Influence of local and regional prey availability on breeding performance of African penguins *Spheniscus demersus*

Richard B. Sherley[1,3,9,*], Les G. Underhill[1,2], Barbara J. Barham[4], Peter J. Barham[2,5], Janet C. Coetzee[6], Robert J. M. Crawford[2,7], Bruce M. Dyer[7], T. Mario Leshoro[8], Leshia Upfold[7]

[1]Marine Research Institute, and [2]Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, Cape Town, South Africa

[3]School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK

[4]Penguin Datasystems, Bristol BS6 6QS, UK

[5]H. H. Wills Physics Laboratory, University of Bristol, Bristol BS8 1TL, UK

[6]Branch Fisheries, Department of Agriculture, Forestry and Fisheries, Rogge Bay 8012, South Africa

[7]Oceans and Coasts, Department of Environmental Affairs, Rogge Bay 8012, South Africa

[8]Robben Island Museum, Robben Island 7400, South Africa

[9]*Present address:* Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, Cape Town, South Africa

ABSTRACT: Population trends of African penguins *Spheniscus demersus* in the Western Cape, South Africa, and their breeding success have been linked to the abundance of their main prey, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. During the late 1990s and early 2000s, both fish species increased markedly in abundance, but after 2004, sardine biomass decreased to below average levels. In addition, adults of both stocks were principally located to the east of Cape Agulhas from 2001 to 2009 and were thus distant from seabird colonies on South Africa's West Coast. The number of African penguin pairs counted at Robben Island from 2001 to 2009 and the fledging period of chicks from successful nests increased and decreased in apparent response to the biomass of sardine prior to each breeding season, possibly linked through adult condition at the onset of breeding. Breeding success and chick-fledging rates increased during the study period and showed positive relationships with local food availability, indexed through the annual industrial catch of anchovy made within 56 km (30 nautical miles) of the colony. In addition, chick-fledging rates were depressed in 2-chick broods during years when anchovy contributed <75 % by mass to the diet of breeding birds. Previously reported relationships between the overall abundance of forage fish in South Africa and penguin breeding success were not supported. Taken together, these results highlight the combined importance of ensuring adequate local food availability for seabirds during the reproductive cycle and safeguarding regional prey abundance during the non-breeding season.

KEY WORDS: Breeding performance · Fisheries–seabird interactions · Seabird conservation · Nesting success · Ecosystem approach

INTRODUCTION

Food abundance is often unpredictable in marine habitats due to spatial and temporal variability in oceanographic conditions (e.g. Weimerskirch 2007).

Accordingly, prey availability impacts seabird biology, particularly during breeding, when central-place foraging constraints operate (Orians & Pearson 1979). However, functional relationships between prey availability or quality and different seabird

parameters can be difficult to detect: they can take different forms (e.g. Montevecchi 2007, Piatt et al. 2007) and the signals may be masked by life-history adaptations (Burger & Piatt 1990). Environmental change can exacerbate the situation by altering the trophic interactions between predators and their prey (Durant et al. 2007) or disrupting relationships between prey availability at different spatial scales (Grémillet et al. 2008, Durant et al. 2010).

In South Africa, a change in the relative abundance of adult sardine *Sardinops sagax* J. and anchovy *Engraulis encrasicolus* L., attributed to differential fishing pressure and changes in the marine environment, was noted during the late 1990s and early 2000s (Fairweather et al. 2006, Roy et al. 2007, Coetzee et al. 2008). Consequently, adults of both stocks were principally located off the South Coast (Fig. S1 in the supplement at www.int-res.com/articles/ suppl/ m473p291_supp.pdf) from 2001 to 2009, resulting in a spatial mismatch between the bulk of the adult forage fish and seabirds nesting at colonies on the West Coast (Fig. S1; Grémillet et al. 2008). During the same period, sardine and anchovy abundance increased (from 2000 to 2003) to values far exceeding those recorded previously, after which the estimated biomass of adult sardine decreased following 6 yr of poor recruitment (2004 to 2009), while that of anchovy remained relatively high until 2009 (Coetzee et al. 2008, de Moor et al. 2008, J. Coetzee unpubl. data).

These patterns are thought to have influenced the population demography of several seabird species endemic to the region, including the African penguin *Spheniscus demersus* L. (Crawford et al. 2008a, 2011). This species feeds predominantly on anchovy and sardine (Fig. S2 in the supplement; Crawford et al. 2011) and has a restricted foraging range of 20 to 45 km during the breeding season (Pichegru et al. 2009, 2011), making it more vulnerable to changing environmental conditions than highly mobile or generalist species (Furness & Tasker 2000). The population declined rapidly between 2001 and 2009, and the species is currently considered endangered (Crawford et al. 2011). Previous studies have documented high spatial and temporal variability in breeding success, thought to relate to food availability (Crawford et al. 1999, 2006), and have linked breeding success to the overall abundance of both anchovy and sardine (e.g. Crawford et al. 1999, 2006) and linked population trends to the total biomass of sardine off South Africa (Crawford et al. 1999, 2001).

Given the widespread changes noted in the ecosystem, broad-scale annual estimates of total biomass may now be inappropriate measures of food availability around seabird colonies (Durant et al. 2010). Accordingly, there is a need to consider alternative resource indices (see Durant et al. 2010) and document the form of relationships between seabird parameters and prey variability at more appropriate spatial scales (e.g. Piatt et al. 2007). Furthermore, African penguins on the West Coast primarily feed their chicks on anchovy and sardine recruits as the fish migrate southwards from nursery grounds on the West Coast to their spawning grounds on the Western Agulhas Bank (Fig. S1) and South Coast (Crawford et al. 2006). Recruitment, particularly of anchovy, was relatively high over much of the 2000s (see Hutchings et al. 2009); thus, food availability during the breeding season on the West Coast may not have depended solely on the abundance or distribution of the adult forage fish during the last decade.

The present study examines the breeding performance of African penguins at Robben Island (33° 48′ S, 18° 22′ E; West Coast; Fig. S1) over 9 breeding seasons (2001 to 2009). We consider how prey availability on both local and regional spatial scales may influence breeding productivity and whether previously reported positive relationships between adult forage fish biomass and penguin breeding success (e.g. Crawford et al. 1999, 2006) have persisted following the large-scale changes in the forage fish abundance and distribution observed during the study period.

