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Growth and decline of a penguin colony and the influence on nesting density and reproductive success

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Abstract Colonial breeding is characteristic of seabirds but nesting at high density has both advantages and disadvantages and may reduce survival and fecundity. African penguins (*Spheniscus demersus*) initiated breeding at Robben Island, South Africa in 1983. The breeding population on the island increased in the late 1990s and early 2000s before decreasing rapidly until 2010. Before the number breeding peaked, local nest density in the areas where the colony was initiated plateaued, suggesting that preferred nests sites were mostly occupied, and the area used by breeding birds expanded. However, it did not contract again as the population decreased, so that nesting density varied substantially. Breeding success was related positively to the prey available to the breeding birds and negatively to local nest density, particularly during the chick-rearing period, suggesting a density-dependence operating through social interactions in the colony, possibly exacerbated by poor prey availability when the breeding population was large. Although nest density at Robben Island was not high, nesting burrows, which probably reduce the incidence of aggressive encounters in the colony, are scarce and our results suggest that habitat alteration has modified the strength of density-dependent relationships for African penguins. Gaining a better understanding of how density dependence affects fecundity and population growth rates in colonial breeders is important for informing conservation management of the African penguin and other threatened taxa.

Keywords Colonial breeding · Colony growth · Density-dependence · Nesting success · Population dynamics · Seabird conservation

Introduction

Colonial nesting is an almost universal characteristic of seabirds (Coulson 2002), suggesting that the behaviour must impart a net fitness benefit, or at least did so during the recent evolutionary past. However, the ultimate causative factors of coloniality are debated (reviewed by Coulson 2002). Nesting at high density can have both selective advantages, such as collective defence against predators (e.g., Ashbrook et al. 2010) or information exchange (e.g., Weimerskirch et al. 2010), and disadvantages, such as increased rates of parasite transmission (e.g.,

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Brown and Brown 2004), depletion of local food resources (e.g., Lewis et al. 2001; Ballance et al. 2009) and higher incidence of extra-pair copulation (e.g., Hoi and Hoi-Leitner 1997).

Negative density dependence, usually operating through intraspecific competition where density affects per capita resource availability, has been shown to decrease survival (Nicoll et al. 2003; te Marvelde et al. 2009) and reproductive success (Hunt et al. 1986; Forero et al. 2002; Schuetz 2011) when colonies are large. However, in small colonies the benefits of group breeding can also produce positive (or inverse) density dependence, where per capita growth rates increase with increasing density (Allee effects; Courchamp et al. 1999; Kramer et al. 2009).

Both negative density dependence (e.g., Stokes and Boersma 2000; Tella et al. 2001) and Allee effects (e.g., te Marvelde et al. 2009; Votier et al. 2009) have been demonstrated in seabirds and there is evidence that survival and fecundity can be maximised at intermediate colony sizes or densities (Brunton 1999; te Marvelde et al. 2009). Thus, for species of conservation concern, or those that breed in small, geographically isolated colonies, understanding the nature of density dependence could influence management decisions at both population and colony levels (e.g., Yearsley et al. 2003).

African penguins (*Spheniscus demersus*) breed between central Namibia and Algoa Bay, South Africa. Despite a period (1997–2004) during which the numbers breeding in South Africa increased, the overall population decreased substantially through the 20th century and into the first decade of the 21st century (Crawford et al. 2011). Historically, the population at Dassen Island, South Africa, exceeded 500,000 pairs and three colonies have held ca. 20,000 pairs since 1978 (Crawford et al. 2007). By 2009, there were ca. 26,000 pairs breeding at 28 colonies, most hosting breeding populations of fewer than 1,000 pairs (Crawford et al. 2011).

The increase in the late 20th century occurred mainly in South Africa's Western Cape and included the formation of two new mainland colonies as well as the re-colonisation of Robben Island after an absence of more than 180 years (Crawford et al. 1995, 2011). The colony at Robben Island grew over two decades from nine breeding pairs in 1983 to become the third largest colony overall (with ca. 8,500 pairs) by 2004. However, the number breeding there subsequently decreased rapidly to ca. 2,600 pairs in 2010 (Crawford et al. 2011).

The African penguins on Robben Island have been the subject of a long-term research project since 1983, which has included monitoring of breeding success (e.g., Crawford et al. 1995, 2011; Sherley et al. 2012, 2013). In this paper we report on how the area used for breeding at Robben Island changed as the number breeding grew and then decreased. We further consider how nesting densities varied with the expansion and contraction of the surface area of the colony and how nesting density and population size may have influenced breeding success from 2001 to 2010. Given the endangered status of the African penguin (Crawford et al. 2011), and the concerns over seabird conservation globally (Croxall et al. 2012), understanding how the density of and interactions amongst conspecifics in seabird colonies impacts fitness is important to guide future policy regarding research and management of seabirds.

