Chapter 11

Breeding patterns and factors influencing breeding success of African Penguins *Spheniscus demersus* in Namibia

Jessica Kemper[1,2]*, Les G. Underhill[1], Jean-Paul Roux[3], Peter A. Bartlett[3], Yves J. Chesselet[3], Joan A.C. James[3], Rian Jones[3], Neville-Nash Uhongora[3] and Silvia Wepener[3]

[1] Avian Demography Unit, University of Cape Town, Rondebosch 7701, Cape Town, South Africa
[2] African Penguin Conservation Project, c/o Ministry of Fisheries and Marine Resources, PO Box 394, Lüderitz, Namibia
[3] Lüderitz Marine Research, Ministry of Fisheries and Marine Resources, PO Box 394, Lüderitz, Namibia
* Corresponding author: e-mail: jkemper@mfmr.gov.na / Spheniscus03@yahoo.co.uk

We describe breeding seasonality patterns and assess breeding success of African Penguins *Spheniscus demersus* at the four most important breeding colonies in Namibia. Penguins bred throughout the year; peak nesting activities varied between localities and between years. At Mercury Island, most penguins bred between October and January and at Ichaboe Island between October and December. At Halifax Island, breeding usually peaked between July and August and in early December. Breeding was less seasonal at Possession Island but reached a peak between November and January. Least breeding took place during April and May at all four islands. From 2 780 monitored nests, an average of 0.61 chicks were fledged per breeding attempt. The incidence of fledging two chicks from one clutch was high; between 43.3% and 64.1% of successful attempts produced two fledglings. Egg-laying date was the most important determinant of nest success. Nests initiated at the end of October at Mercury, Ichaboe and Halifax Islands had a higher probability of survival than at any other time of the year. At Possession Island, the best time for egg-laying was about a month earlier. Poorly-timed breeding was probably the key factor responsible for the poor breeding success at Halifax Island compared to the other three localities. Vulnerability to flooding, nest position within a colony (with centrally positioned nests more likely to be successful than nests at the edge of a colony), and nest type were other important explanatory variables. Breeding success estimates for Namibian localities compared well with those obtained from localities in South Africa but are insufficient to keep the African Penguin population in Namibia stable.

Keywords: African Penguins, Namibia, breeding seasonality, breeding success, nest characteristics, egg-laying date

Introduction

To be successful, a penguin nest site must provide a place where adult penguins, their eggs and chicks are safe from predators and where they are able to cope with environmental factors such as distance to a food source, intense heat and potential flooding. Large-scale removal of guano from most of the Namibian islands has changed the characteristics of many seabird colonies breeding there, including those of African Penguins *Spheniscus demersus* (Frost *et al.* 1976, Kemper *et al.* submitted 1). As a result, the majority of penguins which nested in burrows scraped into the guano now nest on the surface, where they are exposed to predation by Kelp Gulls *Larus dominicanus* and direct solar insolation. Namibia supports a regional population of African Penguins. The four main penguin breeding localities in Namibia (Table 1), which account for c. 96% of the Namibian population, differ in a number of features, particularly local food availability, nesting habitat, predation intensity and topography.

African Penguins are primarily inshore foragers when breeding (Wilson 1985). Food quality and availability are thought to be more reliable at Mercury and Ichaboe Islands, where penguins feed on abundant Pelagic Goby *Sufflogobius bibarbatus*, than at localities south of Lüderitz (Crawford *et al.* 1985, 1991). At Possession Island, diet is dominated by cephalopods (Crawford *et al.* 1985, Cordes *et al.* 1999). Their quality as a food source is considered inferior to Pelagic Goby (Heath & Randall 1985). However, penguins there could benefit from occasional shoals of Anchovy *Engraulis capensis* reaching the vicinity of the island from the south (Cruickshank *et al.* 1990, Hampton 2003).

The quality of available nest sites differs between islands. At Mercury and Ichaboe Islands, virtually all nest sites are situated on the surface and most penguins there breed in relatively large, dense colonies. Boulders offer partial protection to some nest sites at Ichaboe Island. At Halifax Island, there is a variety of nest types (Kemper *et al.* submitted 1), although 70% of nests there occur in three distinct surface colonies. At Possession Island, the majority of penguins nest solitarily or in loose, small colonies beneath bushes, with the remainder breeding in aggregations of sandy burrows or in abandoned buildings. There are few surface nest colonies at Possession Island and isolated surface nesting is uncommon.