MATERIALS AND METHODS

Nest monitoring and counts

The methods used to monitor African penguin nests at Robben Island between 2001 and 2009 are described by Sherley et al. (2012). Briefly, visits to marked nests were made between mid-March and mid-September (the main breeding season at this site) at a target interval of 5 d. Nests were added to the sample throughout the breeding season, and in all years, a small number of breeding attempts were first monitored after chicks had hatched (ca. 15% in total). Nest contents were recorded at each visit; chicks were classified into 5 development stages (P0 to P4; Barham et al. 2007) and considered to have fledged if they reached the final stage (after which they left the nest). Breeding attempts from birds de-oiled following oil spills were excluded because they breed less successfully than unoiled birds (Barham et al. 2007).

The number of penguins breeding at Robben Island in each year (2001 to 2009) was estimated from counts of occupied nest sites conducted in May to coincide with the peak of breeding activity at the island (Crawford et al. 1995). The census techniques and annual counts are summarised by Crawford et al. (2011).

Breeding success

An extension of the Mayfield (1961) method was used to compute breeding success, with parametric survival models used to determine survival probabilities for the nest contents (Sherley et al. 2012). The number of days over which a nest's contents was estimated to have survived during incubation (incubation days) and chick-rearing (chick days) was calculated to the nearest half day by taking the mid-point between monitoring visits (Mayfield 1961). If the hatching date could not be reliably estimated because of an unusually long inter-visit interval, the estimate for the number of incubation days was constrained to be ≤41 d (Sherley et al. 2012). Eggs that were incubated for >50 d and did not hatch were assumed to be infertile and scored as failing. To avoid inflating the estimates of incubation success, their incubation days estimates were reduced to 40 d.

Following Sherley et al. (2012), survival (S) of the nest contents at time t was defined as follows:

$$S(t) = \exp(-\exp[-\alpha - \beta] \cdot t) \qquad (1)$$

where α and β were the intercept and coefficient from the model, and t was a representative incubation (40 d) or fledging period (74 d). Year was used as the explanatory variable to generate annual estimates of the survival of the nest contents. Because daily mortality rates differ for different nesting stages (Seddon & van Heezik 1991), breeding success was the product of the nest content survival rates during incubation and chick rearing (Sherley et al. 2012). Approximate 95% confidence intervals were derived from asymptotic theory (see Sherley et al. 2012). The models were specified using the 'survreg' function of the 'survival' package (see Crawley 2007) for R v2.10.1 (R Development Core Team 2009).

Fledging success and fledging periods

The model described above was insensitive to partial failure of a breeding attempt, so we also calculated the probability that a chick would fledge in 1-chick broods (OCB) and 2-chick broods (TCB), irrespective of the fate of any sibling. Breeding attempts were classified as OCB or TCB based on the chicks present at the first visit post-hatching, so some broods could have been misclassified. In breeding attempts in which chicks fledged, we also calculated the mean (±1 SD) number of days elapsed between hatching and fledging (fledging period). African penguin chicks are nidicolous and fledge at close to adult size and weight (Seddon & van Heezik 1991). We therefore assumed that the fledging period would vary in response to food availability and the rate at which parents could provision them (e.g. Quillfeldt et al. 2007). In 5 breeding attempts, fledging period estimates were <50 d. This was considered unusually short (Seddon & van Heezik 1993), and these data were excluded as artefacts of the monitoring protocol (variation in inter-visit intervals).

Relationships with prey availability

Estimates (with known precision) of the size of the sardine and anchovy stocks were obtained from twice-yearly surveys conducted by the South African Department of Agriculture, Forestry and Fisheries (DAFF) from 2000 to 2009. Surveys between Hondeklip Bay and Port Alfred (see Fig. S1 in the supplement) in November provided estimates of total biomass, and surveys between the Orange River Mouth and Cape Infanta (Fig. S1) in May gave estimates of recruitment biomass (both in millions of tonnes; see de Moor et al. 2008).

Annual catches (t) of sardine and anchovy made by the South African purse-seine fleet within 30 nautical miles (hereafter 56 km) of Robben Island were estimated by DAFF (2001 to 2009). The geographic coordinates for each set of the nets and sets of zero catches were not reported, so catches were assigned to 10' latitude × 10' longitude grid cells, and fishing effort could not be calculated (Hutchings et al. 2009). Although the fishery operates throughout the year, the majority of the catch on the West Coast is taken between March and October (Pichegru et al. 2009), which corresponds to the penguin breeding season on Robben Island (Crawford et al. 1995). Annual catches were thus used as an index of local prey availability.

Data on African penguin diet (2001 to 2009) were obtained from Crawford et al. (2011) and are summarised in Figs. S2 & S3 in the supplement. Anchovy dominated the diet of African penguins sampled during the present study (Fig. S2; Crawford et al. 2011),

and the percentage contributions of the 2 species to the diet were correlated during the study period ($r = 0.69$, df = 7, $p = 0.04$). In addition, although it varies seasonally and with fish condition (Schülein et al. 1995), anchovy generally has ca. 80 to 90% of the energetic value of sardine (Balmelli & Wickens 1994). We therefore included the percentage contribution of anchovy to the diet (rather than sardine or the combined values) in the models investigating the relationships between prey availability and breeding performance.

The relationships between variables indexing prey availability (Table 1) and the breeding performance of African penguins at Robben Island were assessed by linear regression models using the 'lm' function from the 'stats' package of R v2.10.1 (R Development Core Team 2009; Table 1). Breeding success, the number of penguins breeding, the mean fledging period and the probability of an individual chick fledging in OCB and TCB were the dependent variables. The breeding success, fledging probabilities and fledging periods were estimated with various degrees of precision each year (different annual sample sizes), so we weighted the linear models using the standard error of each annual estimate.