Methods

Breeding population size and estimates of nest density

Counts of all active nest sites at Robben Island (33°48′S, 18°22′E) were carried out at least once a year from 1983 to 2010 during the peak of breeding in late-May or early-June (Table S1 in Electronic Supplementary Material, ESM; Crawford et al. 2011). In years when multiple counts were made, the highest number of breeding pairs counted represented the breeding population for that year (Total-Pop; see ESM for further details). We considered all discrete groups of adjacent nests (sub-colonies) on the island to comprise the colony (Ainley 2002). In 1990, the colony was divided into a number of census zones (Fig. 1a), each of which was checked for nests and counted separately in subsequent years. As the colony grew, additional census zones were created (Fig. 1a).

To determine nest density (nests m^{-2}) in each year, the surface area (m^2) used for breeding was estimated using the GPS coordinates for the corners of the occupied census zones and the measure area feature in Google Earth Pro™. From these data, we determined the annual nest density in the areas where nests were monitored for breeding success (Den-Mon) and separately in each of three distinct areas of the colony where monitoring took place: census zones N to V (Den-NV; Fig. 1a), census zone IC, (Den-IC; Fig. 1a) and census zones IB, W, X, Y and Z (Den-IBZ; Fig. 1a).

Estimates of local nest density

Nearly all (95 %) penguin nests at Robben Island occur in either (1) areas with dense growth of large bushes (*Acacia cyclops* and *Myoporum tenuifolium*), often with several nests under a single bush; or (2) areas of tree plantations (*Pinus pinaster*, *Cupressus* spp. and *Eucalyptus* spp.) where nests occur singularly at the base of tree trunks or in clusters under fallen trees. The aggregated nature of penguin nests meant that the local nest density (number of close neighbours) was much higher than accounted for in our estimates of nest density above, as nests would have

