Penguins in the Coal Mine:
Unraveling Sentinel Species Responses to Human-Caused Stressors

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Abstract

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Given the urgent need to understand the rapid changes in marine systems, seabirds can serve as effective sentinel species, offering valuable insights into marine conditions and food webs across a range of spatiotemporal scales. I explore the use of seabirds—specifically Magellanic penguins (*Spheniscus magellanicus*) at the large, but declining breeding colony of Punta Tombo, Argentina—as sentinel species in multiple contexts.

First, I examined the effects of extreme heat on Magellanic penguin adults and chicks. Due to climate change, extreme weather events are becoming more frequent and severe, leading to an increase in direct, adverse thermoregulatory impacts on wildlife. I document the magnitude of an unprecedented, single-day, heat-related mortality event of Magellanic penguin adults and chicks. Mortality rates of adults were unevenly distributed across the colony, suggesting that the presence of microclimates or easier beach access were important factors to penguin survival.

Next, I examined how intrinsic traits, specifically sex and body size, affect the foraging success of adult Magellanic penguins, before examining how extrinsic factors, like commercial fishing impact their foraging success. Many seabird species are sexually size dimorphic, with males and females often displaying different foraging behaviors. Sex-specific differences in foraging are often attributed to sexual size dimorphism, yet few have quantified the foraging success of males and females and/or of large and small conspecifics. We found males brought back 38% more food than females and males were more efficient foragers than females, bringing back 69% more food per day. Size did not influence foraging success or foraging efficiency suggesting sex-specific foraging behaviors or roles during breeding are driving differences in foraging success and efficiency.

Understanding competition between fisheries and seabirds is critical for developing ecosystem-based management strategies that balance fisheries harvest and conservation goals. I assessed the effect of commercial fishing hours on the foraging success and foraging efficiency of chick-provisioning Magellanic penguins. We found that (1) as the average number of fishing hours increased within the penguins' foraging area, adult foraging efficiency decreased, and (2) both adult sex and the timing of fishing effort relative to chick age influenced this effect. When adults were feeding small chicks, an increase in the number of fishing hours within the foraging range was associated with reduced foraging efficiency, especially for males. When adults were raising large chicks, however, foraging metrics had no relationship to fishing hours, likely because adults can leave larger chicks for longer and are thus less spatially and temporally constrained in their foraging efforts. These results indicate fishing may not be affecting the amount of food breeding adults acquire on a foraging trip, but the rate at which they acquire it.

DEDICATION

I dedicate this to my supportive parents, my animal-loving grandmother, and my grandfather, who says that getting outside is “a good thing to do.”

Chapter 1

Unprecedented heat mortality of Magellanic Penguins

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Abstract

Extreme weather events are becoming more frequent and severe, leading to an increase in direct, adverse thermoregulatory impacts to wildlife. Here we document an unprecedented, single-day, heat-related mortality event of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Chubut Province, Argentina, one of the largest breeding colonies for this species. We found 264 dead adults and 90 dead chicks in the breeding colony and along the beaches after recording the highest temperature in the shade (44°C on 19 January 2019) since the study started in December 1982. We found dead adults and chicks in postures used to release heat, i.e., lying prone with flippers and feet extended away from the body and/or bills open. We found no evidence for other causes of mortality other than heat (e.g., disease, toxic algae, starvation). Adults potentially died of dehydration, because dead adults were in significantly worse body condition than adults that survived. Dead adults had either empty stomachs or < 50g of food and 27% of the dead adults died traveling between the nesting area and the water. More males died than females (83% male, 17% female, $n = 94$). In one section of the colony, ~5% of 1153 adults died in the heat. Mortality rates of adults were unevenly distributed across the colony, suggesting that the presence of microclimates or easier beach access were important factors to penguin survival. The body condition indices of dead and live chicks were similar and chicks that died from heat had food in their stomachs (mean = 405 ± 128g, $n = 14$) suggesting food likely inhibited their ability to thermoregulate. Documenting the effects of extreme weather events on populations is crucial to predicting how they will respond to climate change because these events, although rare, are expected to become more frequent and could have severe impacts on populations.

Keywords: Heat mortality, extreme weather events, seabird, Magellanic Penguin, climate change, dehydration, thermoregulation, body condition

Introduction

Understanding how heat stress and extreme weather events affect organisms is becoming critical, since both are increasing in frequency and severity as a result of human-induced climate change (Diffenbaugh et al. 2017, Ummenhofer and Meehl 2017) and predicted to continue to increase in frequency and severity (Duffy and Tebaldi 2012, IPCC 2014). Thermoregulation helps endotherms manage extreme temperatures and maintain thermal homeostasis, but it comes at a cost, since organisms have finite resources to allocate to maintenance, growth and reproduction (Stearns 1989, Nord and Nilsson 2019). Most studies of how climate change affects endotherms focus on indirect effects (Oswald and Arnold 2012). In birds, extreme weather and thermal stress affect reproductive success (Boersma and Rebstock 2014, Ropert-Coudert et al. 2015), foraging success and efficiency (Finney et al. 1999), stress levels (Romero et al. 2000, Krause et al. 2016a, 2016b), behavior (Reichert et al. 2012), habitat (Bonter et al. 2014), prey availability (Jones et al. 2019, Piatt et al. 2020), and fledging success (Cunningham et al. 2013). However, with increasing average and extreme temperatures, direct thermoregulatory impacts, e.g., heat-related mortality, are expected to increase for many animals (McKechnie and Wolf 2010, McKechnie et al. 2021) and humans (Shindell et al. 2020).

Thermal stress has the potential to kill thousands to hundreds of thousands of organisms in a single day (Finlayson 1932, Wells et al. 1961), which can have long-term consequences on populations (Fey et al. 2015). In a recent analysis of 727 mass-mortality events across invertebrate, amphibian, fish, bird, reptile, and mammal species, 25% of mass-mortality events were directly related to climate processes ((Fey et al. 2015). Hot thermal stress events have been rare, but started to occur in the 1980s (Fey et al. 2015). Understanding the impacts of extreme events was recently identified as a major gap in population and community ecology (Altwegg et al. 2017). Mass mortality from extreme weather events is rare and often not published in scientific literature, but some events are reported in news outlets (Fey et al. 2015). With the frequency and severity of heat-related mortality predicted to increase, it is important to document these events in peer-reviewed literature.

Here we document unprecedented, heat-related mortality of Magellanic Penguins (*Spheniscus magellanicus*) at the Punta Tombo, Argentina breeding colony. We found 264 dead adults and 90 dead chicks after 19 January 2019 when air temperature in the shade reached 44°C. In the region around the Punta Tombo breeding colony, the average air temperature is predicted to increase 1.5 – 2.5°C within the next century (Nuñez et al. 2009). We put this single day, heat mortality event into the context of a 35-year study and, because we were at the breeding colony on the hot day, we were able to assess individual body condition before penguins became too decomposed or were scavenged. Because chicks and likely adults receive most of their water from their food (Janes 1997), we predicted individuals in worse body condition were more likely to die because they would not be hydrated enough to pant and lower their body temperature sufficiently. We assessed if more individuals left the colony on hotter days to escape the heat.

Prolonged periods of heat are known to decrease adult survival of penguins (Ganendran et al. 2016). Magellanic Penguins exhibit many of the ideal characteristics for seabirds to be successful indicators of changes in thermoregulatory constraints, as suggested by Oswald and Arnold (2012), such as long migrations, exposed breeding sites, and dependence on marine prey. More empirical data on how organisms respond to extreme environmental variation can improve models predicting the effects of climate change (Angilletta and Sears 2011). Understanding the direct effects of extreme weather can increase our ability to predict how species, populations, communities and ecosystems will respond to climate change.

Methods

Since 1982, the second author and her students have studied the Magellanic Penguin colony at Punta Tombo, Chubut Province, Argentina (44.0458S, 65.2238W; (Boersma et al. 1990). With ~200,000 breeding pairs, Punta Tombo is one of the largest breeding colonies of this species, covering about 400 ha, but the number of active nests declined by 36% from 1987 to 2014 (Rebstock et al. 2016). The colony is in a coastal, arid desert where penguins nest in bushes and burrows for protection from the elements and predators (Stokes and Boersma 1991). Some penguins nest nearly 1 km inland (Rebstock et al. 2016).

Magellanic Penguins arrive at Punta Tombo to start breeding in September and October, chicks fledge from late January to early February, and adults leave the colony to go to sea, typically migrating north to winter offshore of northern Argentina and southern Brazil, after molting from late February through early April (Boersma et al. 1990, Boersma and García-

Borboroglu 2013). From 1982/83 to 2017/18 (excluding 2011/12), researchers stayed at the colony from late September/early October to late February/March. In 2018/19, the study timeframe was similar except no researchers were present at the colony during late November and most of December.

For 35 breeding seasons (1983/84 – 2018/19, excluding 2011/12), we recorded daily maximum temperature with a Sper Scientific min/max thermometer, placed in the middle of a dense *molle* bush (*Schinus johnstonii*) for shade. To further shade the thermometer from all sun angles, we placed it inside a three-sided wooden box, several centimeters larger than the thermometer on all sides, with loose plastic strips over the opening to allow air flow. Plastic on the bottom and top of the thermometer case suspended the thermometer inside the box. Temperature was recorded in the same manner and location throughout the study. To examine temperature trends from 1983/84 – 2018/19, we regressed the proportion of days with a maximum temperature greater than 25°C per breeding season (n days with max temp > 25/total days per season) against year. Total days per season was determined by the number of days we recorded temperature during a breeding season. The total days per season varied because we arrive and depart the colony at slightly different days each year. Additionally, we regressed the maximum temperature for each breeding season against year. We used a 25°C threshold because in previous years we found adults and chicks died from heat in temperatures as low as 26°C and 25°C, respectively (author unpublished data).

After the high temperature of 44°C on 19 January 2019, three researchers surveyed ~240 ha in and around the 400-ha colony (Figure 1) for six days to look for recently dead adults and chicks that showed signs of a heat-related death. The ~240 ha correspond to existing study areas and parts of the colony where we were simultaneously conducting our annual population survey.

External signs of a heat-related death were an open bill, one or both flippers extended from the body, and one or both feet extended behind the body (Figure 2). When we found dead adults and chicks, we marked the underside of their flippers with a marker to ensure they were only counted once. Although we found dead penguins across six days after the hot day, we had high confidence all the penguins died on 19 January 2019. Each morning we walked through the same section of the colony (~ 14 ha) where we had found and marked adults dead the day after the hot day so that we were able to observe the rates of bloating and decomposition to compare to individuals found later. We never found new dead adults in this section, indicating adult and chick mortality was confined to the hot day of 19 January 2019.

To determine the proportion of penguins that died from heat on the hot day, we surveyed two existing study areas (a northwestern section and a central section; see Figure 1) and counted all adults and chicks alive and dead. We used a chi-squared test to test for significant differences in mortality rates among adults and chicks in the two study sections. To sex adults, we measured bill depth (Boersma and García-Borboroglu 2013).We necropsied recently dead adults and chicks to exclude other possible causes of mortality (e.g., consuming toxic algae) and to weigh stomach contents. A bright red or pink stomach lining indicates an individual consumed prey contaminated with toxic algae (Shumway et al. 2003). We quantified stomach contents by weighing the penguin with a spring scale before and after we removed the stomach contents. We excluded predation as a cause of death by looking for external wounds. The main predators of adult Magellanic Penguins are southern sea lions, elephant seals, southern giant petrels, foxes, and wild cats and the main predators of chicks are gulls, skuas, armadillos, foxes and skunks (Boersma and García-Borboroglu 2013) making predation simple to rule out because external wounds are apparent. Starvation was ruled out by looking for a prominent keel bone and comparing the weight of dead adults to adults that had starved in previous years.

More penguins are found on beaches on hot days (Pozzi et al. 2013), so we quantified the number of individuals who left the breeding colony on the hot day of 19 January 2019. Adults typically leave the nesting area ~07:00 and return ~19:00 (author unpublished data). We also quantified how the number of penguins leaving the nesting area related to the daily maximum temperature in January for the years 2016-2019. We limited analysis to January to account for the changing frequency at which adults forage depending on the stage of the breeding season and the age of the chick(s) (Boersma and Rebstock 2009). Adults were counted exiting the colony with three automatic weigh scales (hereafter referred to as “scales”) placed side-by-side across a dry riverbed. When a penguin walked across a scale, the scale recorded the time of crossing, direction of travel, weight of the penguin, and, if present, the number of the radio frequency identification (RFID) chip implanted under the skin of the tarsus. The scales miss crossings when multiple penguins are on the scale simultaneously, but still capture 70% of crossings during periods of high traffic, compared to 85% of crossings during periods of low traffic (authors unpublished data).

Body Condition Index

We weighed adults and chicks that had died within one or two days before carcasses dried out or were scavenged. Penguins were weighed with a spring scale to the nearest 50 g. We measured bill length and bill depth and, unless the penguin was in rigor mortis, flipper length and foot length. We then compared their body condition to live adults and chicks weighed and measured between 11 and 27 January 2019 using a Welch two sample t-test. We used both the residual body condition index (BCI), which has previously been used with Magellanic Penguins at Punta Tombo (Hood et al. 1998), and the scaled mass index (SMI) which may account for several biases associated with a residual BCI (Peig and Green 2009). The SMI method uses a single morphological measure that is closely correlated with mass and scales the mass of individuals to what would be expected for the average length of the single morphological measure. We used Pearson's correlation coefficients to determine which of our four morphological measurements were most closely correlated to mass. To determine the scaling factor for the SMI (b_{SMA} in Equation 2 of Peig and Green 2009) we used a standardized major axis regression of mass against the length measurement using the methods of (Warton et al. 2006) with the R SMATR package. We used the same SMATR package to check which morphological measurements scale similarly to mass for both sexes.

To increase the sample size of live adults, we included the weights of adults with RFID chips that crossed the scales on 20 January 2019, the day after the hot day, because we knew those adults survived the hot day. The maximum temperature recorded in the shade on 20 January was 34°C. We used penguin weights recorded by the scales in January 2019 and their corresponding morphological measurements from a prior year to calculate body condition index, because adult morphological measurements are stable among years (Koehn et al. 2016).

Not all adults and chicks found dead were used in all analyses. Only adults and chicks found dead within one or two days of the hot day were used to calculate body condition index so we could get an accurate weight before the body became too dehydrated or scavenged. We were only able to necropsy and sex a subset of individuals because of time restraints. For clarification, sample sizes of each group are included in Table 1.

Results

We found 264 adults and 90 chicks that died on 19 January 2019 (Table 1). All dead adults and chicks showed signs of heat death from their posture and a sample were confirmed as heat deaths with a necropsy (Table 1). We underestimated death from heat because we likely missed dead penguins hidden under bushes, in deep burrows, and in parts of the colony we did not search. None of the adults or chicks had an irritated red/pink stomach lining ($n_{adults} = 26$, $n_{chicks} = 14$), and no live penguins showed signs of consuming prey contaminated with toxic algae (e.g., disoriented stumbling, vomiting), ruling out a toxic algal bloom as the cause of death. No adults or chicks had any external wounds, indicating they were not killed by predators. Adults that died of starvation in other years weighed 2.76 ± 0.47 kg for females ($n = 6$) and 2.04 ± 0.27 kg ($n = 10$) for males, which is much less than the dead adults we weighed from the heat death event (3.9 ± 0.50 kg, $n = 30$). Mortality appeared localized to Punta Tombo on 19 January 2019. There was no heat-related mass mortality observed at the nearby Magellanic Penguin breeding colonies of Pedral (143km north-northeast of Punta Tombo) and San Lorenzo (240km northeast of Punta Tombo) (Figure 3; P. García-Borboroglu, personal communication).

To provide context for the magnitude of the heat death event on 19 January 2019 we examined how many of our tagged birds were found dead from heat since the study began. Between the 1982/83 and 2019/20 breeding seasons at Punta Tombo, we marked 16,738 adults and later found 391 of those marked adults dead. Of those adults found dead in previous years, only seven appeared to have died from heat in temperatures ranging from 26°C to 43°C. Tagged dead birds were found each year between 1982/83 and 2019/20, but the seven adults that died from heat were found in the 1995/96, 2001/02, 2010/11 and the 2013/14 breeding seasons. As for chicks, we followed 3,496 chicks between 1983/84 and 2010/11 and ~1% (40 of the 3,496 chicks) died from heat (Boersma and Rebstock 2014). None of the adults or chicks found dead from the heat on 19 January 2019 were marked or part of the ongoing, long-term study.

Severe Temperature Anomaly

The maximum temperature recorded in the shade on 19 January 2019 was 44°C. This is the highest temperature recorded in the 35 years of the study. Although we have no data from the 2011/12 breeding season, air temperature records from the nearest airport (Almirante Marcos A. Zar, Trelew, Argentina; for location see Figure 3) did not exceed 40°C between September 2011 and February 2012 (https://www.ncdc.noaa.gov/cdo-web/). The airport in Trelew is approximately 91 km north of Punta Tombo, but is 22km inland, so the airport is generally hotter than Punta Tombo. For example, for the 2018/19 season the average max air temperature was nearly 4°C greater at the airport (27.6 ± 5.8°C, $n = 65$ days) than Punta Tombo (24 ± 6.6°C, $n = 110$ days, $P < 0.001$). At Punta Tombo, the maximum temperatures in the days leading up to 19 January 2019 were 36°C on 15 January, 20°C on 16 January, and 26°C on 17 January. We were not able to accurately record maximum temperature on 18 January because our thermometer was dislodged from the bush and fell to the ground. A backup temperature logger placed in the same location as our main thermometer recorded a maximum temperature of 26°C on 18 January. In seven prior breeding seasons (1983/84, 1984/85, 1988/89, 1992/93, 2010/11, 2013/14, 2017/18), air temperature recorded in the shade reached between 40 and 43°C, but we observed no heat-related mass mortality in these years.