Table 1: Summary description of the four main African Penguin breeding localities in Namibia

Breeding locality	Position	Size (ha)	Estimated number of:	
			adult penguin individuals*	nests at peak breeding*
Mercury	25°43'S 14°50'E	3.0	12 499	2037
Ichaboe	26°17'S 14°56'E	6.5	5 989	864
Halifax	26°37'S 15°04'E	10.0	3 771	669
Possession	27°01'S 15°12'E	90.0	1 387	445

*estimate for 2004 (Kemper 2006)

Kelp Gulls are the only potential predators of penguin eggs or small chicks at any of these islands, particularly between October and February, when they breed. Gull numbers differ between islands. Mercury Island has one resident breeding pair and the number of roosting gulls rarely exceeds ten. Ichaboe Island supports a relatively small Kelp Gull breeding population numbering fewer than 100 pairs, although up to 900 individuals may roost there throughout the year (Ministry of Fisheries and Marine Resources (MFMR) unpubl. data). The breeding population of Kelp Gulls at Halifax Island numbers about 350 pairs (Kemper *et al.* submitted 1). Large numbers of Kelp Gulls occur at Possession Island, including approximately 1 500 breeding pairs and up to 3 000 individuals roosting (MFMR unpubl. data).

The islands differ in their topography. Ichaboe, Halifax and Possession Islands are largely flat; Mercury Island mainly consists of steep east- or west-facing slopes, with few level areas available to breeding penguins. Rainstorms in the region are rare but can be severe. Flooding of nests by rain is most likely at Ichaboe Island, where a wall surrounding the island prevents excess water from draining. At Possession Island, a low-lying colony of burrows is particularly prone to flooding by rainwater. At Mercury Island, and to a lesser extent at Halifax Island, flooding of nests close to the water's edge is relatively common during springtide or rough seas.

This paper describes breeding seasonality patterns of African Penguins at the four most important breeding colonies in Namibia, assesses their breeding success rates, and evaluates the potential contribution of breeding success to the continuing decline of the Namibian penguin population. Special reference is made to differences in breeding success between localities, seasons and years, and the importance of nest site characteristics with respect to breeding success.

Methods

As the breeding activity of penguins was lowest during the months of April and May (this study), a year was defined as the period from 1 May to 30 April in this study. Counts of active nest (containing eggs or chicks) were used to describe general breeding seasonality patterns at each of the four localities. Counts were done monthly at Mercury (since 1994), Ichaboe (since 1992) and Halifax (since 1996) Islands and every two weeks at Possession Island (since 1996). Since June 2000 at Halifax Island and since July 1996 at Possession Island, nests with chicks were distinguished from those with eggs during the counts .

In addition, since December 1996 at Mercury and Ichaboe Islands, and since December 1999 and April 2000 at Possession and Halifax Islands. Also, since January 2000 at each locality, a number of nest site characteristics were noted for each nest monitored(Table 2). For the above, observations up to the end of May 2004 were included in this study. Because egg-laying in African Penguins is rarely observed

(pers. obs), only nests containing eggs which appeared to have been recently laid were monitored. The date on which monitoring was initiated was noted for each nest, and the nest contents were recorded weekly thereafter. The hatching date of each chick was estimated from the approximate age of the chick when it was first observed. Since nests were checked weekly, the error associated with hatching date was about three days. Egg-laying dates were then back-calculated from the estimated hatching dates, assuming the length of the incubation period to be 40 days (Randall & Randall 1981, Williams & Cooper 1984). For nests which failed before hatching and for which an egg-laying date could therefore not be calculated, half the incubation duration (20 days) was subtracted from the date the nest was found.

Chicks were considered to have fledged if they were fully feathered (but see discussion), if unattended by a parent, and if they were not to be found at their nest or at another nest or nearby crèche. When there was doubt, nests were re-checked, sometimes after sunset, when chicks are more likely to be found at their nests (Seddon & van Heezik 1993). In some cases chicks were directly observed leaving the island, always without their parents. Breeding success was measured in terms of the numbers of chicks fledged per nesting attempt or the number of nests producing at least one fledgling.

To reduce the biases in estimating nest success resulting from nests not being found at the beginning of the nesting attempt, the approach developed by Mayfield (1961, 1975), and extended by Underhill (submitted) was used. The extended Mayfield method enables explanatory variables to be incorporated into nest success modelling using the standard hypothesis testing and model selection approaches used, for example, in generalized linear models. Model fitting was undertaken using the RSURVIVAL procedure of GenStat (GenStat Committee 2005). The logarithm of the parameter λ of an exponential distribution was modelled as a linear combination of explanatory variables: e.g. for three explanatory variables,

$$\log \lambda = a + b_1 x_1 + b_2 x_2 + b_3 x_3.$$

Seasonality of breeding was described using a Fourier analysis approach, developed by Zucchini & Adamson (1984) and also used by Underhill *et al.* (1992), Harrison *et al.* (1997) and Underhill & Parsons (submitted). For the Fourier modelling, days of the year were calculated from 1 May, and expressed as an angle (0°–360°) as described in Underhill *et al.* (1992); e.g. 15 June is the 46th day after 1 May, and is represented by the angle 360 × (46/365) = 45.4°. The key property of this approach is that the results do not depend on the choice of day to split the year. First and second "harmonics" in the seasonality model were considered; a harmonic was always fitted as a pair of sine and cosine terms included in the explanatory variables.