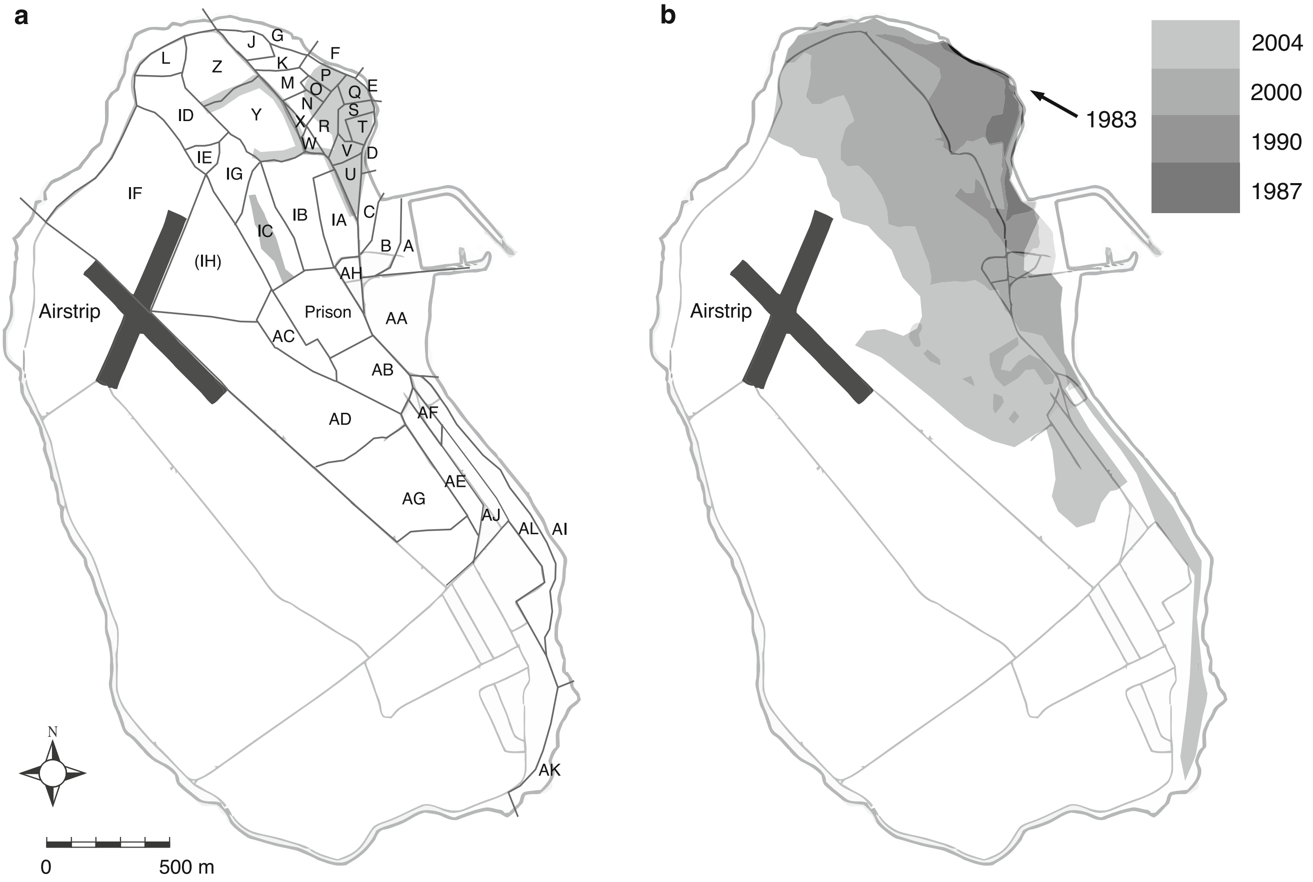

Fig. 1 Robben Island showing **a** the *census zones* used (as of 2010) for the annual count of breeding African penguins as well as the *monitored areas* (*shaded grey*), those parts of the colony in which nests were monitored for breeding success, and **b** the extent of the surface area of the African penguin colony on Robben Island when recolonized in 1983, and in 1987, 1990, 2000 and 2004. The spatial extent of the colony has not decreased since 2004

been absent from much of the census zones devoid of vegetation (Crawford et al. 1995, 2011).

To estimate local nest density, we used Google Earth™ images of the island (from 21 July 2009 and 24 November 2010) and Image-J (National Institutes of Health: http://rsb.info.nih.gov/ij/index.html) to count the number of trees and bushes in specific areas. From these counts, we estimated the number of nests per bush and/or tree (here after nests bush^{-1}) for census zone J (Fig. 1a; J-NPB), an area of nesting habitat type 2 first occupied in 1989, and two zones of nesting habitat type 1 occupied at different times: zone AA (Fig. 1a; AA-NPB), first occupied in 1994; and parts of the colony occupied by 1989 (1987 area in Fig. 1b; Old-NPB). Although there was no active management of the vegetation in the colony during the study, these estimates did not account for natural changes in the available nesting habitat over time (e.g., growth or death of vegetation) or the ca. 5 % of nests which occur in the open, in buildings, in burrows or in artificial nest boxes (Crawford et al. 1995, 2011; Sherley et al. 2012). We compared these estimates of local nest density to the breeding population in each year from 1990 to 2004 using linear and log-linear regression to determine whether the local nest density plateaued prior to the peak in the breeding population in 2004.

Estimates of breeding success

Following Sherley et al. (2012, 2013), we determined nesting success for the incubation (incubation success) and chick-rearing (fledging success) periods using parametric survival models of the form:

$$S(t) = \exp(-\exp(-\alpha - \beta)t) \quad (1)$$

where S is the survival estimate for the nesting stage, α and β are the intercept and coefficient from the model and t is time in days of the nesting attempt (40 days during incubation and 74 days for the fledging period). Overall breeding success (the nesting success for the whole breeding attempt) was determined from the product of incubation and fledging success (see ESM for further details).

Relationships between breeding success, nest density and population size

Breeding success was related to the population size and density using weighted linear regression (see Sherley et al. 2013). The candidate model set was restricted to models with one or two explanatory variables to avoid over parameterisation. We used Akaike's information criterion (AIC_c) to select between models and a ΔAIC_c threshold of 2 to select between models (e.g., Sherley et al. 2013). The explanatory variables (Fig. S1 in ESM) were estimated nest density in the monitored areas (Den-Mon), local density in the area of the colony occupied in 1989 (Old-NPB; this covered much of the monitored areas, Fig. 1) and the total number of pairs breeding at Robben Island (Total-Pop) in each year. Because the breeding population at Robben Island increased until 2004, largely through immigration of first-time breeders (Crawford et al. 2001), and because previous breeding experience can influence breeding success in seabirds (Weimerskirch 1990), we also included an estimate of the proportion of recruits (first-time breeders) in the breeding population (Rec-PerCap) as a candidate variable. This proportion was based on counts of immature birds moulting at the island lagged by 4 years (updated from Crawford et al. 2007, see ESM for more details).

In an effort to distinguish between density-dependence resulting from depletion of local prey resources (e.g., Lewis et al. 2001) and social interactions which can affect breeding success (e.g., collective defence against predators, Ashbrook et al. 2010), we also included the estimated prey available to breeding birds in each season as a candidate explanatory variable in the models. Prey availability was indexed using the natural logarithm of the annual anchovy (*Engraulis encrasicolus*) catch made within 56 km of Robben Island (Catch-Anch; updated from Sherley et al. 2013, see ESM for more details). In addition, because density-dependent food depletion can act at a scale greater than a single colony (Furness and Birkhead 1984), we also included the combined breeding population estimate (RIDI-Pop) for Robben Island and Dassen Island (33°25′S, 18°04′E; counts from Crawford et al. 2011) to estimate the "effective colony size" (sensu Hunt et al. 1986). Robben Island and Dassen Island, ca. 50 km to the north-west, together account for more than 85 % of the penguins breeding on South Africa's west coast, which exploit a common prey resource during the breeding season (Crawford et al. 2011).