Surface air temperatures on 19 January 2019 in the region around Punta Tombo were ~4K higher than the average surface air temperature for this date between 1981 and 2010, according to NOAA temperature anomaly plots (Figure 3). Inland Argentina, west of Punta Tombo, reached ~6K higher than the average surface air temperature for 19 January between 1981 and 2010. On

19 January 2019, we experienced a strong, warm west wind. Despite recording the hottest day since the study began, the number of days at the colony with a maximum temperature greater than 25°C appears to be declining ($P = 0.04$, $n = 36$ years).

Adult Mortality & Behavior

Adults that died from heat were in significantly worse body condition than adults that survived the hot day according to both the SMI and the residual BCI ($n_{\text{live}} = 74$, $n_{\text{dead}} = 30$, $P_{\text{SMI}} < 0.001$, $P_{\text{Residual BCI}} < 0.001$; Figure 4). Out of bill length, bill depth, flipper length, and foot length, we selected bill length as the morphological measurement to calculate the SMI because the scaling exponent was the most similar for males and females and was likely not affected by desiccation or rigor mortis. Bill depth is most closely correlated with mass (Pearson Correlation Coefficient: bill depth = 0.56, flipper length = 0.52, foot length = 0.51, bill length = 0.49), but the scaling factors for males and females (i.e., b_{SMA} in Equation 2 of Peig and Green 2009) are most similar using bill length (Bill Depth: female $b_{\text{SMA}} = 3.58$, male $b_{\text{SMA}} = 2.69$, Test for similar slopes: $P = 0.098$; Bill Length: female $b_{\text{SMA}} = 3.41$, male $b_{\text{SMA}} = 3.02$, Test for similar slopes: $P = 0.50$). Flipper length, bill length, and foot length scale similarly with mass for males and females ($P_{\text{flipper length}} = 0.71$, $P_{\text{bill length}} = 0.50$, $P_{\text{foot length}} = 0.14$). Flipper length is more highly correlated with mass than bill length or foot length. However, dead adults had shorter flippers than live adults because flippers of a penguin in rigor mortis are usually bent, rigid, and hard to measure (Welch two sample t-test, $P = 0.01$). If we had used flipper length to calculate the SMI we would have found body condition between dead and live adults to be similar (Welch two sample t-test, $P = 0.89$).

More males died than females (83% male, 17% female, $n = 94$). Dead males and females were in similar body condition according to both the SMI and BCI, but our sample size of dead females is small ($n_{\text{dead male}} = 26$, $n_{\text{dead female}} = 4$, $P_{\text{SMI}} = 0.53$, $P_{\text{residual BCI}} = 0.54$). Of the dead adults necropsied, 88% had empty stomachs ($n = 26$).

Of the dead adults found, 27% died while traveling between the nesting area and the ocean ($n = 264$; Figure 5). All other adults were found within the nesting area of the breeding colony. The scales showed more penguins left the nesting area in the morning on hot days than on cooler days to go to the beach or the ocean (Figure 6). Between 08:00 and 09:00 on the hot day of 19 January 2019, the scales recorded 163 $\text{penguins}\cdot\text{scale}^{-1}$ leaving the nesting area. This is the highest number of penguins recorded leaving between 08:00 and 09:00, and more than the average of 94 ± 28 penguins during that same hour for the month of January within the 2015/16 - 2018/19 breeding seasons. On another hot day when the maximum temperature reached 36°C, a similar number of penguins crossed the scales and departed the colony early in the day (163 $\text{penguins}\cdot\text{scale}^{-1}$ left the colony on 27 January 2017 from 07:00 to 08:00). The coldest maximum temperature in January across the 2015/16 – 2018/19 seasons was 18°C. On days where the maximum temperature was 18°C, the peak crossing time was 07:00 to 08:00 and, on average, 87 ± 9 penguins left the colony ($n_{\text{days}} = 2$).

Chick Mortality

The body condition of dead and live chicks was similar according to both the SMI and the residual BCI ($n_{\text{live}}=47$, $n_{\text{dead}}=14$, $P_{\text{SMI}} = 0.47$, $P_{\text{Residual BCI}} = 0.12$; Figure 4). We used bill length as the length measurement for chicks in the SMI method because, although we do not know the sex of the chicks, the same issues for adults surrounding sexual dimorphism and the shortening of flippers after rigor mortis likely apply to chicks as well. In contrast to adults, all 14 necropsied chicks that died from heat had food in their stomachs. The average weight of the stomach contents was 405 ± 128g and ranged from 250g to 700g. The average weight of the chicks necropsied was 2.93 ± 0.31kg.

Spatial Differences in Mortality

A higher proportion of adults died in a central, inland section of the colony (5.3% of 1153 adults) compared to a northwestern section closer to the ocean (0.7% of 1139 adults; $\chi^2 = 39.75$, df = 1, $P < 0.0001$, Figure 1). Similar proportions of chicks died in the same sections (2.9% of 556 chicks in central; 4.5% of 425 chicks in northwestern; ($\chi^2 = 1.34$, df = 1, $P = 0.25$, Figure 1). The approximate area of the central and northwestern sections is 0.20 km^2 and 0.30 km^2, respectively. More dead adults were found on the shorter, south beach (43 dead in 1.3km of beach) than the longer, north beach (12 dead in 3.4km of beach; Figure 1).

Discussion

As extreme climatic events gain more attention in the face of anthropogenic climate change, debate surrounds what is defined as an extreme event in an attempt to standardize this exponentially growing field of study (Van de Pol et al. 2017). Proposed definitions are centered on whether the event is climatologically extreme or if the biological response is extreme (Van de Pol et al. 2017). This event fits both definitions: this was the hottest temperature we recorded in the shade throughout the 35-year study and more penguins died from heat in a single day than any other since the study began in 1982.

We posit individuals died as a result of the extreme heat on 19 January. Individuals could have been dehydrated from the 36°C on 15 January, but adults had the opportunity to go to the ocean for a drink before the extreme heat on 19 January. A warm western wind on 19 January likely exacerbated the extreme temperature at Punta Tombo by transporting heat from the hotter inland region out to the coast. In previous years we have found penguins dead from heat when maximum air temperatures were between 25°C and 43°C in the shade. Other factors contributing to mortality could be wind speed, humidity, nest cover, and individual body condition. However, this is the first mass heat death mortality event at Punta Tombo, indicating a maximum air temperature threshold for Magellanic Penguins was likely surpassed on 19 January.

Adult vs. Chick Physiological Constraints

Both adults and chicks died on the hot day, but their physiological constraints were potentially not the same. Most dead adults had no food in their stomachs, while dead chicks had stomachs full of food suggesting chicks were relatively hydrated and adults were not. Penguin chicks receive all their water from their food (Janes 1997) and adults get water from food and trips to the ocean to drink. There are no water sources within the breeding colony and a trip to the ocean to drink may be costly because some penguins must walk nearly 1 km from their nest to the ocean. Where the adults died (i.e., on beaches or *en route* to them), their poor body condition index, and their empty stomachs suggest they had been fasting on land prior to the hot day and were not well hydrated, so could not survive panting through the hottest part of the day. Most heat is dissipated through the feet and flippers when the environmental temperature is lower than the body temperature (Drent and Stonehouse 1971, Boersma 1975), but penguins also pant to lower body temperature through evaporative water loss. The rate of panting increases with increasing body temperature (Boersma 1975), thus penguins must balance panting to lower body temperature and conserving water to avoid dehydration (Dawson 1982). Dehydration inhibits heat dissipation as the volume of blood available for use in heat dissipation is reduced (Miyake 2013) and the volume of water available to evaporate from respiratory surfaces is reduced (Bartholomew and Dawson 1954). Dehydrated adults or adults in poor body condition could have perished directly from dehydration or would have been more likely to die from additional heat exposure as they made the trip to the ocean to cool down and/or drink than hydrated adults in good body condition.

In contrast to adults, chicks with full stomachs of food were unlikely to be dehydrated as they get all their water from their food (Janes 1997). Heat stress inhibits orthostatic tolerance (i.e., ability to regulate blood pressure; (Schlader et al. 2016), thus, chicks could have experienced conflicting blood flow demands to the epidermis for heat dissipation and to the stomach for digestion, and so were unable to regulate their blood pressure. Additional heat generated from digestion could have also contributed to chick mortality. The metabolic rate of many organisms will increase after a meal (referred to as the specific dynamic action, heat increment of feeding, or diet-induced thermogenesis; (Maynard and Loosli 1969)), generating heat. Many studies have focused on how heat produced by specific dynamic action can be substituted for thermoregulatory heat production (Costa and Kooyman 1984, Hawkins et al. 1997). However, during periods of heat stress, the additional heat generated from specific dynamic action could be detrimental. In King Penguin chicks, the specific dynamic action increased linearly with meal size (Janes and Chappell 1995). This suggests a chick with a larger meal may be more susceptible to heat mortality than a chick with a smaller meal.

Spatial Differences in Mortality

The proportion of adults found dead was not consistent across the colony, indicating that the presence of microclimates or easier access to the beaches may have played an important role in survival. Comparing central and northwestern sections of the colony, we found more dead adults in the central, inland part of the colony (Figure 1), which sits at a higher elevation and is exposed to the sun for a longer period of the day than the latter. The central section is also slightly farther inland, and inland nests at Punta Tombo are on average 1.6°C hotter than more coastal nests (Stokes and Boersma 1998). We found more adults dead on the beach adjacent to the central section than the beach closest to the northwestern section, further suggesting adults in the central section were more heat stressed. In a catastrophic heat mortality event of Western Gulls on Santa Barbara Island, USA, mortality was also unevenly distributed over the island (Salzman 1982). Chick mortality was not related to cover, age or size of the chicks, but areas with high mortality had higher ground and air temperatures and lower wind speeds (Salzman 1982). Adults from the central section at Punta Tombo likely experienced higher temperatures for longer and/or had a longer walk to the beach than penguins in the northwestern section.

Adult Mortality & Behavior

In the central section of the colony, 5% of adults died from heat. Adult mortality of long-lived seabirds is the demographic parameter most likely to have the greatest effect on a population's growth rate (Jenouvrier et al. 2005). Seabirds typically have low fecundity and high adult survival (Bennet and Owens 2002), so high mortality of adults can have a large impact on the population size (Wooller et al. 1992, Jenouvrier et al. 2005). Annual adult survival of Magellanic Penguins at Punta Tombo ranges from 0.61 to 0.99 for females and 0.71 to 0.99 for males (Gownaris and Boersma 2019a). Heat-related mortality was male biased (83% male), but that may simply reflect the colony's overall sex-ratio bias (3 males:1 female, (Gownaris and Boersma 2019b). However, it could have been male biased because we have found males are more likely to be sighted in the colony than females (Boersma and Rebstock 2010). Punctuated adult mortality events, like this one, will likely contribute to population decline (Frederiksen et al. 2008) and could further skew sex ratios.

Even if a bird does not die in heat, heat avoidance behavior is often costly because it increases time away from the nest, leaving eggs and chicks exposed to predation (Oswald et al. 2008, Cook et al. 2020). More penguins are found on the beaches at Punta Tombo on hot days (Pozzi et al. 2013), and more adults leave the colony in the morning on hot days. However, once Magellanic chicks are ~30 days of age, adults begin to leave their chicks unattended to forage farther from the colony (Boersma et al. 1990, Boersma and García-Borboroglu 2013). Penguins at breeding colonies experiencing more frequent and more severe hot days, particularly while brooding chicks, will likely display more heat avoidance behavior, likely decreasing their reproductive success.

Body Condition Index: SMI vs. Residual BCI

Debate surrounds which method is most appropriate to determine body condition index and few authors provide justification for their choice of method (Peig and Green 2010). We used the residual BCI, previously used with Magellanic Penguins at Punta Tombo (Hood et al. 1998), and the SMI, which Peig and Green (2009) argue accounts for several biases associated with a residual BCI. We found both methods showed dead adult Magellanic Penguins killed by heat to be in worse body condition than live adults. However, the single morphological measurement selected for the SMI must be selected carefully.

The single morphological measurement that is used with the SMI should be closely correlated to mass and should scale similarly with mass for males and females (Peig and Green 2009). Of our four body length measurements, flipper length met those two criteria yet gave an inflated body condition index because the shorter flippers of dead individuals made dead individuals appear to have a higher body condition index than if we used a length measurement unaffected by desiccation and/or rigor mortis. The residual BCI method used four measurements to represent the size of the penguin, but measuring more body parts takes time. With careful selection of the single morphological measurement for the SMI, we found results were similar between the residual BCI and the SMI.

With the increase in maximum temperatures from global climate change, the impacts of thermal stress and heat-related mortality are predicted to increase for many species, humans included. Short-term adult mortality events of long-lived seabirds are likely to increase with global climate change and will likely impact adult survival and population growth rates. Seabird breeding colonies are often remote and not frequently visited, so the importance of punctuated mortality events is likely to go unnoticed. Documenting these rare events is important to understanding the ecological impacts of extreme weather and their impact on wildlife.

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Tables and Figures

Table 1. Sample sizes of groups used in analyses. Only adults and chicks found dead within one or two days of the hot day were used to calculate body condition index so we could get an accurate weight before the body became too dehydrated or scavenged. We were only able to necropsy and sex a subset of individuals because of time restraints.

	ADULTS	CHICKS
TOTAL FOUND DEAD FROM HEAT	264	90
# NECROPSIED	26	14
# DEAD W/BODY CONDITION CALCULATION	30	14
# ALIVE W/BODY CONDITION CALCULATION	74	47
# SEXED W/BILL DEPTH MEASUREMENT	94	0

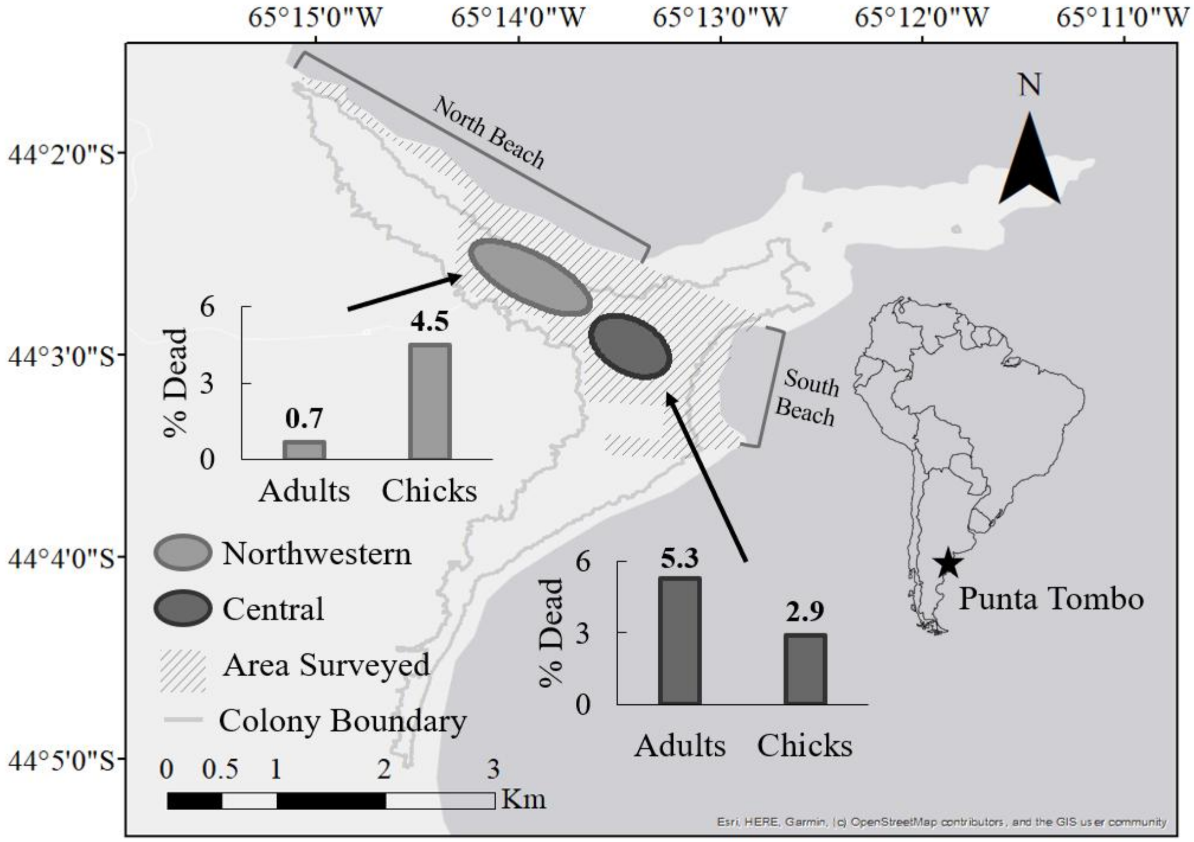

Figure 1. A higher proportion of adult Magellanic Penguins died in the more inland, central section of the colony (5.3% of 1153 adults; dark gray oval) than in a northwestern section (0.7% of 1139 adults; light gray oval). Similar proportions of chicks died in the same sections (2.9% of 556 chicks in central; 4.5% of 425 chicks in northwestern). The area surveyed for dead birds includes ~240 ha in and around the 400 ha breeding colony. More dead adults were found on the south beach (*n* = 43) than the north beach (*n* = 12).

Figure 2. Dead adult Magellanic Penguins in the heat-relief posture with feet extended behind the body, flippers extended away from the body, and bills open, as if the penguins died while panting.

