



Sex-specific migratory behavior in a marine predator results in higher risks to females

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ABSTRACT: Protecting migratory species requires knowledge of their distributions throughout the year. Spatial or temporal segregation of females and males during part of the annual cycle complicates conservation measures and can lead to sex-biased mortality. Females and males of many seabird species use separate areas during the nonbreeding season, and sex-biased bycatch in fisheries is common. We satellite-tracked 8 female and 8 male post-breeding adult Magellanic penguins *Spheniscus magellanicus*, including 7 pairs, from Punta Tombo, Argentina, during their fall northbound migration. Our results agreed with recent studies from other colonies, and provided more accurate locations than the geolocator tags used in those studies. Females stayed 47 km closer to shore than males. On average, females and males reached similar latitudes from northern Argentina to southern Brazil. Females tended to stay farther north, however, with some males heading south by June. Body size did not influence how far offshore a penguin migrated, when controlling for sex. On average, females left the colony 2 d before their mates, and did not encounter them at sea. The mean distance between mates at sea was more than 350 km. Females are likely exposed to fishing gear and pollution more than males because the females stayed closer to shore and stayed farther north than males. Migratory routes varied among individuals. The large area that penguins use during their nonbreeding season makes protection of the population difficult.

KEY WORDS: Migration · Sexual segregation · Sex-biased mortality · Satellite tracking · *Spheniscus magellanicus* · Magellanic penguin

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1. INTRODUCTION

Migratory species face threats that vary with the habitats they use and the national, provincial, and conservation/management jurisdictions where they occur across the year (Lascelles et al. 2014). Migratory species often move great distances across multiple jurisdictions between breeding and nonbreeding areas, and often range more widely outside the breeding season than when breeding (Thiebot & Dreyfus 2021). The distances moved during migration and the nonbreeding period can pose additional challenges to protecting migratory species compared to more sedentary species for which place-based protections are easier to implement (Blondin et al. 2022). Conser-

vation of migratory species therefore requires information on their distribution and movements outside the breeding season (Stokes et al. 2014, Harrison et al. 2018).

Protecting migratory species can be more challenging when females and males segregate spatially or temporally outside the breeding season. Spatial or temporal segregation of the sexes is common in migratory animals, and has been well studied in ungulates (Ruckstuhl 2007, Wearmouth & Sims 2008), terrestrial birds (Morbey & Ydenberg 2001, Komar et al. 2005), and, increasingly, seabirds (De Felipe et al. 2019, Reyes-González et al. 2021). Failure to account for sexual segregation can lead to biased population estimates and consequent errors in management

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(Bowyer 2004). Sexual segregation increases the area that needs to be protected or extends the time when protection is necessary.

Using separate areas exposes the sexes to distinct threats and prey availability, which can lead to sex-biased mortality (Wearmouth & Sims 2008, Gianuca et al. 2017). Nonbreeding habitats of females are being lost faster than those of males in some Neotropical migratory landbirds such as golden-winged warblers *Vermivora chrysoptera* (Bennett et al. 2019). Ranges of males are more likely to overlap with humans, their infrastructure, or livestock than those of females in some mammals, such as American black bears *Ursus americanus* (Gantchoff et al. 2019). Females of several species of freshwater turtles were killed on roads more often than males, as the females nested along road edges (Aresco 2005). Fisheries bycatch of seabirds, a major threat for many species, was sex-biased in 65% of 123 fisheries sampled globally, apparently due to spatial segregation of the sexes (Gianuca et al. 2017). In albatrosses and petrels killed in longline fisheries, sex biases were found in about two-thirds of fisheries studied, also attributed to sexual segregation at sea (Bugoni et al. 2011). In addition to increased bycatch risk (Crawford et al. 2017), foraging in areas of intense fishing effort could lead to lower prey availability due to prey depletion (Sherley et al. 2018, Campbell et al. 2019) or to increased access to fisheries discards (Beck et al. 2021). Sexual segregation at sea also increases the risk of sex-biased mortality from toxic algal blooms, oil slicks, and other pollution (Phillips et al. 2011, Pichegru et al. 2013, Beck et al. 2023).

Sexual size dimorphism, because of size-dependent locomotor abilities, is frequently suggested as an underlying reason for spatial segregation of the sexes during migration (Phillips et al. 2004, Wearmouth & Sims 2008, Yamamoto et al. 2019). Within a seabird species, larger and heavier individuals can dive deeper than smaller and lighter individuals (Walker & Boersma 2003, Ratcliffe et al. 2013). Birds with longer wings fly more efficiently than birds with shorter wings (Winkler & Leisler 1992). In penguins, larger species swim faster with minimal energy expenditure than smaller species (Sato et al. 2010), and species with longer wings dive deeper than species with shorter wings (Haidr 2023).

Thermoregulatory abilities may also be size-dependent, leading individuals of each sex to seek separate thermal habitats (Magory Cohen et al. 2021). Additional reasons for size to influence space use include competitive exclusion of one sex from productive areas by the other sex, size-mediated

predation risk, and sex-specific targeting of prey species with separate distributions (Wearmouth & Sims 2008).

Sexual segregation outside the breeding season may not be related to sexual size dimorphism. In many species of migratory birds, including seabirds, males arrive before females at the breeding locations (Boersma et al. 1990, Morbey & Ydenberg 2001, De Felipe et al. 2019). Energetic needs of the sexes may depend on sex-specific breeding roles and investment (Wearmouth & Sims 2008).

Recent studies suggest that breeding adult Magellanic penguins *Spheniscus magellanicus* in Argentina segregate by sex during migration and winter, but details vary among studies. Females stayed closer to shore (Barrionuevo et al. 2020) or dove less deeply (Yamamoto et al. 2019) than males. Yamamoto et al. (2019) and Dodino et al. (2021) found that females migrated farther north than males. Barrionuevo et al. (2020), conversely, found that females and males migrated to similar latitudes, but total path lengths of females were greater than those of males.

Mortality at sea during the winter is higher for females than for males in Magellanic penguins (Vanstreels et al. 2013, Marques et al. 2018, Gownaris & Boersma 2019). Magellanic penguins are captured in fishing gear in the wintering area (Cardoso et al. 2011, Fogliarini et al. 2019) and encounter oil pollution during migration and winter (Gandini et al. 1994, García Borboroglu et al. 2006, Wagner et al. 2023). Females are more likely than males to be caught in some fisheries (Fogliarini et al. 2019) and are more likely to be stranded on beaches (Vanstreels et al. 2013). Oceanographic conditions, including the Rio de la Plata river plume, in the nonbreeding area affect overwinter survival and breeding in the following season. A strong Rio de la Plata plume decreases survival of juveniles and adult females (Clark-Wolf et al. 2023). The surviving females return to the colony for breeding later and in worse body condition than when the plume is weak (Rebstock & Boersma 2018).

