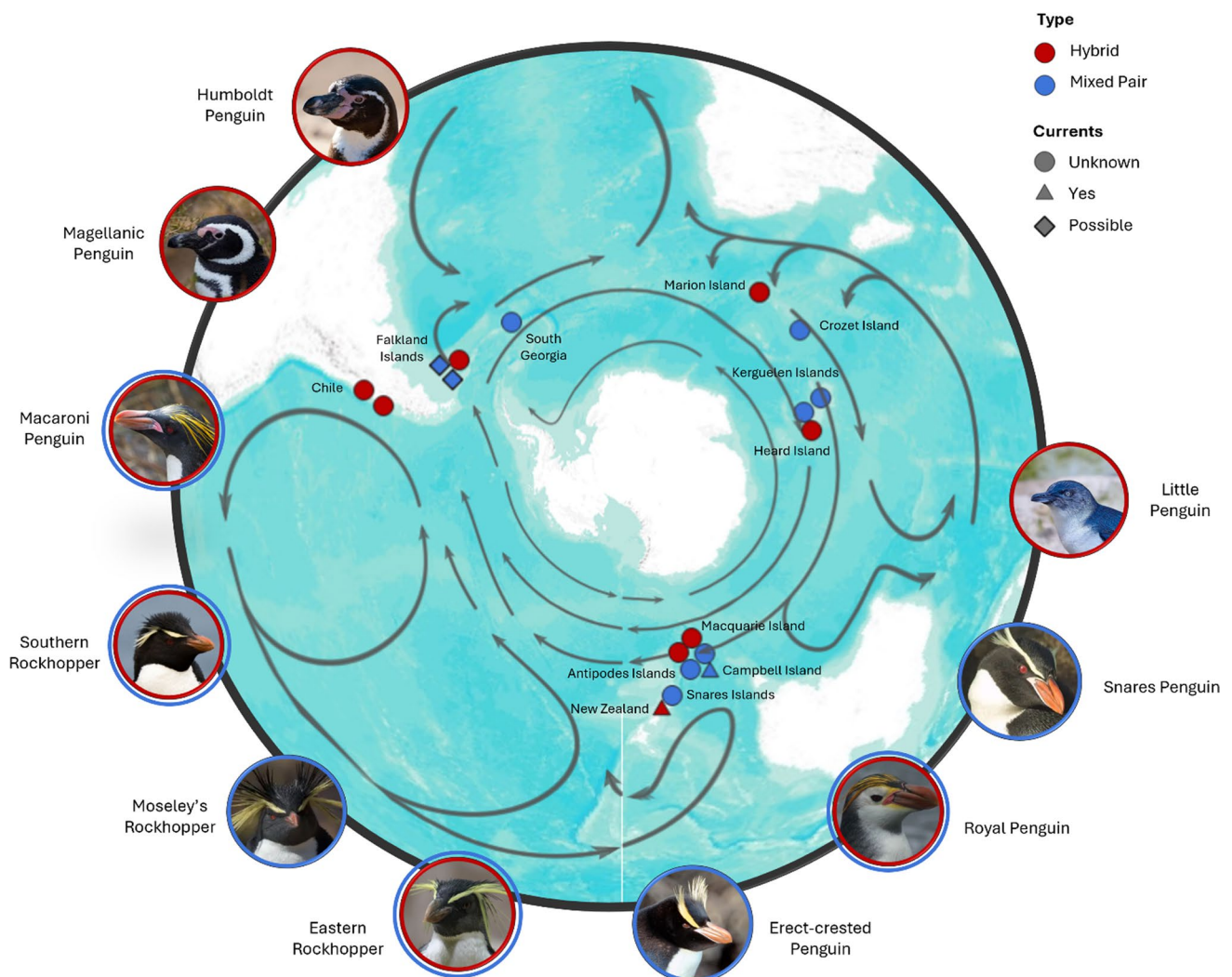


Fig. 1 Overview of hybrid penguin records—mixed pairs (blue) and putative hybrid individuals (red)—in relation to prevailing ocean currents around Antarctica. Pictures around the map show the hybridiz-

ing penguin species (image credits and source of ocean currents can be found in the Appendix). More details about the mixed pairs and hybrids can be found in Table 1