We limited the explanatory variable set (Table 1) to those we considered most likely to describe the conditions affecting birds during breeding at Robben Island. Anchovy dominated the recruitment biomass (Hutchings et al. 2009) upon which African penguins fed (Crawford et al. 2006), so we favoured explanatory variables relating to anchovy availability during the breeding season. However, as the number of penguins breeding each year in the Western Cape (Fig. S1) appears to relate to the abundance of adult fish (particularly sardine; Crawford et al. 2001, 2008b, Durant et al. 2010), we also considered a possible role for sardine biomass estimated in the November prior to the onset of the breeding season (Table 1). Because the biomass surveys suggested that the sardine stock was predominately off the South Coast in 7 yr of the present study (J. Coetzee unpubl. data), we also considered just the biomass of sardine located to the west of Cape Agulhas (from Hondeklip Bay to Cape Agulhas; Fig. S1, Table 1). Time series used in the analysis are presented in Fig. S4 in the supplement.

A number of studies have shown non-linear relationships between seabird parameters and food abundance (e.g. Furness 2007, Piatt et al. 2007, Cury et al. 2011). We, therefore, selected *a priori* both linear and log models for each explanatory variable. We used the corrected Akaike's information criterion (AICc) to select between models and a ΔAICc threshold of 2 to select the best supported model (Burnham & Anderson 2002).

RESULTS

Numbers breeding

Counts of penguins at Robben Island in May were positively related to the natural logarithm of the sardine biomass during the November survey 6 mo earlier (TotalBioSard y_{-1}: $r = 0.89$, df = 7, $p = 0.0013$;

Table 1. Explanatory variables tested against indices of African penguin breeding performance at Robben Island, 2001 to 2009. Both linear and log models were tested for each explanatory variable. Where y_0 is appended, breeding performance was related to estimates of the explanatory variable from the same year, while y_{-1} denotes estimates from the previous November. For locations see Fig. S1 in the supplement at www.int-res.com/articles/suppl/m473p291_supp.pdf

Variable name	Description
TotalBioAnch y_0	Estimated biomass of anchovy between Hondeklip Bay and Port Alfred (Fig. S1) from the November survey of the year corresponding to the measure of breeding productivity.
TotalBioSard y_{-1}	Estimated biomass of sardine between Hondeklip Bay and Port Alfred from the November survey of the year prior to the measure of breeding productivity.
BioSardWA y_{-1}	Estimated biomass of sardine west of Cape Agulhas (Hondeklip Bay to Cape Agulhas; Fig. S1) from the November survey of the year prior to the measure of breeding productivity.
TotalRecAnch y_0	Total estimated biomass of recruit (young-of-the-year) anchovy between the Orange River mouth and Cape Infanta (Fig. S1) from the May survey of the year corresponding to the measure of breeding productivity.
CatchAnch y_0	Total annual catch of anchovy made within 56 km of Robben Island during the year corresponding to the measure of breeding productivity.
AnchPercDiet y_0	Annual percentage contribution of anchovy to the diet of African penguins at Robben Island in the year corresponding to the measure of breeding productivity.

Fig. 1). The model ($p = -4.25 + 2.01 \times \ln(b)$, where $p =$ number of breeding pairs, and $b =$ total sardine biomass in millions of tonnes) had good predictive power (adjusted $R^2 = 0.76$) and AICc support (Table 2, Model A1). There was also a positive relationship with the sardine biomass west of Cape Agulhas (r = 0.82, df = 7, p = 0.007), but these explanatory variables were correlated (r = 0.83, df = 7, p = 0.006), and support for this model was poor (Model A2, Table 2).

Breeding success

Breeding success was estimated from 1221 breeding attempts during incubation and 1041 breeding attempts during chick rearing. There was significant inter-annual variation for both the incubation ($\chi^2 = 54.94$, df = 8, p < 0.001) and fledging periods ($\chi^2 = 66.77$, df = 8, p < 0.001; Fig. 2A,B). Breeding success (Fig. 2C) was positively related to the log of the anchovy catch within 56 km of Robben Island during the same year (CatchAnch y_0: r = 0.84, df = 7, p = 0.005; Table 2, Model B1). The best fitting regression line ($h = -0.125 + 0.282 \times \ln(c)$, where $h =$ breeding success [proportion fledging at least 1 chick], and $c =$

Fig. 1. *Spheniscus demersus* and *Sardinops sagax*. Number of breeding pairs of African penguins counted at Robben Island during the annual nest census (2001 to 2009) in relation to the total biomass of sardine in South Africa estimated in the preceding November (TotalBioSard y_{-1}). The line represents the fit of Model A1 (Table 2)

anchovy catch [$\times 10^4$ t]) explained 66% of the variance in breeding success (Fig. 3, Table 2). A negative relationship between breeding success and sardine biomass west of Cape Agulhas (BioSardWA y_{-1}: r = 0.80, df = 7, p = 0.010) was also significant but was assigned low AIC weight (Table 2, Model B3).

Fledging success

Fledging success and fledging periods were estimated for 1060 breeding attempts. For OCB, a linear fit between anchovy catches (CatchAnch y_0) and fledging probabilities was significant (r = 0.69, df = 7, p = 0.039) and was given the greatest support (Table 2, Model 1C). However, the fledging probabilities only showed a weak response to the explanatory variables (Table 2), and 9 models contributed to 90% of the summed AICc weights. Neither the linear (r = 0.36, df = 7, p = 0.34) nor the logarithmic (r = 0.35, df = 7, p = 0.35) relationships with the contribution of anchovy to the diet were significant for nests with OCB, and the fledging probability was more variable than in the TCB when anchovy contributed >90% of the diet (Fig. 4).

In TCB, the chick-fledging probabilities were positively related to the percentage of anchovy in the diet (r = 0.77, df = 7, p = 0.014; Table 2, Model D1: $f = -2.33 + 0.624 \times \ln(d)$, where $f =$ fledging probability, and $d =$ anchovy in diet [% by mass]). In 3 of the 9 years (2003, 2004 and 2006), the diet consisted of <75% anchovy, and the probability of a chick fledging was <0.5 (Fig. 4A). A negative relationship between the chick-fledging probabilities and sardine biomass from the previous November was also given tentative support (r = 0.71, df = 7, p = 0.033; AICc weight = 0.126; Table 2, Model D3).