We tracked the fall migration of breeding adult female and male Magellanic penguins using satellite transmitters from the large but declining breeding colony at Punta Tombo, Argentina (Gownaris & Boersma 2019, Clark-Wolf et al. 2023). Our main objective was to identify important areas at sea for each sex during fall northbound migration, at a much finer spatial scale than is possible with geolocator tags. This information is crucial to effective conservation of the species outside the breeding season. In addition, we tested whether females stay closer to shore and go farther north than males during fall

migration, previously reported patterns that would expose females to more threats at sea than males. We also tested the role of size dimorphism in sex-specific distributions during fall migration.

Finally, we tracked pairs to find out if mates leave the colony together and stay together at sea during fall migration, as previously reported in some species with biparental care and long-lasting pair bonds, such as swans, geese, and cranes (Black 2001, Alonso et al. 2004). Migratory seabirds, including Magellanic penguins, typically have long-lasting pair bonds (Bried & Jouventin 2002, Boersma et al. 2013, Wagner et al. 2022), but few have extended parental care outside of breeding colonies (Burger 1980, Boersma et al. 2017). Biparental care is necessary to raise young in most seabird species (Bried & Jouventin 2002), and synchronization of arrival and breeding behavior increases breeding success (Fayet et al. 2017).

2. MATERIALS AND METHODS

2.1. Study area and species

We did fieldwork at the large breeding colony at Punta Tombo, Argentina (44° 03' S, 65° 13' W), where we have studied penguins since 1982. Males return to breed in September and early October, and females arrive several days to a few weeks later. Females lay 2 eggs, generally in October, and mates take turns incubating. Chicks hatch in mid-November to early December, and both parents brood, guard, and feed the chicks (Boersma et al. 1990, 2013, Wagner & Boersma 2019). Chicks fledge (leave the colony to spend the winter at sea) in mid-January through February (Boersma et al. 2013, Cappello & Boersma 2021). After their chicks fledge, adults take a long foraging trip to regain weight before they molt (Boersma et al. 2013). They remain on land for 2–3 wk while molting, replacing all feathers simultaneously, then begin their migration to northern Argentina, Uruguay, and southern Brazil, typically in April (Stokes et al. 1998, Boersma et al. 2013). Outside of the breeding season, Magellanic penguins are not constrained to return to land.

2.2. Tag attachment and location data smoothing

We tracked 16 adult post-breeding penguins (8 females and 8 males), including 7 presumed breeding pairs. We sexed penguins by bill measurements (Boersma et al. 2013). We used discriminant functions reviewed, evaluated, and adjusted by Vanstreels et

al. (2011) to test our sex classifications. All of our classifications agreed with the classifications of 2 functions based on bill depth and bill length, which classified females correctly 100% of the time (Vanstreels et al. 2011). Using 2 adjusted functions, which improved classifications of males to 86% but reduced accuracy for females to 83% (Vanstreels et al. 2011), we classified all penguins except 1 female correctly. However, we sexed that female by cloacal size (Boersma & Davies 1987) between the laying of the 2 eggs in 2015, so we are confident in our classification. We tagged all penguins at nest sites. Breeding adults generally molt in a nest, but not always in the nest in which they bred (G. A. Rebstock & P. D. Boersma pers. obs.).

We did not follow penguins throughout the breeding season due to COVID-19 restrictions. We saw 3 pairs together with chicks several times in January or February, so we are certain they bred together in this season. We saw 4 pairs together only in April, so we are less certain that they bred together. However, their behavior towards each other (e.g. sitting side by side in or next to the nest, allopreening) indicated they were likely mates. The pair we tagged in nest H04O moved together between 2 nests in April, giving us more certainty that they were mates. We do not have records of the pairs nesting together in other seasons, but on average, only 50% of pairs reunite the next year, and following the first year of mating together, 71% of pairs divorce (Wagner et al. 2022). The female in one nest left the colony before we could tag her, and the male in another nest did not finish molting in time to receive a tag (Table 1).

All individuals were marked in previous seasons, except 1 male, which we banded in April 2022. One female was marked with a stainless-steel flipper band (Boersma & Rebstock 2010) and a radio-frequency identification (RFID) chip. All other penguins were marked with 2 × 10 mm web tags (Boersma & Rebstock 2010) and 134.2 kHz RFID chips (Agrident), injected under the skin of the lower left tarsometatarsus (Boersma & Rebstock 2009).

We used SPOT-275C Argos satellite transmitters (platform transmitting terminal tags, PTTs; Table 2). We attached tags between 4 and 13 April 2022, after penguins finished their annual molt. We attached the tags to feathers with neoprene glue and tape, and covered the tape with epoxy to keep the ends of the tape in place during migration (Wilson et al. 1997). We positioned the tags on the penguins' lower backs to reduce drag (Bannasch et al. 1994). We programmed tags to transmit every hour.

We smoothed the data using the state-space model 'Crawl' in R (Johnson et al. 2008) and estimated a

Table 1. Magellanic penguins satellite-tracked during northbound migration from Punta Tombo, Argentina. Plus signs (+) indicate the pairs we were most certain bred together; asterisks (*) indicate penguins that were seen in the following breeding season (October–February). Migration start: date of the first Argos location > 10 km from the colony, excluding a short trip by 1 female (dates are given as mo/d/yr and are based on Argos locations); Transmission duration: days from migration start date until the last transmission date; Max. distance to colony: straight-line distance from the colony to the location farthest from the colony; Last location distance to colony: straight-line distance from the colony to the centroid of locations in the last 24 h of transmission. Distances are based on locations from the state-space model ('Crawl') output

Nest	Sex	Migration start	Last transmission	Transmission duration (d)	Distance to colony (km)		Weight at tagging (kg)
					Max.	From last location	
720X	F+*	4/10/2022	6/7/2022	58	1266	864	2.95
720X	M+	4/14/2022	6/18/2022	65	457	59	3.6
H04O	F*	4/9/2022	5/22/2022	43	1500	1493	3.45
H04O	M	4/10/2022	6/27/2022	78	1521	1323	3.6
H07O	F*	4/12/2022	6/16/2022	65	1387	1219	3.25
H07O	M	4/14/2022	5/28/2022	44	1054	536	3.5
H07U	F*	4/10/2022	5/30/2022	50	1243	1224	3.2
H07U	M*	4/12/2022	6/14/2022	63	1658	1535	3.25
H09K	F+	4/13/2022	7/10/2022	88	1756	1680	2.95
H09K	M+*	4/17/2022	7/11/2022	85	1405	1289	4.2
H09R	F+*	4/9/2022	6/27/2022	79	1421	1418	3.1
H09R	M+	4/12/2022	6/13/2022	62	1229	235	3.35
511D	F*	4/15/2022	6/21/2022	67	1530	1463	3.1
511D	M*	4/14/2022	7/21/2022	98	1709	1545	3.7
704M	F	4/13/2022	6/29/2022	77	1722	1705	3.5
H09L	M*	4/10/2022	6/29/2022	80	822	807	3.4

location every 30 min for each tag. We used Argos error ellipse information for the model error structure. As we did in previous studies (Rebstock et al. 2022a,b), we first deleted locations with location class Z, for which Argos does not provide an error estimate, as well as locations with duplicate times, keeping the location closest to the 2 surrounding locations. We then removed locations on land that were also more than 5 km from the colony. Finally, we ran a custom filter to remove large spikes in the track line, i.e. locations that represent a large movement away from the track line followed immediately by a return. Removing these spikes improved the performance of the state-space model (Rebstock et al. 2022a,b).