Table 1 Overview of hybrids and mixed pairs between different penguin species in the wild. Locations, where potential interbreeding was reported, are divided into three regions: South America (SA), Indian Ocean (IO), and New Zealand (NZ). For each case, I have provided the type of observation (hybrid or mixed pair), the supporting evidence (observation, morphology or genetics), and the associated sources. Based on the breeding distribution of both species, I have inferred whether the hybridization event could be explained by the prevailing ocean currents

Species1	Species2	Location	Type	Evidence	Currents?	Source
Little Penguin <i>Eudyptula minor</i> (subsp.)		Australia/New Zealand (NZ)	Hybrid	Genetics	Yes	Grosser et al. (2015)
Humboldt Penguin, <i>Spheniscus humboldti</i>	Magellanic Penguin, <i>Spheniscus magellanicus</i>	Southern Chile (SA), Chile/Argentina (SA)	Hybrid, Hybrid	Genetics, Genetics	Unknown, Unknown	Simeone et al. (2009); Hibbets et al. (2020)
Macaroni Penguin, <i>Eudyptes chrysolophus</i>	Royal Penguin, <i>Eudyptes schlegeli</i>	Several locations (NZ)	Mixed pair ^a	Observation	Unknown	References in Morrison and Sagar (2014)
Southern Rockhopper Penguin, <i>Eudyptes [c.] chrysocome</i>	Moseley's Rockhopper Penguin, <i>Eudyptes moseleyi</i>	Falkland Islands (SA)	Mixed pair	Observation	Possible ^b	Crofts and Robson (2015)
Southern Rockhopper Penguin, <i>Eudyptes [c.] chrysocome</i>	Erect-crested Penguin, <i>Eudyptes sclateri</i>	Falkland Islands (SA)	Mixed pair	Observation	Possible ^b	Napier (1968)
Southern Rockhopper Penguin, <i>Eudyptes [c.] chrysocome</i>	Macaroni Penguin, <i>Eudyptes chrysolophus</i>	Falkland Islands (SA)	Hybrid	Observation	Unknown	White and Clausen (2002)
Eastern Rockhopper Penguin, <i>Eudyptes [c.] filholi</i>	Royal Penguin, <i>Eudyptes schlegeli</i>	Macquarie Island (NZ), Macquarie Island (NZ), Campbell Island (NZ)	Hybrid, Hybrid, Mixed pair	Morphology, Observation, Observation	Unknown, Unknown, Yes	Simpson (1985); Hull and Wiltshire (1990); References in Morrison and Sagar (2014)
Eastern Rockhopper Penguin, <i>Eudyptes [c.] filholi</i>	Macaroni Penguin, <i>Eudyptes chrysolophus</i>	Heard Island (IO), Marion Island (IO), Campbell Island (NZ)	Hybrid, Hybrid, Mixed pair	Morphology, Morphology, Observation	Unknown, Unknown, Unknown	Woehler and Gilbert (1990); Woehler and Gilbert (1990); References in Morrison and Sagar (2014)
Eastern Rockhopper Penguin, <i>Eudyptes [c.] filholi</i>	Erect-crested Penguin, <i>Eudyptes sclateri</i>	Campbell Island (NZ), Antipodes Islands (NZ)	Mixed pair, Mixed pair	Observation, Observation	Unknown, Unknown	References in Morrison and Sagar (2014); References in Morrison and Sagar (2014)
Snares Penguin, <i>Eudyptes robustus</i>	Erect-crested Penguin, <i>Eudyptes sclateri</i>	Snares Islands (NZ)	Mixed pair	Observation	Unknown	Morrison and Sagar (2014)

Records of captive hybrids include Adelie Penguin (*Pygoscelis adeliae*) x Gentoo Penguin (*Pygoscelis papua*), Magellanic Penguin (*Spheniscus magellanicus*) x African Penguin (*Spheniscus demersus*), and Humboldt Penguin (*Spheniscus humboldti*) x African Penguin (*Spheniscus demersus*)

^aUncertain whether it concerns hybrids or a rare phenotype (see main text for further explanation)

^bAssuming dispersal from the closest colony

flow between different Gentoo Penguin populations that might represent multiple species (Levy et al. 2016; Vianna et al. 2017; Clucas et al. 2018; Cole et al. 2022).

