



Changes in habitat use and nesting density in a declining seabird colony

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Abstract Seabirds in expanding colonies select the highest-quality nesting habitat, but habitat selection has seldom been studied in declining colonies. We studied a colony of Magellanic penguins (*Spheniscus magellanicus*) that declined from 314,000 active nests in 1987 to 201,000 in 2014. As expected, nest quality and reproductive success were higher in burrow habitats than in other habitats, and nest density decreased with distance from shore. Contrary to predictions, the steepest declines did not occur in the poorest-quality habitat (scrub) or near the inland colony edge and the colony area did not shrink. In agreement with predictions, penguins shifted from nests with less cover to nests with more cover. The highest nest densities and the steepest declines were in habitats of large bushes and bush clusters. As the population declined penguins abandoned nests on the edges of large bushes. Constraints on penguin habitat-use changes include strong area and nest-site fidelity, increased avian predation in high-density areas, soil characteristics, and the costs of making and maintaining nests. Contrary to conventional wisdom we found low-

density, poor-quality scrub habitat (which covers >70 % of the colony area) contained 45 % of active nests, produced 44 % of fledglings, and was as important as high-quality habitat for reproductive output. Our research shows that all habitats in a declining colony of seabirds have value for conservation.

Keywords Colonial seabird · Habitat quality · Magellanic penguin · Nest quality · Population decline · *Spheniscus magellanicus*

Introduction

Habitat selection affects animal distribution as well as individual survival, foraging, and breeding success (Cody 1985; O'Shaughnessy et al. 2014; Patenaude-Monette et al. 2014; Pitman et al. 2014). Birds breed in heterogeneous habitats, with some habitats being more suitable, i.e., resulting in higher fitness, than others (Brown 1969; Fretwell and Lucas 1970; Rodenhouse et al. 1997). Even within a breeding colony, habitat often varies and affects nest-site quality (Kokko et al. 2004). High-quality nest sites provide better protection from heat, cold, rain, flooding, predators, and intraspecific aggression than low-quality nest sites (Boersma 1986; Stokes and Boersma 1998; Tulp et al. 2012; Boersma and Rebstock 2014). Pairs using high-quality nests typically have better reproductive success and therefore higher fitness than pairs in lower-quality nests although this is sometimes related to individual quality of breeders (Calladine 1997; Rodenhouse et al. 1997; Stokes and Boersma 1998; Hamer et al. 2002; García-Borboroglu and Yorio 2004).

In expanding colonies and during annual settlement, birds should occupy the best nest sites available, to

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maximize their fitness. Newly recruiting or arriving individuals should select nest sites in the best habitats where they can acquire and hold a nest (Brown 1969; Fretwell and Lucas 1970). Patterns of settlement consistent with habitat selection to maximize fitness are documented in seabirds as diverse as cormorants (Velando and Freire 2003), gulls (Oro 2008), gannets (Pyk et al. 2013), and penguins (Sherley et al. 2014), and in passerines and other animals (Rodenhouse et al. 1997).

When seabird colonies decline, the opposite pattern is expected, with the poorest nest sites abandoned first, and the best nest sites abandoned last (Krohn 1992). As a colony declines, pairs breeding in poor-quality nest sites should switch to higher-quality nest sites as they become available, and new recruits should also select any empty higher-quality nest sites (Rodenhouse et al. 1997). Declines in poorer nesting habitat, therefore, should be steeper than declines in higher-quality habitat.

Nests in peripheral areas of colonies often have lower reproductive success than centrally-located nests (Coulson 1968; Gochfeld 1980; Siegel-Causey and Hunt 1981; Lynch et al. 2010a; Svagelj and Quintana 2011); as breeding populations decrease, peripheral nests should be abandoned before central nests and the area of the colony should shrink. Site fidelity of breeders (Krohn 1992) and the tendency of new recruits to select nest sites near their natal nests (Priddel et al. 2006) or in the same habitat as their natal nests (Davis and Stamps 2004) may disrupt this pattern. Lower-quality pairs or nests may cluster around higher-quality pairs or nests, forming multiple centers of high quality throughout a colony (Burger and Shisler 1980; Velando and Freire 2001). For penguins, breeding in peripheral areas near the water may be advantageous because walking farther inland has energetic costs and, for temperate penguins, inland areas have higher temperatures than areas near the water (Stokes and Boersma 1998; Walker et al. 2004).

As seabird populations decline around the world (Croxall et al. 2012), individual colonies will decline, which could prompt colony-based conservation actions. What should these actions be? Understanding habitat use in declining seabird colonies should inform management decisions on habitat protection or restoration, predator control, and other interventions. Few studies, however, have documented habitat use in declining seabird colonies. Among studies of declining colonies, some supported predictions (Cordes et al. 1999; Robertson et al. 2001; Naveen et al. 2012), others did not (Coulson et al. 1982; Sherley et al. 2014; Morrison et al. 2015), and Gilchrist (1999) gave one example supporting the predictions and one example inconsistent with predictions.

We studied a large but declining colony of Magellanic penguins (*Spheniscus magellanicus* Forster) at Punta Tombo, Argentina. Penguins first colonized the site in the

1920s, and the colony grew to be the largest colony of the species by the 1960s (Boersma et al. 1990; Schiavini et al. 2005), but was declining by the 1980s (Boersma 2008).

We documented the decline in the breeding population from 1987 to 2014. We made three predictions about how penguins would select nesting habitats and four predictions about how penguins would alter their habitat selection when the colony was in decline. In accordance with habitat-selection theory we expected that penguins would: (1) have the highest nest density and ratio of active to total nests in the habitat with the highest-quality nests, (2) have the highest reproductive success in the habitat with the highest-quality nests, and (3) preferentially select nests near the center of the colony and/or the areas closest to the water. In a declining colony penguins should change nest sites to maintain optimum habitat selection and we expected: (4) declines in nest density to be greatest in the poorest-quality habitats, (5) declines in nest density to be greatest near the inland edge of the colony, (6) penguins to shift from poorly covered nests to nests with more cover regardless of the habitat, and (7) the area of the colony to shrink because penguins abandon peripheral areas.

Materials and methods

Study area and species

Since 1982 we have studied Magellanic penguins at Punta Tombo, Chubut Province, Argentina (Fig. 1; 44°03'S, 65°13'W) (Boersma et al. 1990), in arid coastal Patagonia with vegetation dominated by bushes [Table S1 in Electronic Supplementary Material (ESM)] (Stokes and Boersma 1991). Magellanic penguin colonies are irregular in shape, bounded by the high-tide line but lacking a sharp inland boundary, with some inland nests isolated from each other by 50 m or more.

Magellanic penguins in the south Atlantic are migratory (Stokes et al. 2014). Breeding adults arrive at Punta Tombo in September or early October and lay two eggs, mostly in October (Boersma et al. 1990; Boersma and Rebstock 2014). Chicks hatch in November or early December, are brooded or guarded by one parent for about a month, then left alone while both parents forage. An unguarded chick may remain in its nest, or move to a nearby nest. Chicks fledge in January or February (Boersma et al. 1990, 2013).