Fledging periods

Although the values for 2001 and 2002 were estimated with low precision (Fig. 5A), the data suggested an increase in the mean (±1 SD) fledging period from 68.7 ± 7.6 d in 2004 to 78.2 ± 12.2 d in 2009. Fledging periods were negatively related to the log of the sardine biomass from the previous November (TotalBioSard y_{-1}: r = 0.92, df = 7, p < 0.001; Fig. 5B). The best fitting model ($g = 86.03 - 2.57 \times \ln(b)$, where $g =$ the mean fledging period [d], and $b =$ the sardine biomass [$\times 10^6$ t]) explained 81% of the variation in the fledging periods and had 88% of the summed AICc weights (Table 2, Model E1).
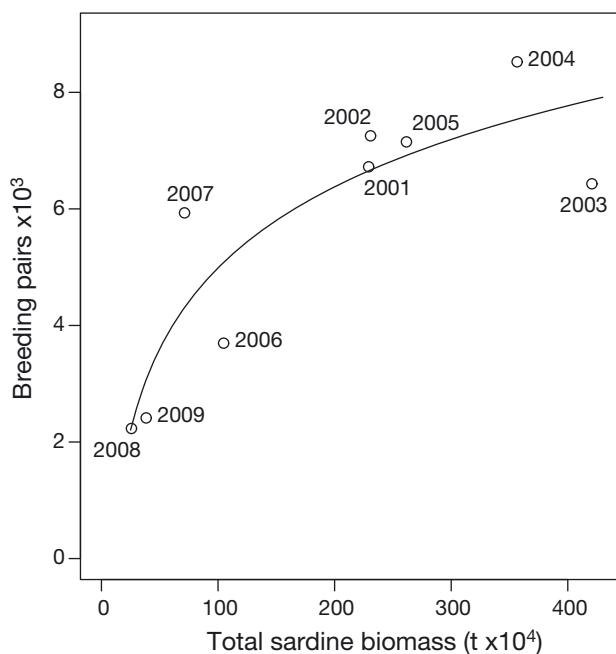
Table 2. *Spheniscus demersus.* Regression models relating African penguin breeding performance at Robben Island (2001 to 2009) to forage-fish abundance in South Africa. For each response, models that contributed to 90% of the summed AICc weight and had greater support than the null model are shown, along with the number of model parameters (K), AICc value, difference from the lowest AICc value (ΔAICc) and the relative support (AICc weights) given to each model. See Table 1 for model abbreviations. y_0 indicates an explanatory variable from the same year and y_{-1} from the previous year; Ln() is the natural logarithm; + indicates a positive relationship between variables and − indicates a negative one. na: not applicable

Model no.	Model	K	AICc	ΔAICc	AICc weight	+/−	Adjusted R^2	p
No. breeding pairs								
A1	Ln(TotalBioSard y_{-1})	2	129.76	0.00	0.789	+	0.76	0.001
A2	Ln(BioSardWA y_{-1})	2	134.03	4.27	0.093	+	0.62	0.007
A3	TotalBioSard y_{-1}	2	134.58	4.82	0.071	+	0.60	0.009
A4	Intercept only	1	140.52	10.76	0.004	na	na	na
Breeding success								
B1	Ln(CatchAnch y_0)	2	−55.10	0.00	0.397	+	0.66	0.005
B2	CatchAnch y_0	2	−54.58	0.52	0.307	+	0.64	0.006
B3	BioSardWA y_{-1}	2	−53.42	1.68	0.172	−	0.58	0.010
B4	Ln(BioSardWA y_{-1})	2	−51.68	3.42	0.072	−	0.50	0.021
B5	Intercept only	1	−36.42	18.68	0.000	na	na	na
Fledging success: 1-chick broods								
C1	CatchAnch y_0	2	−54.10	0.00	0.310	+	0.40	0.039
C2	Ln(CatchAnch y_0)	2	−53.60	0.50	0.242	+	0.37	0.048
C3	Intercept only	1	−51.66	2.43	0.092	na	na	na
Fledging success: 2-chick broods								
D1	Ln(AnchPercDiet y_0)	2	−66.48	0.00	0.336	+	0.54	0.014
D2	AnchPercDiet y_0	2	−66.30	0.18	0.308	+	0.53	0.016
D3	TotalBioSard y_{-1}	2	−64.51	1.97	0.126	−	0.43	0.033
D4	BioSardWA y_{-1}	2	−63.55	2.93	0.078	−	0.37	0.050
D5	Ln(TotalBioSard y_{-1})	2	−62.85	3.63	0.055	−	0.31	0.068
D6	Intercept only	1	−61.69	4.79	0.031	na	na	na
Fledging period								
E1	Ln(TotalBioSard y_{-1})	2	10.43	0.00	0.875	−	0.81	<0.001
E2	TotalBioSard y_{-1}	2	14.59	4.16	0.109	−	0.71	0.003
E3	Intercept only	1	20.87	10.43	0.005	na	na	na
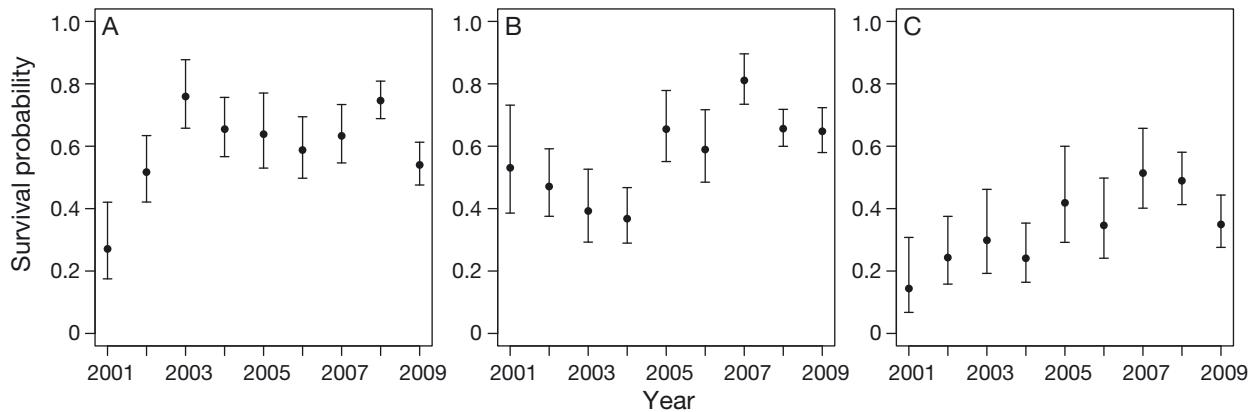
Fig. 2. *Spheniscus demersus.* Survival probabilities (and 95% confidence limits) of the nest contents during (A) the average incubation period (40 d), (B) the average chick-rearing period (74 d) and (C) the overall breeding success (the product of A and B) of African penguins at Robben Island during 2001 to 2009