Table 2: Nest site characteristics recorded for 1 577 monitored nests at the four main breeding localities of African Penguins in Namibia

Category	Attribute	Number of nests	Additional notes
Nest type	Surface	954	
	Bush	296	*Lycium decumbens*
	Boulder	71	Under boulders, in rock crevices
	Artificial	192	Plastic / rock shelters, tyres planks, metal drums
	Buildings	64	Old brick and wood sheds and guano collector accommodation
Substrate	Non-porous	104	Rock, concrete, metal, wood
	Porous	380	Gravel, sand, sacking, shells
	Guano	1093	
Nesting material	Soft	579	Seaweed, feathers, leaves
	Hard	366	Shells, pebbles, dry guano clusters, bones, twigs
	Mixed	592	
	None	40	
Side cover (Top cover)	0	597 (946)	No cover
	1	315 (87)	25% cover
	2	180 (31)	50% cover
	3	393 (44)	75% cover
	4	92 (469)	Full cover
Slope	0	871	Flat
	1	314	1°−5°
	2	217	6°−12°
	3	175	>12°
Orientation	0	298	Flat, fully exposed
	1	375	NW to NNE
	2	543	NE to ESE
	3	137	SE to SSW
	4	224	SW to WNW
Colony size	Isolated	576	≤10 nests within 100 m^2
	Small	311	≤50 nests
	Medium	324	≤50 nests
	Large	366	>150 nests
Colony position	Edge	884	≤three nests deep
	Centre	117	>three nests deep
Flooding	Likely	171	
	Not likely	1406	
Distance to landing beach	0–500 m	1577	Continuous variable

Results

Breeding seasonality patterns

African Penguins were recorded breeding, either incubating eggs or rearing chicks, throughout the year at all four main breeding localities in Namibia. Peak nesting activities varied between localities and between years (Figures 1 and 2). At Mercury Island, peak nesting was between October and January; at Ichaboe Island, breeding peaked between October and December. At Halifax Island, breeding usually peaked between July and August and in early December. Breeding was less seasonal at Possession Island but reached a peak between November and January. Breeding activities at all four islands were generally lowest during April and May. At Mercury Island, the number of active nests at peak breeding was, on average, 6.3 times higher than during times of least breeding activity; this ratio was lower at Ichaboe Island (3.4), Halifax Island (3.0) and Possession Island (2.1).

For the years 2000 to 2004, the timing of the primary incubation peak at Halifax Island was restricted to a three week period between 25 June and 18 July; the timing of secondary incubation peaks varied between 9 October in 2003 and 21 December in 2001 (Figure 3). At Possession Island, the timing of incubation activities was variable between 1996 and 2004. In 1996 and 1997, incubation peaks were observed during March and February (Figure 3). Between 1999 and 2004, incubation activities peaked between 18 October (2003) and 28 November (1998). Between 1996 and 2000 and in 2002, secondary incubation peaks were observed during March; in 2001, 2003 and 2004, incubation had a secondary peak in July. At both islands, incubation took place throughout the year.

Breeding success

Between December 1996 and April 2004, a total of 2 780 nests were monitored. General breeding success parameters for each island are summarized in Table 3. There were no major environmental anomalies during the period spanned by this study. Apart from a few heat waves (e.g. Kemper *et al.* submitted 1), infrequent rain events causing dozens of nests to be abandoned simultaneously, and heavy storms occasionally washing away nests close to the water's edge at Mercury and Halifax Islands, no locality-wide mass nest abandonment was recorded.