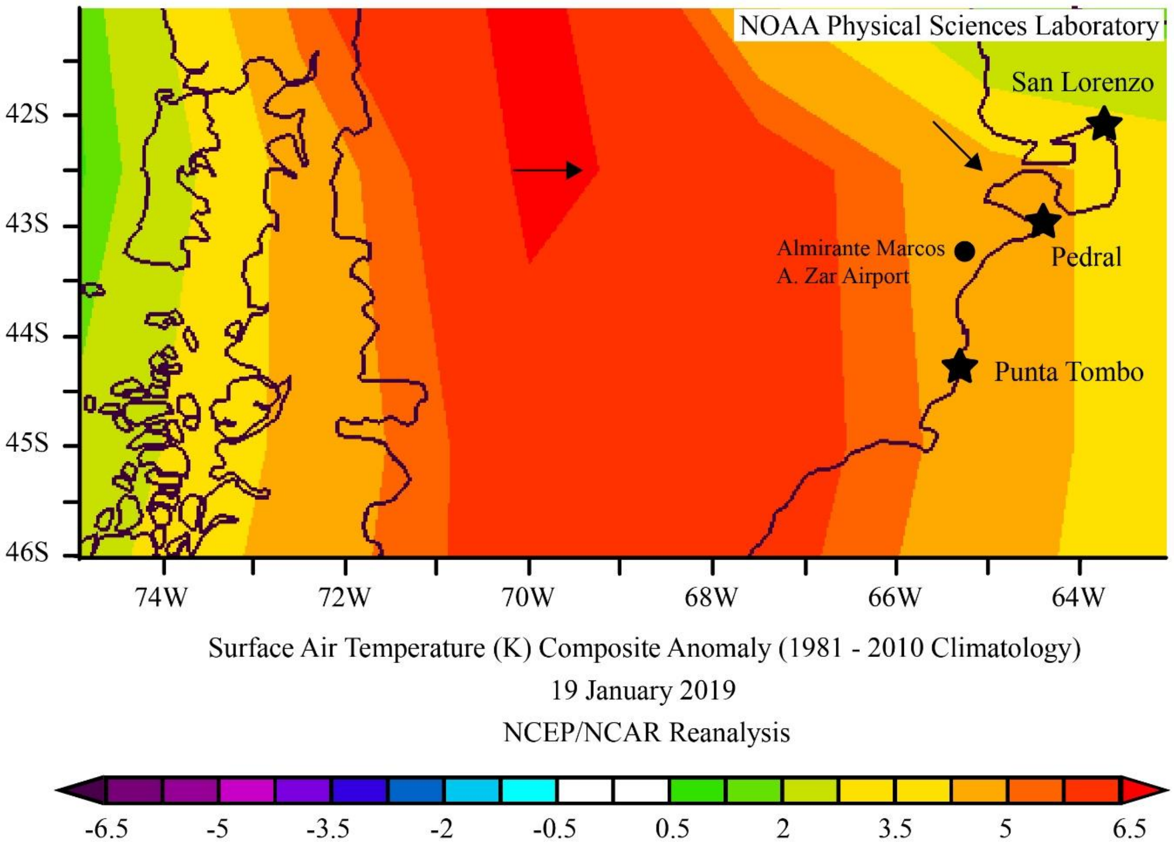

Figure 3. Temperatures on 19 January 2019 were higher than the average between 1981 and 2010 at the Punta Tombo Magellanic Penguin breeding colony, where mass heat mortality occurred. The temperature scale unit of measure is Kelvin. Arrows represent surface vector winds. No mass heat mortality was observed at the San Lorenzo or Pedral breeding colonies. Image and vector wind direction provided by the NOAA/ESRL Physical Sciences Division, Boulder Colorado from their website at http://www.esrl.noaa.gov/psd/

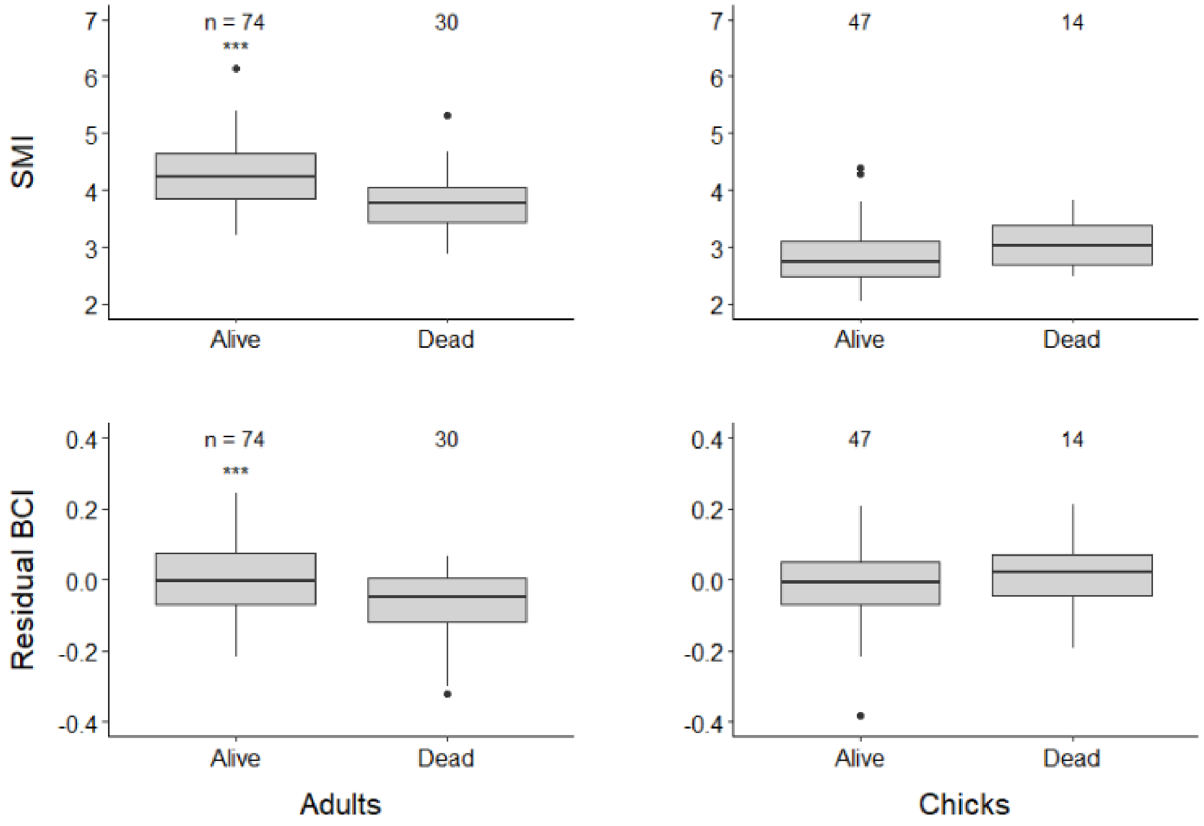

Figure 4. Adult Magellanic Penguins that died on the hot day of 19 January 2019 were in worse body condition than adults that survived the hot day (left) according to both the scaled mass index (top) and the residual body condition index (bottom; n_{live}=74, n_{dead}=30, $P_{\text{SMI}} < 0.001$, $P_{\text{Residual BCI}} < 0.001$). The body condition of dead and live chicks were similar (right) using both the scaled mass index and the residual body condition index (n_{live}=47, n_{dead}=14, $P_{\text{SMI}} = 0.47$, $P_{\text{Residual BCI}} = 0.12$) but all dead chicks had food in their stomachs. *** = P value < 0.001.

Figure 5. Of the dead adult Magellanic Penguins found, 27% were between the nesting area and the ocean, apparently dying on their way to the ocean (*n* = 264).

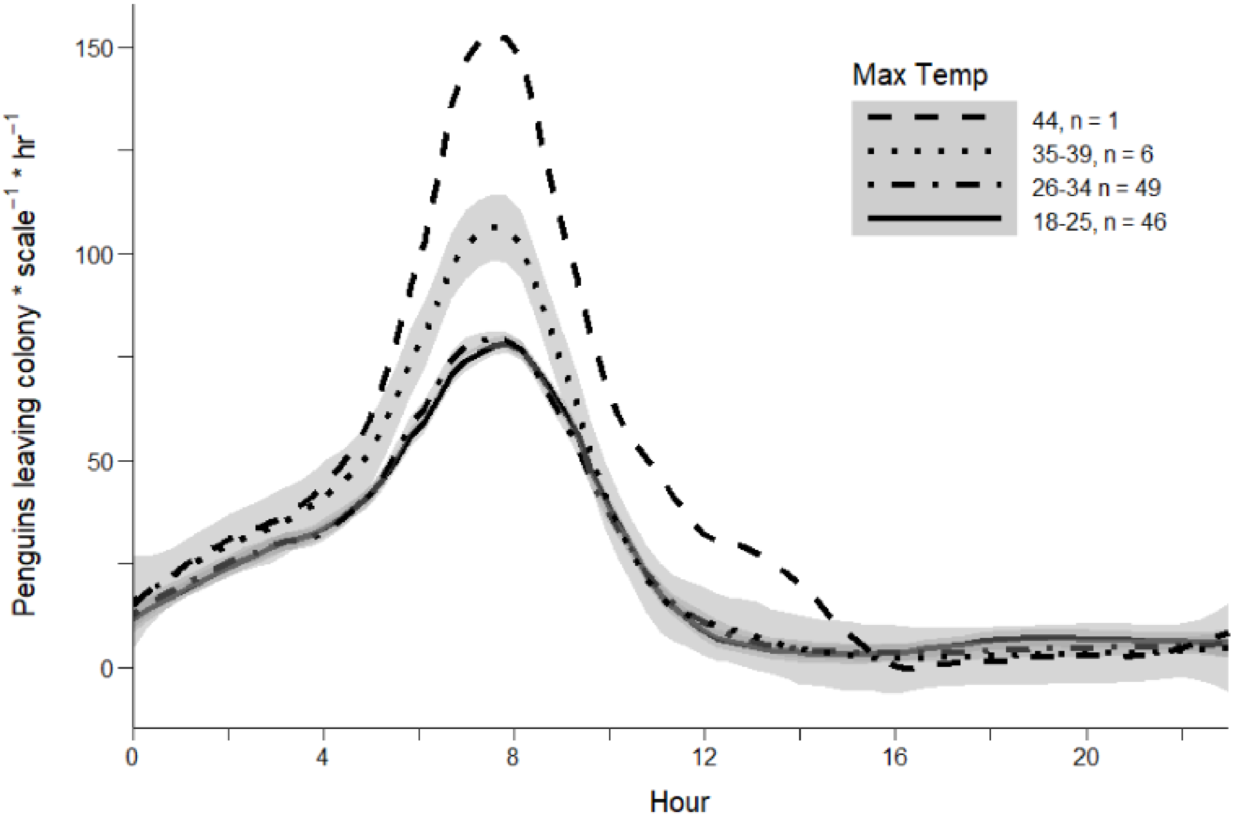

Figure 6. More Magellanic Penguins leave the Punta Tombo colony between 07:00 and 09:00 on hot days. We used automatic weigh scale data in January from the breeding seasons 2015/16 – 2018/19. The curves are fit with loess smoothing with the span at 30%. Grey boundaries around the lines represent standard errors. In the figure caption, n represents the number of days within each temperature range.

Chapter 2

Sex, not body size, predicts foraging success and efficiency of a marine predator

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Abstract

Body size can affect species' foraging success and efficiency which consequently influence survival and/or reproductive success. Males of most seabird species (74%) are larger than females and threatened species are more likely to have skewed sex ratios than non-threatened species. Recent studies of declining seabird colonies found that female mortality is higher than male mortality and suggest this is because larger males have higher foraging success than smaller females, however few have quantified the foraging success of males and females and/or of large and small conspecifics. We used automatic weigh scales and linear mixed models to quantify the foraging success of sexually size dimorphic Magellanic penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina between the 2015/16 and 2018/19 breeding seasons ($n_{\text{foraging trips}} = 802$, $n_{\text{individuals}} = 137$). We found males brought back 38% more food (mean = 0.18 kg, SE = 0.03 kg) than females even though males are only 18% larger in mass than females. Size did not have an influence on foraging success (i.e. large males did not bring back more food than smaller males). Males were more efficient foragers than females, bringing back 69% more food (mean = 0.29

kg/day, SE = 0.04 kg/day) per day than females. These results suggest it is not size but other sex-specific foraging behaviors that are driving differences in foraging success, foraging efficiency, and potentially mortality rates.

Introduction

An organism's body size relates to important physiological and ecological traits (Peters 1983; e.g., metabolic rate (Hemmingsen 1960), cost of movement (Fedak and Seeherman 1979), time spent sleeping (Zepelin and Rechtschaffen 1974), and ingestion rate (Farlow 1976)) and is under selective pressure, allowing species to persist and adapt as food resources fluctuate (e.g., Darwin's finches; Grant and Grant 2002). Body size can also constrain what food resources an individual can access (Mittelbach 1981), affecting individual foraging success and consequently survival and reproductive success (Lynch 1977).

Within a species, sex-specific body size differences (i.e., sexual size dimorphism) may arise from a combination of mechanisms (e.g., sexual selection (Darwin 1871, Fairbairn 2007), intersexual competition hypothesis (Lande 1980, Slatkin 1984, Reeve and Fairbairn 2001), dimorphic niche hypothesis (Darwin 1871, Hedrick and Temeles 1989, Andersson 1994), and fecundity hypothesis (Selander 1972, Snyder and Wiley 1976)). With some exceptions, females are commonly larger than males in invertebrates, amphibians, and reptiles, while males tend to be larger in birds and mammals (Andersson 1994). Although many studies have investigated the drivers of sexual size dimorphism (e.g., Fairbairn and Shine 1993, Zavalaga et al. 2007, Cook et al. 2013, Trefry and Diamond 2017), few have examined its direct consequences under rapid global change. For example, if sexual size dimorphism arose to allow species to partition resources and reduce intersexual competition, then rapid changes in prey abundance or distribution could lead to size- or sex-specific consequences. Here, we examine how an individual's sex and body size affect its foraging success, efficiency, and trip frequency in a sexually size-dimorphic seabird, the Magellanic Penguin (*Spheniscus magellanicus*).

Across seabirds, males are larger than females in ~75% of species (Fairbairn and Shine 1993). The size dimorphism is rarely more than 20% of average mass (Schreiber & Burger 2001) but can still result in tradeoffs. Larger individuals can dive deeper and for longer (Wienecke and Robertson 1997, Zavalaga et al. 2007), consume a greater size range of prey (Koffijberg & Vaneerden 1995, Kato et al. 2000, Forero et al. 2002), have a more efficient metabolism (Peters 1983), have a more favorable surface-area-to-volume ratio for conserving heat (Lustick 1984), have a larger food storage capacity (Jackson 1992), and, for flying seabirds, larger individuals can forage more efficiently in strong winds than smaller individuals (Shaffer et al. 2001). Smaller individuals, conversely, have lower total energy requirements (Ellis and Gabrielsen 2002), greater maneuverability (Weimerskirch et al. 2006), and, in light wind conditions, smaller flying seabirds can travel greater distances more efficiently to forage than larger ones (Shaffer et al. 2001).

Independent of size, sex can also drive variation in foraging behavior. Males and females may have different foraging locations (Austin et al. 2019), prey preferences (Bearhop et al. 2006, Camphuysen et al. 2015), or foraging strategies (Weimerskirch et al. 2006). Sex-specific foraging behavior may help reduce intraspecific competition (González-Solís et al. 2000, Bearhop et al. 2006, Camphuysen et al. 2015), or be driven by sex-specific reproductive roles (Lewis et al. 2005, Austin et al. 2019).

Most research on sex-specific foraging behavior is conducted on sexually size-dimorphic species, and many have argued that size is what drives sex-specific foraging behavior (González-

Solís et al. 2000, Lewis et al. 2005, Bearhop et al. 2006), yet analyses relevant to this issue have not always accounted for individual size. Studies of monomorphic species have found significant differences in the foraging behavior of males and females (Lewis et al. 2002, Peck and Congdon 2006, Pinet et al. 2012). To date, only a few studies of foraging behavior have attempted to disentangle the effects of sex from body size (Zavalaga et al. 2007, Orben et al. 2015).

Male Magellanic Penguins are 17% heavier than females (Boersma and García-Borboroglu 2013), have larger bills (8% longer and 15% deeper; Boersma and García-Borboroglu 2013), dive deeper during the breeding season (Walker and Boersma 2003), and consume a greater size range of prey (Forero et al. 2002) than females. At one of the species' largest breeding colonies (Punta Tombo, Argentina), males have a higher annual survival probability than females (males: mean = 0.89, SD = 0.11; females: mean = 0.85, SD = 0.13). This has led to an increasingly male-biased sex ratio. At the average age of male sexual maturity, seven years, the average sex ratio was 3 males to 1 female for the 1989 – 2009 cohorts at Punta Tombo and, as each cohort aged, the cohort sex ratio became increasingly male biased (Gownaris and Boersma 2019). Higher male survival probabilities may be due to their larger body size, which may enable them to dive deeper and for longer and eat a larger size range of prey. Even so, there has not been consistent selection for larger individuals (Koehn et al. 2016).

We sought to determine whether sex or body size is a better predictor of individual foraging success and efficiency in Magellanic Penguins. Understanding this relationship can help elucidate drivers of variation in survival and reproductive success in this top marine predator. If body size best predicts foraging metrics, it suggests a certain size allows better access to prey. Conversely, if foraging metrics differ by sex, independent of body size, it could indicate males and females have different chick provisioning rates, nutrient requirements, or foraging strategies.