2.3. Device effects

Back-mounted tags increase drag on swimming penguins (Bannasch et al. 1994, Wilson et al. 2004, Ropert-Coudert et al. 2007), and may affect their swimming and foraging performance. We therefore tested for effects of the satellite tags on swimming speeds. We compared swimming speeds of penguins that were foraging to feed large chicks (> 30 d old) in January–February 2018, 2019, and 2020. Penguins carried 1 of 3 types of tags: the SPOT satellite tags used here, small GPS tags with short antennae, or larger GPS tags with no external antennae (Table 2).

Table 2. Tracking tags used during migration (SPOT-275 tags) and to compare Magellanic penguin swimming speeds at Punta Tombo, Argentina, when penguins were foraging for chicks > 30 d old (all tags). For the speed comparison, we combined F2G and nanoFix GPS tags, which are both small tags with short antennae

Tag type/model	Manufacturer	Length (mm)	Width (mm)	Height (mm)	Antenna length (mm)
Satellite transmitter (PTT)/SPOT-275	Wildlife Computers (Redmond, WA, USA)	86	17	17	185
GPS/F2G	Sirtrack/Lotek (Havelock North, NZ)	66	28	16	37
GPS/nanoFix-Geo	PathTrack (Otley, UK)	60	19	16	40
GPS/F5G	Sirtrack/Lotek (Havelock North, NZ)	85	28	20	Internal only

We calculated speed using the state-space model output and deleted zeros (locations at the nest when the penguins were not moving) and speeds $> 15 \text{ km h}^{-1}$ (approximately 2.35 times cruising speed of a Magellanic penguin [Wilson et al. 2004]; or our mean plus 5 times our standard deviation). We also excluded unusually long trips, greater than 6 d, made by 2 females, both with small GPS tags, and 2 males, both with SPOT satellite tags.

We ran mixed-effects regressions ('lmer' in the 'lme4' package in R; Bates et al. 2015) with swimming speed as the response, tag type, trip duration, sex nested in flipper length (as a measure of size), sex, and year (as a factor) as fixed predictors, and penguin ID as a random factor. We square-root transformed swimming speed to improve the residuals (log transforming shifted the distribution too far to the right).

2.4. Important areas at sea by sex

To identify important areas at sea for each sex, we calculated sex-specific minimum convex polygons for each half-month period during which at least half of the tags transmitted (April–June). We used minimum convex polygons instead of kernels because the penguins were migrating and tracks were mostly linear. Kernel analyses with small values of the smoothing parameter (h) resulted in many disconnected polygons, and analyses with large h values resulted in very broad polygons that overlapped land and offshore waters that the penguins did not use. Minimum convex polygons thus defined the migratory paths better than kernels.

We first projected the penguin locations using the Lambert azimuthal equal-area projection ('spTransform' in 'sp'; Pebesma & Bivand 2005), with the center of the projection equal to the midpoint of the penguin locations. We used 'mcp' ('adehabitatHR'; Calenge 2006) to compute the minimum convex polygons. We used 90% of locations to represent both wintering areas and migration corridors, which are important for conservation of migratory species. We removed land from the polygons using 'st_difference' ('sf'; Pebesma 2018).

2.5. Comparing proximity to shore for females vs. males

We compared distance from shore between females and males using a linear mixed-effects model ('lmer' in 'lme4'). Fixed effects were sex, shelf width, shelf width squared, and the interaction between sex and

shelf width. Penguin ID was a random effect. We included shelf width because penguins can be farther from the coast where the shelf is wide than where it is narrow, assuming penguins stay over the continental shelf. We also included shelf width squared to account for a nonlinear relationship. Penguins were necessarily close to shore immediately after leaving the colony, where the shelf is widest, and in the north where the shelf is narrowest, but could be farther from shore in the middle of their migration paths, where shelf width is intermediate.

We calculated the distance from shore for each penguin location using 'st_distance' ('sf'). We used the coastline from the 'rnatuarearth' package (South 2017) to make a line string for the coast. We projected penguin locations and the coastline using the azimuthal equidistance projection. In this case, the 'st_distance' function finds the distance between each penguin location (point) and the nearest point of the coastline. Note that the nearest point of the coastline is not necessarily at the same latitude as the penguin location, as the penguins we tracked did not enter large gulfs and estuaries. We square-root transformed distance to shore to improve the regression residuals.

Shelf width was calculated with 'dist2isobath' ('marmap'; Pante & Simon-Bouhet 2013), which uses great circle distances. Shelf width is the sum of the distance between each penguin location and the coast (0 m isobath) and the distance between the penguin location and the 200 m isobath. This may be less than the distance between the coast and the 200 m isobath along a line of latitude. We standardized shelf width and shelf width squared to prevent large differences in the scales of the variables in the model.

2.6. Comparing distance north of the colony for females vs. males

We compared the northern-most latitude reached by females and males, using linear regression ('lm' in 'stats'; R Core Team 2020). The response was the maximum (northern-most) latitude reached by a penguin while its tag was transmitting, and predictors were sex and the number of days that the tag transmitted, because the tags did not transmit over the entire nonbreeding season.

We also compared the final latitude of females and males while their tags transmitted, using linear regression. The response was the latitude of the centroid of locations for the last 24 h the tag transmitted, and predictors were sex and the number of days that

the tag transmitted. We found the centroid of locations using 'centroid' ('geosphere'; Hijmans 2019), and the distance from the colony to the centroid using 'distVincentyEllipsoid' ('geosphere').