DISCUSSION

To breed successfully, seabirds must have access to stable or abundant food resources within a limited range from their colony (e.g. Piatt et al. 2007, Durant et al. 2010). Although they can buffer reduced food availability (Burger & Piatt 1990), compensating has energetic costs, and seabirds will favour their own

survival above that of their progeny (Cairns 1987, Burger & Piatt 1990). As a result, breeding success often shows a curvilinear response to changes in food
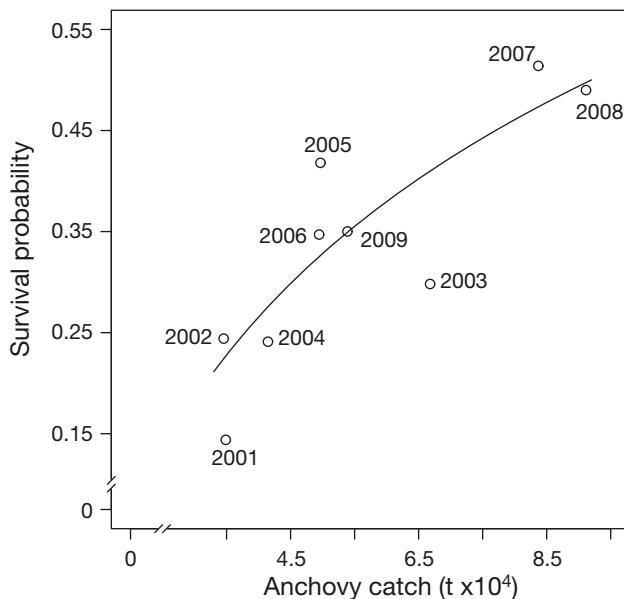
Fig. 3. *Spheniscus demersus* and *Engraulis encrasicolus*. Relationship between breeding success (probability of the nest contents surviving the nesting period) of African penguins and the catch of anchovy made within 56 km of Robben Island in the same year (CatchAnch y_0), 2001 to 2009. The line shows the best fitting regression model (Model B1, Table 2)

availability which is apparently robust across various life-history strategies, habitats and population sizes (e.g. Furness 2007, Piatt et al. 2007, Cury et al. 2011). In the present study, breeding success showed a positive, non-linear response to an apparent increase in the abundance of anchovy close to the colony during the latter years of the study. However, responses may differ among species or parameters (e.g. Montevecchi 2007, Piatt et al. 2007), and while an apparent decrease in the estimated abundance of sardine corresponded to a non-linear decrease in the breeding population counted at Robben Island and a non-linear increase in fledging periods, the link between fledging rates and diet composition seemed to only respond to severe decreases in local food availability in the present study (Fig. 4A).