In addition, because we examined foraging success and efficiency at the level of a foraging trip, rather than at the level of an individual penguin (using something such as, e.g., foraging success per month), we wanted to examine whether individuals were making up for lower foraging success and efficiency per trip by taking more frequent trips. This information was critical for further contextualizing our results in terms of the potential implications for observed differences in sex-specific survival and chick provisioning rates.

Methods

Study System

We conducted our study at the breeding colony of Punta Tombo, in Chubut Province, Argentina (44.0458°S, 65.2238°W). Although one of the Magellanic penguin's largest colonies, with ~120,000 breeding pairs (Boersma unpublished data), the population at Punta Tombo has declined by 57% since 1987 (Rebstock et al. 2016, Clark-Wolf et al. 2023) even as colonies to the north are increasing (García-Borboroglu et al. 2022). At Punta Tombo, penguins nest under bushes and burrows (Stokes and Boersma 1998) and are serially monogamous (Wagner et al. 2022), with females typically laying two-egg clutches. Both parents then care for the chicks until they either die or fledge ~10 weeks later (Cappello and Boersma 2021). Breeding success is largely determined by prey location and abundance (Boersma et al. 2009); on average, 39% of chicks die of starvation—the most frequent cause of chick death (Boersma and Rebstock 2014). Magellanic penguins forage primarily on pelagic schooling fishes such as anchovy (*Engraulis anchoita*) and hake (*Merluccius hubbsi*), and to a lesser extent crustaceans (*Artemisia longinaris*) and squid (*Loligo* and *Illex* sp.) (Frere et al. 1996, Forero et al. 2002).

Foraging trip distance of breeding adults varies during chick-rearing, depending on whether adults are caring for chicks ≤ 30 days of age (hereafter "guard stage"), or chicks > 30 days of age (hereafter "post-guard stage"; Boersma and Rebstock 2009). During the guard stage, males and females take turns making short provisioning trips (guard stage trip distance: mean = 61 km, SE = 3.9 km; Boersma and Rebstock 2009) and brooding their chicks. During the post-guard stage, chicks can thermoregulate, so they can be left alone at the nest while adults take longer provisioning trips (post-guard trip distance: mean = 111 km , SE = 5.0 km; Boersma and Rebstock 2009). Female and male trip lengths at Punta Tombo are similar and negatively correlated with reproductive success; as trip length increases, the probability of losing both chicks increases (Boersma and Rebstock 2009a).

We focused on confirmed breeding adults in this study. Nonbreeders have lower energetic requirements because they are not feeding chicks and only have to maintain their own body condition. Thus, we assumed that the influence of sex and size on foraging success would likely be more pronounced in breeders during periods of high energy requirement. To determine an individual's breeding status and breeding outcome, we checked marked nests on a 10-day schedule. We considered adults to be breeders if they were the adult seen most frequently in a nest with either eggs or chicks, and were sighted in the nest at least five times during breeding. If the nest wasn't checked until after chicks hatched, adults were considered breeders if they were the only adult of their sex seen in the nest.

Measuring Body Size & Sexing

At the time adults were implanted with radio frequency ID (RFID) tags (more info on RFID tagging in *Foraging Success and Efficiency*), we measured the bill length and depth to the nearest 0.01cm and flipper length and foot length to the nearest 0.1cm. Sex was determined by bill depth; previous work shows this is a reliable sexing method with 95% accuracy (Bertellotti et al. 2002). Measurements do not change once an individual is an adult (Koehn et al. 2016), but adults are likely to be remeasured at some point in the study. To account for repeated measures, we used the average measurement. Through visual examination of the distribution of differences across measures for an individual, we identified and removed unreliable measurements.

Foraging Success and Efficiency

To noninvasively quantify the foraging success and efficiency of Magellanic penguins at Punta Tombo, we deployed automatic weighbridges along a heavily used pathway during the 2015/16 through 2018/19 breeding seasons. The pathway led from the shoreline to a nesting area of the colony where we had implanted a subset of females and males with RFID tags (see Boersma and Rebstock 2009b for RFID implantation methods). The weighbridges consisted of an electronic scale and an RFID reader. If a penguin implanted with an RFID crossed the weighbridge, its weight, direction of travel (into or out of the colony), the date and time, and its unique RFID number were recorded automatically.

We defined foraging success as the difference between consecutive outgoing and incoming weights (Δ mass kg/foraging trip), and foraging efficiency as the change in mass divided by the length of the foraging trip (Δ mass kg/day). The change in mass for both metrics includes stomach contents (i.e., the chick meal) as well as any mass the adult assimilated or expended during transit (Lescroël et al. 2010). Penguins can choose to walk around the weighbridges, so to ensure we were capturing a foraging trip, we used consecutive leaving (to forage) and arrival (at nesting area) crossings with time intervals less than the average foraging trip length plus two standard deviations, as recorded by GPS tags deployed concurrently on breeding adults during the corresponding chick-rearing stage. Average foraging trip length plus two standard deviations, as determined by the GPS tags, during guard and post-guard stages were 3.17 and 4.63 days, respectively, during the years we deployed the weighbridges. We limited foraging trips to the guard and post-guard stages because we recorded few foraging trips during incubation, and the temporal and spatial constraints of incubation foraging trips are different than chick provisioning trips. Any trip recorded by the weighbridges that exceeded these trip lengths for the respective season stage was removed, as it likely indicated the penguin had walked around the weighbridges.

To ensure the weighbridges accurately weighed penguins, we caught 325 penguins ($n_{2015/16} = 202$, $n_{2016/17} = 38$, $n_{2017/18} = 65$, $n_{2018/19} = 20$) immediately after they crossed a weighbridge and compared the weighbridge weight to a weight taken with a 6 kg spring scale that weighed to the closest 0.05kg. To determine if year or weighbridge ID had an effect on weight accuracy, we built a series of linear models with weighbridge weight as the response variable, spring scale weight as the predictor variable in all models, and including all possible combinations of weighbridge ID and year. The model with the lowest AIC included year as a predictor but did not include weighbridge ID (Supplementary Table 1), indicating weighbridge accuracy varied by year but not by weighbridge. However, the R^2 values between spring scale weight and weighbridge weight were ≥ 0.98 for all years, indicating that weighbridge weights are very strongly correlated with spring scale weights (Supplementary Figure 2).

The average absolute difference and standard deviation between the weighbridge weight and the spring scale weight for all years combined was 0.089kg ± 0.076kg ($n = 325$). The average spring scale weight for this sample was 4.36kg, making the average error 2% of the average total mass. For the study period, we captured 802 foraging trips of breeding adults

(n_{female} = 430, n_{male} = 372) during chick-rearing with the weighbridges. See Table 1 for the number of trips per year, season stage, and sex.

Foraging Trip Frequency

To quantify foraging trip frequency, we calculated the number of foraging trips per day as the total number of trips during a tracking tag deployment divided by the number of days the tracking tag was deployed. Tracking tags were deployed during guard and post-guard stages on breeding adults from the 1995/96 breeding season to the 2022/23 breading season, excluding 2011/12 and 2020/21. Six types of tags (with various sizes, shapes, and levels of accuracy) were used over this period as tracking tag technology improved. Some tags obtained and sent location data via satellite (ST10 and ST20 made by Sirtrack, SPOT-275C made by Wildlife Computers) while others communicated with satellites for location information but where archival tags and had to be physically retrieved to collect the data (nanoFix-GEO made by PathTrack, F2G 134A and F5G 334A/434A made by Sirtrack). Tags were attached and data were filtered and processed as described in Rebstock et al. 2022. Only complete foraging trips where the tag captured the penguin leaving the nesting area, foraging, and returning to the nesting area were used to ensure reliable trip duration. If the battery died or the tag fell off during the trip, these data were removed from the analysis.

Hypotheses & Structure of Models

We formulated several competing hypotheses for how sex and size could affect foraging success and efficiency and built statistical models associated with each. Our first hypothesis posits that sex, not size, drives foraging metrics (Hypothesis 1; Model notation: sex; Figure 1A,), and we predict males will have higher foraging success and efficiency than females as in many dimorphic and monomorphic seabirds, males provision chicks more than females (Gray and

Hamer 2001, Cornioley et al. 2017). Our second hypothesis posits that size, not sex, drives foraging success and efficiency, and that the effect of size on foraging success is linear (Hypothesis 2; Model notation: size; Figure 1B). Again, we expected that males would have higher success on average because, as the larger sex, they can dive deeper and for longer than females (Walker and Boersma 2003) and eat a larger size range of prey (Forero et al. 2002); thus, our third hypothesis posits that size and sex interact to drive foraging success, for a combination of the reasons outlined above, and that the effect of size on foraging success is linear (Hypothesis 3; Model notation: sex + size:sex; Figure 1C). We also hypothesized a nonlinear relationship between size and foraging outcomes, either including (Hypothesis 4; Model notation: sex + size:sex + size^2:sex; Figure 1D) or excluding (Hypothesis D; Model notation: size + size^2; Figure 1E) an interacting effect of sex, because as body size increases, we expect the volume or stomach capacity of an individual to increase cubically. Finally, we considered a null hypothesis of no relationship between size or sex and foraging success and efficiency (Hypothesis 6; Model notation: Intercept; Figure 1F). Note that for the models associated with Hypothesis 3 and Hypothesis 4, because size and sex are highly correlated, we included an effect of sex plus an effect of size nested within sex, rather than a simple interaction.

We examined the relationship between linear size metrics (bill length, bill depth, flipper length, foot length) and each of the foraging metrics (foraging success and foraging efficiency) separately, as there is evidence that each of these morphometrics could influence foraging success in unique ways. For examples, shags and penguins with larger bills can capture larger prey (Kato et al. 2000, Forero et al. 2002). Flippers propel penguins through the water (Davis and Renner 2003) allowing them to capture prey. Feet are used as rudders (Davis and Renner 2003) and may be important for maneuverability while foraging. We also examined the relationship between an overall body size metric and our foraging metrics. Overall body size was calculated as the first principal component (PC1) of a principal components analysis (PCA) of all four linear size measurements (PC1 explained 80% of the variance). All morphometrics were standardized (z-scored) prior to analysis and the PCA was conducted with the standardized morphometrics.

To compare our competing hypotheses, we built two sets of 22 linear mixed effects models, with either foraging success or foraging efficiency as the response variable. This model set encompassed one model associated with Hypothesis 1 (Figure 1A), one model associated with Hypothesis 6 (Figure 1F), and five models associated with each of the Hypotheses 2 through 5 (Figure 1B – 1E), where each of the five models included a different size metric (see Tables 2 and 4 for all models).

Along with the sex and size structure, all models included season stage (guard or post-guard), the number of chicks in the nest at the start of the trip (1 or 2), and ID tag type (all penguins had either a web tag or a flipper band in addition to the RFID tag). Trip duration was included as a predictor in the set of foraging success models but not in the set of foraging efficiency models, as it is incorporated in the response variable. These predictors were included in all models as there is strong evidence that they can influence foraging success and efficiency. For example, Magellanic Penguin foraging constraints vary with season stage (Boersma and Rebstock 2009a), seabirds can adjust provisioning based on brood size (Ricklefs 1990), and Magellanic Penguin trip duration is related to reproductive success and foraging site fidelity (Boersma and Rebstock 2009a, Rebstock et al. 2022a). While many studies show that flipper bands increase swimming costs and reduce adult penguin survival (citations within Jackson and Wilson 2002), some found no effect on forage trip duration (Boersma and Rebstock 2009b) or over-winter survival (Hindell et al. 1996). Year and individual ID were included as random effects in all foraging success and foraging efficiency models to account for repeated measures at each of these scales; the results of likelihood ratio tests supported this decision.

Because we measured foraging success and efficiency at the foraging trip level, rather than at the level of an individual (e.g., using a metric such as weight gain on all foraging trips that an individual took in a month) we wanted to evaluate whether individuals could be compensating for lower foraging success and efficiency per trip by taking more frequent trips. To determine if foraging trip frequency varied with sex, we built linear mixed effects models with the number of trips per day as the response variable and all possible combinations of sex, season stage, and device model as predictors. We opted not to include body size metrics and ID tag type in trip frequency models based on results of the foraging success and efficiency models. Device model was included as a predictor because tag technology greatly improved across the 25 years we deployed tags, and the size and shape of the tags can affect swimming and foraging (Bannasch et al. 1994, Wilson et al. 2015). Penguin ID was included as a random effect in all trip frequency models, but not year, based on the results of likelihood ratio tests.

Model Implementation

Prior to model building, we calculated Pearson correlation coefficients and confirmed that no predictors, except the size metrics with each other, as well as size and sex, were highly correlated ($r > 0.7$). While the five size metrics were highly correlated with each other, they never appeared in the same models. As mentioned previously, rather than build models with a simple interaction between sex and size, we built models with an effect of sex and an effect of size nested within sex. Residuals were evaluated for normality, homogeneity of variance, and independence. As described above, we used likelihood ratio tests to evaluate the importance of including penguin ID and year as random effects.

To rank the models, we used an information-theoretic approach (Burnham and Anderson 2002). Models were ranked by Akaike Information Criterion (AIC) where lower AIC values indicate more parsimonious models. To compare all other models to the top-ranked model, we calculated ΔAIC, the difference between each candidate model AIC and the lowest overall AIC value. During model selection, models were fit with maximum likelihood estimation. To evaluate the effect size of the parameters, models were fit with restricted maximum likelihood. We found a long-tailed distribution in our residuals, so we bootstrapped (n = 1000) the 95% confidence intervals (CIs) reported in the most competitive models. Any predictors with a 95% CI that encompassed zero were considered uninformative. Models were built using the *lme4* package (Bates et al. 2015) in R 4.2.0 ("R Core Team" 2024).

Results

Foraging Success (Δ mass kg/foraging trip)

The foraging success model representing Hypothesis 1, estimated as the change in mass during a foraging trip, (sex) was the most strongly supported, based on AIC (Table 2). In this model, males were estimated to bring back more food (mean = 0.18 kg, SE = 0.03 kg) than females (Table 3), as we had expected. On average, breeding adults brought back more food during the post-guard stage (post-guard mean = 0.17 kg, SE = 0.02 kg) than the guard stage, and more food if they had two chicks (two chick mean = 0.12 kg, SE = 0.03 kg) compared to one (Table 3). Trip duration and ID type (web tag or flipper band) were not significant predictors of foraging success (Table 3).

Other comparable models (<2 ΔAIC) included the model representing Hypothesis 4 (sex + size:sex + size^2:sex) with bill depth as the size metric, and the model representing Hypothesis 3 (sex + size:sex) with flipper length or PC1 as the size metric (Table 2). In the two models representing Hypothesis 3, the confidence intervals on the size coefficients for both males and females overlapped zero, indicating no size effect (Table 3). In the sex + size:sex + size^2:sex structure with bill depth as the size metric, the confidence intervals on the size:sex and size^2:sex coefficients for males overlapped zero, indicating no size effect. For females, the coefficients for the size metrics were negative and confidence intervals did not overlap zero (Table 3), indicating that the relationship between female bill depth and foraging success is negative and nonlinear (i.e., as size increases, foraging success decreases exponentially).

Foraging Efficiency (Δ mass kg/day)

With foraging efficiency (Δ mass kg/day) as the response variable, the most supported two models (within <2 ΔAIC) included one model associated with Hypothesis 4 (sex + size:sex + size^2:sex) with bill depth as the size metric and another model associated with Hypothesis 1 (sex) (Table 4). In the sex + size:sex + size^2:sex model, the confidence intervals of size coefficients for both males and females overlapped zero, indicating no discernible effect of size (Table 5).

In the model that included only sex, males were estimated to bring back 55% more per day (mean = 0.29 kg/day, SE = 0.04 kg/day) than females (Table 5). During the post-guard stage, breeding adults brought back 21% more per day (mean = 0.09 kg/day, SE = 0.03 kg/day) than during the guard stage and 18% more per day (mean = 0.08 kg/day, SE = 0.04 kg/day) if they had two chicks compared to one (Table 5). ID type had no significant effect on foraging efficiency (Table 5).

Trip Frequency (trips/day)

The most supported trip frequency model, according to AIC, included sex and season stage. As determined by this most supported model, males took more trips per day than females, on average (Table 6). Trip frequency varied with season stage, with adults making more trips during the guard stage than the post-guard stage (Table 6). Device type did not influence trip frequency. The second-ranked competing model had a ΔAIC of 3.16 and only included sex as a predictor.

Discussion

Our results suggest sex-specific foraging behaviors are driving differences in foraging success, efficiency, and potentially mortality rates. We found males brought back 30% more food than females (Figure 2) even though males are only 18% larger in mass than females. Males were more efficient foragers than females, bringing back 55% more food per day than females (Figure 2).

We found little to no support for an effect of size on either foraging success (Δ mass kg/foraging trip) or foraging efficiency (Δ mass kg/day). In the top four competing foraging success models (as ranked by AIC), most of the confidence intervals for the size coefficients overlapped zero, indicating no effect of size on foraging success (Table 3). In only one of the top competing models with a sex + size:sex + size^2:sex structure and bill depth as the size metric, confidence intervals for females' size metric did not overlap zero and the effect size was negative, suggesting females with larger bills have lower foraging success than females with smaller bills. In all other competing models, small females were predicted to have similar foraging success and efficiency as large females and small males were predicted to have similar foraging success and efficiency as large males. In the top two foraging efficiency models (as ranked by AIC), size had no effect on foraging efficiency (Table 5).