2.7. Testing the role of size dimorphism in sexual segregation

Magellanic penguin males are larger and heavier than females, although there is overlap in size and mass (Boersma et al. 2013). We used 2 measures of size in penguins: weight (kg) as a measure of overall body size and body condition, and flipper (wing) length (cm) as a measure of underwater 'flight' (swimming) efficiency. We weighed penguins with a spring scale and measured flipper length when we attached the satellite tags. Both weight (linear regression: $F_{1,14} = 9.4$, $p = 0.009$, adjusted $R^2 = 0.36$) and flipper length (linear regression: $F_{1,14} = 10.7$, $p = 0.006$, adjusted $R^2 = 0.39$) were strongly correlated with sex. To test the effects of size independent of sex, we used the residuals from regressions of weight and flipper length on sex. We calculated the mean distance to shore for each penguin (mean of the distances calculated above). We regressed mean distance on the residuals for weight and flipper length.

2.8. Comparing migration start timing of mates and proximity of mates at sea

To determine if mates left the colony together, we defined the start of migration as the date of the first location at sea more than 10 km from the colony. One female swam 22 km from the colony, then returned, so we excluded those early locations. We used dates of the Argos transmissions rather than state-space model output because the model sometimes did not capture the first few locations at sea.

To determine if mates stay together at sea, we calculated the distance between mates for each hour that we had predicted locations for both penguins. Although the model predicted 2 locations per hour, the times depended on Argos transmission times, and the times for a pair rarely matched. We calculated the midpoint of the 2 locations per hour using 'midPoint' ('geosphere'). We used 'distVincentyEllipsoid' to calculate distances.

We used the R language and environment, version 3.6.3 (R Core Team 2020), for the state-space model, statistics, and mapping. We used bathymetric data from the ETOPO1 database hosted on the National

Oceanic and Atmospheric Administration (NOAA) website, accessed through 'getNOAA.bathy' ('marmap'). Values are reported as means \pm SD.

3. RESULTS

Tags transmitted 43–98 d before the batteries died or the tags came off (Table 1). Most (12 of 16) penguins reached wintering areas off the mouth of the Rio de la Plata ($\sim 36.5^\circ$ S) or the coast of Uruguay (Fig. 1). Three males turned south before reaching 36.5° S. Penguins reached the Rio de la Plata (1200–1300 km from Punta Tombo) in 24 to 70 d. Hence, the 3 males that did not reach 36.5° S could have done so within the time their tags transmitted (44–80 d).

All penguins left the colony in a northeasterly direction, but followed individual trajectories (Fig. 1). Two females spent more than 1 mo near the colony before swimming north and reaching Uruguayan waters. One female and 2 males returned south after reaching $37\text{--}36^\circ$ S. Two males stayed south of $\sim 41^\circ$ S. All except 1 penguin stayed over the continental shelf, in water less than 200 m deep. One male traveled over the continental slope, in water up to 1540 m deep, before returning to the continental shelf south of the Rio de la Plata.

We re-sighted 5 females and 3 males at Punta Tombo, without their tags, between October 2022 and February 2023 (Table 1). They were missing feathers where the tags had been. All appeared healthy and in good condition. Our automated scale and RFID reader system recorded an additional female and male, but we never saw them and did not locate their nests. We found 3 females and 3 males incubating eggs. We did not find all of the penguins during early incubation, so the others could have had eggs that they lost before we found them.

3.1. Device effects

Overall, penguins averaged 3.8 ± 2.2 km h⁻¹ when foraging for large chicks. Swimming speeds were similar between penguins carrying GPS tags with short antennae and penguins carrying satellite tags with long antennae (Table 3; linear mixed-effects regression: $t = 1.4$, $p = 0.15$). Swimming speeds were also similar between penguins with larger GPS tags without external antennae and penguins with satellite tags with long antennae (Table 3; $t = 0.6$, $p = 0.58$). In contrast, the penguins we tracked during fall migration averaged 2.04 ± 1.4 km h⁻¹. Females

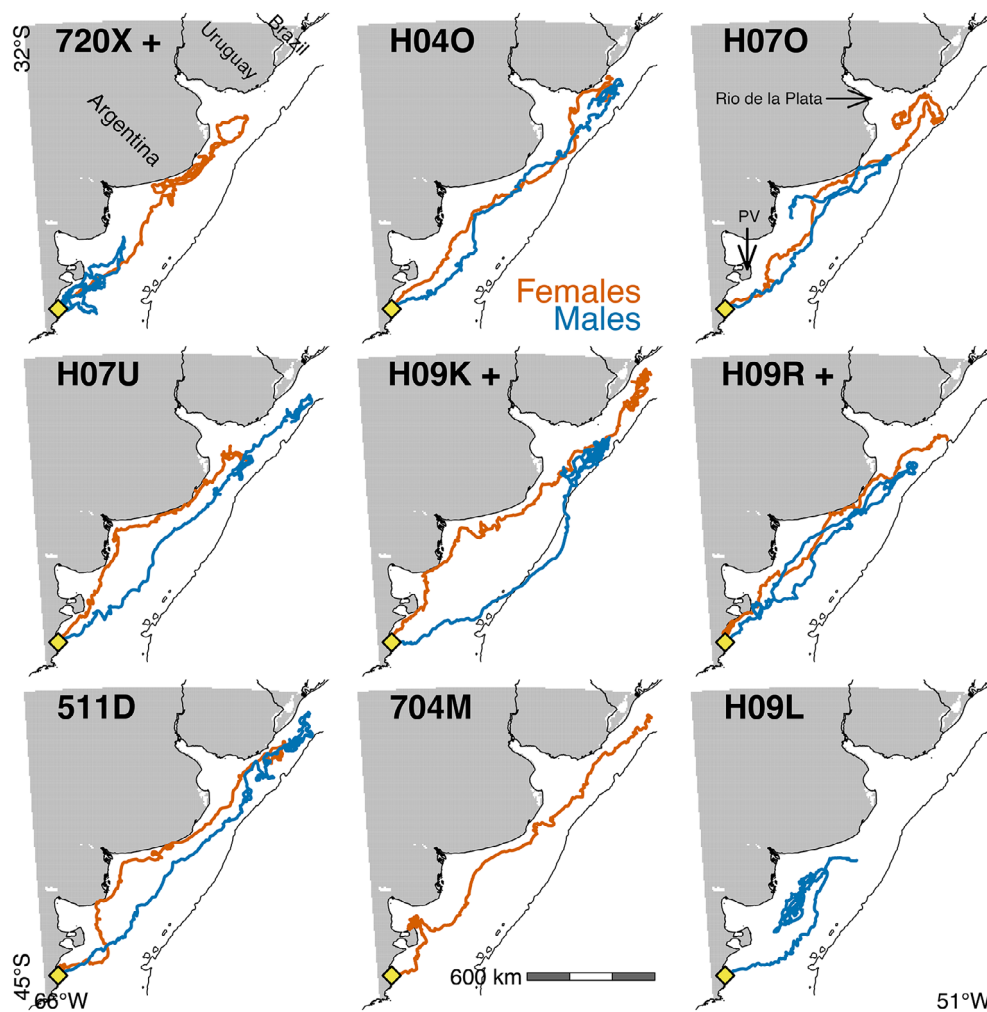


Fig. 1. Breeding adult Magellanic penguins tracked from Punta Tombo, Argentina (yellow diamond), after the breeding season and annual molt (April–July) 2022. Each panel shows 1 presumed breeding pair, except the bottom center and bottom right panels, which show a female and male, respectively, whose mates we were not able to tag. A plus (+) following the nest number indicates the pairs that we were most certain bred together. Nest numbers are in the upper left of each panel. PV: Peninsula Valdés. The gray line offshore shows the edge of the continental shelf (200 m isobath)

swam $2.06 \pm 1.4 \text{ km h}^{-1}$; males swam $2.01 \pm 1.3 \text{ km h}^{-1}$.