Finally, we used the data on nest density in the three monitored areas to conduct within-year comparisons of breeding success (using the parametric survival models) from nests in a high density and low density section of the colony in five randomly selected years. Nest density was compared using ANOVA and Tukey's Honest Significant Difference. All models were specified in R v2.10.1 (R Development Core Team 2009).

Results

Population size, colony area and nest density

From 1983 to 1986 the breeding population grew from 9 to 227 pairs in a small coastal area north of the harbour (Fig. 1b). New breeding areas were colonised from 1987 to 1989 and again from 1990 to 1999 (Figs. 1b, 2). During this period, the population exceeded 4,000 pairs, predominately growing in the areas occupied from 1990 onwards (Fig. 2). The colony attained a maximum density of 0.03 nests m^{-2} in 1999. The breeding population continued to grow until 2004, with additional areas occupied from 2000

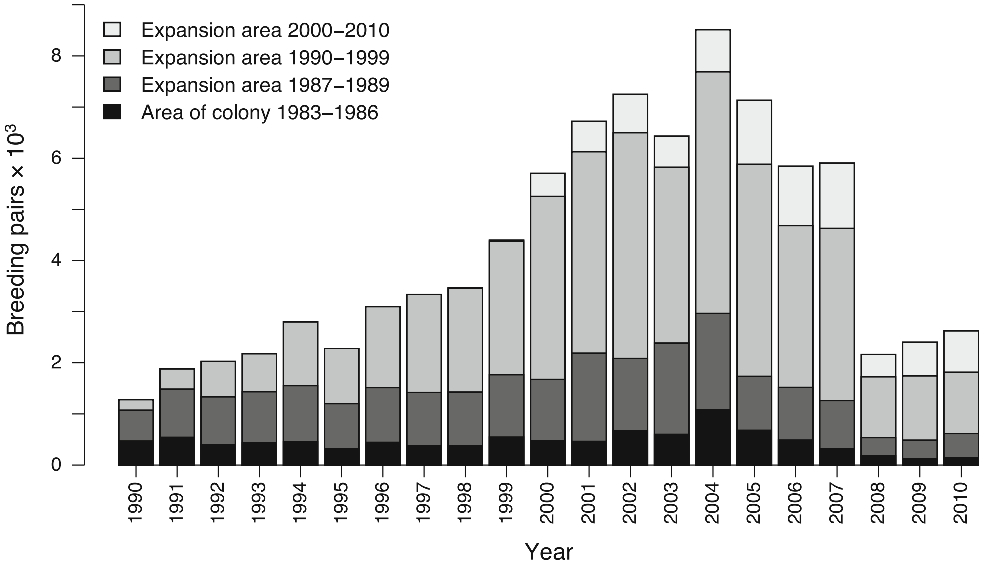

Fig. 2 Numbers of African penguin nests counted in different areas of Robben Island from 1990 to 2010. *Black bars* represent the number of nests found in the area occupied by breeders when the island was re-colonized (1983–1986). *Dark grey bars* indicate numbers in those areas that were occupied by penguins from 1987–1989, *intermediate grey bars* show numbers in areas that were occupied from 1990–1999, and *light grey bars* show numbers in areas occupied from 2000 onwards. Figure 1b shows the extents of the areas occupied at the start of these time periods