Females could compensate for their lower foraging success and efficiency by making more trips, yet when we examined trip frequency, we found that males made more trips per day than females (Table 6). The higher foraging success, efficiency, and trip frequency of males could be driven by one or a combination of several mechanisms: sex-specific reproductive roles, sexual foraging segregation, intraspecific competition, or other environmental factors.

The higher foraging success and efficiency of males could be explained by the sexes' reproductive roles. Sexual size dimorphism, in some cases, may have evolved from sex-specific reproductive roles (Lewis et al. 2005 and citations within). However, in both sexually size-monomorphic and -dimorphic seabirds, one sex will provision chicks more than the other. Males of the sexually monomorphic Manx shearwaters (*Puffinus puffinus*) feed their chicks more frequently than females (Gray and Hamer 2001). Monomorphic common terns (*Sterna hirundo*) have distinct parental roles, with females spending significantly more time incubating and defending the nest while males do a majority of chick provisioning (Wiggins and Morris 1987). In some sexually dimorphic species, like the Emperor penguin (*Aptenodytes forsteri*), chicks get larger meals from males and reproductive success is related to male, not female, body mass (Cornioley et al. 2017). Male wandering albatross (*Diomedea exulans*) take shorter and faster trips than their smaller female conspecifics, while still providing larger meals (Weimerskirch and Lys 2000). Not only do male seabirds tend to provision their chicks more than females, but males tend to be more fixed in their reproductive investment (Weimerskirch et al. 2000, Gray and Hamer 2001). In several seabird species, females, but not males, adjust their food provisioning to their brood size or the begging of their chicks (Quillfeldt et al. 2004, Leclaire et al. 2010, Spelt and Pichegru 2017). According to other metrics, male and female Magellanic penguin reproductive investment seems to be divided evenly; for example, males and females spend similar time incubating and both sexes provision and defend chicks; Boersma and García-Borboroglu 2013). Our results, however, indicate that males provision chicks with more food per foraging trip and more frequently than females (see also Forero et al. 2002).

Sexual segregation during foraging (either through spatial, temporal or diet segregation) can reduce competition between the sexes (Mancini et al. 2013) and could result in sex-specific foraging success and efficiency. At Punta Tombo, there is some evidence that males and females use similar foraging grounds (Boersma and Rebstock 2009a), but this could be colony specific. At one colony in their southern range, for example, females took longer foraging trips during incubation (Raya Rey et al. 2012), indicating that they may be foraging in a different location than males. The Magellanic penguin diet is opportunistic and varies with prey availability and environmental conditions (Thompson 1993, Frere et al. 1996, Clausen and Pütz 2002, Boersma et al. 2009), yet stable isotope analysis has indicated that the diets of male and female Magellanic penguins do differ, though slightly, at the end of chick-rearing (Forero et al. 2002, Raya Rey et al. 2012). During periods of low prey abundance, males and females may adopt different foraging strategies, with females extending their trip distance (horizontal direction) and males diving deeper (vertical direction; Raya Rey et al. 2012). If females are extending their foraging range during periods of low prey availability, they may need to invest more in self-maintenance and thus, provision chicks less.

Sexual segregation during foraging could be a result of reducing intraspecific competition; thus, colony size can influence the degree of sex-specific foraging differences. At a large colony, local prey is likely to be depleted, causing individuals, on average, to travel farther for food than they would at smaller colonies (i.e., Ashmole's Halo (Birt et al. 1987, Lewis et al. 2001, Ainley et al. 2006)). Our study is limited to Punta Tombo, one of the largest breeding colonies for this species, but there is strong evidence that intraspecific competition has sex-specific consequences on foraging behavior and that colony size can influence the degree of sex-specific foraging differences. At a smaller Magellanic penguin breeding colony, Isla de los Estados, with 1,600 breeding pairs, the sexes showed only slight differences in foraging behavior and no differences in diet (Rosciano et al. 2018). Adelie penguins (*Pygoscelis adeliae*) at the large Cape Crozier breeding colony (~275,000 breeding pairs) start to extend their foraging range as the chick-rearing period progresses, but females swim farther and males dive deeper (Lescroël et al. 2010, 2014).

Environmental conditions could be masking the effect of size on foraging success and efficiency. For example, in thick-billed murres (*Uria lomvia*), foraging behavior metrics were significantly correlated with body size and predicted the wintering foraging strategies of individuals (Orben et al. 2015). This pattern was seen across three different colonies where the body size of individuals was similar within each colony but differed across colonies. Other work has found that environmental conditions, like the predictability of prey, could influence intersexual foraging behavior; when prey are unpredictable, this can reduce intersexual behavioral differences (Courbin et al. 2018). In future work, it may be productive to examine the effect of size on foraging metrics across colonies experiencing different environmental conditions.

Conclusions

Here we determined that sex, not body size, best describes the individual foraging success and efficiency of a long-lived seabird, the Magellanic penguin, at a declining colony. We found that males had higher foraging success, efficiency, and trip frequency than females. These results can help elucidate drivers of variation in survival and reproductive success of this top marine predator. The higher foraging success and efficiency of males could be driving the higher survival of males, resulting in a strongly male-biased sex ratio at the Punta Tombo breeding colony. Given that males provision chicks more than females, reproductive success may be related more to the foraging success of males than females.

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Tables & Figures

Table 1. The number of breeding Magellanic penguin foraging trips at the Punta Tombo, Argentina breeding colony recorded by the weighbridges per year, season stage and sex used in the foraging success and foraging efficiency linear mixed models. These trips come from 137 unique individuals.

Breeding Season	**♀ Guard**	**♀ Post-Guard**	**♂ Guard**	**♂ Post-Guard**
2015/16	70	159	54	118
2016/17	49	18	58	14
2017/18	47	45	54	39
2018/19	7	35	9	26

Table 2. Model selection results, including the number of parameters (*K*), the value of the log likelihood function at its lowest (optimal) value (logLik), Akaike's Information Criterion (AIC), and the difference between AIC for a given model and AIC for the top-ranked model (ΔAIC). Foraging success (Δ mass kg/foraging trip) of Magellanic Penguins is the response variable in all models. The predictor variables (i.e., model structures) are described in the main text and correspond to the six different hypotheses outlined in Figure 1. The notation following each model structure indicates the corresponding hypothesis number (e.g., H1 = Hypothesis 1). Models with size included one of five different size metrics (bill depth, bill length, flipper length, foot length, or the first principal component of a principal components analysis integrating all size variables). All models also included season stage, number of chicks in the nest, trip duration, and tag type as fixed effects and penguin ID and year as random effects. Models within 2 AIC of the top-ranked model are bolded.

Foraging Success (Δ mass kg/foraging trip)

Model Structure	**Size Metric**	***K***	**logLik**	**AIC**	**ΔAIC**
Sex (H1)		**9**	**-195.77**	**409.55**	**0**
Sex + Size:Sex + Size^2:Sex (H4)	**Bill Depth**	**13**	**-192.39**	**410.78**	**1.24**
Sex + Size:Sex (H3)	**Flipper**	**11**	**-194.48**	**410.95**	**1.41**
Sex + Size:Sex (H3)	**PC1**	**11**	**-194.64**	**411.28**	**1.73**
Sex + Size:Sex (H3)	Bill Length	11	-194.81	411.62	2.07
Sex + Size:Sex (H3)	Bill Depth	11	-194.96	411.91	2.37
Sex + Size:Sex (H3)	Foot Length	11	-195.74	413.49	3.94
Sex + Size:Sex + Size^2:Sex (H4)	PC1	13	-193.77	413.54	3.99
Sex + Size:Sex + Size^2:Sex (H4)	Flipper	13	-194.14	414.29	4.74
Sex + Size:Sex + Size^2:Sex (H4)	Bill Length	13	-194.34	414.68	5.13
Sex + Size:Sex + Size^2:Sex (H4)	Foot Length	13	-194.97	415.93	6.39
Size (H2)	Bill Depth	9	-199.46	416.91	7.37
Size + Size^2 (H5)	Bill Depth	10	-198.48	416.96	7.42
Size (H2)	PC1	9	-201.22	420.43	10.89
Size + Size^2 (H5)	PC1	10	-201.18	422.36	12.81
Size (H2)	Foot Length	9	-202.48	422.96	13.41
Size + Size^2 (H5)	Foot Length	10	-202.11	424.22	14.68
Size (H2)	Bill Length	9	-204.11	426.22	16.67
Size + Size^2 (H5)	Bill Length	10	-203.81	427.62	18.07
Size (H2)	Flipper	9	-205.39	428.77	19.23
Size + Size^2 (H5)	Flipper	10	-205.38	430.75	21.21
Intercept (H6)		8	-208.94	433.88	24.34

Table 3. Effect sizes from competing linear mixed models (see bolded models in Table 2) relating sex and size to foraging success (Δ mass kg/foraging trip) in Magellanic Penguins. 95% confidence intervals (CI) are bootstrapped (*n* = 1000).

Variable	Effect Size	95% CI
Foraging Success ~ Sex		
Intercept	0.52	0.37 - 0.67
Sex - Male	0.18	0.11 - 0.24
Season Stage - Post-Guard	0.17	0.12 - 0.21
Number of Chicks - 2	0.12	0.07 - 0.17
Trip Duration	0.02	0 - 0.04
ID Type - Web Tag	-0.02	-0.09 - 0.04
Foraging Success ~ Sex + Size:Sex - Size^2		
Intercept	0.20	-0.14 - 0.56
Sex - Male	0.53	0.17 - 0.91
Size - Bill Depth:Female	-0.75	-1.42 - -0.08
Size - Bill Depth:Male	0.01	-0.36 - 0.42
Size - Bill Depth:Female^2	-0.39	-0.74 - -0.05
Size - Bill Depth:Male^2	-0.04	-0.23 - 0.13
Season Stage - Post-Guard	0.17	0.12 - 0.22
Number of Chicks - 2	0.11	0.06 - 0.17
Trip Duration	0.02	0 - 0.04
ID Type - Web Tag	-0.02	-0.09 - 0.04
Foraging Success ~ Sex + Size:Sex (Flipper Length)		
Intercept	0.50	0.33 - 0.65
Sex - Male	0.24	0.14 - 0.33
Size - Flipper Length:Female	-0.03	-0.09 - 0.03
Size - Flipper Length:Male	-0.04	-0.12 - 0.02
Season Stage - Post-Guard	0.17	0.12 - 0.21
Number of Chicks - 2	0.12	0.07 - 0.17
Trip Duration	0.02	0 - 0.04
ID Type - Web Tag	-0.02	-0.08 - 0.04
Foraging Success ~ Sex + Size:Sex (PC1)		
Intercept	0.55	0.33 - 0.75
Sex - Male	0.40	0.05 - 0.79
Size - PC1:Female	-0.02	-0.11 - 0.07
Size - PC1:Male	-0.08	-0.19 - 0.02
Season Stage - Post-Guard	0.17	0.12 - 0.22
Number of Chicks - 2	0.12	0.07 - 0.17
Trip Duration	0.02	0 - 0.04
ID Type - Web Tag	-0.02	-0.09 - 0.04

Table 4. Model selection results, including the number of parameters (*K*), the value of the log likelihood function at its lowest (optimal) value (logLik), Akaike's Information Criterion (AIC), and the difference between AIC for a given model and AIC for the top-ranked model (ΔAIC). Foraging efficiency (Δ mass kg/day) of Magellanic Penguins is the response variable in all models. The predictor variables (i.e., model structures) are described in the main text and correspond to the six different hypotheses outlined in Figure 1. The notation following each model structure indicates the corresponding hypothesis number (e.g., H1 = Hypothesis 1). Models with size included one of five different size metrics (bill depth, bill length, flipper length, foot length, or the first principal component of a principal components analysis integrating all size variables). All models also included season stage, number of chicks in the nest, and tag type as fixed effects and penguin ID and year as random effects. Models within 2 AIC of the top-ranked model are bolded.

Foraging Efficiency (Δ mass kg/day)

Model Structure	**Size Metric**	***K***	**logLik**	**AIC**	**ΔAIC**
Sex + Size:Sex + Size^2:Sex (H4)	**Foot Length**	**1**	**-481.96**	**987.93**	**0**
Sex (H1)		**8**	**-486.22**	**988.44**	**0.51**
Sex + Size:Sex (H3)	Foot Length	1	-485.31	990.63	2.7
Sex + Size:Sex + Size^2:Sex (H4)	Bill Depth	1	-483.5	990.99	2.56
Sex + Size:Sex (H3)	Bill Length	1	-485.84	991.68	3.24
Sex + Size:Sex (H3)	Flipper Length	1	-486.03	992.06	3.63
Sex + Size:Sex (H3)	PC1	1	-486.04	992.07	3.64
Sex + Size:Sex (H3)	Bill Depth	1	-486.05	992.11	3.67
Sex + Size:Sex + Size^2:Sex (H4)	Flipper Length	1	-484.66	993.33	4.89
Size (H2)	Bill Depth	8	-488.71	993.42	4.99
Sex + Size:Sex + Size^2:Sex (H4)	PC1	1	-485.16	994.32	5.88
Size + Size^2 (H5)	Bill Depth	9	-488.43	994.86	6.43
Sex + Size:Sex + Size^2:Sex (H4)	Bill Length	1	-485.55	995.11	6.67
Size (H2)	PC1	8	-491.34	998.69	10.25
Size + Size^2 (H5)	PC1	9	-491.34	1000.6	12.25
Size (H2)	Bill Length	8	-493.15	1002.3	13.86
Size + Size^2 (H5)	Bill Length	9	-493.09	1004.1	15.74
Size (H2)	Flipper Length	8	-496.28	1008.5	20.12
Size + Size^2 (H5)	Flipper Length	9	-496.13	1010.2	21.82
Size (H2)	Foot Length	8	-499.52	1015.0	27.12
Size + Size^2 (H5)	Foot Length	9	-499.52	1017.0	29.11
Intercept (H6)		7	-505.34	1024.6	36.25

Table 5. Effect sizes from competing linear mixed models (see bolded models in Table 4) relating sex and size to foraging efficiency (Δ mass kg/day) in Magellanic Penguins. 95% confidence intervals (CI) are bootstrapped (*n* = 1000).

Variable	**Effect Size**	**95% CI**
Foraging Efficiency: Sex		
Intercept	0.37	0.19 - 0.55
Sex - Male	0.29	0.2 - 0.37
Season Stage - Post-Guard	0.09	0.02 - 0.16
Number of Chicks - 2	0.08	0.01 - 0.15
IDType - Web Tag	0.04	-0.05 - 0.12
Foraging Efficiency: Sex + Size:Sex - Size^2		
Intercept	0.36	0.18 - 0.53
Sex - Male	0.29	0.17 - 0.41
Size - Foot Length:Female	0.11	-0.05 - 0.26
Size - Foot Length:Male	0.13	-0.1 - 0.36
Size - Foot Length:Female^2	0.09	0 - 0.18
Size - Foot Length:Male^2	-0.09	-0.2 - 0.02
Season Stage - Post-Guard	0.09	0.03 - 0.16
Number of Chicks - 2	0.07	0 - 0.15
IDType - Web Tag	0.04	-0.04 - 0.12

Table 6. Effect sizes from the most supported linear mixed effects model, based on AIC, showing the effect of sex and season stage on trip frequency (number of trips per day; n_{trips} = 345) for breeding male and female Magellanic Penguins across the 1995/96 to 2022/23 breading seasons, excluding 2011/12 and 2020/21. Males took more trips per day than females and all breeding adults took fewer trips during the post-guard stage. Device type did not affect trip frequency. 95% CIs are bootstrapped (*n* = 1000).

Variable	**Effect Size**	**95% CI**
Trip Frequency: Sex + Season Stage		
Intercept	0.68	0.52 - 0.84
Sex - Male	0.18	0.05 - 0.31
Season Stage - Post-Guard	-0.19	-0.35 - -0.03

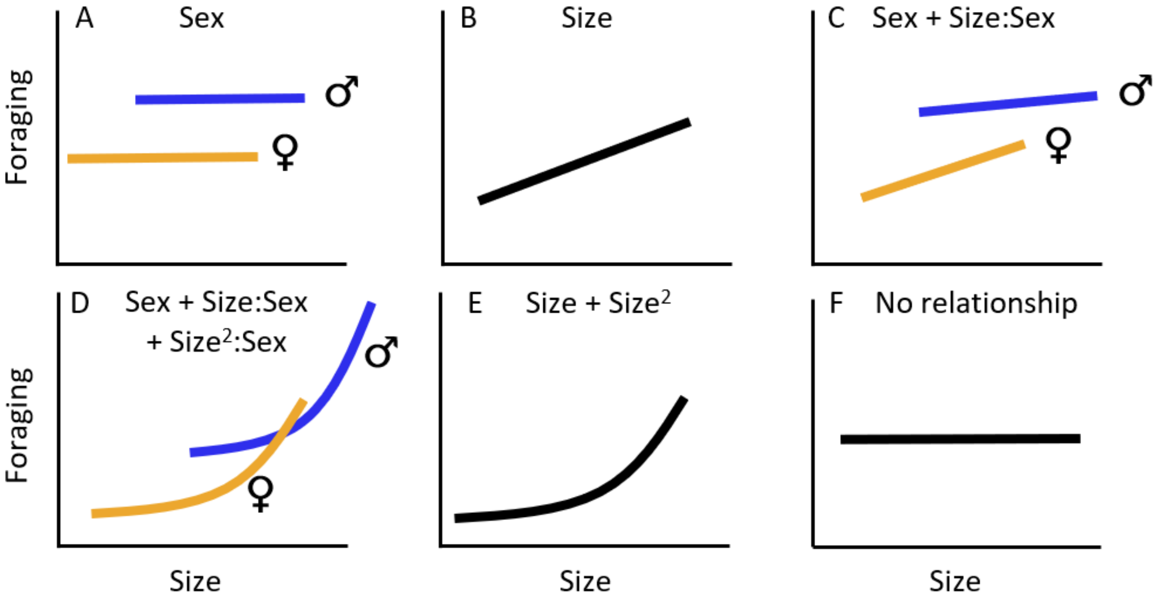


Figure 1. Hypothesized relationships between foraging outcomes (e.g., foraging success and foraging efficiency) and sex and size metrics (bill length, bill depth, flipper length, foot length, PC1 of all measures) in breeding Magellanic Penguins.