Most penguins laid two eggs and overall average clutch size was 1.84 (sd = 0.37). Clutch size was smallest at Ichaboe Island (1.80). The proportion of one-egg to two-egg
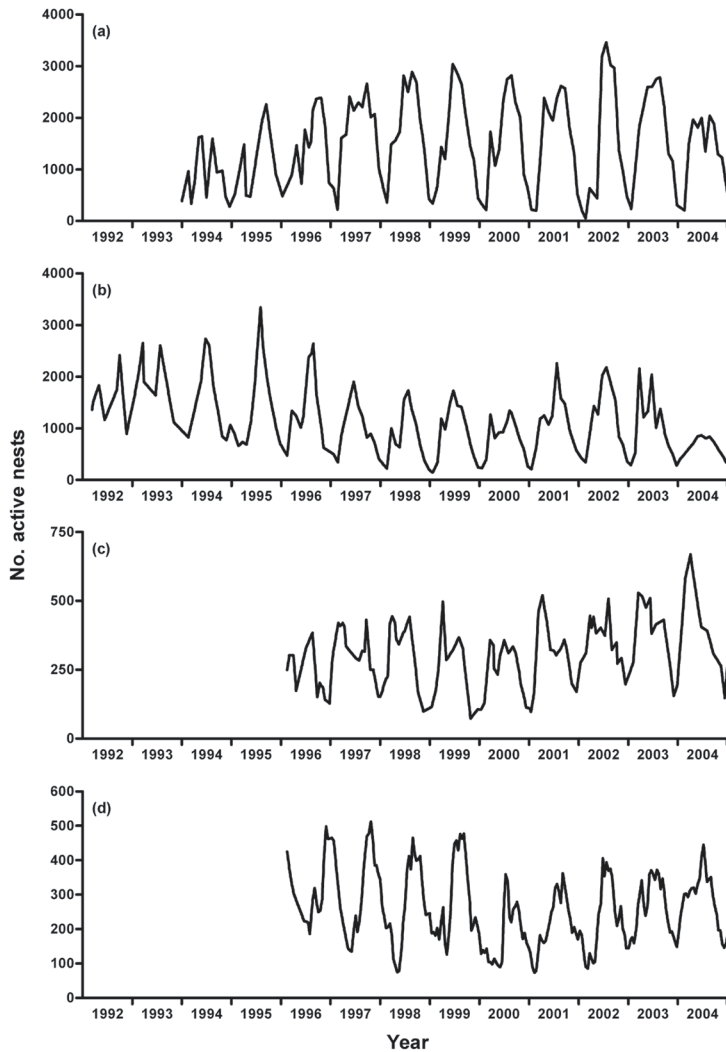
Figure 1: Time series of monthly counts of active nests for (a) Mercury, (b) Ichaboe and (c) Halifax Islands and of two-weekly counts of active nests for (d) Possession Island, Namibia. Years run from 1 May to 30 April the next year

Figure 2: Standardized, average seasonal breeding patterns of African Penguins, derived from counts of active nests (solid line), and associated coefficients of variation (dashed line) at the four main breeding localities in Namibia; (a) Mercury, (b) Ichaboe, (c) Halifax and (d) Possession Islands

clutches differed between islands ($\chi^2_3 = 35.26$, $P < 0.001$). At Mercury Island, 63.2% of nests survived incubation, compared to 57.3% at Ichaboe Island, 52.0% at Halifax Island and 58.6% at Possession Island. Each nest produced an average of 0.95 (sd = 0.89) hatchlings; nests at Possession Island hatched the highest number of chicks per nest (1.04, 0.93) and Halifax Island the fewest (0.86, 0.90). The proportion of 2-egg nests surviving incubation where both chicks hatched, differed between islands ($\chi^2_3 = 25.46$, $P < 0.001$).

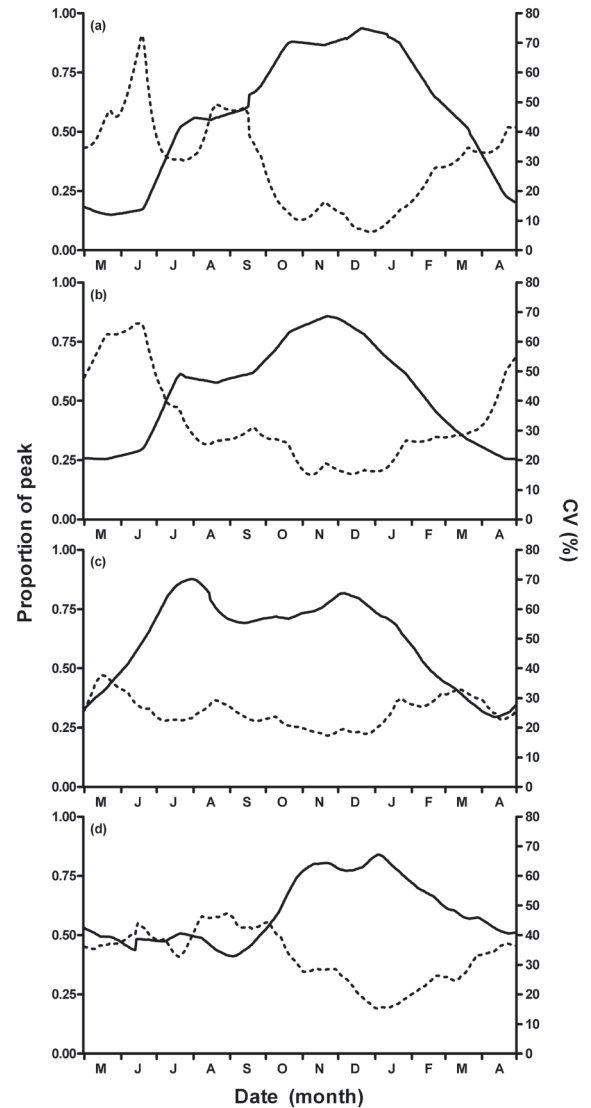Chick mortality decreased with age. Of the 939 chicks in the sample which died before fledging, 56.34% died within 20 days of hatching (Figure 4a). For the first 12 days after hatching, a greater percentage of chicks died at Ichaboe and Possession Islands than at Mercury and Halifax Islands (Figure 4b). After that, the observed daily mortality rate was simi-