Magellanic penguins nest in burrows that they dig and under bushes, with few nesting in open scrapes (Stokes and Boersma 1991). Burrow nests generally have more protection from the sun, rain, and predators, and have higher reproductive success, than nests under bushes (Stokes and Boersma 1998; Boersma and Rebstock 2014), although reproductive success in the highest-quality bush and

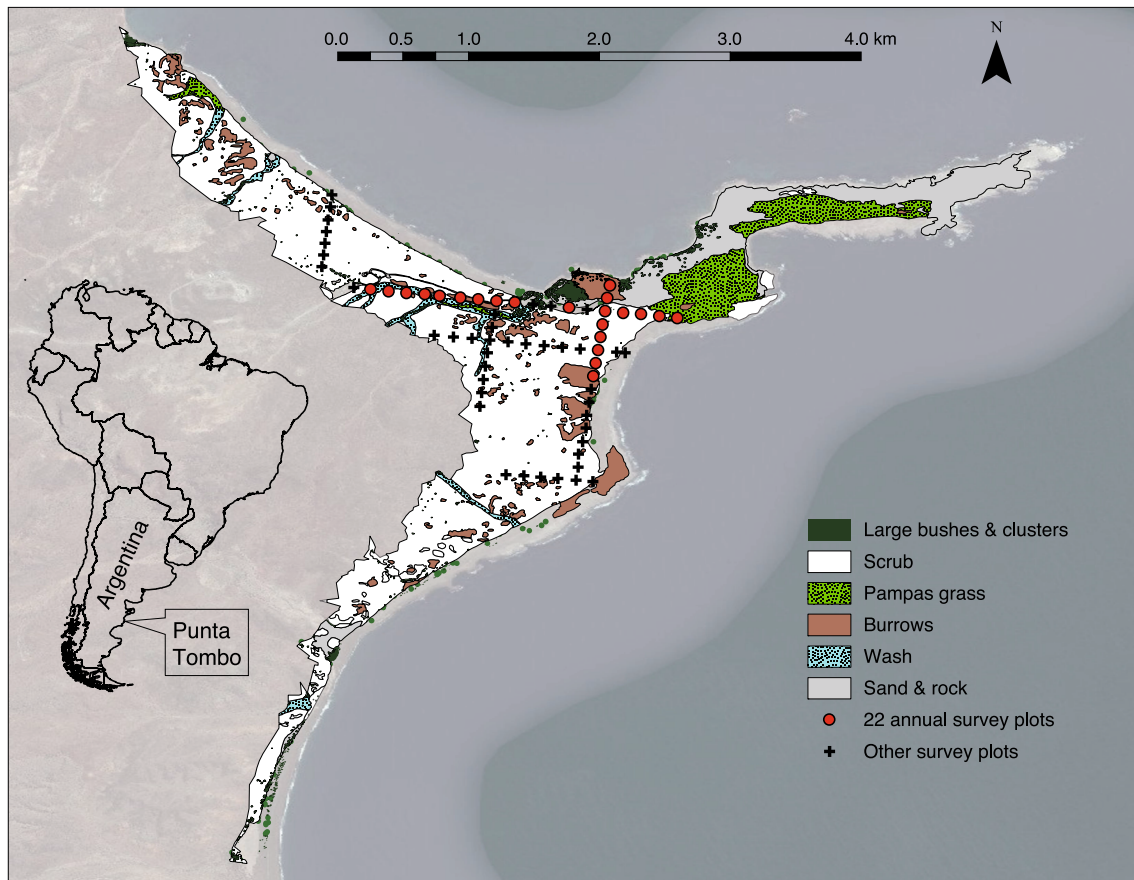


Fig. 1 The Magellanic penguin colony at Punta Tombo, Argentina, occupies about 400 ha. Habitats are shown in polygons. The large-bush and bush-cluster habitats are combined as “large bushes and clusters”. 1240 of the smaller bushes in this habitat are not shown. Large burrow areas and small burrow areas are combined as

“burrows”. Habitats that penguins do not use for nesting, sand, rock, parking lots, and a trail walked by tourists are combined as “sand and rock”. The 22 standard staked plots surveyed annually 1987–2014 are *circles*. Staked plots surveyed in some years are *crosses*. The inset map shows the location of Punta Tombo

burrow nests is similar (Stokes and Boersma 1998). Temperatures are higher in inland nests than in nests near the coast. Experimental and longitudinal data showed that nest characteristics matter independently of individual quality in breeding penguins (Stokes and Boersma 1998). Not all burrows or other nest sites are used each season, with about 10 % of burrows unoccupied (Stokes and Boersma 1991).

Colony and habitat mapping

We used hand-held GPS devices (Garmin Ltd., Olathe, Kansas or Magellan, Santa Clara, California) to determine the boundaries of the colony in October 1996, 2003, 2006, and 2009. Three to five people searched for the outermost active nests and recorded their latitudes and longitudes. We plotted the outermost nests and created a colony polygon in ArcMap 10.0 (Esri, Redlands, California) except in 1996 when we created a map on graph paper.

We created a habitat map of the penguin colony by digitizing habitats on the Bing Maps Aerial basemap in

ArcMap. We defined seven habitats, two predominantly bare of vegetation, two predominantly covered by bushes, and three mixed habitats (Table S2, Figs. S1–S6 in ESM). We divided the mostly-bare areas into large burrow areas ($\geq 100 \text{ m} \times 50 \text{ m}$, Figs. S1, S2 in ESM) and small burrow areas ($< 100 \text{ m} \times 50 \text{ m}$) because the smaller areas may have edge effects that the larger areas lack. The bush-dominated habitats included large bushes (smallest dimension $< 10 \text{ m}$, Fig. S2 in ESM) and bush clusters (smallest dimension $\geq 10 \text{ m}$, Fig. S3 in ESM). The three mixed habitats were scrub habitat (areas with scattered small bushes, Figs. S1, S4 in ESM), washes (dry streambeds, Figs. S4, S5 in ESM), and pampas grass (Figs. S1, S6 in ESM). We removed areas of bare rock, sand (not suitable for burrows), and man-made structures such as buildings and parking lots from the habitat maps, making the sum of the habitat areas less than the area within the mapped boundaries. We traced habitats at a resolution of 1:3000 and tagged large bushes and traced bush clusters at 1:1000. We calculated the area of each habitat in ArcMap.

Annual surveys

In 1986, we established a permanent grid with lines running 1.5 km north to south and 2 km east to west and permanent markers (rebar stakes hammered into the ground) every 100 m (Stokes and Boersma 1991), using a theodolite to find the grid locations to mark (Fig. 1). Like others, we used the same plots every year to control for spatial variation (Greenwood and Robinson 2006) such as vegetation and soil characteristics, which affect nest density (Stokes and Boersma 1991). Using fixed plots yields an index of population size and can show trends in population (Lancia et al. 1994; Bart and Earnst 2002; Greenwood and Robinson 2006). Rodway and Lemon (2011) found that, for burrow-nesting seabirds, six to eight permanent plots of 100 m²–400 m² showed trends similar to the trends found by full-colony transect surveys. We did two surveys (one in October and one in January or February) each breeding season from 1987 (the 1987–88 season) through 2014, excluding 2011, and we refer to the sampling period as 1987–2014 (Table S3 in ESM).