3.2. Important areas at sea by sex

Minimum convex polygons showed variation in penguin locations by date and sex (Fig. 2). In early April (Fig. 2), female tracks extended about twice as far from the colony as male tracks, because females generally left the colony (median date left = 11 April) earlier than males (median date left = 13 April). In late April and early May (Fig. 2), females and males were about equally far north,

Table 3. Comparison among tracking-tag types of swimming speeds of Magellanic penguins foraging to feed chicks >30 d old at Punta Tombo, Argentina. Satellite tags were SPOT 275 tags. GPS tags with small antennae were F2G or nanoFix Geo tags. GPS tags without external antennae were F5G tags. See Table 2 for tag dimensions and manufacturers. We did not put F5G tags on females

Tag type	Speed (km h^{-1})		N penguins	N locations
	Mean	SD		
Females				
Satellite tag	3.9	2.37	2	1703
GPS tag with small antenna	3.7	2.14	7	4527
Males				
Satellite tag	3.8	2.24	11	7814
GPS tag with small antenna	3.9	2.15	10	6665
GPS tag without external antenna	3.7	2.07	9	6453

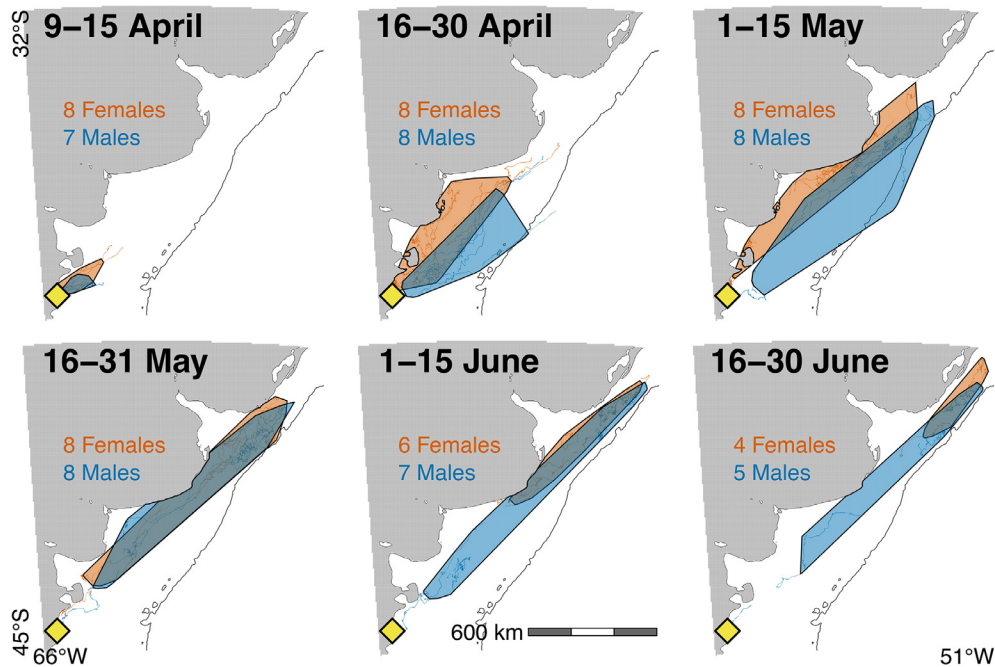


Fig. 2. Areas used by breeding adult Magellanic penguins tracked from Punta Tombo, Argentina (yellow diamond), after the breeding season and annual molt (April–July) 2022. Colored polygons are minimum convex polygons (MCPs), calculated for 90% of penguin locations by half-month period (the first period is shorter because penguins left the colony starting 9 April). Land areas were removed from the MCPs. Colored lines represent penguin tracks during each period. The gray line offshore is the edge of the continental shelf (200 m isobath). One male left the colony on 17 April, and is not included in the 9–15 April panel. Tags stopped transmitting starting in late May. July is not included, as fewer than half of the tags were still transmitting

but males were farther from shore than females. By the middle of May, some penguins had reached the mouth of the Rio de la Plata, and into Uruguayan waters. In late May (Fig. 2), females and males overlapped almost completely, with locations extending from near the Peninsula Valdés to the coast of Uruguay. In early June (Fig. 2), northern-most locations of females and males overlapped, but some males remained or returned much farther south than females. In late June (Fig. 2), for penguins with tags still transmitting, females continued to stay farther north than males.

3.3. Females stayed closer to shore than males

Although the locations of females and males overlapped in late May and off northern Argentina to southern Brazil in early June, they often used separate areas during migration (Fig. 2). Females swam significantly closer to shore (62.4 ± 43.3 km) than males (109.3 ± 51.4 km; linear mixed-effects regression: $t = 4.0$, $p < 0.0001$). One male swam beyond the continental shelf (Fig. 1, center panel), but even without that male outlier (>200 km from shore), females stayed closer to shore than males on average (without the outlier: males = 100.9 ± 45.5 km; $t = 3.8$, $p =$

0.0002) (Fig. 3). As expected, the width of the shelf positively affected distance to shore ($t = 22.6$, $p < 0.0001$) and shelf width squared negatively affected distance ($t = -26.2$, $p < 0.0001$). Furthermore, the interaction between sex and shelf width was significant ($t = 16.5$, $p < 0.0001$), with females staying closer to shore and males staying farther offshore where the shelf was widest.

3.4. Females stayed farther north than males

Females reached slightly, but not significantly, more northern latitudes ($34.42 \pm 1.31^\circ$ S) than males ($36.28 \pm 2.91^\circ$ S; Fig. 4) (linear regression: $t = -2.09$, $p = 0.057$). Days that the tags transmitted had little effect on the northern-most latitude reached ($t = 1.76$, $p = 0.10$). The full regression model ($F_{2,13} = 3.1$, $p = 0.08$) accounted for 22% of the variance, however. Males had more variability in their northern-most latitudes than females (Fig. 4).