Table 3: General breeding success parameters for African Penguins at the four main breeding localities in Namibia. Means (sd) are reported

| Breeding success parameter	Mercury	Ichaboe	Halifax	Possession
Number of nests monitored	674	1240	571	295
Nests monitored since	December 1996	December 1996	April 2000	December 1999
Clutch size	1.86 (0.35)	1.80 (0.40)	1.89 (0.31)	1.88 (0.32)
Number of chicks hatched per nest	0.99 (0.85)	0.94 (0.89)	0.86 (0.90)	1.04 (0.93)
Percentage of nests surviving incubation	63.2%	57.3%	52.0%	58.6%
Percentage of nests producing at least one fledgling	48.66%	41.13%	28.90%	42.71%
Number of fledglings per nesting attempt	0.70 (0.80)	0.61 (0.80)	0.44 (0.74)	0.71 (0.87)
Number of fledglings per successful nest	1.43 (0.50)	1.49 (0.50)	1.52 (0.50)	1.64 (0.48)
Percentage of nests fledging two chicks	21.07%	19.76%	15.06%	27.80%
Percentage of successful nests fledging two chicks	43.30%	48.04%	52.12%	64.06%
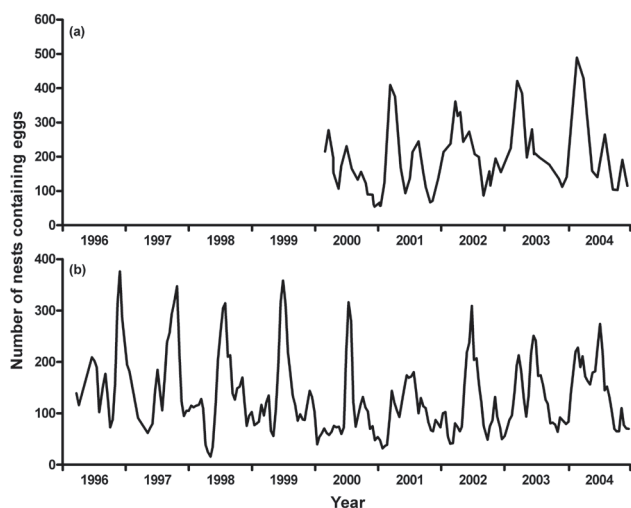
Figure 3: Time series of counts of African Penguin nests containing eggs at (a) Halifax Island since June 2000 and at (b) Possession Island since July 1996. Years run from 1 May to 30 April

Table 4: Survival, from egg laying to fledging of at least one chick, of African Penguin nests in Namibia, in relation to three explanatory variables: island, breeding year and seasonality. Results of a generalized linear model of the parameter λ of exponential distribution. The coefficients for the islands are in relation to Mercury Island and for years are in relation to 1996. Negative coefficients for the islands or the years indicate smaller modeled values for the parameter λ, which translates into higher breeding success (see text for details)

Explanatory variable	Regression coefficient	sd	t
Constant	−4.957	0.115	
Mercury Island	0		
ΔIchaboe Island	−0.138	0.070	−1.98
ΔHalifax Island	−0.134	0.087	−1.54
ΔPossession Island	−0.158	0.102	−1.54
1996	0		
Δ1997	0.209	0.148	1.41
Δ1998	0.340	0.166	2.05
Δ1999	−0.067	0.143	−0.47
Δ2000	0.427	0.130	3.27
Δ2001	0.473	0.138	3.42
Δ2002	0.463	0.136	3.41
Δ2003	0.276	0.150	1.84
Mercury and Ichaboe Islands			
sin θ	0.022	0.049	0.46
cos θ	0.524	0.050	10.44
Halifax Island			
sin θ	−0.067	0.080	−0.84
cos θ	0.533	0.098	5.42
sin 2 θ	−0.051	0.088	−0.58
cos 2 θ	−0.323	0.090	−3.61
Possession Island			
sin θ	−0.201	0.116	−1.73
cos θ	0.308	0.128	2.40

Figure 4: Chick mortality expressed as (a) percentage of African Penguin chicks which died before fledging at the four main breeding localities in Namibia, (b) percentage of surviving chicks in relation to chick age per breeding locality, (c) percentage of surviving chicks which had survived the previous interval of 10 days

lar for Mercury, Ichaboe and Halifax Islands, but was lower for Possession Island. The fewest chicks survived at Ichaboe Island. Chicks which survived the first two 10-day intervals after hatching had an increasingly better chance to survive a subsequent 10-day interval (Figure 4c).