In each survey we counted nests, penguins, eggs, and chicks within a 100-m² circle centered at the rebar marker using a rope with 2 knots tied 5.64 m apart to delineate the edge of the circle. The counter looked in every nest site in the circle, and determined the nest status (active or inactive) and type (burrow, live bush, dead bush, or scrape). An active nest in October contained a penguin or egg; in January or February, it had to contain a penguin, chick, or egg, or have abundant guano at the nest entrance. Active nests may be empty when checked late in the season because both adults are foraging and the chicks are in another nest, but abundant guano indicates the nest likely had chicks during the season. In 2006–2014, we also counted ancient nests, nests that had grass growing in the nest cup and had not been used in at least the last two years.

Roof cover is the most important nest characteristic predicting reproductive success (Stokes and Boersma 1998). In 2007–2014, we assessed the quality of each nest as one of five roof-cover categories: best = 100 % cover over the nest cup, good = 80–99 % cover, average = 60–79 % cover, poor = 1–59 % cover, worst = 0 % cover, an open scrape. Roof cover is a subjective judgement but either PDB or GAR was present each year to train and calibrate new observers before the start of the survey.

Breeding penguins usually remained in their nests during the surveys but if a penguin ran out of a nest we counted the nest as active. We counted penguins within the circle but not associated with a nest as wandering, not breeding. We recorded the two or three bush species that covered the most area in each circle and estimated the percent of the circle covered by bushes, by grasses or herbaceous plants, and by bare soil or rock.

Estimating breeding population size of the colony

We estimated the breeding population of the colony in October 2012 using a separate stratified-random survey. We selected 10 random points in each of the seven habitats, using ArcMap, and surveyed plots that were completely within each habitat. We used 100-m² circles in the burrow, wash, pampas-grass, and scrub habitats, following the protocol of our annual surveys. We used 10-m² circles in large bushes and bush clusters, which were seldom large enough for a 100-m² circle. If a bush was not large enough for a 10-m² circle, we counted nests inside a rectangle contained in the bush and measured its dimensions. We sampled as many 10-m² circles as fit in each large bush or bush cluster because these plots were much smaller than those in the other habitats. We combined the counts in all the circles in a bush or cluster. Hence, area of each plot was not constant in the large-bush and bush-cluster habitats.

Analyses

Population decline

We tested for trends in the number of active nests using the annual fixed-plot surveys and linear regression of the mean active-nest density in October surveys on year. We used the same 22 plots surveyed in each October 1987–2014 (27 years) to avoid confounding spatial and temporal differences. We tested whether number of plots, survey start date, or using different observers affected our results (Sect. 2 in ESM). We also regressed the number of empty plots (plots with no active nests) on year, using the 22 plots surveyed in all years.

We estimated the number of active nests in the colony from the 2012 stratified-random survey as the sum of the total nests in each habitat (see below). We also summed the bootstrap means for each habitat to calculate 95 % confidence intervals for the total breeding population. We used the linear regression equation for 22 plots and the total population size in 2012 to estimate the breeding population in 1987 and 2014.

Predictions of habitat use

Prediction 1: the habitat with the highest-quality nests should have the highest density of nests and the highest ratio of active to total nests

We ranked the seven habitats by nest quality (cover). We calculated the percentage of nests in each nest-cover category in each habitat in the 2012 stratified-random survey. The highest-quality habitat was the habitat with the highest percentage of best- and good-quality nests.

We calculated density (number of nests counted divided by area surveyed), and number of active nests (density times total area) in each habitat from the 2012 stratified-random survey. We used a bootstrap method to calculate the 95 % confidence limits for each habitat and for the total breeding population. We resampled the counts with replacement 1000 times for each habitat and calculated the mean of each sample. The 95 % bootstrap confidence intervals are the 25th and 975th values from a ranked list of the 1000 means. The confidence intervals may be asymmetrical around the mean.

Prediction 2: the habitat with the highest-quality nests should have the highest reproductive success

We estimated reproductive success using the annual surveys by dividing the number of chicks found in January or February in all plots in each habitat by the number of active nests in October of the same breeding season and habitat (Cooper et al. 1997; Commission for the Conservation of Antarctic Marine Living Resources 2004; Wanless et al. 2009). We selected 18 years in which we surveyed the most plots twice because not all plots were surveyed twice in the same season. We combined large with small burrow areas, and large bushes with bush clusters because of small sample sizes. The burrow-, scrub-, and large-bush/bush-cluster-plot groups were not the same as in the population-trend analysis because of plots not surveyed twice in all years.

We compared reproductive success among habitats using ANOVA with habitat and year as factors. We excluded the wash habitat because reproductive success in wash plots was zero in all but 2 years and the residuals for the wash plots were problematic. We did a Tukey test for multiple comparisons following the ANOVA. We did not transform reproductive success because reproductive success estimated in this way has no theoretical maximum. Chicks move between nests and plots, and a nest can have more than two chicks during the January/February survey. Tests for heteroskedasticity and nonnormality of the residuals were not significant.

Prediction 3: the center of the colony and/or the areas closest to the water should have the most breeding penguins

To determine if nest density decreased with distance from the shore, we used data from October 1987 and 2006, the years with the most plots (Table S3 in ESM), and used a Spearman's rank correlation. Many of these plots were 33 m apart (instead of 100 m) and were not permanently staked. We calculated the shortest distance between each plot and the coastline using ArcMap, and excluded plots

that we surveyed outside the mapped boundaries of the colony ($n = 738$ in 1987, $n = 656$ in 2006). About one-third of the plots ($n = 243$) were sampled in both years. We used two years to show that the relationship is general, not restricted to one year.

To determine if empty plots were located near colony edges, we created a 100-m buffer inside the colony boundaries using ArcMap. We used all 1643 plots surveyed from 1987 to 2014 and counted the number of empty plots that overlapped the buffer on the coastal and inland edges and the number of empty plots >100 m from the colony boundaries.

Predictions of changes in habitat use as the colony declined

Prediction 4: declines in nest density should be greatest in the poorest-quality habitats

We regressed mean nest density in each habitat on year, 1987 and 1991–2014 to test whether nest density declined, combining large with small burrow areas and large bushes with bush clusters. To compare trends in the plots by habitat we regressed active nests (after centering by habitat) on year, habitat, and their interaction. The coefficient of the interaction term is the difference in slopes between groups (UCLA: Academic Technology Services. Statistical Consulting Group 2011).

Prediction 5: declines in nest density should be greatest near the inland edge of the colony

Using all 1643 plots surveyed, we visually identified plots in ArcMap that were close to the inland and northern edges of the colony to test for trends in number of active nests in peripheral areas. We surveyed eight plots near the northern extreme of the colony twice, once in 1987 or 1989 and again in 2006. We compared means between 1987/1989 and 2006 using a paired t test. We surveyed six plots near the inland edge of the colony (within 120 m of the edge) in 22 years (1987 and 1993–2014) and regressed mean active nests on year. We mapped the distribution of plots with significant increases or decreases, and those with no significant trends. We also mapped plots that were surveyed twice, showing the spatial distribution of areas of higher, lower, and equal nest density after 17 or 19 years.