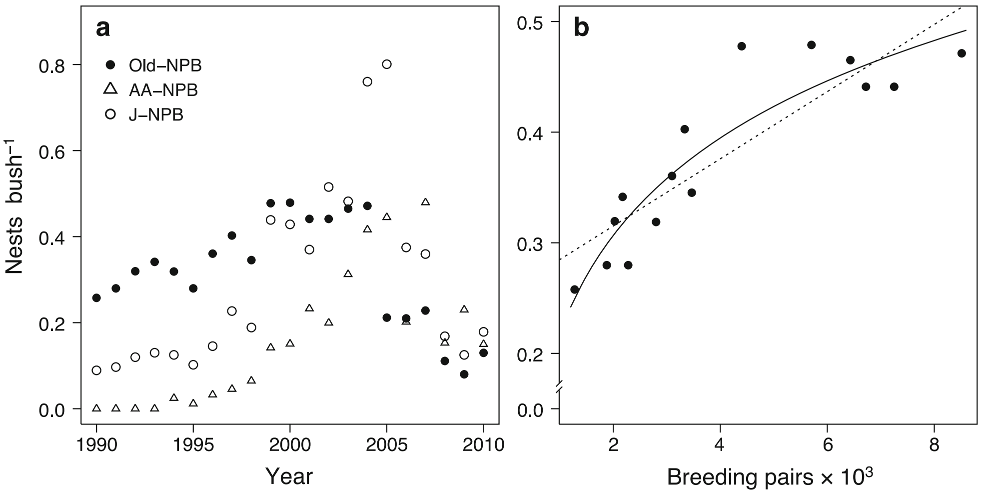

Fig. 3 Estimated local nest density (nests bush^{-1}) of African penguin nests **a** in areas of different nesting habitat (AA-NPB and Old-NPB, type 1; J-NPB, type 2) occupied before 1990 (Old-NPB, 1989; J-NPB, 1989) and after 1990 (AA-NPB, 1994); and **b** in parts of the colony occupied by 1989 (Old-NPB) in relation to the breeding population for the corresponding year (Total-Pop). The *dashed line* represents the linear relationship ($\mathrm{AIC_c} = -47.35$) and the *solid line* the log-linear relationship ($\mathrm{AIC_c} = -53.75$). The scales of the vertical axes differ

(Figs. 1b, 2), but the population in the areas occupied before 1990 generally increased at a slower rate than the overall population and remained at a relatively stable nest density of ca. 0.01 nests m^{-2}. As the population declined from 2005 onwards, the overall area used for breeding did not contract and the number of nests declined at much the same rate across the island (Fig. 2). Overall nest density was <0.002 nests m^{-2} during this period.

In the area occupied in 1994, AA-NPB rose to 0.44 nests bush^{-1} by 2005 before falling as the colony declined (Fig. 3a), while J-NPB increased with the growth of the population until 1998 and then was relatively stable between 0.37 and 0.52 nests bush^{-1} from 1999 to 2003, before increasing to around 0.80 nests bush^{-1}, as numbers at Robben Island exceeded 7,000 pairs (Figs. 2, 3a). In both zone J (J-NPB: $r = 0.95$, $df = 12$, $P < 0.001$) and AA (YZ-NPB: $r = 0.95$, $df = 12$, $P < 0.001$) the local nest densities were linearly related to the size of the breeding population (Total-Pop) up to 2004 ($\Delta\mathrm{AIC_c} > 5$ between models). In contrast, Old-NPB exceeded 0.4 nests bush^{-1} in 1997 and remained between 0.35 and 0.48 until the colony declined in 2005 (Fig. 3a). The relationship with log(Total-Pop) was significant ($r = 0.92$, $df = 13$, $P < 0.001$) and was preferred to the linear relationship ($\Delta\mathrm{AIC_c} = 10.97$) suggesting that the local nest density plateaued prior to the peak in the annual number breeding (Fig. 3b).

Relationships between breeding success, nest density and population size

Breeding success ranged from 0.18 to 0.30 from 2001 to 2004, as the African penguin population at Robben Island was increasing, and from 0.35 to 0.51 during 2005 to 2010 as the population declined (Table S2 in ESM). Nesting success during incubation was not related to any of the explanatory variables used as indices of density or population size (all P values > 0.05), but was positively related to the prey available to the breeding birds during each year (Catch-Anch: $r = 0.84$, $df = 8$, $P = 0.023$). That model had 54 % of the $\mathrm{AIC_c}$ weight and no other model had greater support than the null (intercept only) model for the incubation period (Table 1). Fledging success was negatively related to both local nest density (Old-NPB: $r = 0.80$, $df = 8$, $P = 0.023$) and the combined breeding population at Robben and Dassen Islands (RIDI-Pop: $r = 0.64$, $df = 8$, $P = 0.047$); however, the relationship in the later was only marginally significant and the former model had substantial $\mathrm{AIC_c}$ support relative to the next best model (Table 1).

Overall, breeding success was negatively related to local nest density (Old-NPB: $t = -2.69$, $df = 8$, $P = 0.031$) and positively to the local prey availability around the island (Catch-Anch: $t = 3.10$, $df = 8$, $P = 0.017$, Fig. 4), with the model containing both terms accounting for 45 % of the $\mathrm{AIC_c}$ weighting (Table 1) and the next two models (Catch-Anch only, $\Delta\mathrm{AIC_c} = 1.08$; Old-NPB only, $\Delta\mathrm{AIC_c} = 2.64$) nested in the best supported model and accounting for another 39 % of the $\mathrm{AIC_c}$ weight.