Although the genus *Eudyptula* currently holds only one species (the Little Penguin, *Eudyptula minor*), genetic analyses point to two cryptic lineages, corresponding to Australia (*E. m. novaehollandiae*) and New Zealand (*E. m. minor*), that might represent distinct species (Grosser et al. 2015, 2017; Cole et al. 2019b, 2022). Grosser et al. (2015) found that gene flow occurred primarily from the Australian into the New Zealand lineage, following the prevailing winds and ocean currents. Moreover, genomic analyses detected recent introgression within the New Zealand lineage (Cole et al. 2022).

In the genus *Spheniscus*, wild hybrids between Humboldt Penguin (*Spheniscus humboldti*) and Magellanic Penguin (*Spheniscus magellanicus*) have been documented. In southern Chile, Simeone et al. (2009) observed one mixed pair attending chicks and two adults of intermediate color pattern, one of which tended a chick at a nest. Genetic analyses confirmed the occurrence of one hybrid individual. Another genetic study reported evidence for recent introgression in four out of six putative hybrids (Hibbets et al. 2020). The *Handbook of Avian Hybrids of the World* mentions potential wild hybrids between Magellanic Penguin and African Penguin (*Spheniscus demersus*) based on the occurrence of double chest bands in some individuals, but these claims could not be verified (McCarthy 2006). Finally, captive hybrids between Magellanic Penguin and African Penguin (International Zoo Yearbook 1998), and between Humboldt Penguin and African Penguin (Modesto et al. 2018) are known from several zoos.

Several mixed pairs and putative hybrids have been reported in the genus *Eudyptes* (Fig. 1). However, most cases are based on observations (White and Clausen 2002; Crofts and Robson 2015) or morphological analyses (Simpson 1985; Woehler and Gilbert 1990), requiring genetic confirmation. It is important to note that the number of species within the genus *Eudyptes* differs between taxonomic authorities mainly due to disagreements about the species status of Macaroni/Royal Penguins and the classification of three taxa of Rockhopper Penguins.

Macaroni Penguins (*Eudyptes chrysolophus*) are widely distributed over a circumpolar range whereas Royal Penguins (*Eudyptes schlegeli*) are endemic to Macquarie Island. Royal Penguins, which are characterized by a white-faced phenotype, used to be classified as a subspecies of the Macaroni Penguin, but they have been considered as separate species (Bertelli and Giannini 2005; Ksepka et al. 2006) despite the lack of clear genetic differentiation (Frugone et al. 2018, 2019; Cole et al. 2019a, b, c). Several white-faced penguins have been reported in colonies of Macaroni Penguins (Marchant and Higgins 1990; Morrison and Sagar

2014), but it remains unclear whether these individuals represent rare phenotypes or hybrids between Macaroni Penguin and Royal Penguin (Frugone et al. 2019). Following the IOC World Bird List, I will consider Macaroni Penguin and Royal Penguin as separate species. However, given the uncertainty about the white-faced individuals in Macaroni Penguin colonies, I have included potential mixed pairs with a cautionary note (see Table 1).

Banks et al. (2006) suggested a classification of three distinct species of Rockhopper Penguin, namely Moseley's (or Northern) Rockhopper Penguin (*Eudyptes moseleyi*), Southern Rockhopper Penguin (*Eudyptes chrysocome*) and Eastern Rockhopper Penguin (*Eudyptes filholi*). This classification has been supported by genetic analyses (Frugone et al. 2018; Cole et al. 2019a, b, c), but some authors still consider Southern and Eastern Rockhopper Penguin as a single species with *Eudyptes filholi* as a subspecies of *Eudyptes chrysocome* (Mays et al. 2019). Here, I follow the IOC World Bird List (which recognizes two species—Moseley's and Southern Rockhopper Penguin), but I will discriminate between the three taxa when discussing putative penguin hybrids and mixed pairs (Table 1).

Crofts and Robson (2015) documented a mixed pairing between Southern Rockhopper Penguin and Moseley's Rockhopper Penguin on the eastern Falkland Islands. The pair produced a hybrid chick that did not survive. Moseley's Rockhopper Penguins are vagrants on the Falkland Islands, probably originating from Tristan da Cunha or Gough Island which are located 3800 km northeast from the Falkland Islands. These vagrants might thus have reached the eastern part of the Falkland Islands following the Brazilian ocean current.