Prediction 6: penguins should shift from poor to better nests regardless of the habitat

We used nest type as a proxy for nest quality, as burrow nests usually have higher quality and reproductive success than bush nests. We excluded scrape nests because there

were few (see “[Results](#)”). We calculated the mean proportions of burrow nests and bush nests (live and dead bushes combined) each year using the 22 plots surveyed in all years. We regressed the proportion of burrow nests on year. We did not transform the proportions because it was not necessary (Warton and Hui 2011). Residual plots did not show trends, and tests for heteroskedasticity, skewness, and kurtosis of the residuals were not significant.

Prediction 7: the area of the colony should shrink because penguins abandon peripheral areas

We scanned a map made in 1971 (Boswall and Prytherch 1972) and our map from 1996, georeferenced them using known locations, such as bends in the coastline, and overlaid them with our 2009 map in ArcMap to compare colony boundaries. We then compared the colony area from our maps in 2003 through 2009.

We surveyed 229 plots outside the mapped boundaries of the colony in one to 5 years, mostly 1987–1992 and 2005 or 2006. We counted inactive nests in all years and ancient and inactive nests in 2006. If the colony area shrank before we mapped it we should find former nests outside the mapped boundaries.

Statistics

We used Stata 9.1 (StataCorp LP, College Station, Texas) for statistical tests. Bootstrap procedures used a custom program in MATLAB R2010a (The MathWorks, Natick, Massachusetts). We present results as mean \pm SE unless otherwise stated.

Results

Population decline

The penguin colony at Punta Tombo contained 209,300 active nests in 2012 (Table 1), and declined 36 % from about 314,000 active nests in 1987 to 201,000 nests in 2014 (Fig. 2; Table S4 in ESM, Sect. 3 in ESM). The number of plots, from 22 to 251 did not affect our conclusions, the survey start date did not matter, and observer variance was <10 % (Sect. 2 in ESM).

The number of plots with no active nests increased as expected in a declining colony ($F_{1,25} = 28.3$, $P < 0.0001$, $R^2 = 0.53$). From 1987 to 2001, there was a maximum of 4 empty plots/year, with only 1 or 2 empty plots in 4 years. From 2002 to 2014 there were 3–7 empty plots/year, with 5–7 empty plots in 2008–2014.

Habitat use

Our data mostly supported the three predictions from habitat-selection theory. The habitat with the highest-quality nests had the highest ratio of active to total nests (but not the highest nest density) and the highest reproductive success. Areas closest to the water had the most breeding penguins.

Prediction 1: the habitat with the highest-quality nests had the highest ratio of active to total nests but not the highest density of nests

Burrow habitats had the highest-quality nests (Table 2), and, consistent with predictions, large burrow areas had the highest ratio of active to total nests and small burrow areas and bush clusters had the second highest active-nest ratios (Table 2). Active nests on average were of higher quality with more cover than inactive nests ($\chi^2(4) = 100$, $P < 0.0001$). Active nests accounted for 70 % of the best nests, 62 % of good nests, 37 % of average nests, 25 % of poor nests, and 3 % of the worst nests that had no cover.

Burrow habitats, however, did not have the highest nest densities (Table 1). Bush clusters and large bushes had the highest nest densities but ranked 4th and 6th in nest quality, respectively. Scrub habitat, with the poorest-quality nests and low nest densities held more active nests than any other habitat (Table 1) because of its large extent (>70 % of the colony area).

Prediction 2: the habitat with the highest-quality nests had the highest reproductive success

Reproductive success varied by habitat ($F_{3,51} = 4.5$, $P = 0.007$; Table 3) and year ($F_{17,51} = 9.2$, $P < 0.0001$). Reproductive success was significantly higher in burrow habitats, which had the highest-quality nests (Table 2), than in pampas grass. Reproductive success in the wash habitat was lower than in all other habitats, exceeding zero in only 2 years (1996 and 1998). More chicks fledged from scrub habitat than from burrow habitats even through nest quality was generally poorer in scrub habitat (Table 3), because of the large number of nests in scrub habitat.

Prediction 3: the center of the colony and/or the areas closest to the water had the most breeding penguins

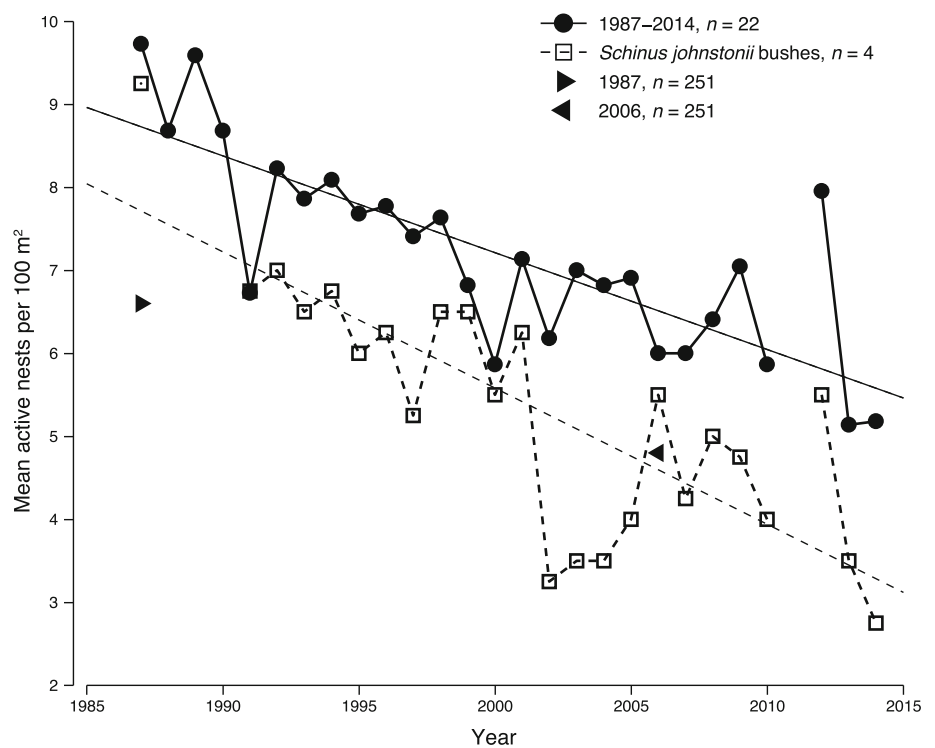
Nest density was higher closer to the shore and lower inland (1987: $r_s = -0.43$, $P < 0.0001$, $n = 738$; and 2006: $r_s = -0.28$, $P < 0.0001$, $n = 656$). Most empty plots were near the edges of the colony and most of the empty plots near the colony edges were inland rather than along the coast (Table 4).