Finally, nest density differed significantly among the three monitored areas ($F_{2,18} = 10.2$, $P = 0.001$), with Den-NV significantly higher than Den-IBZ (Tukey HSD: $P < 0.001$) with inter-annual differences accounted for in the model. However, there were no significant differences in nesting success, either during incubation or chick-rearing

Table 1 Weighted linear regression models relating African penguin breeding success to population size, nest density and prey availability at Robben Island 2001–2010

Model	K	AIC_c	ΔAIC_c	AIC_c weight	+/−	Adjusted R^2	P value
Incubation success							
ln(Catch-Anch)	3	−10.4	0.00	0.535	+	0.43	0.023
Intercept only	2	−7.8	2.60	0.146	na	na	na
Fledging success							
Old-NPB	3	−12.9	0.00	0.597	−	0.60	0.005
Old-NPB + Total-Pop	4	−8.3	4.63	0.059	−, +	0.60	0.018
RIDI-Pop	3	−8.0	4.96	0.050	−	0.33	0.047
Den-Mon	3	−7.8	5.16	0.045	−	0.21	0.051
Old-NPB + Rec-PerCap	4	−7.7	5.21	0.044	−, −	0.57	0.021
Old-NPB + RIDI-Pop	4	−7.3	5.62	0.036	−, +	0.55	0.024
Old-NPB + ln(Catch-Anch)	4	−7.2	5.69	0.035	−, +	0.55	0.025
Intercept only	2	−7.0	5.93	0.031	na	na	na
Breeding success							
Old-NPB + ln(Catch-Anch)	4	−17.9	0.00	0.454	−, +	0.79	0.002
ln(Catch-Anch)	3	−16.8	1.08	0.265	+	0.62	0.004
Old-NPB	3	−15.3	2.64	0.121	−	0.56	0.008
RIDI-Pop + ln(Catch-Anch)	4	−12.3	5.63	0.027	−, +	0.63	0.013
Total-Pop + ln(Catch-Anch)	4	−11.6	6.28	0.020	−, +	0.60	0.017
Den-Mon + ln(Catch-Anch)	4	−11.4	6.47	0.018	−, +	0.59	0.018
RIDI-Pop	3	−11.1	6.83	0.015	−	0.33	0.049
Rec-PerCap + ln(Catch-Anch)	4	−10.9	7.03	0.014	+, +	0.57	0.022
Intercept only	2	−10.2	7.66	0.010	na	na	na

For each response, models given greater support than the null model are shown, along with K (number of model parameters, including the error term), AIC_c value, difference from the lowest AIC_c value (ΔAIC_c) and the relative support (AIC_c weights) given to each model. +/− indicates the direction of any relationship between variables, with respect to the order in which they occur in the model name; ln() = the natural logarithm; na = not applicable. See "Methods" for model abbreviations

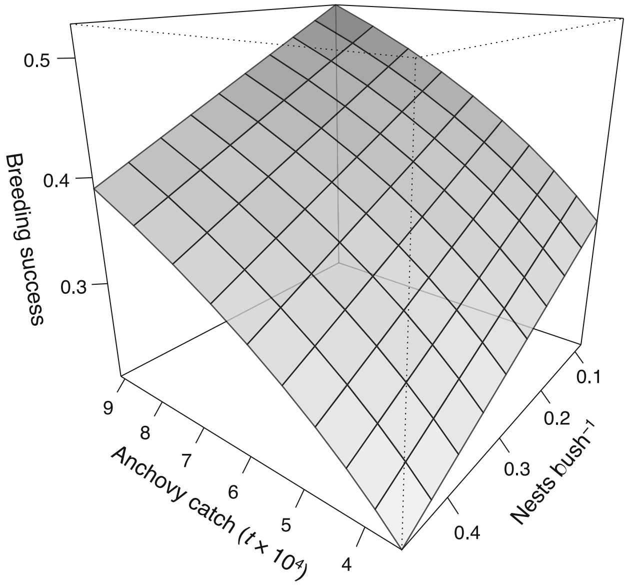

Fig. 4 The relationship between local nest density (Old-NPB; nest bush^{-1}), the annual anchovy catch (t) made within 56 km of the island (Catch-Anch, taken as an index of local prey availability) and breeding success of African penguins at Robben Island 2001–2010. The surface represents the predicted response from the best fitting model in Table 1

between the high (Den-NV) and low density (Den- IBZ) monitored nests in any of the five randomly selected years (Table 2).