Local prey abundance or availability can be difficult or costly to assess, often requiring regular small-scale hydro-acoustic (e.g. Piatt et al. 2007) or aerial surveys (e.g. Suryan et al. 2002). However, our findings suggest that the industrial catch of anchovy made within 56 km of Robben Island provided a good indication of the prey abundance available to breeding penguins. Catch data may offer a useful proxy for top predators in other ecosystems if the operation of the industry matches appropriately to the biology of the predator under consideration. South Africa's anchovy fishery and breeding African penguins both target anchovy
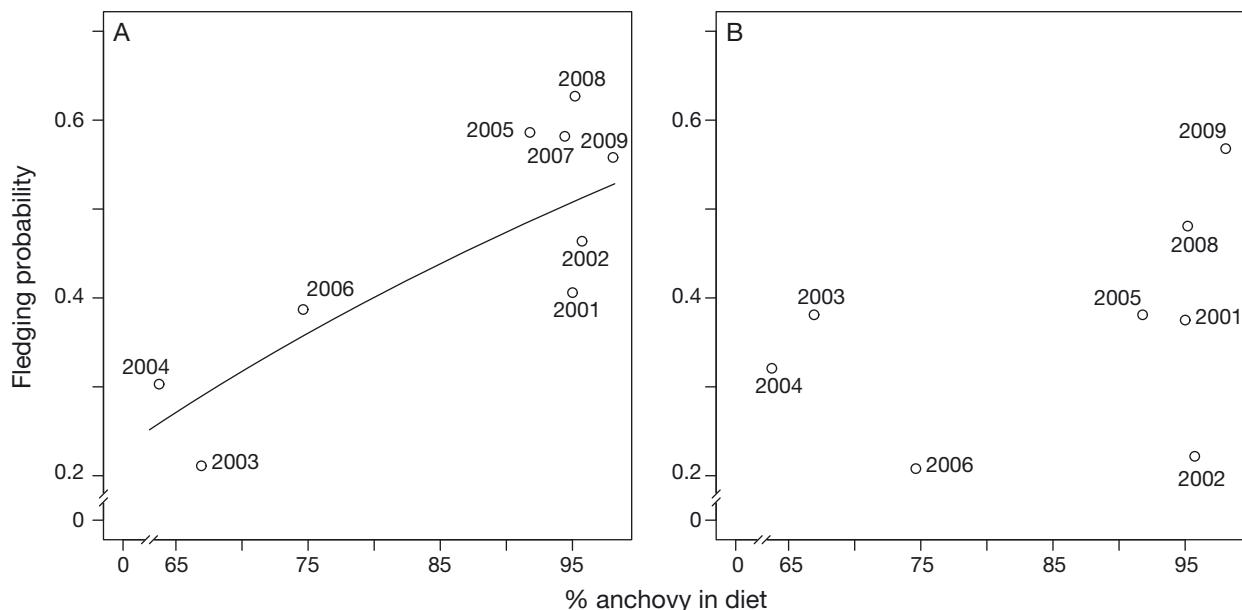
Fig. 4. *Spheniscus demersus* and *Engraulis encrasicolus*. Relationship between the annual percentage contribution of anchovy to the diet of breeding African penguins on Robben Island (AnchPercDiet y_0) and the probability of a chick fledging, regardless of the outcome of the sibling, in (A) 2-chick broods and (B) 1-chick broods between 2001 and 2009. The line in (A) represents the fit of Model D1 (Table 2)
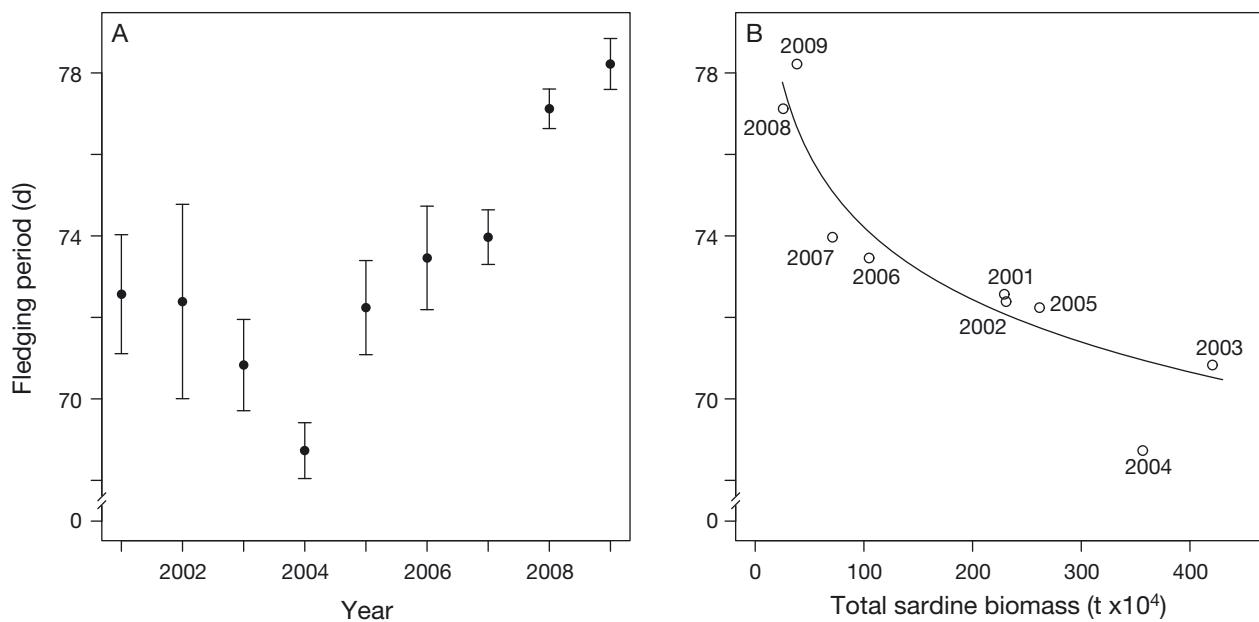
Fig. 5. *Spheniscus demersus* and *Sardinops sagax*. (A) Annual estimates for the mean (±1 SE) fledging period (days) of African penguin chicks in successful breeding attempts at Robben Island, 2001 to 2009. (B) Relationship between the mean fledging period and the total biomass of sardine in South Africa estimated in the preceding November (TotalBioSard y_{-1}). The line represents the fit of Model E1 (Table 2)

recruits in the near-shore waters of the West Coast (Fairweather et al. 2006, Crawford et al. 2011), and the catch data were derived from the total fishing activity during the breeding season (Pichegru et al. 2009). However, all of the measures of prey abundance used in the present study come with caveats. The biannual biomass surveys only provide estimates of prey availability to predators over a large area and can only offer temporal snapshots of the spatial aggregation of the fish in relation to seabird foraging areas. Catch data can be influenced by additional factors besides fish abundance (e.g. economics), high-intensity fishing can depress food availability for seabirds (Frederiksen et al. 2004), and in the present study, catches were not scaled to fishing effort. In addition, seabirds may not always select prey species in proportion to their relative abundance, but may disproportionately target preferred prey items based on accessibility or perceived quality (e.g. Suryan et al. 2000).

African penguins are relatively specialised foragers, at least when provisioning chicks (Crawford et al. 2011). The limited variation in their diet at Robben Island (Crawford et al. 2011; Fig. S2 in the supplement) suggests either little behavioural flexibility to switch to other prey when anchovy is scarce or a paucity of alternative prey. African penguins do target other species (Fig. S2), but the alternative prey

are mostly of poorer energetic value than sardine and anchovy (Balmelli & Wickens 1994, Ludynia et al. 2010). Consequently, when anchovy contributed <75% to the diet (2003, 2004 and 2006; Fig. 4), chick survival was poor (Fig. 2B), and fledging probabilities were below average for chicks in TCB (Fig. 4A).

When food is scarce, the hatching asynchrony in 2-egg clutches sets up a size inequality that reduces the ability of the second hatchling to compete during scramble feeding (Seddon & van Heezik 1991). At these times, the quality or quantity of food delivered to second hatchlings may be insufficient to negate starvation (Seddon & van Heezik 1991), leading to the reduced fledging rates observed in TCB (Fig. 4A). Conversely, fledging probabilities in OCB were not strongly related to anchovy availability within the range of variation in the present study (Fig. 4B). Seabirds that typically lay 2 eggs can often rear 1 chick successfully even under severe food stress (e.g. Stienen & Brenninkmeijer 2006). African penguins seem easily able to buffer low prey availability to meet the minimum demands of raising 1 chick (sensu Burger & Piatt 1990) and have evolved behavioural mechanisms to guard against wasteful brood reduction when food is abundant (van Heezik & Seddon 1996).