Table 1 Area, mean density and the number of nests varied among habitats in the Magellanic penguin colony at Punta Tombo, Argentina in a stratified-random survey in 2012

Habitat	Area of habitat (ha)	Size of plots (m ²)	Area surveyed (m ²)	Mean nest density (number per 100 m ²)	Total nests	95 % confidence intervals
Large burrow areas	22.1	100	1000	20.2	44,710	(33,860, 55,550)
Small burrow areas	13.5	100	1000	16.3	22,070	(13,780, 31,960)
Scrub	253.7	100	1000	3.7	93,880	(60,890, 131,930)
Wash	13.3	100	1000	3.6	4800	(2270, 8000)
Pampas grass	39.1	100	1000	1.3	5080	(390, 13,290)
Large bushes	6.2	11.85 (4.5–40)	118.5	32.9	20,350	(13,450, 35,450)
Bush clusters	4.5	21.6 (10–40)	216.0	40.7	18,430	(12,670, 25,090)
Totals	352.4		5334.5		209,300	(171,100, 256,200)

Ten plots were surveyed in each habitat except large bushes and bush clusters. Mean plot size is shown for these habitats, with range in parentheses

Fig. 2 The number of active Magellanic penguin nests per 100 m² at Punta Tombo, Argentina, declined significantly from 8.7 in 1987 to 5.6 in 2014 ($n = 22$ plots). Trends shown used 22 plots of 100 m² surveyed each year from 1987 to 2014, except 2011 (solid line, black circles) with regression line (thin solid line), and 4 plots dominated by large *Schinus johnstonii* bushes, surveyed each year, 1987 and 1991–2014, except 2011 (dashed line, open squares) with regression line (thin dashed line). The unconnected black triangles represent the mean nest densities estimated from surveys of 251 plots in 1987 and 2006



Changes in habitat use in a declining colony

Our data supported only one of the four predictions of how penguins should change their habitat use in a declining colony. Contrary to predictions, the greatest declines were not in the poorest-quality habitats, or near the inland edge of the colony, and the colony area did not shrink during our study (but did shrink prior to 1971). In agreement with predictions, penguins shifted from poor (bush) nests to nests with more cover (burrow nests).

Prediction 4: declines in nest density were not greatest in the poorest-quality habitats

Nest density declined in burrow, large-bush, and scrub habitats (Table 5). The slope of the decline was greatest in the highest-quality habitat (burrows) and lowest in the worst-quality habitat (scrub), contrary to the prediction. The proportional decline, however, was equal in burrows and scrub, and highest in large bushes (Table 5).

Table 2 Nest quality as determined by cover, and ratio of active to total nests depended on habitat in the 2012 stratified-random survey of Magellanic penguins at Punta Tombo, Argentina. Habitats areordered by rank, based on the percentages of best- and good-quality nests in each habitat. *G* tests were used because 5 of the 28 cells had counts <5. $G_{18} = 146$, $P < 0.0001$

Habitat	Best (100 % cover)	Good (80–99 % cover)	Average (60–79 % cover)	Poor (<60 % cover)	Ratio of active to total nests (%)
Large burrow areas	129 (64 %)	42 (21 %)	20 (10 %)	10 (5 %)	68
Small burrow areas	70 (43 %)	44 (27 %)	26 (16 %)	23 (14 %)	56
Wash	9 (25 %)	13 (36 %)	9 (25 %)	5 (14 %)	36
Bush clusters	23 (26 %)	26 (30 %)	34 (39 %)	5 (6 %)	57
Pampas Grass	2 (15 %)	5 (38 %)	4 (31 %)	2 (15 %)	30
Large bushes	4 (10 %)	16 (41 %)	14 (36 %)	5 (13 %)	43
Scrub	0	5 (14 %)	22 (59 %)	10 (27 %)	26

Large burrow areas had significantly higher quality than all other habitats ($P \leq 0.005$) and scrub had lower quality nests than all other habitats ($P \leq 0.02$). Small burrow areas had higher quality nests than bush clusters ($G = 20.4$, $P = 0.0001$) and large bushes ($G = 19.4$, $P = 0.0002$). All other habitats had similar proportions of nest-cover categories ($P \geq 0.09$)

Table 3 Mean reproductive success of Magellanic penguins (number of chicks in January or February survey divided by number of active nests in October survey) at Punta Tombo, Argentina, in 1991, 1993, 1996, 1998–2008, 2010, and 2012–2014, varied among habitats

Habitat	Number of plots	Reproductive success (mean \pm SD)	Number of chicks fledged
Burrow areas	7	0.62 \pm 0.32	41,000
Scrub	31	0.54 \pm 0.28	51,000
Wash	2	0.08 \pm 0.26	380
Pampas Grass	2	0.41 \pm 0.36	2100
Large bushes/bush clusters	6	0.55 \pm 0.31	21,000

Large and small burrow areas are combined and large bushes and bush clusters are combined. Five of the large-bush/bush-cluster plots were not completely within the bushes so reproductive success and the number of chicks fledged are likely underestimated. The more than 115,000 fledged chicks is based on the total number of active nests in each habitat in 2012 (Table 1) and mean reproductive success

Table 4 Empty plots (survey plots with no active Magellanic penguin nests) were concentrated near the colony edges, especially inland, at Punta Tombo, Argentina, 1987–2014

Location/plot category	Number of plots	Area (ha)
Total plots	1643	402
Empty plots	262	
Empty plots within 100-m buffer (total)	151	185
Empty plots within 100-m buffer along coast	52	122
Empty plots within 100-m buffer along inland side of colony	99	63

Prediction 5: declines in nest density were not greatest near the inland edge of the colony

Active nests near the inland edges of the colony did not decline consistently. In the eight plots near the northern extreme of the colony that we surveyed twice, mean active nests in 1987 or 1989 (2.25) and 2006 (2.13) were similar (paired *t* test: $t = 0.2$, $P = 0.83$). Active nests decreased in three of the plots, increased in three of the plots, and remained zero in two plots (Fig. 3). The six plots near the inland edge of the colony that we surveyed in 22 years did not show a significant decline ($F_{1,20} = 0.9$, $P = 0.88$).

Of the plots that we surveyed in most years, the highest concentration of plots with significant declines in active nests was on the base of the peninsula, near the geographical center of the colony (Fig. 3). Unlike plots near the northern and inland edges of the colony, many of these peninsula plots had at least 10 active nests in the late 1980s, and have declined steeply, from a mean of 12 active nests per 100 m² in 1987 to about 6 in 2014 ($F_{1,20} = 60.1$, $P < 0.0001$, $R^2 = 0.75$, 12 plots declining, 1 plot increasing). Active nests in bushes on the peninsula beyond the base declined the most (P.D. Boersma, personal observation), but we did not survey plots there more than once.