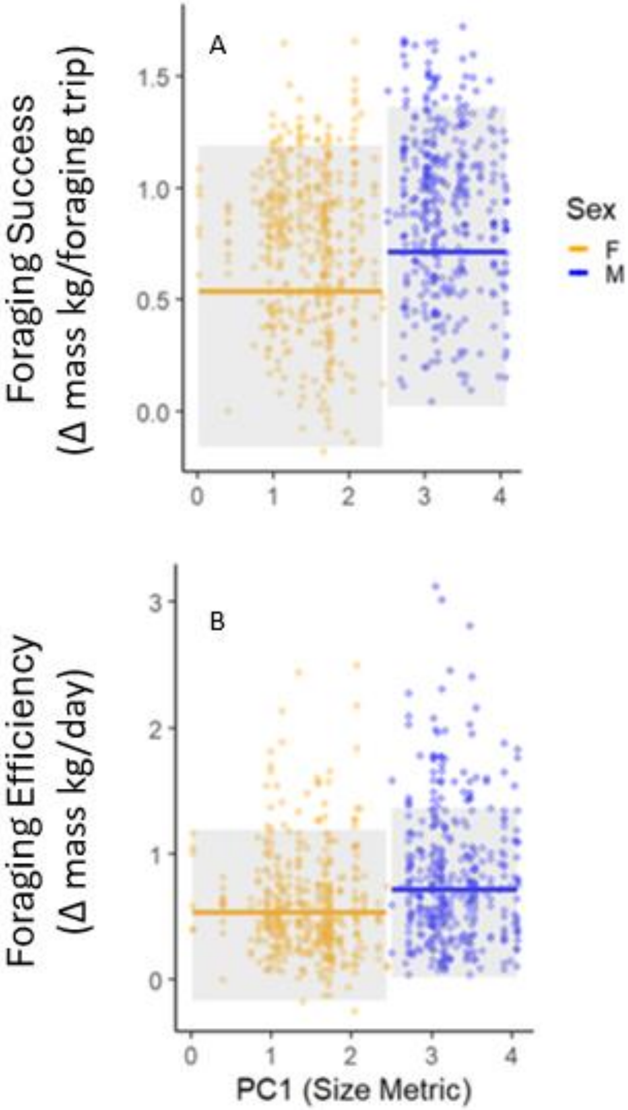
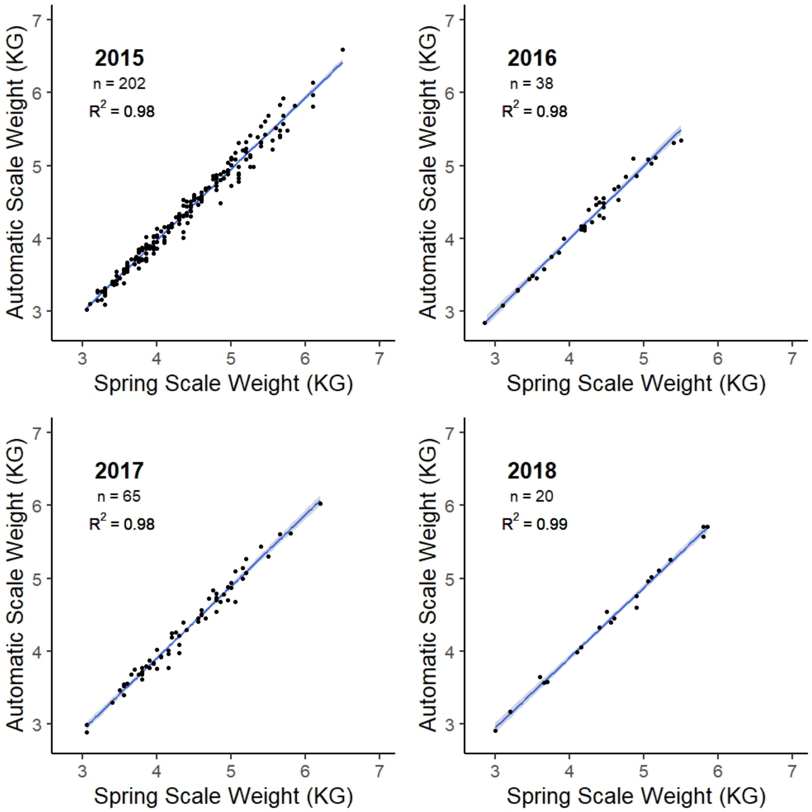


Figure 2. Model predictions from the sex only foraging success (A) and foraging efficiency (B) linear mixed models graphed over the raw data for breeding Magellanic Penguins. Gray bands represent the 95% bootstrapped confidence intervals. Model predictors other than sex were set to average values (i.e., # of chicks = 1, Season Stage = Guard, Trip Duration = 1.58 days). PC1 is used as the size metric here (the first principal component of a principal components analysis including bill length and depth, flipper length, and foot length). The relationship looks similar with all other size metrics on the *x*-axis, differing only in the degree of overlap between the sexes. For foraging success (A), on average females brought back 0.50kg per trip while males brought back 0.69kg. For foraging efficiency (B), females brought back 0.39kg/day, on average, while males brought back 0.66kg/day.

Supplementary Tables & Figures

Supplementary Table 1. Model selection table for linear model with weighbridge weight as the response and spring scale weight as the predictor in all models. Other predictors included Year and Weighbridge ID. Model selection shows year as a significant predictor, suggesting scale accuracy varied with year. Supplementary Figure 1 shows this year-to-year variance is small.

Model	***K***	**logLik**	**AIC**	**ΔAIC**
Year	6	280.95	-549.90	0.00
Year & Weighbridge ID	9	281.62	-545.25	4.65
NULL	3	265.07	-524.15	25.75
Weighbridge ID	6	267.52	-523.04	26.86



Supplementary Figure 1. Linear models showing relationship between weighbridge weight and spring scale weight across all four study years. R^2 values for all years are ≤ 0.98 indicating the year-to-year variance is small.

Chapter 3

Magellanic Penguin foraging efficiency during chick provisioning declines with increased commercial fishing hours

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Abstract

Understanding competition between fisheries and seabirds is critical for developing ecosystem-based management strategies that balance harvest and conservation goals. Best practices for assessing seabird-fisheries competition include estimating the effect of increased fishing on foraging success, yet these data are difficult to obtain at meaningful spatial and temporal scales. Here we assess the effect of commercial fishing hours on the foraging success ($\text{kg}\cdot\text{foraging trip}^{-1}$) and foraging efficiency ($\text{kg}\cdot\text{day}^{-1}$) of provisioning Magellanic Penguins (*Spheniscus magellanicus*) across the 2015/16 – 2018/19 breeding seasons (*n* = 927 foraging trips from 154 individuals). We found that (1) as the average number of fishing hours increased within the penguins' foraging area, adult foraging efficiency decreased, and (2) both adult sex and the timing of fishing effort relative to chick age influenced this effect. When males were feeding small chicks (≤ 30 days of age), an increase in the average number of fishing hours three days prior to the end of the foraging trip reduced their efficiency. When adults were raising large chicks (> 30 days of age), however, foraging metrics had no relationship to fishing hours, likely because adults can leave larger chicks at the nest for longer and are thus less spatially and temporally constrained in their foraging efforts. These results indicate fishing may

not be affecting the amount of food breeding adults acquire on a foraging trip, but the rate at which they acquire it. These results suggest that restricting fishing during the early stage of chick development will have the greatest positive impact on adults provisioning their chicks.

Introduction

Seabirds and commercial fisheries are both major marine consumers, often competing for the same resources (Pikitch et al. 2014). Many seabird species consume forage fish, which are typically defined as small coastal pelagic fish (e.g., anchovy and sardines), euphausiid crustaceans (krill), and squid (Cury et al. 2011, Pikitch et al. 2014). Forage fish also support a large fraction of commercial fishing targets. In 2014, for instance, forage fish accounted for 20% of the value of global fisheries (Pikitch et al. 2014), but since forage fish are typically a low value species they made up 30% of global fisheries catch in 2008 (Alder et al. 2008). Additionally, since forage fish are important prey for larger fish, they supported other commercial fisheries worth twice as much (Pikitch et al. 2014).

While seabird populations, and thus the total amount of forage fish they consume, have declined (Grémillet et al. 2018), global fishery catch has increased, leading to heightened or persistent seabird-fisheries competition in most of the world’s oceans (Grémillet et al. 2018). Understanding the functional relationships between commercial fisheries and seabird foraging is crucial to prevent the collapse of forage fish stocks, an important commodity for humans (Alder et al. 2008, Pikitch et al. 2014), and the collapse of ecosystems that rely on these fish as a key lower trophic level species (Cury 2000). Much research has focused on seabird-fisheries competition likely because, in some systems, seabirds are known to be reliable indicators of forage fish abundance and thus, indicators of ecosystem health (Velarde and Daniel 2019).

Without directly investigating how commercial fishing may be affecting prey availability, an immense body of work has demonstrated the link between prey availability and seabird population parameters. One notable example identifies the minimum forage fish biomass needed to sustain seabird populations, showing how reproductive success declines with reduced prey beyond a threshold (Cury et al. 2011). There is strong evidence showing changes in forage fish abundance reduces seabird reproduction (Furness and Tasker 2000, Crawford et al. 2006) and adult survival (Oro and Furness 2002, Robinson et al. 2015, but see Hilborn et al. 2017).

Other work has attempted to draw direct links between reductions in prey availability due to commercial fishing and changes in seabird foraging behavior (Bertrand et al. 2012), reproductive output (Pichegru et al. 2012), and survival rates (Frederiksen et al. 2004). The impacts of fisheries may be dependent on predator diet flexibility (Koehn et al. 2021), or be species-specific (Searle et al. 2023). One of the most extensive studies of seabird-fisheries competition is a decade-long time-area fisheries closure around the critically endangered African Penguin (*Spheniscus demersus*) breeding colonies in South Africa. The fisheries closures prohibited take of anchovy (*Engraulis encrasicolus*) and sardines (*Sardinops sagax*), the penguins' preferred prey, during selected times in relatively small areas near four breeding colonies (Sydeman et al. 2021). The fishery closures corresponded to increased chick survival rates and chick condition, while potentially reducing parental foraging efforts at two of the four colonies (Sherley et al. 2018). Reduced prey abundance has also been shown to reduce adult and juvenile survival rates of African Penguins (Sherley et al. 2014, 2017, Robinson et al. 2015). Even though these experimental closures have been shown to be effective, they remain controversial, and have yet to lead to any significant, durable management action (e.g., McInnes et al. 2024).

Despite this extensive work, the full range of impacts of fisheries on top predators, like seabirds, remain unclear (Free et al. 2021). Few studies, aside from those in South Africa and one in the North Sea (Searle et al. 2023), have explicitly linked the impacts of fisheries on seabird population parameters (Sydeman et al. 2017). Here we outline several challenges (identified in Sydeman et al. 2017) that we are uniquely positioned to address in this study. First, the data needed to examine seabird-fisheries resource competition are often collected on different spatial and temporal scales. Second, best practices call for direct measurements of foraging success, as opposed to looking only at foraging behavior or population parameters, yet these data are difficult to obtain. Examining the effects of seabird-fisheries competition on foraging success is preferred as foraging behaviors may be muted by individual variation (Lescroël et al. 2010) and population-level changes are difficult to detect. For example, seabirds may have large numbers of cryptic prebreeders that can buffer the effects of environmental or anthropogenic perturbations (Votier et al. 2008). Third, in many regions, the extent of illegal fishing has not been quantified. Finally, the effects of fisheries on seabirds may be masked by the natural fluctuation of forage fish populations driven by climatic factors (Checkley et al. 2017).

We tackled each of the above challenges while examining the effects of commercial fishing on the foraging success and efficiency of a top marine predator, the Magellanic Penguin (*Spheniscus magellanicus*), at one of their largest breeding colonies, Punta Tombo, Argentina. For the first challenge, we were able to match penguin foraging metrics spatially and temporally with fishing hours data provided by Global Fishing Watch (Kroodsma et al. 2018). Although these data do not indicate the target prey species of individual vessels, we know ~80% of vessels in the area are trawlers (Kroodsma et al. 2018) likely targeting Argentine anchovy (*Engraulis anchoita*; Paz et al. 2018) and Argentine hake (*Merluccius hubbsi*; Alemany et al. 2014), the main prey of Magellanic Penguins in this region (Forero et al. 2002). For the second, the use of automatic weighbridges allowed us to directly measure foraging success and efficiency of Magellanic Penguins. For the third, we were able to take advantage of recent work using high-resolution satellite images to identify boats with and without Automatic Identification System (AIS) transmissions. This revealed the Patagonian Shelf, where Punta Tombo is located, has one of the world's highest rates of AIS transmissions (~80%)—far above the global average for industrial fishing vessels of 24-28% (Paolo et al. 2024). Finally, to account for short-term variation in forage fish availability, we incorporated sea surface temperature (SST) into our analysis as, in this region, Argentine anchovy and Argentine hake aggregate in cold, nutrient rich waters or at strong thermal gradients (Hansen et al. 2001, Wang et al. 2007).

We predict Magellanic Penguin foraging efficiency, the rate at which food is acquired, will be affected by increased commercial fishing efforts as fisheries either reduce or redistribute prey. These penguins may be able to compensate for the effects of commercial fishing on foraging success, the amount of food acquired per foraging trip, by extending foraging trip duration and distance. As sex is a significant predictor of foraging success and efficiency (Holt et al. in review), we also wanted to examine sex-specific effects of commercial fishing on foraging success and efficiency. Because females have lower foraging success and efficiency than males, we predict that they will be disproportionately affected by fisheries. Males, with the ability to dive deeper and for longer (Walker and Boersma 2003), as well as consume a broader size range of prey (Forero et al. 2002), are likely better able to cope with periods of low or redistributed prey availability compared to females.

Methods

Study System

We examined the effects of commercial fishing on Magellanic penguins at their breeding colony of Punta Tombo, in Chubut Province, Argentina (44.0458°S, 65.2238°W). This colony is one of the species' largest, with ~120,000 breeding pairs (Boersma unpublished data), but the population has declined by 57% since 1987 (Rebstock et al. 2016, Clark-Wolf et al. 2023). Magellanic Penguins are serially monogamous (Wagner et al. 2022), with both parents caring for the chicks until they either die or fledge ~10 weeks later (Cappello and Boersma 2021). Breeding success is largely determined by prey location and abundance (Boersma et al. 2009); on average, 39% of chicks die of starvation—the most frequent cause of chick mortality (Boersma and Rebstock 2014), which indicates breeding penguins at Punta Tombo are food limited. Most chicks starve when they are young (5 – 9 days old; Boersma and Rebstock 2014).

Magellanic Penguins forage primarily on pelagic schooling fishes, such as Argentine anchovy (*Engraulis anchoita*) and juvenile Argentine hake (*Merluccius hubbsi*), and to a lesser extent crustaceans (*Artemisia longinaris*) and small squids (*Loligo* and *Illex* sp.) (Frere et al. 1996, Forero et al. 2002, Yorio et al. 2017). During the breeding season, Magellanic Penguins are central-place foragers (Orians and Pearson 1979), leaving the colony both to feed themselves and to bring back food to regurgitate for their young (Boersma and García-Borboroglu 2013). Foraging trip distance varies as chicks age. Breeding adults take short trips when chicks are young (hereafter "guard stage" when chick age ≤ 30 days old) and they must guard their chicks from predators at the nest and help them thermoregulate (Boersma and Rebstock 2009). Adults take longer trips when chicks are older (hereafter "post-guard stage" when chick age > 30 days old; Boersma and Rebstock 2009). Trip length is negatively correlated with reproductive success, as longer trips correlate with increased chick mortality (Boersma and Rebstock 2009).

This study focused on confirmed breeders as they have higher energetic demands than nonbreeders. As a result, the effects of commercial fishing on foraging metrics are likely to be more pronounced in breeders than nonbreeders. Nonbreeders have lower energetic demands than breeders because they are only maintaining their own condition and not simultaneously feeding chicks, while the daily energetic needs of breeding seabirds are among the highest, relative to body mass, of many marine vertebrates (Nagy et al. 1999). Breeding status was determined by checking marked nests every six to 10 days. We considered adults as breeders if they were frequently seen in nests with eggs, or if they were the only adult of their sex in the nest after chicks hatched.

Foraging Success and Efficiency

We measured foraging success and efficiency with automatic weighbridges between the 2015/16 and 2018/19 breeding seasons in the manner described in Holt et al. (in review). We defined foraging success as the mass difference between consecutive outgoing and incoming weights (Δ mass kg/foraging trip), and foraging efficiency as the change in mass divided by the length of the foraging trip (Δ mass kg/day). The change in mass for both metrics includes both stomach contents (i.e., the chick meal) as well as any mass the adult assimilated or expended during transit (Lescroël et al. 2010). Over the course of the study, we captured 388 foraging trips during the guard stage and 539 foraging trips during the post-guard stage from 154 unique individuals. Foraging trips were evenly distributed across the sexes ($n_{\text{males}} = 444$, $n_{\text{females}} = 483$).