Between 1961 and 1965, one Erect-crested Penguin (*Eudyptes sclateri*) has been resident during each breeding season in a colony of Southern Rockhopper Penguins at West Point Island (Falkland Islands). During the last two seasons, it paired with a Southern Rockhopper Penguin but the eggs did not hatch (Napier 1968). Erect-crested Penguins breed on the Bounty and Antipodes Islands (in the New Zealand region) and could have reached the Falkland Islands through the Pacific Ocean, following the Antarctic Circumpolar Current.

White and Clausen (2002) reported observations of at least six apparent hybrids between Southern Rockhopper Penguin and Macaroni Penguin on the Falkland Islands. Because both species are resident breeders on these islands, I could not infer whether it concerned vagrant individuals.

A museum specimen collected in 1957 from Macquarie Island was initially identified as a Snares Crested Penguin (*Eudyptes robustus*). Reexamination of the specimen indicated that it was a hybrid between Eastern Rockhopper Penguin and Royal Penguin (Simpson 1985). More recently, Hull and Wiltshire (1999) reported a possible hybrid Royal

x Eastern Rockhopper Penguin on Macquarie Island. Both species breed on this island, so it was not possible to deduce whether it involved a vagrant individual. However, Morrison and Sagar (2014) mentioned a mixed pair on Campbell Island where Royal Penguins are vagrants, following the sub-Antarctic ocean currents.

Woehler and Gilbert (1990) used morphological measurements of the bill to describe three hybrids between Eastern Rockhopper Penguin and Macaroni Penguin from Heard and Marion Islands. Mixed pairs have also been observed on Campbell Island although breeding was not confirmed (Morrison and Sagar 2014). Since both species breed on these islands, I could not determine whether the individuals were vagrants.

Mixed pairs between Erect-crested Penguin and Eastern Rockhopper Penguins have been reported on Campbell Island and the Antipodes Islands (Morrison and Sagar 2014). However, because both species breed on these islands, it was not possible to infer the potential influence of ocean currents.

Morrison and Sagar (2014) observed a male Snares Crested Penguin breeding with a female Erect-crested Penguin on the Snares Islands (New Zealand region). Erect-crested Penguins are resident breeders on the Bounty and Antipodes Islands and are known vagrants on Snares Island (Marchant and Higgins 1990). Given the complex dynamics of ocean currents between these islands, it is difficult to infer whether particular currents might have driven the Erect-crested Penguin to Snares Island.

Discussion

Most cases of penguin hybridization resulted from a numerical imbalance at the breeding colony, often involving vagrant individuals that are outnumbered by individuals from the resident species (Morrison and Sagar 2014; Crofts and Robson 2015). Despite the possibilities of hybridization due to vagrancy or mixed breeding colonies, hybrid penguins appear to be quite rare, probably because of strong prezygotic barriers that prevent “wrong” mate choice (Pierotti 1987; Uy et al. 2018). For example, differences in vocalizations and head ornamentation used in courtship displays likely prevent hybridization between Moseley’s and Southern Rockhopper Penguins (Jouventin et al. 2006). However, a few cases suggest that some level of intrinsic postzygotic isolation might affect certain penguin hybrids (Price and Bouvier 2002). A mixed pair between Moseley’s and Southern Rockhopper Penguins on the Falkland Islands produced a hybrid chick that did not survive (Crofts and Robson 2015). Similarly, the eggs from a mixed pair of Erect-crested Penguin and Southern Rockhopper Penguin failed to hatch (Napier 1968). Clearly, more research is

needed to disentangle the interplay between prezygotic and postzygotic reproductive barriers in explaining patterns of penguin hybridization.

In general, limited mate choice at breeding colonies seems to be the main mechanism leading to hybridization between penguin species. This mechanism has been reported in other bird groups (Randler 2006), such as Indigo Buntings (*Passerina cyanea*) and Lazuli Bunting (*Passerina amoena*) (Baker 1996), Speckled Teal (*Anas flavirostris*) and Yellow-billed Pintails (*Anas georgica*) (McCracken et al. 2013), and terns in general (Ottenburghs and Nisbet 2025), and follows Hubb’s principle, which states that ‘Great scarcity of one species coupled with the abundance of another often leads to hybridization: the individuals of the sparse species seem to have difficulty in finding their proper mates’ (Hubbs 1955). A scarcity of conspecifics can arise when vagrant penguins are transported to other colonies by the prevailing ocean currents. In most penguin hybridization events, however, the role of ocean currents was difficult to assess (12 out of 16 records, 75%), because of the uncertain origin of vagrant individuals (Marchant and Higgins 1990) or because the hybridizing species breed on same island (Woehler and Gilbert 1990; Hull and Wiltshire 1999; White and Clausen 2002).