Previous studies have noted positive relationships between breeding success of African penguins and

measures of total small pelagic fish biomass in South Africa (e.g. Crawford et al. 1999, 2006). These effects were not replicated during the present study, possibly because expecting linear or even log-linear relationships with broad-scale measures of prey abundance to persist in ecosystems under flux is too simplistic. Durant et al. (2010) proposed that local food availability on the West Coast became decoupled from overall fish biomass from about 2001 as the adult fish stocks were located principally on the South Coast. This may also explain the negative relationships noted between sardine abundance and breeding and fledging success in the present study (Table 2), as sardine abundance apparently decreased during the study (Fig. S4 in the supplement), but local food availability seemed to increase, and breeding success responded accordingly (Figs. 3 & S4).

Alternatively, the previous relationships between total biomass and breeding success may have been mediated through an influence on the condition of breeding birds. Outside the breeding season, seabirds are not constrained to remain close to breeding colonies (e.g. Barham et al. 2006) and may utilise more distant prey to regain condition after breeding and moulting. In some seabirds, particularly 'capital breeders' (Jönsson 1997), body condition can influence not only the decision to breed but also subsequent breeding success (Chastel et al. 1995). For example, body condition at the onset of breeding has been shown to interact with local feeding conditions to affect breeding success and chick-provisioning behaviour in Adélie penguins *Pygoscelis adeliae* (a capital breeder) foraging in the Antarctic (Ballard et al. 2010) and timing and success of breeding in little penguins *Eudyptula minor* (an income breeder) in temperate South Australia (Robinson et al. 2005).

African penguins are not highly synchronous in the onset of breeding (Crawford et al. 1999) and are sensitive to human disturbance (Hockey & Hallinan 1981), making it difficult to collect data on adult condition prior to egg laying. However, sardine biomass is thought to have influenced the size of the breeding populations at colonies in the Western Cape including Robben Island, Dassen Island, Stony Point and Boulders Beach (locations in Fig. S1) in the past (Crawford et al. 2001, 2008a,b). The longer fledging periods noted when sardine biomass was low in the present study (Fig. 5) suggest that the abundance and spatial distribution of the adult fish stocks could also be important in determining the body condition of birds prior to breeding (see also Durant et al. 2010,

Crawford et al. 2011). If so, the reserves that African penguins obtain prior to the onset of breeding and the ease of finding prey within the vicinity of their breeding colony would likely interact to affect breeding success and chick growth by altering the trade-off between resource allocation to self-maintenance and chick-provisioning behaviour (Ropert-Coudert et al. 2004, Robinson et al. 2005, Saraux et al. 2011). In other words, good body condition prior to breeding may be insufficient to ensure the survival of an adult and its brood if conditions around the colony are poor or mediocre, but in years of abundant local prey resources, seabirds initiating breeding in good condition could invest less in self-maintenance and more in provisioning their brood.

Taken together, our results underline the importance of adequate local food availability for seabirds during the reproductive cycle (e.g. Durant et al. 2010) as well as that of its interaction with a seabird's life cycle and regional prey abundance during the non-breeding season. Small-scale marine protected areas have been used to protect local foraging areas for breeding seabirds in many countries, and Pichegru et al. (2011) have claimed from preliminary results that closures around African penguin colonies in South Africa may benefit breeding adults by reducing the energetic costs of foraging. However, our results imply that these closures may be inadequate to provide benefits at a population level in the absence of other broad-scale measures to ensure food security for top predators, such as 'ecosystems approaches to fisheries' (Shannon et al. 2004), spatial management initiatives to reduce any localised fishery impacts or protection of networks of key foraging areas (Hooker et al. 2011). Seabirds cover large areas during their life-cycle, and a better understanding of how the interactions between resources on different scales affect population demographics will be crucial to reversing the rapid decline of Africa's only breeding penguin and the poor global conservation status of marine birds.

LITERATURE CITED

Ballard G, Dugger KM, Nur N, Ainley DG (2010) Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. Mar Ecol Prog Ser 405:287–302

Balmelli W, Wickens PA (1994) Estimates of daily ration for the South African (Cape) fur seal. S Afr J Mar Sci 14: 151–157

Barham PJ, Crawford RJM, Underhill LG, Wolfaardt AC and others (2006) Return to Robben Island of African penguins that were rehabilitated, relocated or reared in captivity following the *Treasure* oil spill of 2000. Ostrich 77: 202–209

Barham PJ, Underhill LG, Crawford RJM, Leshoro TM (2007) Differences in breeding success between African penguins (*Spheniscus demersus*) that were and were not oiled in the MV Treasure oil-spill in 2000. Emu 107:7–13

Burger AE, Piatt JF (1990) Flexible time budgets in breeding common murres: buffers against variable prey abundance. Stud Avian Biol 14:71–83

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY

Cairns DK (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271

Chastel O, Weimerskirch H, Jouventin P (1995) Body condition and seabird reproductive performance: a study of three petrel species. Ecology 76:2240–2246

Coetzee JC, van der Lingen CD, Hutchings L, Fairweather TP (2008) Has the fishery contributed to a major shift in the distribution of South African sardine? ICES J Mar Sci 65:1676–1688

Crawford RJM, Boonstra HGvD, Dyer BM, Upfold L (1995) Recolonisation of Robben Island by African penguins, 1983–1992. In: Dann P, Norman I, Reilly PN (eds) The penguins: ecology and management. Surrey Beatty & Sons, Sydney, p 333–363

Crawford RJM, Shannon LJ, Whittington PA (1999) Population dynamics of the African penguin *Spheniscus demersus* at Robben Island, South Africa. Mar Ornithol 27: 139–147

Crawford RJM, David JHM, Shannon LJ, Kemper J and others (2001) African penguins as predators and prey — coping (or not) with change. S Afr J Mar Sci 23:435–447

Crawford RJM, Barham PJ, Underhill LG, Shannon LJ and others (2006) The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. Biol Conserv 132: 119–125