Final latitudes of females while tags transmitted ($35.09 \pm 1.82^\circ$ S) were farther north than final latitudes of males ($38.26 \pm 3.65^\circ$ S; linear regression: $t = -2.89$, $p = 0.01$; Fig. 4). The tags transmitted for 65.9 ± 15.2 d for females and 71.9 ± 16.7 d for males

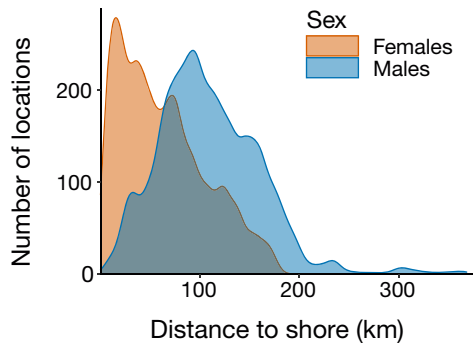


Fig. 3. Breeding female Magellanic penguins tracked from Punta Tombo, Argentina, after the breeding season and annual molt (April–July 2022), stayed closer to shore than males, on average. Density plots of distance between each penguin location and the coastline

($t = 2.10$, $p = 0.056$). Males showed more variability in their final latitudes than females (Fig. 4). Final latitude was significant while the northern-most latitude was not, because several males turned around and headed south after reaching their northern-most latitudes (Fig. 1).

3.5. Size did not affect distance from shore, when accounting for sex

Magellanic penguin males that we tracked were larger and heavier than females on average but with overlap in size and mass of the sexes. In our study, flipper lengths of females averaged 14.88 cm (range 14.2–15.7 cm) and those of males averaged 15.58 cm (15.0–16.2 cm). Females weighed 3.19 kg on average at the time of tag attachment, and males weighed 3.58 kg (Table 1).

Heavier penguins did not swim farther from shore than lighter penguins, when accounting for sex (linear regression: $F_{1,14} = 1.7$, $p = 0.21$). Similarly, penguins with longer flippers did not swim farther from shore than penguins with shorter flippers (linear regression: $F_{1,14} = 0.03$, $p = 0.87$).

3.6. Mates did not leave the colony together or stay together at sea

Mates did not leave the colony together. Penguins left the colony between 9 and 17 April, and mates left 1–4 d apart (Table 1). In 6 of 7 pairs, the female left before the male.

Mates did not stay close to each other at sea (Fig. 5). The mean distance between mates within each hour was

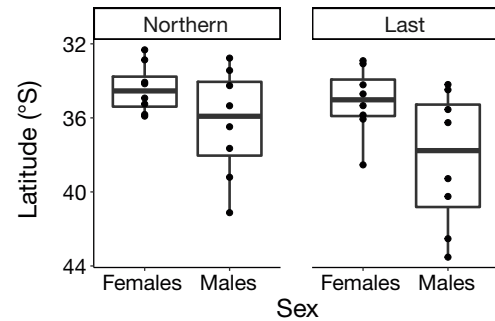


Fig. 4. Breeding female Magellanic penguins tracked from Punta Tombo, Argentina, after the breeding season and annual molt (April–July 2022), reached slightly more northern latitudes than males while their tags transmitted, and stayed farther north, when accounting for the number of days the tags transmitted. Boxes show the 25th and 75th percentiles and the central lines represent the medians. The circles are the latitudes for each penguin. Boxes on the left show the northern-most latitudes; those on the right show latitudes of the centroids of the locations for the last 24 h that the tags transmitted

367 ± 280 km (range = 0.9–1187 km). For the 3 pairs that we are most certain bred together, the mean distance was greater (513 ± 287 km, range = 14–1187 km).

4. DISCUSSION

4.1. Important areas at sea by sex

Our study adds to the growing evidence for spatial segregation of sexes in Magellanic penguins outside the breeding season. Although there was some over-

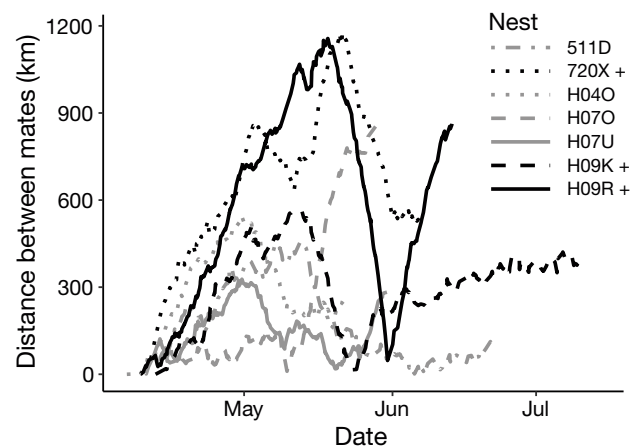


Fig. 5. Magellanic penguin mates tracked from Punta Tombo, Argentina, after the breeding season and annual molt (April–July 2022), did not stay together at sea. Each line represents a presumed breeding pair, and the legend lists the nest numbers. Distance between mates was calculated for each hour that both tags transmitted. Plus signs (+) and dark lines indicate the 3 pairs that we are most certain bred together

lap, females and males tended to use distinct areas, with distributions of females being closer to shore in April and early May, and more restricted to lower latitudes in June. Individual variation was high, and a larger sample from multiple years would be more conclusive; nevertheless, our results were consistent with studies from other colonies that all showed sexual segregation.

The northern areas used disproportionately by females outside the breeding season overlapped with important areas for pinnipeds, sea turtles, albatrosses (González Carman et al. 2016), other seabirds (Krüger et al. 2017), and cetaceans (Berninsone et al. 2020). These areas also have high bycatch rates of marine mammals, turtles, and birds (Petry & Fonseca 2002, Franco-Trecu et al. 2019) and high levels of pollution (Braga et al. 2008, Lohmann & Belkin 2014). Near-shore areas used by females during northbound migration, between about 40 and 39°S, are also used by other marine megafauna (Copello et al. 2014) and are also heavily impacted by human activities (Kopprio et al. 2015).

Use of separate areas leads to sex-biased mortality and skewed adult sex ratios in many species. Female Andean condors *Vultur gryphus* forage in more human-impacted landscapes and have higher mortality than males (Lambertucci et al. 2012). Female Trinidadian guppies *Poecilia reticulata* avoid aggressive males by selecting areas with high predation rates (Darden & Croft 2008). Some exploited sharks in the Pacific Ocean segregate by sex, and catch rates are higher for the sex that uses areas with higher fishing effort (Mucientes et al. 2009). Sex-biased mortality of seabirds in fisheries is common and is attributed to spatial segregation of the sexes at sea (Bugoni et al. 2011, Gianuca et al. 2017). Female Magellanic penguins have higher mortality in gillnets in the wintering area of southern Brazil than males (Fogliarini et al. 2019).