Nonetheless, ocean currents do appear to contribute to hybridization dynamics in penguins. When it was possible to infer the most likely origin of vagrant individuals, the pattern of hybridization could generally be explained by the prevailing ocean currents (4 out of 16 records, 25%). Indeed, for several (sub)species combinations, the occurrence of hybridization aligned with the ocean currents, namely recent gene flow between Little Penguin subspecies (Grosser et al. 2015), Southern Rockhopper Penguin x Moseley’s Rockhopper Penguin (Crofts and Robson 2015), Southern Rockhopper Penguin x Erect-crested Penguin (Napier 1968), and Eastern Rockhopper Penguin x Royal Penguin (Morrison and Sagar 2014). The most convincing case involved hybridization between two cryptic lineages of the Little Penguin. Genetic analyses of nuclear markers revealed that genes primarily flow from the Australian into the New Zealand lineage, following the prevailing winds and the ocean currents (Grosser et al. 2015). This example highlights the usefulness of genetic data to infer the origin of hybrid individuals and to test whether hybridization patterns align with oceans currents (Vianna et al. 2020; Cole et al. 2022). More population genetic studies are thus required to confidently link ocean currents to patterns of penguin hybridization.

Prevailing winds and ocean currents can thus be conducive to hybridization, but they might also act as barriers between colonies and species, promoting isolation and potentially leading to speciation. Specifically, the different characteristics of particular ocean regimes, such as sea surface temperature or prey availability, can prevent dispersal

between neighboring breeding areas (Friesen 2015; Munro and Burg 2017). For example, Southern Rockhopper Penguins on both sides of the Subtropical Convergence (where ocean temperatures differ by 10 °C) are genetically distinct in mitochondrial DNA (Jouventin et al. 2006). Additionally, strong upwelling along the southern coast of Australia might prevent dispersal between Little Penguin colonies (Overeem et al. 2008). These examples highlight the complex and context-dependent role of ocean currents, which can either facilitate genetic exchange or reinforce reproductive barriers, ultimately shaping the evolutionary trajectories of marine species (Friesen 2015; Munro and Burg 2017; Lombal et al. 2020).

This complexity becomes even more apparent when comparing Northern and Southern Hemispheres, where the influence of prevailing winds and ocean currents on genetic patterns in seabirds is shaped by different geographic contexts (Lombal et al. 2020). In the Northern Hemisphere, the presence of extensive landmasses disrupts the continuity of oceanic and atmospheric circulation, often limiting the dispersal of seabirds and contributing to genetic structuring among populations (Friesen 2015). In contrast, the Southern Hemisphere is characterized by vast expanses of open ocean and more continuous wind and current systems, which can either facilitate or inhibit dispersal (Munro and Burg 2017). While it is clear that winds and ocean currents shape patterns of gene flow in both hemispheres, the extent to which contrasting geographic configurations—the fragmented oceans of the north versus the open expanses of the south—drive these differences remains insufficiently understood, highlighting a valuable opportunity for further comparative research.

Taken together, hybridization patterns in penguins can be explained by a combination of abiotic (i.e., prevailing ocean currents) and biotic (i.e., numerical imbalance at breeding colonies) factors. It remains to be determined whether similar dynamics influence hybridization in other bird groups, such as terns (Ottenburghs and Nisbet 2025) and long-distance migrants (Leighton et al. 2021), whose movements might also be affected by strong wind and ocean currents.

Appendix

Image credits

Little Penguin: <https://www.goodfon.com/animals/wallpaper-ptitsa-pingvin-goluboi-sinii-bereg.html>.

Erect-crested Penguin: <https://snl.no/hornpingvin>.

Eastern Rockhopper: <https://www.flickr.com/photos/flowcomm/14205224511>.

Southern Rockhopper: https://upload.wikimedia.org/wikipedia/commons/e/ee/Gorfou_sauteur_-_Rockhopper_Penguin.jpg.

Magellanic Penguin: <https://www.flickr.com/photos/anschieber/17328245866>.

