Correspondence

Female-biased stranding in Magellanic penguins

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Magellanic penguins (*Spheniscus magellanicus*) have been reported to become stranded along the coasts of northern Argentina, Uruguay and southern Brazil during the austral winter [1–3]. This location is more than a thousand kilometers distant from their northernmost breeding colony in northern Patagonia. Curiously, females typically outnumber males at stranding sites (approximately three females per male) [2]. To date, no conspicuous sex differences have been reported in their migratory movements [3], although records are lacking during the peak stranding season. Consequently, the reason(s) for the female-biased stranding remain unknown, despite the growing necessity for understanding their behavior outside the breeding season [3]. We recorded at-sea distributions of Magellanic penguins throughout the non-breeding period using animal-borne data loggers and found that females reached more northern areas than males and did not dive as deep during winter (Figure 1). Such sexual differences in spatial domains might be driven by mechanisms related to sexual size dimorphism, such as the avoidance of intraspecific competition for food resources [4], differences in thermal habitat preference [5] or differences in the ability to withstand the northward-flowing ocean circulation [6]. Individual penguins that winter in northern areas are likely to be at greater risk of natural [7] and anthropogenic threats [8], and probably more so in females, as more females than males tend to frequent areas closer to the sites where penguins strand. Our results highlight the importance of understanding the spatial domains of each sex throughout the annual cycle that are associated with different mortality risks.

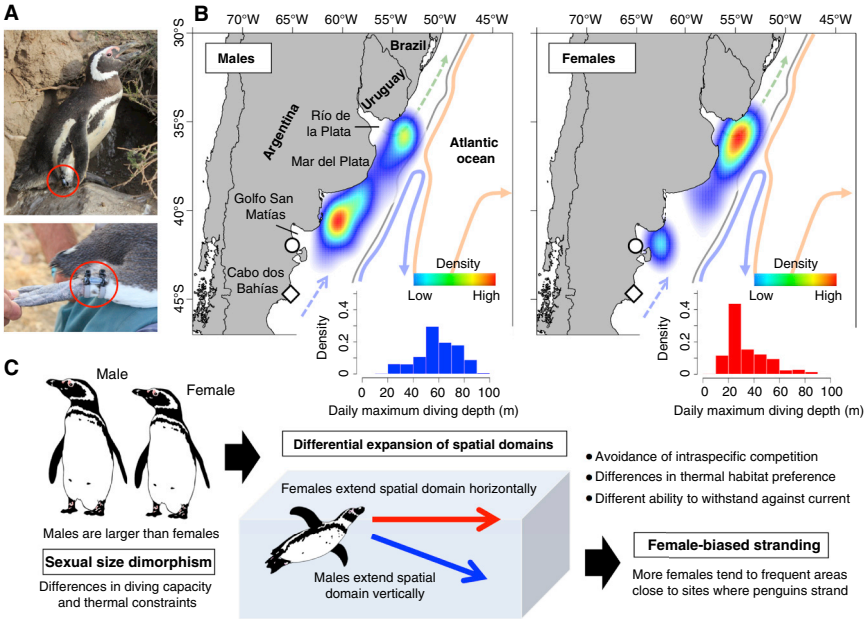

Figure 1. Migratory and wintering behavior of Magellanic penguins.
(A) Attachment of a geolocator to an adult penguin (red circles). (B) Kernel density distributions and histograms of daily maximum diving depths of males and females during the wintering period (May–August). The open diamond indicates the study colony (Cabo dos Bahías), the open circle represents the northernmost breeding colony of Magellanic penguins in the Atlantic (Islote Lobos, 41°S), and the background black line represents 200 m depth-isobath. Schematic diagram of the upper layer circulation of currents in the study region modified from [S1,S2]: the Malvinas/Falkland Current (thick blue arrow), Patagonian Current (dashed blue arrow), Brazil Current (thick orange arrow), and La Plata River plume flowing northward (dashed green arrow), for more detailed surface current velocities during the study period, see Figure S1A. (C) A schematic diagram of key processes for female-biased wintering stranding in Magellanic penguins.