Table 5 Active-nest density of Magellanic penguins decreased in large-bush, burrow, and scrub habitats from 1987 to 2014 (surveys in 1987, 1991–2010, and 2012–2014) at Punta Tombo, Argentina

Habitat	Slope (regression coefficient)	Percent change (number of active nests per 100 m ² in 1987 and 2014)	<i>n</i>	<i>F</i> _{1,22}	<i>P</i>	<i>R</i> ²
Burrow areas	-0.21 ± 0.06	-25 % (22.0, 16.8)	5	12.8	0.002	0.37
Scrub	-0.05 ± 0.013	-26 % (5.0, 3.7)	32	13.4	0.001	0.38
Wash	-0.002 ± 0.01		2	0.02	0.88	
Pampas grass	0.001 ± 0.03		2	<0.01	0.97	
Large bushes	-0.16 ± 0.03	-57.5 % (7.7, 3.3)	4	38.8	<0.0001	0.64

The regression slope was significantly lower in scrub than in large bushes (*P* = 0.01) and burrows (*P* = 0.001). Slopes were similar in large bushes and burrows (*P* = 0.38). *n* = number of plots surveyed each year. The large-bush plots were dominated by large *Schinus johnstonii* bushes, but were not completely within the bushes. We do not show percent change and *R*² for habitats where trends were not significant

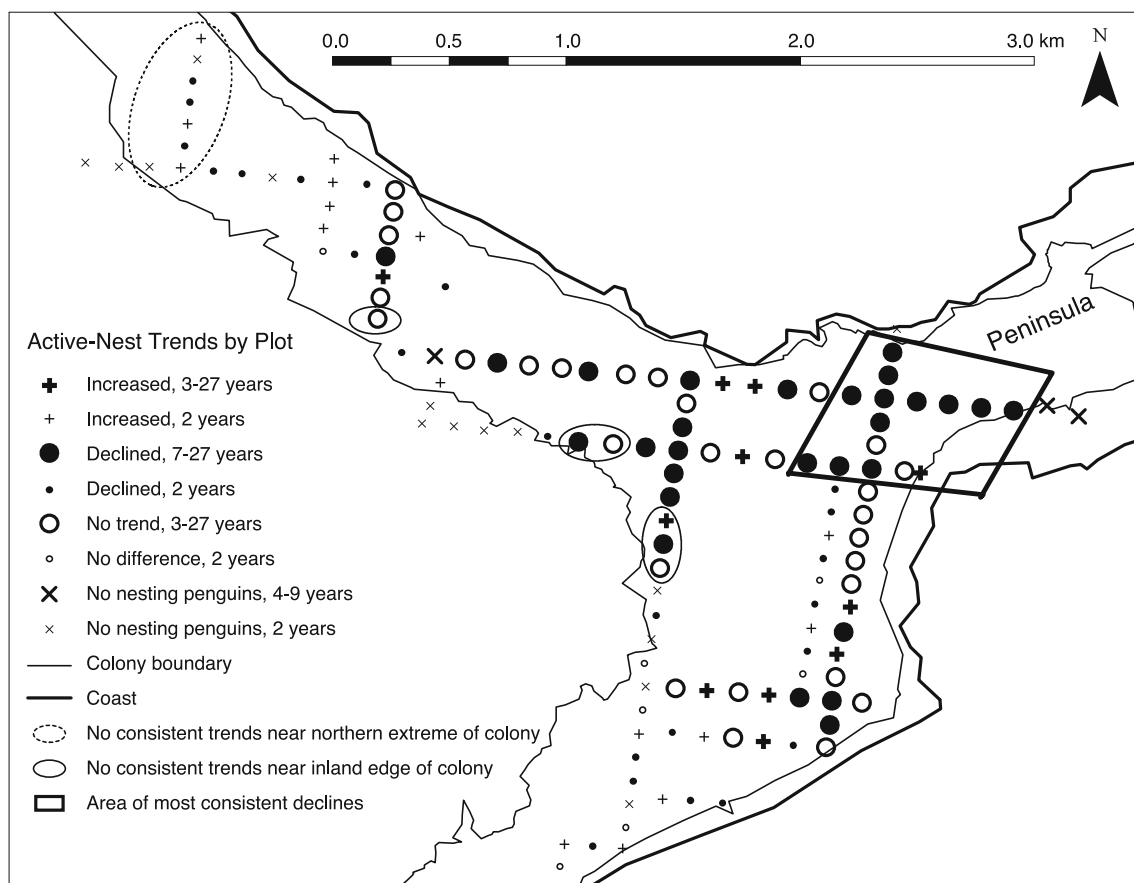


Fig. 3 Declines in density of active Magellanic penguin nests at Punta Tombo, Argentina from 1987 to 2014 were most consistent on the base of the peninsula, near the geographic center of the colony (plots enclosed in bold polygon). Small symbols represent plots surveyed twice, once in 1987 or 1989 and again in 2006. Large

symbols represent plots surveyed >2 times between 1987 and 2014 (62 of 71 plots were surveyed ≥22 times). 8 plots near the northern extreme (enclosed in dashed oval) and 6 plots near the inland edge of the colony (enclosed in ovals) did not show consistent increases or declines

Prediction 6: penguins shifted from poor to better nests regardless of the habitat

Burrow nests increased relative to bush nests by 0.3 % per year (*F*_{1,25} = 5.2, *P* = 0.03), an increase from approximately

46 % burrows in 1987 to approximately 53 % in 2014 in the 22 plots surveyed in all years. Using all plots surveyed in October 1987–2014 but only counting each plot once, 51 % of 10,574 active nests were under live bushes, 5 % were under dead bushes, 43 % were in burrows, and 0.5 % were scrapes.

Prediction 7: the area of the colony did not shrink; penguins did not abandon peripheral areas

The colony area has remained similar since we first mapped it in 1996. The penguin colony occupied 402 ± 4 ha in 2003, 2006, and 2009 (Fig. 1), with the largest and smallest estimates differing by about 8 ha or 2 %. Our 1996 map had similar boundaries to our 2009 map. The northern boundary of the colony was similar from 1971 to 2009. Boswall and Prytherch's (1972) map was similar to our maps for the northern part of the colony. Their map excluded low-density areas so it did not extend as far inland or as far south as our map (Sect. 3 in ESM).

The colony area, however, shrank prior to being mapped in 1971. We found 34 inactive and ancient nests in 26 of the 229 plots we surveyed from 1987 to 2006 outside the mapped boundaries of the colony, indicating that the colony area was larger in the 1960s when there were more breeding pairs.

Discussion

The habitat-selection predictions were supported but most of the predictions of changes in habitat use in a declining population were not supported. As expected, the habitat with the highest-quality nests had the highest reproductive success and the highest ratio of active to total nests, and nest density decreased with distance to shore. As the colony declined, however, breeders did not always change their habitat use as theory predicted. We found Magellanic penguins shifted from lower-quality bush nests to higher-quality burrow nests regardless of the habitat, but the greatest declines in nest density were not in the habitats with the poorest nests or near the inland edge of the colony. The colony area shrank before 1971, but remained stable afterwards as the population continued to decline. All habitats in a declining colony, we found, had more equal value than predicted by theory. For conservation, our results indicate that all areas within a declining colony should be protected, not just the highest-quality habitat.