4.2. Females stayed closer to shore and farther north than males

Females stayed closer to shore on average than males during their northbound migration, as Barrionuevo et al. (2020) also found. Yamamoto et al. (2019) did not test distance to shore, but they reported that females did not dive as deep as males at the same latitude. The shallower dives of females may be because females stayed in shallower waters closer to shore than males (see Yamamoto et al. 2019, their Fig. S1).

There was less agreement in studies that reported maximum distance from the colony or distance the

penguins swam. Dodino et al. (2021) and Yamamoto et al. (2019) found that females went farther north than males. Barrionuevo et al. (2020) found that females had significantly longer total path lengths than males. Pütz et al. (2007), however, found that the sexes were similar in the maximum distance from the colony and the minimum distance traveled. We found that females and males reached similar latitudes during the autumn migration, but females remained farther north than males while their tags transmitted.

There are several reasons to expect inconsistent details in migratory patterns among studies of Magellanic penguins, including inter-colony and interannual variations, and the types of tags used. Magellanic penguins breeding in the northern part of the range generally follow their main prey, Argentine anchovy *Engraulis anchoita* (Yorio et al. 2017, Marques et al. 2018), which migrate north along the continental shelf as far as 23°S (Costa et al. 2016). Penguins breeding in the southern part of their range migrate seasonally, but do not simply follow their prey north in autumn. Important prey species sprat *Sprattus fuegensis*, lobster krill *Munida gregoria*, and squid *Loligo gahi* (Clausen & Pütz 2002, Barrionuevo et al. 2018, Dodino et al. 2022) do not migrate north in winter (Clausen & Pütz 2003, Arkhipkin et al. 2004, Diez et al. 2018). However, in winter, sprat (Diez et al. 2018) and *L. gahi* (Arkhipkin et al. 2004) may occur below the depth where they are readily available to Magellanic penguins, ~100 m (Walker & Boersma 2003, Yamamoto et al. 2019). Furthermore, migration tracks and timing for the same colony vary among years (Pütz et al. 2007, Stokes et al. 2014), similar to foraging locations and distance from the colony during the breeding season (Rebstock et al. 2022b).

Two types of tags were used in migration tracking studies, Argos satellite transmitters and geolocators. Satellite transmitters are about 2 orders of magnitude more accurate than geolocators (Halpin et al. 2021). However, satellite tags have not lasted the entire non-breeding period because of battery or attachment limitations (Pütz et al. 2000, 2007, Stokes et al. 2014), leading to a tradeoff between location accuracy and temporal coverage.

4.3. Device effects

Back-mounted tags increase drag on swimming penguins, depending on size, shape, placement of tag, and antenna presence or size (Bannasch et al. 1994, Wilson et al. 2004, Ropert-Coudert et al. 2007). We found that penguins carrying satellite tags with

long antennae swam at similar speeds to penguins carrying small GPS tags with short antennae and larger GPS tags with no external antennae. The antennae on the tags we used were flexible, and mounted at an angle, pointing towards the rear, both of which reduce the drag from the antenna (Wilson et al. 2004). The tags also have a small cross-sectional area and a sloping front, which also reduce drag (Banasch et al. 1994, Vandenabeele et al. 2015). We concluded that the antennae on the satellite tags did not significantly affect swimming performance of the migrating penguins.

We expected tracked penguins to skip the next breeding season if tags affected their foraging over the winter. Females are smaller and less likely to return during the breeding season than males (Boersma & Rebstock 2010, Gownaris & Boersma 2019), but we found 6 of 8 females and only 4 of 8 males in the colony in October 2022 to February 2023. One of the females that weighed the least at the time of tagging was among those that returned, suggesting that tags did not have a disproportionate effect on smaller penguins. Our resighting rate of tracked penguins in the following season (62.5%) was within the range of resighting rates of penguins that did not carry tracking tags at Punta Tombo, 45–99% depending on year and ID type (Boersma & Rebstock 2010, Gownaris & Boersma 2019). Our resightings represent a minimum of the penguins that returned to breed, as penguins at Punta Tombo frequently change nest sites and mates (Boersma et al. 2013, Wagner et al. 2022), and we may not find them in the large colony of 400 ha and > 100 000 breeding pairs (Rebstock et al. 2016).

In addition, our results were consistent with those from studies using small, leg-mounted geolocator tags (Yamamoto et al. 2019, Barrionuevo et al. 2020, Dodino et al. 2021), which presumably do not increase drag as much as larger back-mounted tags with antennae (Wilson et al. 2004). We conclude that although the tags affected penguins in some ways that we could not measure, the effects were similar for females and males, and did not bias our comparison of the sexes.

4.4. Spatial segregation at sea and sexual size dimorphism

Sexual size dimorphism explains spatial segregation between the sexes in some species (Phillips et al. 2004), although spatial segregation has also been found in species with similar sizes of females and males (Hedd et al. 2014, Reyes-González et al. 2021).

Larger individuals may prefer deeper water (farther offshore) because they can dive deeper than smaller individuals (Walker & Boersma 2003, Ratcliffe et al. 2013). Yamamoto et al. (2019) found that the average dive depth was deeper for males than for females during migration. Females may seek warmer water nearshore because they are smaller than males on average (Wearmouth & Sims 2008, Magory Cohen et al. 2021). Size dimorphism, however, does not appear to be the reason that females stay closer to shore than males during migration in Magellanic penguins. Larger penguins, independent of sex, did not go farther offshore than smaller penguins.

Larger penguins generally swim faster than smaller penguins (Sato et al. 2010). Yamamoto et al. (2019) suggested that female Magellanic penguins migrated farther north than males because females were less able than males to maintain their position in the north-flowing current on the Patagonian shelf. Swimming speeds were similar between females and males, perhaps because of the small size dimorphism by sex.

Additional hypotheses to explain sexual segregation include social factors such as exclusion of one sex by the other from favorable areas, and size-dependent predation risk (Wearmouth & Sims 2008). Males may be more aggressive than females, as in other penguins (Spurr 1974, Viñuela et al. 1995), but we have no data on social behaviors at sea, such as competitive exclusion. Magellanic penguins have small sexual-size dimorphism, with some overlap between the sexes. Large predators that could take Magellanic penguins at sea, such as large sharks (Randall et al. 1988), pinnipeds (Boswall 1972), or orcas *Orcinus orca* (Jehl 1975), likely could take either sex. Some smaller predators, such as giant petrels *Macronectes*, may be restricted to smaller individuals, although giant petrel predation on adult Magellanic penguins is relatively rare and may occur only near breeding colonies (Ryan et al. 2008, Finger et al. 2023). Predation on Magellanic penguins at sea outside the breeding season is unknown, but some wintering areas overlap with distributions of potential predators (González Carman et al. 2016).