We recorded the migratory and diving behavior of 14 Magellanic penguins (eight males and six females) during the non-breeding period in 2017 using LAT 2500 geolocators (Figure 1A; Supplemental Information). The Magellanic penguins finished breeding in late February, commenced their migration throughout April and returned to the breeding colony between mid-September and mid-October (Table S1). During the wintering period, females predominantly utilized areas to the east of the Río de la Plata Estuary (<36°S), whereas males were mainly concentrated in areas between the north of the Golfo San Matías and Mar del Plata (ca. 38–41°S; Figure 1B). Distances between the colony and the centroids of the wintering distribution ranged from 268 to 1023 km for males and 371 to 1202 km for females (Figure S1A). During winter, males reached comparatively deeper waters than females: 58.6 ± 16.4 m for males and 35.3 ± 16.2 m for females (GLMM, $t = 4.95$; $p < 0.01$; Figure 1B).

The tracking of the Magellanic penguins' movements throughout the entire non-breeding period revealed sex-related differences in their spatial domains (defined as the horizontal and vertical spatial extent) during winter, with males tending to exploit food resources vertically and females horizontally (Figure 1B). Such differences in spatial domains might be caused by a set of non-exclusive mechanisms related to sexual size dimorphism (male Magellanic penguins are heavier and larger than females). First, differences in the spatial domains of the two sexes may reflect niche partitioning, as a consequence of the avoidance of intraspecific competition for food resources [4]. Body size is allometrically correlated with diving capacities, and larger-bodied individuals can dive deeper. Indeed, we found that females utilized shallower waters to a greater extent than males, even when the two sexes were distributed at similar latitudes (Figure S1B). Second,

thermal constraints may drive sexual differences in the spatial domains. Lower water temperatures induce greater heat loss, and insulation is reduced with an increase in diving depth via compression of the feather air layer, resulting in elevated metabolic rate [5]. Thermoregulatory ability is theoretically correlated with body mass, and as penguins spend most of their time at sea during the non-breeding period, the smaller females may preferentially seek out warmer waters at lower latitudes and shallower depths in which to forage. Third, both sexes might use the northward-flowing ocean circulation of the Patagonian Current along the continental shelf (possibly some extension of Malvinas/Falkland Current along the shelf break; Figure 1B) during migration [6], with females possibly drifting more to the north owing to their lower swimming ability. Furthermore, the effect of current is probably more pronounced in females as they typically utilize shallower depths than males (Figure 1B) [9].

Although the sample size was relatively small, our results highlight the size dimorphism-based sexual differences in spatial domain usage during the non-breeding period in Magellanic penguins, and demonstrate that the distribution range of tagged females took them closer than the males to the sites where penguins strand. Several factors might threaten Magellanic penguins along the coasts from northern Argentina to southern Brazil. Although individual penguins that travel northward can exploit the areas of higher primary and secondary productivity provided by the Río de la Plata plume [8], winter oceanographic conditions, for example a larger plume [7], probably reduce their foraging efficiency and disperse prey species. This might necessitate additional energy expenditure by penguins with respect to locating and capturing prey [7] or by migrating farther north [1] and encountering the oligotrophic southward-flowing Brazilian Current, all of which could contribute to a deterioration in body condition. In addition, areas of the Río de la Plata plume front sustain industrial fisheries [8], and petroleum chronic pollution has been a serious concern from southern Brazil through northern Argentina (see more details in the Supplemental Information). These natural and anthropogenic factors likely increase the probability of stranding, and particularly so in females, as more females than males tend to frequent northern areas; this phenomenon presumably relates to the female bias in the stranding of Magellanic penguins (Figure 1C).

Sex-related differences in the spatial domain could theoretically bias the risk of mortality if one of the sexes is more exposed to potential threats of both anthropogenic and natural origin, which would generate a skewed sex ratio of breeding individuals and could consequently affect population viability [10]. Our study accordingly highlights the necessity of gaining a better understanding of the long-term spatial domains of species and populations throughout annual cycles, including any differences between sexes, that are potentially associated with different mortality risks.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures, one figure and one table can be found with this article online at https://doi.org/10.1016/j.cub.2018.11.023.

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AUTHOR CONTRIBUTIONS

T.Y. and K.Y. conceived the study; T.Y., G.B., and F.Q. organized and conducted the fieldwork; T.Y. analyzed the data; and T.Y. and K.Y. drafted the manuscript. All authors discussed the results and commented on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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