Crawford RJM, Sabarros PS, Fairweather T, Underhill LG, Wolfaardt AC (2008a) Implications for seabirds off South Africa of a long-term change in the distribution of sardine. Afr J Mar Sci 30:177–184

Crawford RJM, Underhill LG, Coetzee JC, Fairweather T, Shannon LJ, Wolfaardt AC (2008b) Influences of the abundance and distribution of prey on African penguins *Spheniscus demersus* off western South Africa. Afr J Mar Sci 30:167–175

Crawford RJM, Altwegg R, Barham BJ, Barham PJ and others (2011) Collapse of South Africa's penguins in the early 21st century. Afr J Mar Sci 33:139–156

Crawley MJ (2007) The R book. John Wiley & Sons, Chichester

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T and others (2011) Global seabird response to forage fish depletion — one-third for the birds. Science 334:1703–1706

de Moor CL, Butterworth DS, Coetzee JC (2008) Revised estimates of abundance of South African sardine and anchovy acoustic surveys adjusting for echosounder saturation in earlier surveys and attenuation effects for sardine. Afr J Mar Sci 30:219–232

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33: 271–283

Durant JM, Crawford RJM, Wolfaardt AC, Agenbag K, Visagie J, Upfold L, Stenseth NC (2010) Influence of feeding conditions on breeding of African penguins — importance of adequate local food supplies. Mar Ecol Prog Ser 420:263–271

Fairweather TP, van der Lingen CD, Booth AJ, Drapeau L, van der Westhuizen JJ (2006) Indicators of sustainable fishing for South African sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus.* Afr J Mar Sci 28: 661–680

Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson LJ (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. J Appl Ecol 41:1129–1139

Furness RW (2007) Responses of seabirds to depletion of food fish stocks. J Ornithol 148(Suppl 2):247–252

Furness RW, Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar Ecol Prog Ser 202:253–264

Grémillet D, Lewis S, Drapeau L, van der Lingen CD and others (2008) Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and seasurface temperature to predict marine predator distributions? J Appl Ecol 45:610–621

Hockey PAR, Hallinan J (1981) Effect of human disturbance on the breeding behaviour of jackass penguins *Spheniscus demersus.* S Afr J Wildl Res 11:59–62

Hooker SK, Cañadas A, Hyrenbach KD, Corrigan C, Polovina JJ, Reeves RR (2011) Making protected area networks effective for marine top predators. Endang Species Res 13:203–218

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM and others (2009) The Benguela Current: an ecosystem of four components. Prog Oceanogr 83:15–32

Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78: 57–66

Ludynia K, Roux JP, Jones R, Kemper J, Underhill LG (2010) Surviving off junk: low-energy prey dominates the diet of African penguins *Spheniscus demersus* at Mercury Island, Namibia, between 1996 and 2009. Afr J Mar Sci 32:563–572

Mayfield H (1961) Nest success calculated from exposure. Wilson Bull 73:255–261

Montevecchi WA (2007) Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. Mar Ecol Prog Ser 352: 213–220

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of ecological systems. Ohio State University Press, Colombus, OH, p 154–177

Piatt JF, Harding AMA, Shultz M, Speckman SG, van Pelt TI, Drew GS, Kettle AB (2007) Seabirds as indicators of marine food supplies: Cairns revisited. Mar Ecol Prog Ser 352:221–234

Pichegru L, Ryan PG, Le Bohec C, van der Lingen CD and others (2009) Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. Mar Ecol Prog Ser 391: 199–208

Pichegru L, Ryan PG, van Eeden R, Reid T, Grémillet D, Wanless R (2012) Industrial fishing, no-take zones and endangered penguins. Biol Conserv 156:117–125

Quillfeldt P, Strange IJ, Masello JF (2007) Sea surface temperatures and behavioural buffering capacity in thin-billed prions *Pachyptila belcheri*: breeding success, provisioning and chick begging. J Avian Biol 38:298–308

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org

Robinson S, Chiaradia A, Hindell MA (2005) The effect of body condition on the timing and success of breeding little penguins *Eudyptula minor.* Ibis 147:483–489

Ropert-Coudert Y, Wilson RP, Daunt F, Kato A (2004) Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips. Behav Ecol 15:824–830

Roy C, van der Lingen CD, Coetzee JC, Lutjeharms JRE (2007) Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. Afr J Mar Sci 29:309–319

Saraux C, Robinson-Laverick SM, Le Maho Y, Ropert-Coudert Y, Chiaradia A (2011) Plasticity in foraging strategies of inshore birds: how little penguins maintain body reserves while feeding offspring. Ecology 92:1909–1916

Schülein FH, Boyd A, Underhill LG (1995) Catch trends and oil-to-meal ratios of pelagic fish taken from the northern and the southern Benguela system—seasonal patterns and temporal trends, 1951–1993. S Afr J Mar Sci 15: 61–82

Seddon PJ, van Heezik Y (1991) Hatching asynchrony and brood reduction in the jackass penguin: an experimental study. Anim Behav 42:347–356

Seddon PJ, van Heezik Y (1993) Behaviour of the jackass penguin chick. Ostrich 64:8–12

Shannon LJ, Cochrane KL, Moloney CL, Fréon P (2004) Ecosystem approach to fisheries management in the southern Benguela: a workshop overview. Afr J Mar Sci 26: 1–8

Sherley RB, Barham BJ, Barham PJ, Leshoro TM, Underhill LG (2012) Artificial nests enhance the breeding productivity of African penguins (*Spheniscus demersus*) on Robben Island, South Africa. Emu 112:97–106

Stienen EWM, Brenninkmeijer A (2006) Effect of brood size and hatching sequence on prefledging mortality of Sandwich terns: Why lay two eggs? J Ornithol 147: 520–530

Suryan RM, Irons DB, Benson J (2000) Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. Condor 102: 375–385

Suryan RM, Irons DB, Kaufman M, Benson J, Jodice PGR, Roby DD, Brown ED (2002) Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*. Mar Ecol Prog Ser 236:273–287

van Heezik YM, Seddon PJ (1996) Scramble feeding in jackass penguins: within-brood food distribution and the maintenance of sibling asymmetries. Anim Behav 51: 1383–1390

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep-Sea Res II 54:211–223