Fishing Hours

We aimed to match penguin foraging trip metrics with commercial fishing data both spatially and temporally. To align the foraging trips spatially with fishing activity, we defined a general foraging area for the population of breeding adults based on GPS and Argos tracking tag data. For temporal alignment, we averaged fishing hours within these general foraging areas across various time windows surrounding each individual foraging trip. This allowed us to determine the temporal scale at which fishing hours most affected penguin foraging metrics.

To determine a general foraging area, we calculated 90% utilization distributions using tracking data from all foraging breeding adults between the 2012/2013 and 2023/24 breeding seasons. Over this period, five types of tags (with various sizes, shapes, and levels of accuracy) were used as tracking tag technology advanced. Some tags obtained and sent location data via Argos satellite (ST20 made by Sirtrack, SPOT-275C made by Wildlife Computers) while others communicated with satellites for location information but were archival tags and had to be physically retrieved to collect the data (nanoFix-GEO made by PathTrack, F2G 134A and F5G 334A/434A made by Sirtrack). Tags were attached and their data filtered and processed as described in Rebstock et al. 2022.

Foraging tracks and thus, foraging areas, were categorized into two stages: guard and post-guard. We created the 90% utilization distributions using the *adehabitatHR* package version 0.4.22 in R (Calenge 2011). The guard stage is fully encompassed by the post-guard stage (Figure 1).

Once we had general foraging areas for the guard and post-guard stages, we overlaid daily fishing hours at a 0.1° resolution using data from Global Fishing Watch (Kroodsma et al.

2018). This dataset only includes vessels with transmitting AIS devices, but a recent study shows ~80% of vessels in this Patagonian Shelf region have their AIS devices active (Paolo et al. 2024). To temporally align fishing hours with each penguin foraging trip, we calculated the average fishing hours within different time windows surrounding each foraging event. Specifically, we selected three, five and 31-day windows, with the end of each window tied to the end of each foraging trip. We selected three- and five-day windows as these correspond to the average foraging trip length plus two standard deviations for the guard and post-guard stages, respectively (guard stage forage trip duration + 2SD = 3.17 days, post-guard stage forage trip duration + 2SD = 4.63 days), as determined from tracking tag data. The 31-day window was included to assess whether increased fishing activity before the foraging trip affected foraging success and efficiency.

The main fisheries on the Patagonian shelf include the Argentine anchovy *(Engraulis anchoita*; Paz et al. 2018), Argentine hake (*Merluccius hubbsi*; Alemany et al. 2014) and shortfin squid (*Illex argentinus*; Crespi-Abril et al. 2013). Although data from Global Fishing Watch does not indicate the target prey species of individual vessels, we know ~80% of vessels in the area are trawlers (Kroodsma et al. 2018) likely targeting anchovy and hake. The sizes of anchovy eaten by penguins and taken by fisheries overlap (Gandini et al. 1999). It is less clear whether the sizes of hake taken by fisheries and penguins overlap (Gandini et al. 1999). Penguins are likely eating small, juvenile hake (Gandini et al. 1999). Hake fisheries typically target adults yet, since the mid-1990s, they have started to target juvenile hake (Bezzi et al. 2004). Even when hake fisheries are targeting adults, bycatch of juvenile hake can be extensive (Romero et al. 2010).

SST

To account for short-term environmental variation and local prey availability, we calculated the average SST within the entire general foraging range for each trip, using a 30-day window that ended on the trip’s last day. We used a larger area than the area used to calculate fishing hours to capture the oceanographic front that is driving the primary productivity of the area (Boersma et al. 2009). The Peninsula Valdes front, a thermal tidal mixing front, forms in austral spring (Acha et al. 2004), attracting spawning anchovy (Hansen et al. 2001) and Argentine hake (Sabatini 2004). This front persists through the austral autumn, when the stratification of the shelf waters deteriorates (Acha et al. 2004). We used a 30-day average of SST across this front to capture fine-scale distributions of prey consistent with other studies (e.g., Brusa et al. 2023).

The area was determined using the same tracking tag data as described above, but we also included tracking tag data from incubation trips. During incubation, adults are neither as spatially nor temporally constrained as chick-rearing adults and thus forage at a greater distance from the colony along the tidal mixing front (Boersma and Rebstock 2009). With this tracking tag data that extended farther from the colony into the tidal mixing front, we calculated the 90% utilization distribution (Figure 2) using the *adehabitatHR* package version 0.4.22 in R (Calenge 2011). Last, we calculated a 30-day SST average within the aforementioned area for each foraging trip, with the end of the 30-day average ending on the last day of the foraging trip. Daily SST data were obtained from the NOAA Coral Reef Watch at a 5km resolution (https://coastwatch.noaa.gov/erddap/griddap/noaacrwsstDaily.html).

Model Structure, Selection, and Implementation

To determine the effect of fishing hours on foraging success and efficiency, we fit a series of linear mixed models in a hierarchical Bayesian framework with either foraging success or foraging efficiency as the response variable. We used all possible combinations of SST, the three different fishing hour time windows, and allowed for an interaction between sex and fishing hours to determine if fishing affects the sexes similarly (See Supplementary Tables 1-4 to see all possible models). All models included sex and the number of chicks in the nest at the start of the adult foraging trip, as those are important predictors for our foraging metrics (Holt et al. in review). Year and individual ID were included as random effects in all models to account for repeated measures; the results of likelihood ratio tests supported this decision.

Models were grouped into four groups by foraging metric (foraging success or efficiency) and chick-rearing stage (guard or post-guard). Within each of those groups, we ranked models with a leave-one-out cross-validation approach (Supplementary Tables 1-4), using the *loo* package version 2.8.0 in R (Vehtari et al. 2015). Parameter estimates of the most supported models are presented in the results. We considered any predictors with a 95% credible interval that did not cross zero to be informative and any predictor with an 80% credible interval that did not cross zero weakly informative.

Prior to model building, we calculated Pearson correlation coefficients and confirmed no predictors were highly correlated ($r > 0.7$). Residuals were evaluated for normality, homogeneity of variance, and independence. We used the *rstanarm* package, an R interface to Stan, for drawing samples from the posterior distributions of model parameters (Goodrich et al. 2024). *Rstanarm* fits regression models using Hamiltonian Monte Carlo via Markov Chain Monte Carlo. We ran three chains from 4,000 iterations after 1,000 warmup iterations and assessed convergence using the potential scale reduction factor ($\hat{R} \leq 1.05$; Gelman 2013) and visual chain inspection. All analyses were conducted in R version 4.4.1 ("R Core Team" 2024).

Results

Effects of fishing hours during the Guard Stage

We found weak evidence that increased fishing hours were associated with decreased foraging success during the guard stage for males and found no effect of fishing on female foraging success (Table 1, Figure 3A). The most supported model, of the foraging success models of the guard stage, included the average fishing hours within a 3-day window and an interaction between fishing hours and sex (Supplementary Table 1). Males had higher foraging success than females during the guard stage, and breeding adults with two chicks had higher foraging success than adults with one (Table 1). Average SST was positively correlated with foraging success in the guard stage (Table 1).

As for the effect of fishing hours on foraging efficiency, we found strong evidence that as the average number of fishing hours increased, male foraging efficiency decreased (Table 2, Figure 3C). We found weak evidence that female foraging efficiency decreased as the average fishing hours increased (Table 2, Figure 3C). The most supported model, of the foraging efficiency models during the guard stage, included average fishing hours within a 3-day window and an interaction between fishing hours and sex (Supplementary Table 2). Males had higher foraging efficiency than females and breeding adults with two chicks had higher foraging efficiency than adults with one chick (Table 2). Average SST was positively correlated with foraging efficiency in the guard stage (Table 2).

Effects of fishing hours during the Post-Guard Stage

During the post-guard stage, fishing hours did not affect foraging success as the credible interval for the fishing hours coefficient overlapped zero (Table 3, Figure 3B). The most supported model, of the foraging success models during the post-guard stage, included average fishing hours within a 31-day window and no interaction between fishing hours and sex (Supplementary Table 2). Males had higher foraging success than females, breeding adults with two chicks had higher foraging success than adults with one chick, and average SST was negatively correlated with foraging success (Table 3).

During the post-guard stage, we found no evidence that fishing hours affected foraging efficiency (Table 4). The most supported model, of the foraging efficiency models in the post-guard stage, included SST and did not include the average fishing hours (Supplementary Table 4). Males had higher foraging efficiency than females (Table 4). We found weak evidence that breeding adults have higher foraging efficiency when they have two chicks compared to one (Table 4). Average SST was negatively correlated with foraging efficiency (Table 4).

Discussion

We found that foraging efficiency, the rate of food acquisition, decreased for males and females as commercial fishing increased within the foraging range. However, foraging success, the amount of food acquired per foraging trip, was only weakly affected by increasing commercial fishing and only in males. The timing of fishing effort relative to chick age and the sex of the foraging adult influenced these effects. Only when chicks were small (guard stage; chick age ≤ 30 days) did we find commercial fishing negatively associated with penguin foraging metrics, with male foraging metrics being more negatively impacted than those of females.

These results have strong implications for reproductive success for two reasons: 1) Chicks are most likely to starve in the first half of the guard stage (Boersma and Rebstock 2014) the period when commercial fishing reduced foraging success and efficiency and 2) Commercial fishing especially impacts the foraging of males, who likely provision chicks larger meals and at faster rates than females (Holt et al. in review). It appears when chicks are older (post-guard stage; chick age > 30 days old) and breeding adults are less constrained spatially and temporally in their foraging efforts, adults are better able to compensate for the effects of commercial fishing. These results have direct conservation applications. Restricting fishing during the early stage of chick development, rather than when chicks are older, could have a greater positive impact on adults provisioning their chicks. Assessing chick growth or mortality rates in association with fishing hours would strengthen this recommendation.

We found sex-specific effects of commercial fishing on penguin foraging metrics, but not in a way that aligned with our predictions. We expected increased fishing hours to affect females more than males, since previous work has shown females have lower foraging success and efficiency than males during chick rearing (Holt et al. in review), and males may be more flexible in their diet as they dive deeper (Walker and Boersma 2003) and eat a larger size range of prey (Forero et al. 2002) than females. Given the potential limitations in female diet flexibility, we predicted that reduced or redistributed prey from commercial fishing would disproportionately reduce female foraging metrics more than males. Instead, we found a weak negative effect of fishing hours on foraging success for males and no effect on females during the guard stage. Males' foraging metrics may be more affected by fishing hours if they are responsible for most of the chick provisioning (Holt et al. in review), while females may primarily be focusing on maintaining their condition, requiring fewer prey.

Assessing seabird-fisheries competition comes with many challenges, some of which we have addressed in this study, but our solutions could be improved upon. A challenge we attempted to tackle was accounting for the fluctuation of prey due to oceanographic conditions. We incorporated an oceanographic measure, SST, as a proxy for short-term, local prey availability. A more direct measure of prey availability, like acoustic data, would be preferred. Interestingly, we found the relationship between SST and our foraging metrics depended on the stage of the season. During the guard stage, warmer SST coincided with higher foraging success (Table 1) and efficiency (Table 2), while during the post-guard stage lower SST coincided with higher foraging success (Table 3) and efficiency (Table 4). Our results during the post-guard stage align with a preponderance of studies relating colder SST or stronger thermal gradients to more successful penguin foraging (Boersma et al. 2009, Scheffer et al. 2010, Berlincourt and Arnould 2015, Van Eeden et al. 2016). We believe this relationship does not hold during the guard stage as adults need to make short and fast foraging trips to protect small chicks at the nest and help small chicks thermoregulate (Boersma et al. 2009). Hence, when chicks are small during the guard stage, SST may not be an appropriate proxy for fine-scale prey availability in this system.

The current available dataset in this region for assessing fishing effort only quantifies the number of hours boats spend fishing. A direct measure of commercial fisheries landings or catch per unit effort and the target prey species of individual vessels, would improve this study. Broadly, we know ~80% of the commercial fishing boats in the area are trawlers (Kroodsma et al. 2018) that *likely* target Argentine anchovy (Paz et al. 2018) and hake (Alemany et al. 2014). Even though we are not able to definitively match the penguin diet with the target prey species of commercial fishing vessels, fisheries do not have to target the same prey species as local seabirds to alter seabird foraging as fisheries could instead be redistributing prey (Sydeman et al. 2017).

Most studies of seabird-fisheries competition assume the mechanism to be exploitative competition where one group outcompetes another group and depletes a limited resource, making that resource less accessible to the other (Sydeman et al. 2017). However, there are several examples of seabird-fisheries interactions that suggest interference competition, where one group prevents another from accessing a resource, could be the mechanism reducing the foraging of seabirds (Sydeman et al. 2017). Fisheries may change the horizontal or vertical distribution or the aggregation behavior of forage fish (Garrison 2000, Haugland and Misund 2011). For example, fisheries may have redistributed sardine from the Western Cape to the Agulhas Bank (Coetzee et al. 2008), with negative consequences for nearby African Penguins. In the North Sea, only surface-feeding black-legged kittiwakes (*Rissa tridactyla*) were affected by a nearby sandeel fishery, whereas diving seabirds, like the common murre (*Uria aalge*) and the European shag (*Phalacrocorax aristotelis*), were unaffected (Searle et al. 2023). This suggests the fishery could have pushed sandeels deeper in the water column, making them inaccessible to the surface-feeders. Even though we are unable to differentiate between exploitative and interference competition, however, the ecological effects on Magellanic Penguins remain the same.

As almost all adults crossing the weighbridges were not carrying tracking tags, we constructed general foraging areas from tagged adults not crossing the weighbridges (Figure 1) to spatially match the foraging trips with the fishing data. Using tracking tags with accelerometers to record the locations of prey capture events would allow for direct spatial alignment of fishing effort and penguin foraging metrics. Although we are focusing on the effects of fishing within the colony's foraging range on individual foraging trips, rather than on the effects of fishing that foraging adults directly encounter on their trips, there is evidence that fishing can reduce or redistribute prey in its surrounding area (Ohayon et al. 2021).

The effects of fishing on prey availability vary across spatial and temporal scales, and depend on factors such as the mobility of the target species (Ohayon et al. 2021). Examining the total fishing hours within the guard and post-guard stages, across all years of the study (2015/16 – 2018/19 breeding seasons) we find the main fishing hotspots overlap with the edge of the penguin foraging range and most of the foraging range experiences low levels of fishing (Figure 1). Even though the fishing hotspots do not completely overlap with the penguin foraging range, we believe high levels of fishing on the edge of the foraging range can still reduce prey availability within the foraging range. From work examining the "edge effects" of fisheries operating up against the boundaries of no-take Marine Protected Areas (MPAs), we know fisheries can reduce prey density within MPAs, near the edge of the reserves (Ohayon et al. 2021) especially when the species target of the fisheries is highly mobile (Ohayon et al. 2021). As anchovy and hake, the target prey of the commercial fisheries near the Punta Tombo breeding colony, are mobile, we believe fisheries are likely to reduce prey in the area around the apparent fishing hotspots.

Understanding the relationship between foraging seabirds and commercial fisheries is critical to reducing both the negative effects on seabird population parameters and on commercial fisheries take. If forage fish stocks crash, this can have devastating effects on seabirds, fisheries, and whole ecosystems that rely on the lower trophic level forage fish. For example, after decades of overfishing sardines in Namibia, many seabird populations collapsed. Penguins, gannets and cormorants decreased by 90%, 95% and 76%, respectively (Crawford

2007). The Namibian Islands Marine Protected Area was implemented in 2009 to assist seabird and sardine fishery recovery (Crawford 2007, McInnes et al. 2024). However, fish stocks were so depleted they have never rebounded, the sardine fishery in Namibia was closed in 2018, and the African Penguin population in this region has not recovered (McInnes et al. 2024).

This sardine fishery is a cautionary tale and does not have to be the fate of other forage fish – seabird – fisheries interactions. The establishment of fisheries no-take zones have alleviated the negative impacts on marine species (Sydeman et al. 2017, Searle et al. 2023). In the Alaskan North Pacific, fishing for most forage fish and euphasiid crustaceans was prohibited in 1997 and fisheries competition with marine wildlife has not become an obvious issue in this area (Witherell 2000). The results of the time-area fisheries closure experiment around the African Penguin colonies in South Africa suggest that relatively small closure areas can positively affect the breeding success of a target species while having very little effect on commercial fisheries (McInnes et al. 2024). The effect of fisheries closure on the survival rate of chicks ranged from 2 – 11% (Sherley et al. 2018). Population models predict this increase in chick survival can improve the African Penguin population growth rate by ~0.5% - 1.2% per year (Sherley et al. 2018). For a rapidly declining species, that could become extinct in the wild by 2035 (Sherley et al. 2020), policy action to reduce the effects of commercial fishing is imperative.

Conclusions

Our study suggests that commercial fishing does not strongly affect the amount of food breeding adults acquire, but the rate at which they acquire it. We identified a distinct period of the breeding season where breeding adults were most susceptible to the effects of commercial fishing. Only when chicks were small, did adults have reduced foraging success and efficiency. These results suggest that restricting fishing during the early stage of chick development could have the greatest positive impact on adults provisioning their chicks. Assessing chick growth or mortality rates in association with fishing hours would strengthen this recommendation. These findings have direct implications for management and conservation strategies that can help effectively balance the interests of wildlife conservationists, tourism and commercial fisheries.

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Tables & Figures

Table 1. Parameter estimates with 80% and 95% credible intervals from the most supported linear mixed model relating fishing hours to foraging success (Δ mass kg/foraging trip) during the guard stage in Magellanic Penguins. **Bold**: 95% CIs did not overlap zero, indicating strong support. *Italics*: 80% CIs did not overlap zero, indicating weak support.