Overall, 40.68% of nesting attempts produced at least one fledgling, with an average of 0.61 (0.80) fledglings per nesting attempt, or 1.49 (0.50) fledglings per successful nesting attempt. Two chicks were 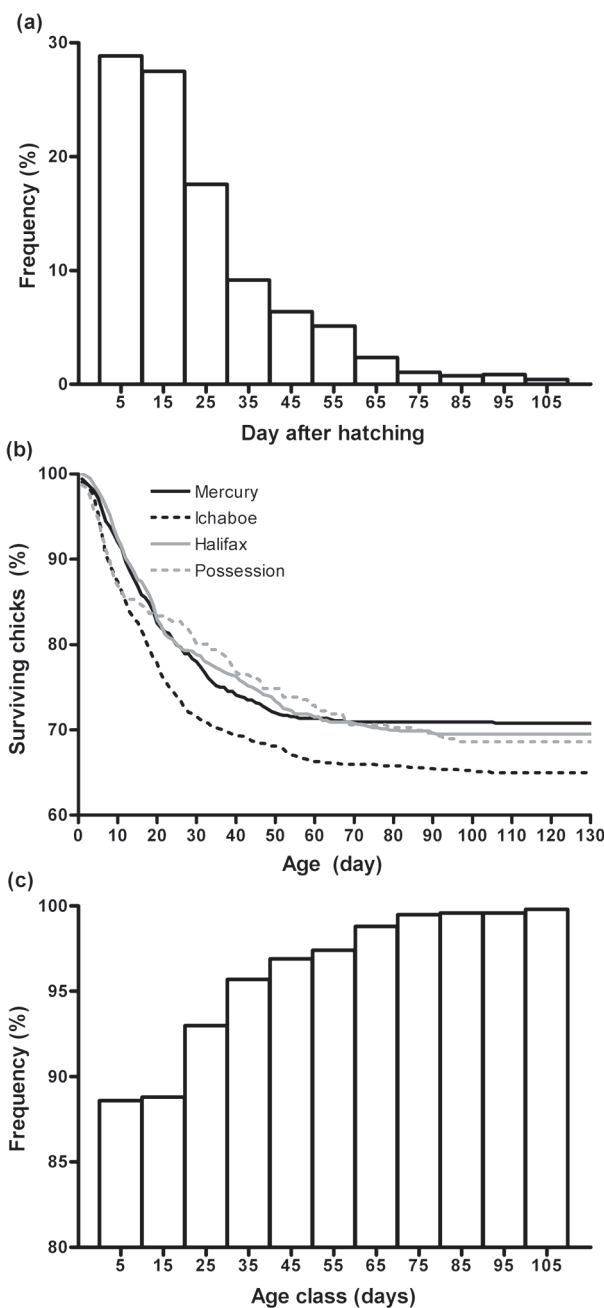fledged in 20.0% of all nesting attempts and in 49.1% of all successful attempts. The number of nests fledging two chicks differed between islands ($\chi^2_3 = 20.70$, $P < 0.001$); pairs at Possession Island fledged two chicks nearly twice as often as at Halifax Island. Successful nests fledging two chicks were more common at localities south of Lüderitz ($\chi^2_3 = 16.72$, $P < 0.001$).

At Mercury Island, 6.5% of all monitored nests contained one or more eggs ($n = 42$ nests) or a small chick ($n = 2$) which had rolled from a nest situated further up the slope. In three cases, monitored nests ended up with five eggs and in one case with six eggs. Egg-rolling was rare at Ichaboe Island; 14 monitored nests (1.1%) at some stage contained a rolled egg. In one case all three eggs in the clutch were hatched and raised to fledging. No cases of egg-rolling were reported from Halifax or Possession Islands.
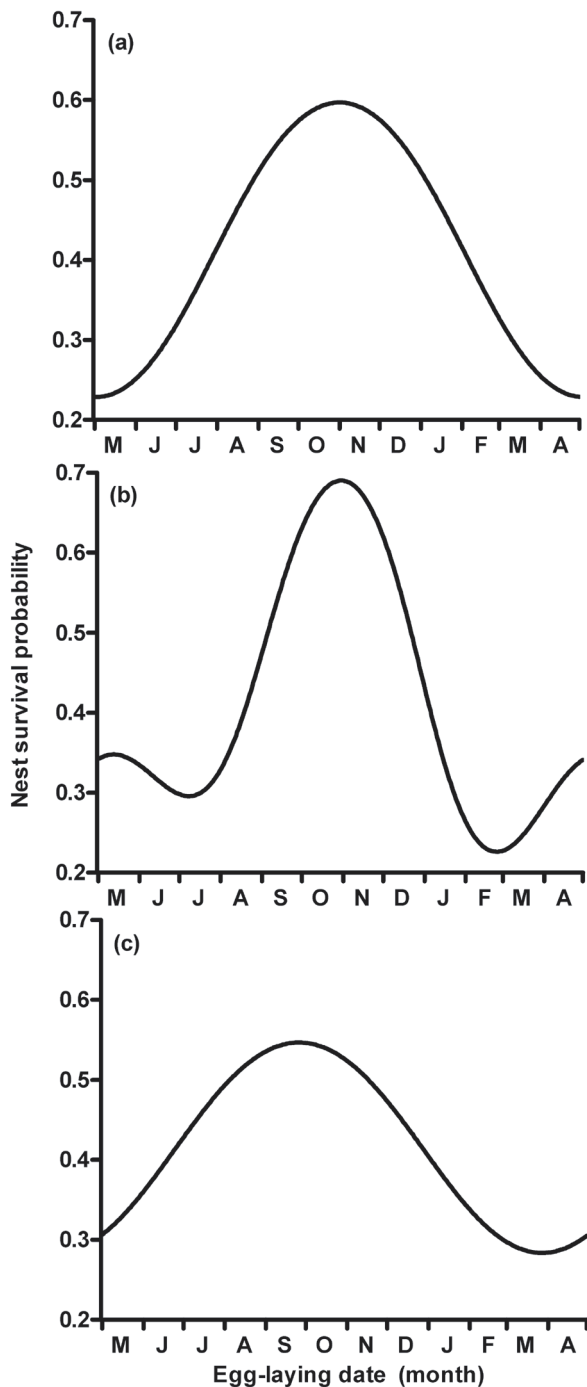
Figure 5: Relationship between egg-laying date and the modelled probability of nest success of African Penguins at (a) Mercury and Ichaboe, (b) Halifax and (c) Possession Islands, Namibia