Population decline

We found a significant linear decline in the density of active nests, but interannual fluctuations were large. The linear trend in nest density mirrors a decline in the population. Sample sizes from 22 to 251 plots did not alter the results showing that large sample sizes are not needed to detect these trends. The interannual variability, however, reflects the proportion of penguins attempting to breed each year, as Magellanic penguins sometimes skip a breeding

season (Boersma and Rebstock 2010). Long-lived birds make trade-offs between survival and reproduction when conditions are poor (Jenouvrier et al. 2003; Lee et al. 2007; Zabala et al. 2011). The breeding population, not the total population, determines the reproductive output of the colony, and the proportion of breeders affects long-term population dynamics in seabirds (Jenouvrier et al. 2005; Sandvik et al. 2012).

We likely detected nearly all active nests in October regardless of survey date. Magellanic penguins have high breeding synchrony (Boersma et al. 1990; Boersma and Rebstock 2014) and males attend their nests for 3–4 weeks before eggs are laid (Williams and Boersma 1995) so multiple counts during incubation are not necessary. Neither the date of the survey in October (although laying dates varied among years) nor observer variance (<10 %) affected active nest count.

Habitat use

Prediction 1: the habitat with the highest-quality nests had the highest ratio of active to total nests but not the highest density of nests

The highest densities of nests occurred under large bushes and bush clusters, not in the highest-quality habitat (burrows). Competitive interactions resulted in higher density in poor habitats in some mammals, land birds (Van Horne 1983) and seabirds (Oro 2008). At Punta Tombo, the higher density in large bushes is because the poorer large-bush and bush-cluster habitats can hold more nests than the better burrow habitats, bush nests are less costly to make than burrow nests, and all nests under large bushes except the outermost nests are protected from predators by the peripheral nests. The footprint of a burrow is larger than that of a bush nest because of the tunnel between the burrow entrance and nest cup (Boswall and MacIver 1975; Stokes and Boersma 1991). Many pairs of penguins can nest under a large bush simultaneously. The cost of making and maintaining a burrow nest is higher than the cost of a bush nest because of the amount of soil that penguins must remove to make new burrows or dig out collapsed burrows to make them suitable (Stokes and Boersma 1991). At the scale of a large bush or bush cluster, but not at the scale of the colony, peripheral nests protect interior nests from predators. In addition, penguins are less likely to fight if their nests are separated by branches, as in large bushes, reducing aggressive interactions that decrease reproductive success at high densities (Stokes and Boersma 2000). Branches also hinder predators and protect unattended chicks from aggressive nonbreeding penguins (Seddon and Van Heezik 1993; P.D. Boersma, unpublished data).

Prediction 2: the habitat with the highest-quality nests had the highest reproductive success

Burrow habitats had the highest-quality (highest-cover) nests and the highest reproductive success because burrows offer more protection from weather and aerial predators than bush nests (Frere et al. 1992; Stokes and Boersma 1998; Gandini et al. 1999; García-Borboroglu et al. 2002; Boersma and Rebstock 2014). Seabirds that nest in covered sites generally have higher reproductive success than conspecifics that nest in the open (Frost et al. 1976; Cordes et al. 1999; Paredes and Zavalaga 2001; Muzaffar et al. 2015). The substrate of burrows matters, as reproductive success is affected by burrow collapse and flooding (Thompson and Furness 1991; Stokes and Boersma 1998; Paredes and Zavalaga 2001; Sherley et al. 2012).

Wash habitats, with the third-highest average nest quality, had the lowest reproductive success because washes flood during large rain storms, killing eggs and chicks (Boersma et al. 2004; Boersma and Rebstock 2014). Nests in low-lying areas were most likely to flood in other seabird colonies (Bonter et al. 2014). Scrub habitat at Punta Tombo produces more fledglings than burrow habitats even though it has the lowest-quality nests on average because of its large area.

Prediction 3: the center of the colony and/or the areas closest to the water had the most breeding penguins

Nest density decreased with distance to shore, as predicted, at least partly because of the distribution of habitats. Soil suitable for burrowing (Stokes and Boersma 1991) and most of the largest bushes are closer to the shore than to the inland edge of the colony. The disadvantage of peripheral nests in seabird colonies is often because predators have easier access to peripheral nests than to central nests (Siegel-Causey and Hunt 1981; Kazama 2007) although lower-quality pairs that tend to fledge fewer young often use the peripheral nests (Coulson 1968). Predation rates at Punta Tombo, in contrast, are higher in higher-density areas (Stokes and Boersma 2000), which are not peripheral areas. Mammalian nest predators such as armadillos (*Chaetophractus villosus*), skunks (*Conepatus humboldti*), and weasels (*Galictis cuja*) breed within the colony (P.D. Boersma and G.A. Rebstock, personal observation) and do not approach it from outside. Peripheral nests are far apart so predators that breed outside the colony such as foxes (*Lycalopex culpaeus*, *L. griseus*), kelp gulls (*Larus dominicanus*), and Antarctic skuas (*Stercorarius antarcticus antarcticus*) can pass between them without interference from breeding penguins. Penguins cannot mob avian predators the way many colonial birds do (Kazama and Watanuki 2010).

Nonetheless, nests around bush clusters on the inland and northern edges of the colony had lower densities, later egg dates, fewer eggs, and fewer live chicks than nests around bush clusters in the center of the colony (Gochfeld 1980), a pattern apparent for the past 30 years. Nesting inland has higher energetic costs to get to the nest than nesting close to the beach (Walker et al. 2004) and exposes penguins, eggs, and chicks to higher air temperatures and more water loss (Stokes and Boersma 1998).

If nesting inland is more costly than nesting close to the shore, why do penguins walk up to 700 m inland to nest? Slope of the land partially determines where penguins enter (García-Borboroglu et al. 2002) and disperse within the colony as penguins prefer to walk inland on low slopes such as washes. Penguins usually nest farther inland and at higher densities along washes than in the surrounding scrub habitat. Our data showed similar average nest densities between wash and scrub habitats but washes had more variable density than scrub habitat (Table 1) because of varying topography. Furthermore, some large *Lycium* bushes that make good-quality nests are scattered throughout scrub habitat.

Changes in habitat use as the colony declined

Prediction 4: declines in nest density were not greatest in the poorest-quality habitats

The largest declines in nest density were in large bushes and bush clusters, the habitat with the highest nest density, not in scrub, the lowest-quality habitat. The large bushes contained both high-quality (near the bush centers) and low-quality (near the bush edges) nests. In the early 1980s there were often up to four layers of nests from the center to the periphery of large bushes. Nests near the edges of large bushes usually have low reproductive success and may be the last sites settled and the first sites abandoned when the number of breeding penguins increases or decreases. The nests at the very edges of large bushes declined noticeably from 1982 to 1987 (P.D. Boersma, personal observation), before our surveys began.