Discussion

Negative density dependence can regulate population growth in colonial species at high densities (e.g., Courchamp et al. 1999) and breeding success may decrease as nesting density increases in seabird colonies (e.g., Hunt et al. 1986; Stokes and Boersma 2000; Tella et al. 2001). Our data suggest a correspondence between lower nest density and increased reproductive success in African penguins. However, the way in which density dependence limits populations can vary, both in terms of the life-history traits affected (e.g., survival or fecundity) and the proximate mechanisms through which it is expressed. For example, in Magellanic penguins (*Spheniscus magellanicus*), Stokes and Boersma (2000) found negative relationships between breeding success and nest density as a result of increased conspecific aggression in high-density areas of

Table 2 Results of intra-annual comparisons in African penguin nesting success between areas of higher (Den-NV) and lower (Den-IBZ) nest density at Robben Island

Years	Relative density	NS: incubation period			NS: fledging period		
		Den-NV	Den-IBZ	*P* value	Den-NV	Den-IBZ	*P* value
2003	H	0.82 (0.59)	0.55 (0.45)	0.058	0.38 (0.54)	0.24 (0.50)	0.45
2004	H	0.74 (0.43)	0.51 (0.33)	0.061	0.31 (0.44)	0.59 (0.41)	0.064
2005	A	0.73 (0.52)	0.63 (0.35)	0.48	0.60 (0.44)	0.54 (0.32)	0.68
2007	A	0.65 (0.37)	0.60 (0.26)	0.62	0.85 (0.53)	0.73 (0.33)	0.20
2009	L	0.54 (0.24)	0.48 (0.20)	0.46	0.63 (0.34)	0.67 (0.30)	0.69

Values are the survival estimates (± standard error of the model coefficients) for nest contents from parametric survival models and the associated *P* value for the within-year test of significance. Relative density: H = high nest density, the year was above the 75th percentile for all years; L = low nest density, below the 25th percentile for all years; A = average nest density, between the 25th and 75th percentile. NS = nesting success

the colony, while Tella et al. (2001) found evidence of negative density dependence mediated through increased intraspecific competition for prey resources in the same species.

Overall, the negative relationship between fledging success and the local nest density (Old-NPB), but not the total breeding population on Robben Island, coupled with the indication that Old-NPB reached a plateau before the number breeding at the colony peaked in 2004, suggests that social interactions or predation at nest sites, rather than local resource depletion, were driving the relationship in this study. In Magellanic penguins, fights over nest sites (where chicks may be killed), the presence of non-breeding birds (who can start fights and kill chicks) and nest predation were all more prevalent in high-density than low density areas at Punta Tombo, Argentina (Stokes and Boersma 2000). African penguins also fight over nest sites (Eggleton and Siegfried 1979) and will attack chicks that wander from their nest (Seddon and van Heezik 1993). Their chicks are subject to predation by feral cats (*Felis catus*; Crawford et al. 1995, 2011), kelp gulls (*Larus dominicanus*; Wilson 1985) and mole snakes (*Pseudaspis cana*; Underhill et al. 2009) at Robben Island. Kelp gulls in particular are more active in high density areas in Magellanic penguin colonies (Stokes and Boersma 2000), although this effect may depend on the predatory species involved (Brunton 1999).

Although the measures of density reported here (e.g., 0.03 nests m^{-2}) were not high for *Spheniscus* penguins, African penguins nested in burrows dug into guano prior to its commercial harvest in southern Africa (Frost et al. 1976) and there is evidence that changes in nesting habitat may modify the strength of density-dependent relationships in this genus. For example, in 1988 the ca. 6,500 breeding pairs of African penguins at Dassen Island, where burrows make up ca. 30 % of active nests (Frost et al. 1976), nested at 0.2 to 0.88 nests m^{-2} (Crawford et al. 2007), while at Boulders (34°12′S, 18°27′E), where most nests are under vegetation, nest density was 0.03–0.08 m^{-2} in 1997 (Crawford et al. 2000). Similarly, Magellanic penguins at Punta Tombo nested at 0.09 (range 0.01–0.5) nests m^{-2} on average from 1984 to 1991, but nesting density was below 0.1 nests m^{-2} in areas where <33 % of active nests were in burrows and above 0.2 nests m^{-2} where burrows were the predominate nest type (Stokes and Boersma 2000).

Compared to nests on the surface, burrows appear to reduce both predation and intraspecific aggression aimed at chicks (Seddon and van Heezik 1991, 1993) and probably reduce the incidence of aggressive encounters between nesting and prospecting birds because only the nest and its entrance are defended in *Spheniscus* penguins (Stokes and Boersma 2000). However, burrows are scarce at Robben Island (ca. 1.2–4 % of active nests, Crawford et al. 1995, 2011; Sherley et al. 2012), where penguins primarily nest in small aggregations beneath vegetation (Crawford et al. 1995, 2011). As a result, the local density of nests was likely much higher than our measures of nesting density (Den-Mon) would suggest and the plateau in local nesting density in the areas of the colony occupied by 1989 (Old-NPB) suggests that the birds breeding there were intolerant of additional nests in those areas once densities reached ca. 0.4 nests $bush^{-1}$. As the breeding population at Robben Island grew from ca. 1,000 pairs in 1990 to ca. 5,500 pairs in 2000, the increase occurred largely through an expansion of the breeding area, with Old-NPB remaining broadly similar (Figs. 2, 3). In contrast, local nest density in the more recently occupied zone (AA-NPB) only reached similar levels to that in the old colony by 2004 and in zone J it appeared to plateau at around 0.4–0.5, before increasing again in 2004 only as the colony exceeded 8,000 pairs. Although, the later observation could be an artefact of the small size of zone J, these results imply that the absence of high quality nesting habitat in the form of burrows may allow negative density-dependent controls to manifest themselves at lower overall nesting densities.