Factors affecting nest success

Breeding success data, and three explanatory variables (island, year and estimated date of egg-laying), were available for 2 497 nests, and were analysed using the extended Mayfield method. The model of Table 4 was the preferred model, based both on model selection using change of deviance considerations (Dobson 2002) and the Akaike Information Criterion approach (Burnham & Anderson 2002). The estimated date of egg-laying was the key explanatory variable; the most satisfactory seasonal Fourier model included a first-order harmonic which was common to Mercury and Ichaboe Islands, first- and second-order harmonics

for Halifax Island, and a first-order harmonic for Possession Island (Table 4, Figure 5). The change in deviance from a model containing only a constant to this eight-parameter model describing seasonality was 187 ($P < 0.001$). The model suggested that nests in which egg-laying took place around the end of October at Mercury, Ichaboe and Halifax Islands had the best probability of producing fledglings; this date was one month earlier at Possession Island. The amplitude of the harmonic was largest for Halifax Island and smallest for Possession Island.

The modelled value of the parameter λ for an island in a calendar year on a particular date is computed from the regression coefficients of Table 4. For example, the modelled value of λ for Ichaboe Island for the year 2000 for a nest started on 31 October is given by:

$$\log \lambda = -4.957 - 0.138 + 0.427 + 0.022 \sin \theta + 0.524 \cos \theta$$

where $\theta = 181.5°$, because 31 October is the 184th day after 1 May, and converted to an angle becomes $360 \times (184/365) = 181.5°$. Thus $\log \lambda = -5.1924$, and $\lambda = 0.005559$. For the exponential distribution, the probability that a breeding attempt is successful is given by:

$$1 - \text{Pr(breeding attempt fails within } p \text{ days)} =$$

$$1 - \int_0^p \lambda\, e^{-\lambda x} dx = e^{-\lambda p},$$

where, in this case, $p = 124$ days from laying to fledging, so that the probability of success is 0.502.

Similarly, doing these calculations for each year for Ichaboe Island illustrates the extent of the inter-annual variation in breeding success resulting from the regression coefficients of Table 4 – 1996: 0.638, 1997: 0.574, 1998: 0.532, 1999: 0.657, 2000: 0.502, 2001: 0.486, 2002: 0.489 and 2003: 0.553. These values represent the modelled probabilities of a nest started at Ichaboe Island on 31 October of each year being successful in raising at least one chick. Performing these calculations for this date for the year 2000 for each island, the magnitudes of the modelled probabilities of nest success between islands can be illustrated: Mercury Island: 0.453, Ichaboe Island: 0.502, Halifax Island: 0.501 and Possession Island: 0.509. It is clear that the variation between years is larger than the variation between islands.

Further explanatory variables were available for 1577 of the 2497 monitored nests (Table 2). The most parsimonious model which included the explanatory variables for island, year and seasonality, and which incorporated a subset of these 10 explanatory variables was chosen. The best model included three of these 10 variables (Table 5). The key additional explanatory variables were vulnerability to flooding (change of deviance 9.9 with one additional parameter) and nest position within the colony (change of deviance 15.7 with two additional parameters). The addition of nest type to the model decreased the deviance by 9.0, with four degrees of freedom.