Moseley's Rockhopper: <https://animalia.bio/index.php/rockhopper-penguin>.

Humboldt Penguin: <https://www.flickr.com/photos/wwarby/3302583709>.

Royal Penguin: <https://animalia.bio/royal-penguin>.

Snares Penguin: <https://animalia.bio/snares-penguin/1000>.

Macaroni Penguin: <https://www.flickr.com/photos/fernicola/8331027494>.

Ocean currents: https://www.amerigeo.org/datasets/24bfd85e97b042948e6ed4928dc45a8b_0/explore?layer=11&location=-1.425893%2C18.503802%2C1.82.

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Author contributions J.O. conceived the idea, collected and analyzed the data, and wrote the manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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References

- Baker MC (1996) Female buntings from hybridizing populations prefer conspecific males. *Wilson Bull* 108:771–775. <https://doi.org/10.2307/4163756>
- Banks J, Van Buren A, Cherel Y, Whitfield JB (2006) Genetic evidence for three species of rockhopper penguins, *Eudyptes chrysocome*. *Polar Biol* 30:61–67. <https://doi.org/10.1007/s00300-006-0160-3>
- Bertelli S, Giannini NP (2005) A phylogeny of extant penguins (Aves: Sphenisciformes) combining morphology and mitochondrial sequences. *Cladistics* 21:209–239. <https://doi.org/10.1111/j.1096-0031.2005.00065.x>
- Clucas GV, Younger JL, Kao D et al (2018) Comparative population genomics reveals key barriers to dispersal in Southern Ocean