Other seabird species in declining colonies were inconsistent in their changes in habitat use. Declines were greater in poor habitats than in better habitats in thick-billed murre (*Uria lomvia*) (Gilchrist 1999), African penguins (*Spheniscus demersus*) (Cordes et al. 1999), eastern rockhopper penguins (*Eudyptes chrysocome filholi*) (Morrison et al. 2015), and herring gulls (*Larus argentatus*) (Robertson et al. 2001). Species that failed to follow this prediction as colonies declined included thick-billed murre (*Gilchrist 1999*) and African penguins (Sherley et al. 2014). The quality and variation of the habitat and nests may influence whether seabirds follow predicted behavior

as colonies decline. For example, at Robben Island where African penguin nests declined at similar rates throughout the colony, there were only two primary habitat types, bushes and tree plantations, with few penguins nesting in burrows, buildings, or in the open (Sherley et al. 2014). On Possession Island, Namibia, in contrast, most penguins used uncovered surface nests and in this habitat penguin numbers and the area they occupied decreased. Higher-quality nests in burrows and under bushes and rocks increased (Cordes et al. 1999). Punta Tombo has more complex and varied habitats than most penguin colonies, allowing a robust test of the predictions.

Site fidelity is high in many seabird species (Bried and Jouventin 2002) and may inhibit individuals from following predicted behaviors. Breeders are reluctant to change nests especially if they have successfully raised young (Rodenhouse et al. 1997; Bled et al. 2011; Robert et al. 2014). Recruits may also select nests near their natal nests (Priddel et al. 2006) or in the same habitat as their natal nests (Davis and Stamps 2004). Magellanic penguins have high area and nest-site fidelity (Stokes and Boersma 1998) so penguins at Punta Tombo have not disproportionately abandoned the poor-quality habitats. Penguins have higher costs of searching for nest sites than flying birds do (Schmidt-Nielsen 1972) and the probability of finding a high-quality site affects the value of the site (Levins 1968). Hence, the costs of searching for a higher-quality nest may outweigh its value. Moreover, knowledge of an area may constrain movement. Selecting habitat similar to the natal habitat helps recruits minimize search effort and maximize reproductive success (Davis and Stamps 2004). In addition, all habitats at Punta Tombo contain some good-quality nests.

Prediction 5: declines in nest density were not greatest near the inland edge of the colony

Contrary to the prediction, the most spatially consistent decline was close to the colony center. The inland edge and the northern and southern extremes of the colony probably always had lower nest densities than the central area and habitats close to the shore. Lower densities inland compared to near the coast have been documented since 1970 (Gochfeld 1980; Scolaro and Arias de Reyna 1984). Since we began our study in 1982 the southern extreme of the colony has not had a high density of penguins (P.D. Boersma, personal observation) and this area was not included in earlier maps of the colony because of the low density of nests (Boswall and Prytherch 1972; Scolaro and Arias de Reyna 1984). Area and nest-site fidelity plus the presence of some good-quality nests likely kept the low-density peripheral areas from declining much, whereas the higher-density areas had many more nests to lose.

Prediction 6: penguins shifted from poor to better nests regardless of habitat

The proportion of burrow nests (generally high quality) increased and the proportion of bush nests (generally lower quality) decreased. As noted above (prediction 4) African penguins in Namibia shifted from open surface nests to nests with more cover as the colony declined (Cordes et al. 1999), but when nest quality did not vary as much, African penguins did not follow the predictions (Sherley et al. 2014).

Prediction 7: the area of the colony did not shrink; penguins did not abandon peripheral areas

Results for other species were mixed. Chinstrap penguin (*Pygoscelis antarctica*) colonies on Deception Island, Antarctica, shrank as the population declined 39 % over seven years (Naveen et al. 2012). African penguin colonies in Namibia shrank and fragmented as the regional population decreased by 96 % (Cordes et al. 1999). As the African penguin colony on Robben Island, South Africa, declined by 69 %, however, the colony area did not shrink (Sherley et al. 2014). Culling of herring gulls over a decade reduced the population by 80 % but did not decrease the colony area (Coulson et al. 1982). Eastern rockhopper penguin colonies on Campbell Island, New Zealand did not shrink as the population decreased by 21.8 % between 1984 and 2012, although some colonies fragmented (Morrison et al. 2015).

We don't know when the penguin colony at Punta Tombo was at its population peak but the colony area decreased before it was first mapped in 1971 and has not changed since then. The data during our study period (1987–2014) did not support the prediction at the scale of the colony. At the scale of large bushes and bush clusters, the prediction was supported; penguins abandoned peripheral nests around the bushes as the colony declined.

Area and nest-site fidelity restrict penguins from moving between areas. Penguins nest far inland for reasons other than nest-site limitation; hence penguins have not moved closer to the shore or colony core as the population declined and more nests became available. Some peripheral nests are high quality because a few large bushes are scattered throughout the colony. Penguins continued to recruit to peripheral nests at least since the 1970s, as the time from 1970 to 2009 exceeds the breeding lifespan of an individual. Nevertheless, a Magellanic penguin can breed for more than 20 years (Boersma et al. 2013). If young breeders recruit near other existing nests, as many seabirds do (Burger and Shisler 1980; Danchin and Wagner 1997) or near their natal nest (Davis and Stamps 2004; Priddel et al. 2006), the longevity of nests may keep the colony boundaries from changing for decades.

Deviations from predictions of changes in habitat use

The primary reasons why Magellanic penguins did not follow habitat-use predictions when the colony was in decline, include: (1) Magellanic penguins have high area and nest fidelity, (2) predation and aggressive-interaction rates are high in high-density areas, giving low-density areas some advantages, (3) soil characteristics constrain the distribution of nest types and the stability of burrow nests, and there are good-quality nests in all habitats and near the inland edge of the colony, (4) bush nests are less costly to create and maintain than high-quality burrow nests, but reproductive success is low on the peripheries of large bushes, meaning that penguins are quick to colonize those nests and also quick to abandon them, and (5) the population at Punta Tombo is not nest-site limited. Behavioral, social, and geographic factors, as well as the relative cost of a nest type, constrain the habitat use of penguins in a declining colony, making predicted changes in habitat use unrealistic.

The deviations from our predictions have implications for conservation. Many seabirds are declining worldwide and often face colony-based threats such as invasive species, human disturbance, and coastal development (Croxall et al. 2012). Wildlife-based tourism is increasing worldwide with penguin and other seabird colonies popular destinations (Yorio et al. 2001; Lynch et al. 2010b; Watson et al. 2014). Like Magellanic penguins, many seabirds breed over large areas in big colonies (Darby and Seddon 1990; Gaston and Jones 1998; Coulson 2002; Zavalaga et al. 2008). A large colony may extend beyond the boundaries of protected areas, as at Punta Tombo (García Borboroglu et al. 2006). It may be necessary to prioritize parts of a colony for invasive-species removal or protection from predators, tourists, or development. Under expected distributions, the most important parts of a large seabird colony to protect would be the colony core and/or the highest-quality habitat because those areas would have the most nests, produce the most fledglings, show the slowest declines, and be the last areas abandoned if the population decreases. However, we showed that the poorest-quality habitat, scrub, which covers most of a large colony of Magellanic penguins, accounts for more nests and more fledglings than any other habitat and that the largest decline in nest density occurred near the colony core. Hence large, low-density, low-quality scrub habitat is more important than our hypotheses predicted. Our results suggest that large areas of lower-quality habitat should not be dismissed without consideration when planning conservation actions.

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