Sexes may segregate spatially because sex-specific prey species occur in distinct areas (Wearmouth & Sims 2008). There is contradictory evidence, however, for sex-specific diets in Magellanic penguins during the nonbreeding season. Values of $\delta^{15}\text{N}$ were similar for females and males (Silva et al. 2014, Marques et al. 2018, Barrionuevo et al. 2020, Dodino et al. 2021). Results for $\delta^{13}\text{C}$ and trophic niche width were not consistent among the studies cited above, and varied by region (Silva et al. 2014).

Explanations for spatial segregation between the sexes during migration that do not involve sexual size dimorphism include sex-specific arrival times to the breeding colony (Morbey & Ydenberg 2001) and sex-dependent energy requirements related to breeding investment (Lerma et al. 2022). In many seabird species, males arrive at the colony earlier than females to defend nests or territories (Hedd et al. 2014, De Felipe et al. 2019). Magellanic penguin males return to the colony earlier than females (Boersma et al. 1990, 2013). We found strong spatial segregation during April and May, several months before the start of the breeding season and the return of penguins to their breeding colonies in September or October. Sex-specific arrival times are therefore unlikely to explain the greater distance from shore of males during the early part of migration. In blue-footed boobies *Sula nebouxii*, females lose weight during the breeding season but males gain weight (Lerma et al. 2022), likely resulting in sex-specific energy needs after the breeding season. Magellanic penguins lose weight while incubating, but recover after the chicks hatch (Fowler et al. 1994). It is possible that Magellanic penguins have sex-dependent energy requirements after the breeding season, but we have no data.

Migratory paths were variable among individuals, making one explanation of the spatial segregation we found unlikely. Penguins apparently responded individually to factors affecting their foraging and survival.

4.5. Mates did not leave the colony together or stay together at sea

Mates left the colony separately, and did not meet while at sea. Mates in other seabird species studied also migrated separately (Müller et al. 2015, Thiebot et al. 2015). Mates in some seabird species synchronize their returns to the colony (Fayet et al. 2017). We do not know whether mates arrived together, as our tags did not last until the pairs returned. This is unlikely, however, as males generally arrive before females (Boersma et al. 1990).

Female Magellanic penguins usually started the migration earlier than males. Median date of the start of migration from a colony in the Beagle Channel, southern Argentina, was about 3 d earlier for females (26 March) than for males (29 March) (Pütz et al. 2007, Dodino et al. 2021). In 2 studies of penguin migration that tracked pairs (Yamamoto et al. 2019, this study), females left before males in 11 of 13 pairs.

4.6. Implications for conservation

All studies of migrating Magellanic penguins, including ours, found high individual variation in locations and timing. Adult Magellanic penguins occurred in continental-shelf waters from southernmost Argentina to southern Brazil from April through August (Yamamoto et al. 2019, Barrionuevo et al. 2020, Dodino et al. 2021). High variability among individuals and colonies makes defining core areas that need protection problematic. Nevertheless, there were temporal patterns of occurrence outside the breeding season from each breeding colony (Pütz et al. 2007, Stokes et al. 2014, Barrionuevo et al. 2020, this study), suggesting that some temporal zoning of fisheries and other marine activities would benefit migrating Magellanic penguins (Stokes et al. 2014). In addition, management of fisheries and polluting activities to reduce threats everywhere in the ocean would protect penguins and other species regardless of their locations (Trathan et al. 2015, Handley et al. 2020). More studies with relatively accurate satellite tags (Halpin et al. 2021) are needed to define areas used by penguins more precisely than is possible with geolocator tags. In addition, data are needed from more large colonies, and more years, to understand spatial and temporal variation.

Our study showed that females are likely more vulnerable to bycatch in gillnet fisheries than males. Females stayed closer to shore than males on average, and stayed longer off the mouth of the Rio de la Plata or off southern Brazil where they are likely to encounter gillnets (Crawford et al. 2017, Berninsone et al. 2020). In contrast, Dodino et al. (2021) found that females and males had similar overlap with bottom trawl and shrimp fisheries, suggesting similar risk. Their study area, however, lacked major gillnet fisheries. Gillnet fisheries are more common farther north in the penguin wintering area (Crawford et al. 2017, Berninsone et al. 2020), have higher bycatch rates of Magellanic penguins than trawl, shrimp, and longline fisheries (Cardoso et al. 2011, Crawford et al. 2017), and catch more female than male penguins (Fogliarini et al. 2019).

Staying closer to shore and farther north also disproportionately exposes females to pollution. Pollution is worse nearshore than offshore, because most pollution (~80%) is from land-based sources (Hatje et al. 2021). Harmful algal blooms (red tides), which can kill penguins and other seabirds (Shumway et al. 2003, Phillips et al. 2011), are projected to increase in South America as nutrient discharges increase (GliBERT 2020). Harmful algal blooms are often concentrated nearshore or in river plumes because the

nutrients are discharged from terrestrial sources (Glibert 2020). The Rio de la Plata plume is a major source of nutrients and other pollutants within the wintering area of Magellanic penguins (Braga et al. 2008, Lohmann & Belkin 2014). The plume flows northeast along the coasts of Uruguay and Brazil in winter (Acha et al. 2004), making the northern-most wintering area more polluted than more southern areas, which have less riverine inputs. The Rio de la Plata contains the major Argentine and Uruguayan shipping ports (Ash & Carpenter-Lomax 2020), exposing penguins near the river mouth to the pollution generated by shipping (Hatje et al. 2021). Finally, northbound females, but not males, swam nearshore close to the Bahía Blanca system, the Río Colorado and Río Negro mouths, which are affected by industrial pollution, untreated sewage, agricultural runoff, and shipping (Kopprio et al. 2015).

The tendency of females to spend more time near the Rio de la Plata and southern Brazil and closer to shore than males has consequences for the population. The migratory behavior of females exposes them more to entanglement in fishing gear, and more pollution and harmful algal blooms. Greater exposure to these risks helps explain the greater mortality during winter of female Magellanic penguins compared to males (Marques et al. 2018, Gownaris & Boersma 2019), and the increasingly male-biased adult sex ratio at Punta Tombo (Gownaris et al. 2020). Uneven sex ratios, in turn, can lead to population declines, especially in species with obligate bi-parental care of young (Jenouvrier et al. 2010, Gownaris & Boersma 2019).

More protection should be prioritized in areas used by female Magellanic penguins during autumn migration. Although individual variability was high, and some females stayed offshore, enough females likely stay in nearshore areas to result in higher mortality in females than in males. Additional tracking data are needed to confirm our results with larger sample sizes, investigate interannual variability, and quantify the proportion of females that migrate inshore and stay at the Rio de la Plata mouth. Protection of females' nonbreeding areas would likely help the population by reducing mortality of females. Protection of these waters would also help protect other species that use the same area.

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