In some species where chicks are typically attended by at least one parent, poor food availability may interact with high local density to reduce breeding success if parents must leave chicks unattended because they are foraging for longer or simultaneously (Hamer et al. 2007; Ashbrook et al. 2010). Prey availability affected breeding success of African penguins at Robben Island in this and other studies (Crawford et al. 1995, 2011; Sherley et al. 2013) and in particular local prey abundance may have been poor during the first half of the study period (Figs. 4 and S1 in ESM; Sherley et al. 2013). African penguins leave their chicks unguarded at an earlier age when feeding conditions are poor (Seddon and van Heezik 1993), leaving them vulnerable to predation (e.g., Ashbrook et al. 2010) and intraspecific aggression (e.g., Seddon and van Heezik 1991; Hamer et al. 2007). This could explain the relationship between local nest density, prey availability and breeding success in this study (Fig. 4). In addition, the number of young, inexperienced breeders and of non-breeding birds at Robben Island was high from 2001 to 2004 (Crawford et al. 2001) and, while the proportion of recruits (Rec-PerCap) did not appear to influence breeding success directly, the presence of many non-breeding birds at the island could have increased aggressive interactions at nest sites. However, the absence of significant intra-annual differences in nesting success between the high and low density areas of the colony, particularly during the two years of high local nest density (2003 and 2004), suggest that increased predation and intraspecific aggression may have been insufficient to account for the observed relationship alone (although the sample sizes were small in some years, Table 2).

Alternatively, the large populations breeding at Robben and Dassen Islands in the early-2000s (ca. 30,000 pairs, Fig. S1 in ESM) may have exceeded the local carrying capacity, leading to negative density dependence through intraspecific competition. The populations at both islands increased during the late-1990s and early-2000s in response to an increase in spawner sardine and anchovy stocks in the southern Benguela (Crawford et al. 2011). The increased sardine biomass may have allowed a greater proportion of birds (including young adults) to attain breeding condition in this period and although anchovy was abundant in the ecosystem, local prey availability on South Africa's West Coast may have become decoupled from overall forage fish biomass from 2001 onwards (Durant et al. 2010; Crawford et al. 2011; Sherley et al. 2013). Consequently, the resources available around the islands in winter may have been insufficient for ca. 30,000 pairs to breed successfully. In support of this idea, Crawford et al. (2007) used rates of per capita immature recruitment to estimate the carrying capacity of Robben Island as ca. 800 pairs fewer than the maximum number observed to breed at the island during the 2000s, suggesting that negative density dependence acting on local prey resources could have played a role in the initial population decrease after 2004. Although there were probably in excess of 500,000 pairs of African penguins in the southern Benguela in the 1930s, the introduction of commercial purse-seine fishing since the 1950s has likely reduced the density of prey around penguin breeding colonies (Durant et al. 2010), lowering the carrying capacity of the ecosystem. As local nesting density and population size were confounded for much of the time series in this study, it is difficult to rule out local resource depletion as a contributing factor and it is seems that a combination of high local density and large colony size may be particularly disadvantageous when environmental conditions are poor (Tella et al. 2001; Ashbrook et al. 2010).

Although a decrease in the overall population may contribute to improved breeding success, species may exhibit negative per capita growth rates below a critical density (strong Allee effects), increasing the risk of extinction of small or newly established populations (Kramer et al. 2009). In Namibia, African penguins that nested solitarily decreased more rapidly than those in groups (Cordes et al. 1999) and of 40 discrete sub-colonies at Halifax and Possession Islands in 1956 only 3 % with <250 pairs were extant by 1996, as compared with 50 % with 500–1,000 pairs, 67 % with 1,000–5,000 pairs and all larger sub-colonies (Crawford et al. 2001). It has been suggested that African penguins may already be susceptible to Allee effects because it is increasingly difficult for them to form large, cooperative foraging groups at sea as colony sizes decrease (Ryan et al. 2012). If Allee effects are currently operating on the African penguin population, then management actions aimed at slowing the decline in the per capita growth rate, e.g., hand-rearing orphaned chicks (Barham et al. 2008), are likely to be inhibiting their impacts. Gaining a better understanding of whether and how density dependence affects fecundity and population growth rates may, therefore, be important for the conservation of the African penguin.

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