- penguins. *Mol Ecol* 27:4680–4697. <https://doi.org/10.1111/mec.14896>
- Cole TL, Dutoit L, Dussex N et al (2019a) Receding ice drove parallel expansions in Southern Ocean penguins. *Proc Natl Acad Sci*. <https://doi.org/10.1073/pnas.1904048116>
- Cole TL, Ksepka DT, Mitchell KJ et al (2019b) Mitogenomes uncover extinct penguin taxa and reveal island formation as a key driver of speciation. *Mol Biol Evol* 36:784–797. <https://doi.org/10.1093/molbev/msz017>
- Cole TL, Rawlence NJ, Dussex N et al (2019c) Ancient DNA of crested penguins: testing for temporal genetic shifts in the world's most diverse penguin clade. *Mol Phylogenet Evol* 131:72–79. <https://doi.org/10.1016/j.ympev.2018.10.025>
- Cole TL, Zhou C, Fang M et al (2022) Genomic insights into the secondary aquatic transition of penguins. *Nat Commun* 13:1–13. <https://doi.org/10.1038/s41467-022-31508-9>
- Crofts S, Robson BJ (2015) First record of hybridisation between Northern *Eudyptes moseleyi* and Southern Rockhopper Penguins *E. chrysocome*. *Seabird* 28:37–42
- Friesen VL (2015) Speciation in seabirds: why are there so many species...and why aren't there more? *J Ornithol* 156:27–39. <https://doi.org/10.1007/s10336-015-1235-0>
- Frugone MJ, Lowther A, Noll D et al (2018) Contrasting phylogeographic pattern among *Eudyptes* penguins around the Southern Ocean. *Sci Rep* 8:17481. <https://doi.org/10.1038/s41598-018-35975-3>
- Frugone MJ, López ME, Segovia NI et al (2019) More than the eye can see: genomic insights into the drivers of genetic differentiation in Royal/Macaroni penguins across the Southern Ocean. *Mol Phylogenet Evol* 139:106563. <https://doi.org/10.1016/j.ympev.2019.106563>
- Grosser S, Burridge CP, Peucker AJ, Waters JM (2015) Coalescent modelling suggests recent secondary-contact of cryptic penguin species. *PLoS ONE* 10:e0144966. <https://doi.org/10.1371/journal.pone.0144966>
- Grosser S, Scofield RP, Waters JM (2017) Multivariate skeletal analyses support a taxonomic distinction between New Zealand and Australian *Eudyptula* penguins (Sphenisciformes: Spheniscidae). *Emu Austral Ornithol* 117:276–283. <https://doi.org/10.1080/01584197.2017.1315310>
- Hibbets EM, Schumacher KI, Scheppeler HB et al (2020) Genetic evidence of hybridization between Magellanic (*Spheniscus magellanicus*) and Humboldt (*Spheniscus humboldti*) penguins in the wild. *Genetica* 13. <https://doi.org/10.1007/s10709-020-00106-2>
- Hubbs CL (1955) Hybridization between fish species in nature. *Syst Biol* 4:1–20. <https://doi.org/10.2307/sysbio/4.1.1>
- Hull CL, Wiltshire A (1999) An apparent hybrid royal × rockhopper penguin at Macquarie Island. *Aust Bird Watch* 183:95–100
- International Zoo Yearbook (1968) Birds. *Int Zoo Yearb* 8:316–338. <https://doi.org/10.1111/j.1748-1090.1968.tb00496.x>
- International Zoo Yearbook (1998) Birds bred in captivity and multiple generation births 1995/1996. *Int Zoo Yearb* 36:400–484. <https://doi.org/10.1111/j.1748-1090.1998.tb02916.x>
- Jouventin P, Cuthbert RJ, Ottvall R (2006) Genetic isolation and divergence in sexual traits: evidence for the northern rockhopper penguin *Eudyptes moseleyi* being a sibling species. *Mol Ecol* 15:3413–3423. <https://doi.org/10.1111/j.1365-294X.2006.03028.x>
- Kling MM, Ackerly DD (2021) Global wind patterns shape genetic differentiation, asymmetric gene flow, and genetic diversity in trees. *Proc Natl Acad Sci* 118:e2017317118. <https://doi.org/10.1073/pnas.2017317118>
- Ksepka DT, Bertelli S, Giannini NP (2006) The phylogeny of the living and fossil Sphenisciformes (penguins). *Cladistics* 22:412–441. <https://doi.org/10.1111/j.1096-0031.2006.00116.x>
- Lamichhaney S, Han F, Webster MT et al (2020) Female-biased gene flow between two species of Darwin's finches. *Nat Ecol Evol*. <https://doi.org/10.1038/s41559-020-1183-9>
- Leighton GM, Lu LJ, Holop E et al (2021) Sociality and migration predict hybridization across birds. *Proc R Soc b: Biol Sci* 288:20201946. <https://doi.org/10.1098/rspb.2020.1946>
- Levy H, Clucas GV, Rogers AD et al (2016) Population structure and phylogeography of the Gentoo Penguin (*Pygoscelis papua*) across the Scotia Arc. *Ecol Evol* 6:1834–1853. <https://doi.org/10.1002/ece3.1929>
- Lombal AJ, O'dwyer JE, Friesen V et al (2020) Identifying mechanisms of genetic differentiation among populations in vagile species: historical factors dominate genetic differentiation in seabirds. *Biol Rev* 95:625–651. <https://doi.org/10.1111/brv.12580>
- Marchant S, Higgins PJ (1990) Handbook of Australian, New Zealand and Antarctic Birds. Vol. 1, Ratites to ducks; Part A, Ratites to petrels. Oxford University Press, Melbourne
- Mays HL, Oehler DA, Morrison KW et al (2019) Phylogeography, population structure, and species delimitation in rockhopper penguins (*Eudyptes chrysocome* and *Eudyptes moseleyi*). *J Hered* 110:801–817. <https://doi.org/10.1093/jhered/esz051>
- McCarthy E (2006) Handbook of avian hybrids of the world. Oxford University Press, Melbourne
- McCracken KG, Wilson RE, Martin AR (2013) Gene flow and hybridization between numerically imbalanced populations of two duck species on the subantarctic island of South Georgia. *PLoS ONE* 6:e23173. <https://doi.org/10.1371/journal.pone.0082664>
- Modesto P, Biolatti C, Favaro L et al (2018) Molecular genetics unveiled unknown family relationships and hybrids in an ex-situ colony of African Penguins (*Spheniscus demersus*). *J Hered* 109:653–662. <https://doi.org/10.1093/jhered/esy032>
- Morrison KW, Sagar PM (2014) First record of interbreeding between a Snares crested (*Eudyptes robustus*) and erect-crested penguin (*E. sclateri*). *Notornis* 61:109–112
- Munro KJ, Burg TM (2017) A review of historical and contemporary processes affecting population genetic structure of Southern Ocean seabirds. *Emu Austral Ornithol* 117:4–18. <https://doi.org/10.1080/01584197.2016.1271988>
- Napier R (1968) Erect-crested and rockhopper penguins interbreeding in the Falkland Islands. *Br Antarct Surv Bull* 16:71–72
- Ottenburghs J (2021) An evidence-based overview of hybridization in tinamous. *Ornithol Res* 29:113–117. <https://doi.org/10.1007/S43388-021-00049-Y/FIGURES/1>
- Ottenburghs J (2022) Avian introgression patterns are consistent with Haldane's rule. *J Hered* 113:363–370. <https://doi.org/10.1093/jhered/esac005>
- Ottenburghs J (2023) How common is hybridization in birds? *J Ornithol* 164:913–920. <https://doi.org/10.1007/s10336-023-02080-w>
- Ottenburghs J, Nisbet ICT (2025) Hybridization in terns: a review. *Mar Ornithol* 53:83–89
- Ottenburghs J, Kraus R, van Hooft P et al (2017) Avian introgression in the genomic era. *Avian Res* 8:30
- Overeem RL, Peucker AJ, Austin CM et al (2008) Contrasting genetic structuring between colonies of the World's smallest penguin, *Eudyptula minor* (Aves: Spheniscidae). *Conserv Genet* 9:893–905. <https://doi.org/10.1007/s10592-007-9414-z>
- Peters KJ, Myers SA, Dudaniec RY et al (2017) Females drive asymmetrical introgression from rare to common species in Darwin's tree finches. *J Evol Biol* 30:1940–1952. <https://doi.org/10.1111/jeb.13167>
- Pierotti R (1987) Isolating mechanisms in seabirds. *Evolution* 41:559–570. <https://doi.org/10.1111/j.1558-5646.1987.tb05826.x>