Parameter	Coefficient estimate	80% CI	95% CI
Intercept	0.47	(0.30, 0.65)	(0.17, 0.77)
Avg Fishing Hours:3-Day Window	0.00	(-0.03, 0.04)	(-0.05, 0.06)
Sex - M	**0.21**	**(0.17, 0.26)**	**(0.14, 0.29)**
Avg SST	**0.38**	**(0.35, 0.42)**	**(0.33, 0.43)**
nChicks	**0.09**	**(0.05, 0.12)**	**(0.03, 0.14)**
Avg Fishing Hours:Sex - M	*-0.05*	*(-0.09, -0.01)*	*(-0.11, 0.01)*

Table 2. Parameter estimates with 80% and 95% credible intervals from the most supported linear mixed model relating fishing hours to foraging efficiency (Δ mass kg/day) during the guard stage in Magellanic Penguins. **Bold**: 95% CIs did not overlap zero, indicating strong support. *Italics*: 80% CIs did not overlap zero, indicating weak support.

Parameter	Coefficient estimate	80% CI	95% CI
Intercept	0.32	(0.15, 0.50)	(0.03, 0.64)
Avg Fishing Hours:3-Day Window	*-0.05*	*(-0.08, -0.01)*	*(-0.10, 0.01)*
Sex - M	**0.21**	**(0.17, 0.25)**	**(0.14, 0.28)**
Avg SST	**0.29**	**(0.26, 0.32)**	**(0.24, 0.34)**
nChicks	**0.10**	**(0.06, 0.13)**	**(0.04, 0.15)**
Avg Fishing Hours:Sex - M	**-0.07**	**(-0.11, -0.03)**	**(-0.14, -0.01)**

Table 3. Parameter estimates with 80% and 95% credible intervals from the most supported linear mixed model relating fishing hours to foraging success (Δ mass kg/foraging trip) during the post-guard stage in Magellanic Penguins. **Bold**: 95% CIs did not overlap zero, indicating strong support. *Italics*: 80% CIs did not overlap zero, indicating weak support.

Parameter	Coefficient estimate	80% CI	95% CI
Intercept	0.50	(0.41, 0.59)	(0.36, 0.64)
Avg Fishing Hours: 31-Day Window	-0.04	(-0.07, 0.00)	(-0.09, 0.02)
Avg SST	**-0.06**	**(-0.08, -0.04)**	**(-0.09, -0.03)**
Sex - M	**0.13**	**(0.08, 0.18)**	**(0.05, 0.21)**
nChicks	**0.21**	**(0.17, 0.26)**	**(0.14, 0.29)**

Table 4. Parameter estimates with 80% and 95% credible intervals from the most supported linear mixed model relating fishing hours to foraging efficiency (Δ mass kg/day) during the post-guard stage in Magellanic Penguins. **Bold**: 95% CIs did not overlap zero, indicating strong support. *Italics*: 80% CIs did not overlap zero, indicating weak support.

Parameter	Coefficient estimate	80% CI	95% CI
Intercept	0.41	(0.27, 0.55)	(0.18, 0.64)
Avg SST	**-0.16**	**(-0.18, -0.13)**	**(-0.19, -0.12)**
Sex - M	**0.16**	**(0.11, 0.20)**	**(0.09, 0.23)**
nChicks	*0.07*	*(0.02, 0.12)*	*(0.00, 0.14)*

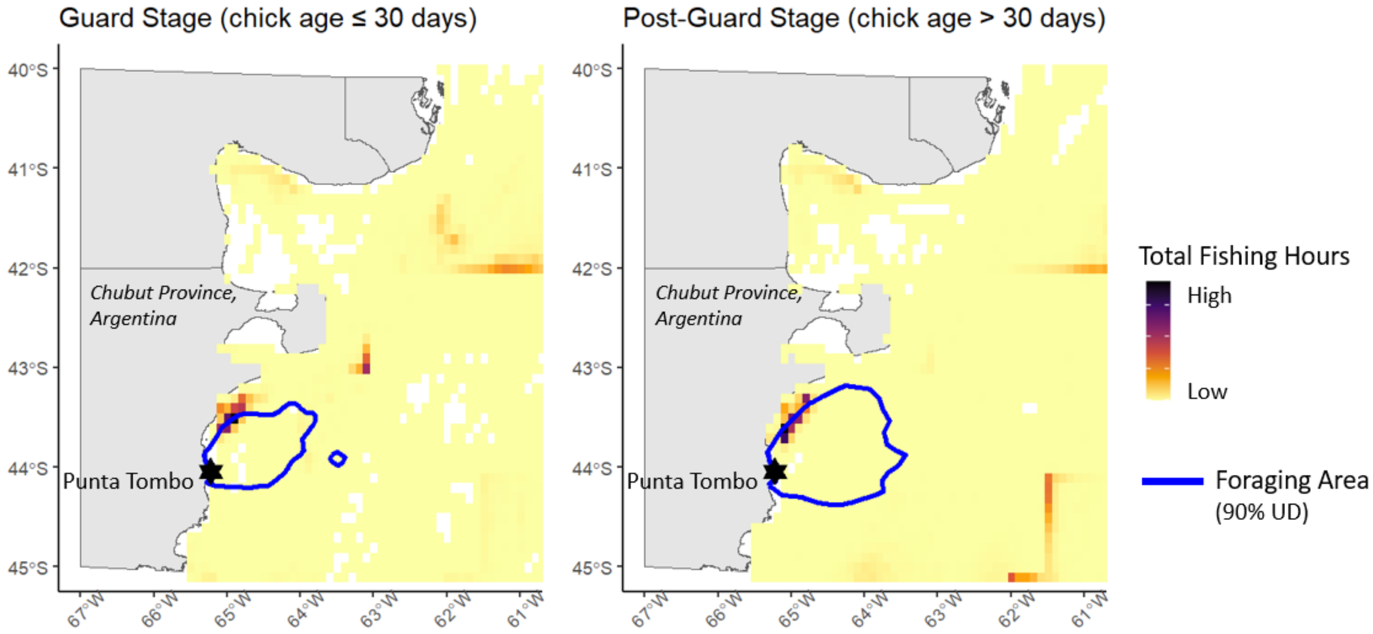

Figure 1. Foraging ranges in the guard and post-guard stages are the 90% utilization distributions constructed from all tracking data from foraging, breeding Magellanic Penguins between the 2012/2013 and 2023/24 breeding seasons at the Punta Tombo colony. These foraging ranges were used to spatially match the penguin foraging metrics with the average number of fishing hours an individual likely encountered. In this figure, we overlay the total fishing hours during the 2015/16 to 2018/19 breeding seasons to highlight fishing hotspots in relation to penguin foraging grounds. Fishing hours data are at a 0.1° resolution and made available by Global Fishing Watch (Kroodsma et al. 2018).

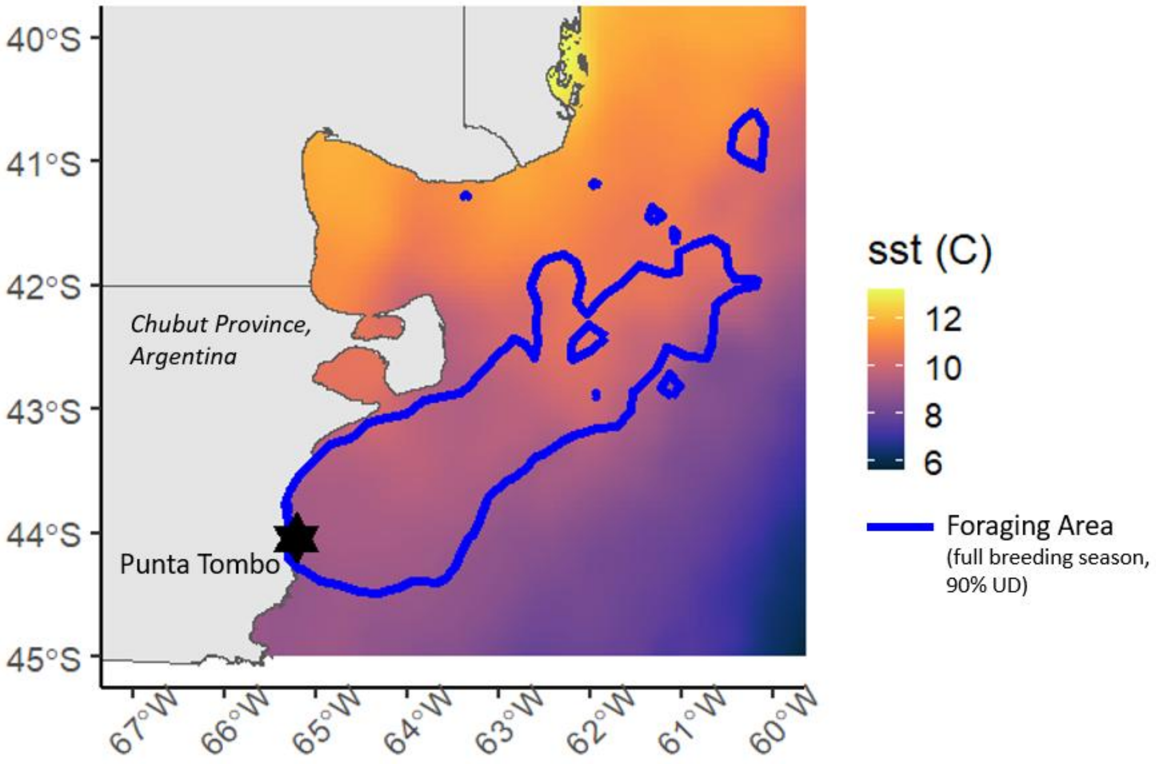

Figure 2. Average sea surface temperature (SST) within the entire breeding season foraging range, was included in the models relating fishing hours to foraging metrics, to capture the oceanographic fronts that are driving the primary productivity of the area (Boersma et al. 2009) and to account for short-term environmental variation and local prey availability. The foraging area is the 90% utilization distribution constructed from foraging, breeding Magellanic Penguins, during all stages of breeding (incubation, guard stage, and post-guard stage) between the 2012/2013 and 2023/24 breeding seasons at the Punta Tombo colony. Daily SST data were obtained from the NOAA Coral Reef Watch at a 5km resolution (*https://coastwatch.noaa.gov/erddap/griddap/noaacrwsstDaily.html*). Here we show the SST from 2015-10-15 as an example.

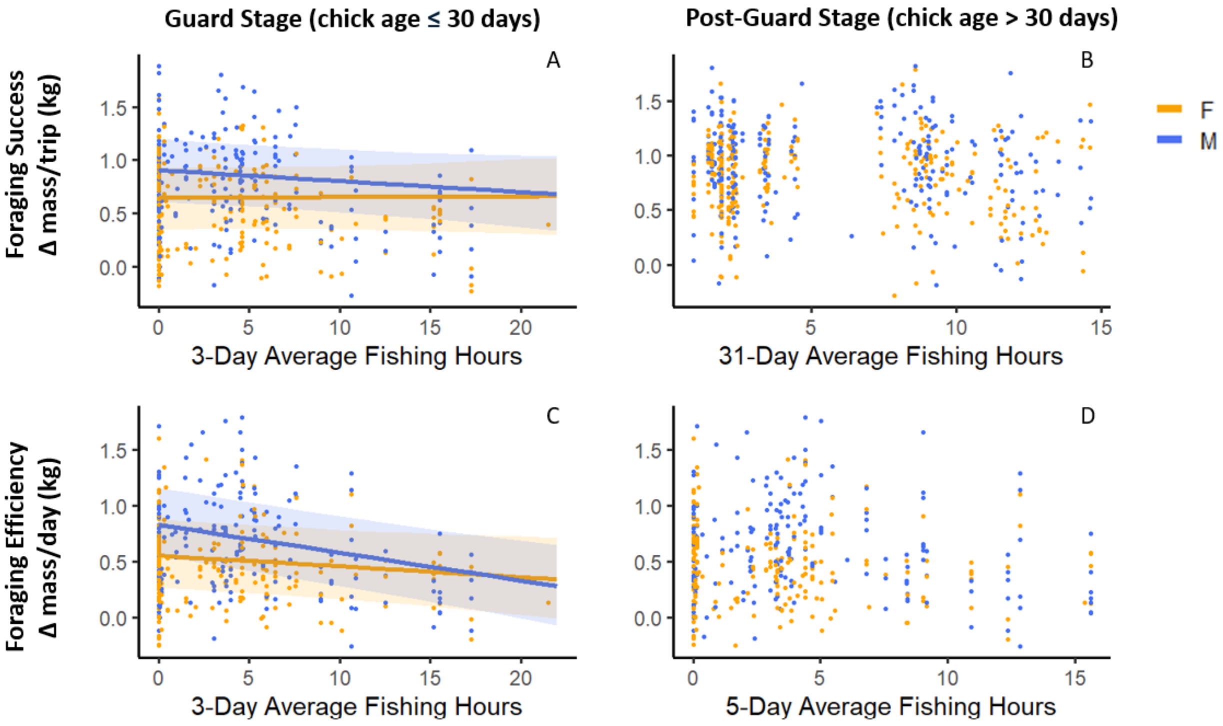

Figure 3. Results from the most supported models relating foraging success (A & B) and foraging efficiency (C & D) to the average number of fishing hours in the guard (A & C) and post-guard stages (B & D) for breeding Magellanic Penguins. Shaded bands represent the 95% credible intervals. Fishing hours negatively associated with foraging success and efficiency during the guard stage, with males experiencing a greater effect than females. Points represent individual foraging trips.

Supplementary Tables

Supplementary Table 1. Leave-one-out cross-validation model selection table for linear mixed models, in a Bayesian framework, relating foraging success to fishing hours in the guard stage for Magellanic Penguins. Here, we show the change in expected log predictive density and standard error for each model compared to the top model. FH represents average fishing hours and the number associated represents the time window (e.g., 3FH = 3-day window of average fishing hours). An asterisk indicates an interaction was allowed.

Model	Δ ELPD	Δ SE
3FH*Sex + SST	0	0
3FH + Sex + SST	-0.1	1.9
SST + Sex	-0.2	2.2
5FH*Sex + SST	-0.6	1.4
31FH + Sex + SST	-0.6	2.2
5FH + Sex + SST	-1	2.1
31FH*Sex + SST	-2.1	2.1
31FH + Sex	-64.4	9.5
31FH*Sex	-65.1	9.4
3FH + Sex	-95.2	11
3FH*Sex	-95.6	11.1
5FH + Sex	-98.8	11
5FH*Sex	-99.8	11
Intercept	-101.8	10.9

Supplementary Table 2. Leave-one-out cross-validation model selection table for linear mixed models, in a Bayesian framework, relating foraging success to fishing hours in the post-guard stage for Magellanic Penguins. Here, we show the change in expected log predictive density and standard error for each model compared to the top model. FH represents average fishing hours and the number associated represents the time window (e.g., 3FH = 3-day window of average fishing hours). An asterisk indicates an interaction was allowed.

Model	**Δ ELPD**	**Δ SE**
31FH + Sex + SST	0	0
SST + Sex	-0.3	1.1
5FH + Sex + SST	-0.7	1.2
3FH + Sex + SST	-1	1.4
31FH*Sex + SST	-1	0.2
3FH*Sex + SST	-1.1	1.7
5FH*Sex + SST	-1.5	1.2
31FH + Sex	-6.8	3.7
Intercept	-7.2	4.1
31FH*Sex	-7.4	3.7
3FH + Sex	-8.2	4.1
5FH + Sex	-8.5	3.9
3FH*Sex	-8.9	4.2
5FH*Sex	-9	4

Supplementary Table 3. Leave-one-out cross-validation model selection table for linear mixed models, in a Bayesian framework, relating foraging efficiency to fishing hours in the guard stage for Magellanic Penguins. Here, we show the change in expected log predictive density and standard error for each model compared to the top model. FH represents average fishing hours and the number associated represents the time window (e.g., 3FH = 3-day window of average fishing hours). An asterisk indicates an interaction was allowed.

Model	**Δ ELPD**	**Δ SE**
3FH*Sex + SST	0	0
3FH + Sex + SST	-1.2	2.2
5FH*Sex + SST	-4.5	2.5
5FH + Sex + SST	-5.4	3
SST + Sex	-7.2	4.2
31FH + Sex + SST	-7.9	4.2
31FH*Sex + SST	-8.8	4
31FH + Sex	-45.5	9.3
31FH*Sex	-46.2	9.2
3FH*Sex	-54.7	9.6
3FH + Sex	-55.2	9.5
5FH + Sex	-62.3	9.5
5FH*Sex	-63	9.6
Intercept	-70.8	9.8

Supplementary Table 4. Leave-one-out cross-validation model selection table for linear mixed models, in a Bayesian framework, relating foraging efficiency to fishing hours in the post-guard stage for Magellanic Penguins. Here, we show the change in expected log predictive density and standard error for each model compared to the top model. FH represents average fishing hours and the number associated represents the time window (e.g., 3FH = 3-day window of average fishing hours). An asterisk indicates an interaction was allowed.

Model	**Δ ELPD**	**Δ SE**
SST + Sex	0	0
5FH + Sex + SST	-0.5	1.2
3FH + Sex + SST	-0.9	0.9
31FH + Sex + SST	-0.9	0.3
31FH*Sex + SST	-1.3	1.1
5FH*Sex + SST	-1.6	1.2
3FH*Sex + SST	-1.8	1
5FH + Sex	-32.6	8.4
5FH*Sex	-33.5	8.3
3FH + Sex	-35.2	8.7
3FH*Sex	-36.1	8.7
Intercept	-38	8.9
31FH + Sex	-38.6	8.9
31FH*Sex	-38.9	8.9