- Price T, Bouvier M (2002) The evolution of F1 postzygotic incompatibilities in birds. *Evolution* 56:2083–2089. <https://doi.org/10.1111/j.0014-3820.2002.tb00133.x>
- Randler C (2006) Behavioural and ecological correlates of natural hybridization in birds. *Ibis* 148:459–467. <https://doi.org/10.1111/j.1474-919X.2006.00548.x>
- Rheindt FE, Edwards SV (2011) Genetic Introgression: an Integral but neglected component of speciation in birds. *Auk* 128:620–632. <https://doi.org/10.1525/auk.2011.128.4.620>
- Simeone A, Hiriart-Bertrand L, Reyes-Arriagada R et al (2009) Heterospecific pairing and hybridization between wild Humboldt and Magellanic penguins in southern Chile. *The Condor* 111:544–550. <https://doi.org/10.1525/cond.2009.090083>
- Simpson KNG (1985) A rockhopper x royal penguin hybrid from Macquarie Island. *Aust Bird Watch* 11:35–45. <https://doi.org/10.3316/informit.602236282662734>
- Uy JAC, Irwin DE, Webster MS (2018) Behavioral isolation and incipient speciation in birds. *Annu Rev Ecol Evol Syst* 49:1–24. <https://doi.org/10.1146/annurev-ecolsys-110617-062646>
- Vianna JA, Noll D, Dantas GPM et al (2017) Marked phylogeographic structure of Gentoo penguin reveals an ongoing diversification process along the Southern Ocean. *Mol Phylogenet Evol* 107:486–498. <https://doi.org/10.1016/j.ympev.2016.12.003>
- Vianna JA, Fernandes FAN, Frugone MJ et al (2020) Genome-wide analyses reveal drivers of penguin diversification. *Proc Natl Acad Sci* 117:22303–22310. <https://doi.org/10.1073/pnas.2006659117>
- White R, Clausen A (2002) Rockhopper *Eudyptes chrysocome* chrysocome x Macaroni *E. chrysolophus* penguin hybrids apparently breeding in the Falkland Islands. *Mar Ornithol* 30:40–42
- White C, Selkoe KA, Watson J et al (2010) Ocean currents help explain population genetic structure. *Proc R Soc b: Biol Sci* 277:1685–1694. <https://doi.org/10.1098/rspb.2009.2214>
- Woehler EJ, Gilbert CA (1990) Hybrid Rockhopper-Macaroni penguins, interbreeding and mixed species pairs at Heard and Marion islands. *Emu Austral Ornithol* 90:198–201. <https://doi.org/10.1071/MU9900198>

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