To illustrate the impact of being vulnerable to flooding, the probability of breeding success of a nest started at Ichaboe Island on 31 October in 2000 was 0.502 for a nest not vulnerable to flooding and 0.390 for a nest that was. Similarly, the impact of colony position can be illustrated: modelled probabilities for nest success for a nest at the edge of a colony was 0.502, a nest in the centre of a colony was 0.637, and a solitary nest was 0.542. For different nest types, the modelled probabilities showed that breeding inside a building generated the largest decrease in nest success: boulder: 0.502, surface: 0.506, artificial: 0.521, bush: 0.544 and building: 0.365.

Discussion

Breeding seasonality patterns

Throughout their range, African Penguins breed through the year (Wilson 1985), although seasonal peaks may vary between localities (Frost *et al.* 1976, Cooper 1980, Randall 1983, Duffy & La Cock 1985, Crawford *et al.* 2006a). This was also the case at the four main African Penguin breeding localities in Namibia. Breeding activities peaked between October and December at Mercury, Ichaboe and Possession Islands, and during July at Halifax Island. The timing and shape of peaks varied between islands and between years. Peak egg-laying at Halifax Island was well synchronized during July between years but was more variable at Possession Island. The timing of peak breeding differed to that reported from localities in South Africa. Peak breeding at Dassen and Robben Islands generally takes place between April and August (Cooper 1980, Wilson 1985, Crawford *et al.* 1999, 2006a, Wolfaardt & Nel 2003). At Malgas (33°03'S 17°55'E) and Marcus Islands and at Stony Point, active nests peak between February and August (Whittington *et al.* 1996, Crawford *et al.* 2006a), and at St Croix Island peak egg-laying is during January with secondary peaks in March/April and June (Randall 1983). The timing of breeding of penguins is thought to coincide with local food availability (Randall & Randall 1981, Crawford *et al.* 2006a). The ability to breed throughout the year could therefore allow some plasticity for the timing of breeding in response to variable local food conditions.

Breeding success

Breeding success averaged 0.61 fledged chicks per breeding attempt. In a few cases, chicks which were not fully feathered were observed going to sea. These were often emaciated and possibly abandoned chicks; high ambient temperature was also a factor for premature fledging (pers. obs). Fledglings are not accompanied by their parents when they leave their colonies and go to sea (pers. obs), and therefore have to find food for themselves before their fledging reserves are depleted, even though they have no experience at catching their food. Breeding success, as defined here, is therefore likely to be an overestimate, because some chicks which had left the nest were probably not old or fat enough to survive the first few days at sea.

Considering the large population decline at Possession Island over the last 50 years (Kemper *et al.* 2001, submitted 2), it seems surprising that the number of fledglings produced per nest was higher there than at any of the other three localities in Namibia. If food availability and quality at Possession Island is inferior to that at islands further north (Crawford *et al.* 1985, 1991, Cordes *et al.* 1999), then the success there could be due to the availability of more protected breeding habitat. Alternatively, if the population decline is due to the lack of local recruitment into the adult population (Kemper 2006), then on average, penguins breeding at Possession Island may be older, more experienced and more likely to breed successfully, than penguins at the other localities. The reverse situation may apply at Halifax Island, where breeding success was particularly poor. If the recent population increase at Halifax Island (Kemper *et al.* submitted 2) is due to recruitment of young birds from elsewhere, the population at this island may consist of breeders that are younger, less experienced and potentially less successful, than the average. The number of fledglings produced per breeding attempt at localities in Namibia compared favourably with estimates obtained from localities in South Africa, where African Penguin breeding success has

Table 5: Survival, from egg laying to fledging of at least one chick, of African Penguin nests in Namibia, in relation to three explanatory variables: vulnerability to flooding, nest position within the colony, and nest type. The explanatory variables of Table 3 were included in the model, but are not shown here. Results of a generalized linear model of the parameter » of exponential distribution. The coefficients for flooding vulnerability are in relation to flooding being unlikely, for colony position are in relation to nests positioned at the edge and for nest type are in relation to nests under boulders. Negative coefficients for flooding vulnerability, nest position in a colony or nest type indicate smaller modelled values for the parameter λ, which translates into higher breeding success (see text for details)

Explanatory variable	Regression coefficient	sd	t
Flooding			
not likely	0		
likely	0.310	0.106	2.92
Colony position			
edge of colony	0		
inside colony	−0.423	0.148	−2.86
solitary	−0.119	0.102	−1.17
Nest type			
boulder	0		
surface	−0.012	0.171	−0.07
artificial	−0.055	0.191	−0.29
bush	−0.124	0.183	−0.68
building	0.379	0.215	1.76

been studied extensively (Table 6 and references therein). Clutch size estimates from Namibian localities agreed with those from Robben Island (Crawford *et al.* 1999) and were marginally higher than those from The Boulders (Murison 1998, Crawford *et al.* 2000) and Dassen Island (Siegfried & Crawford 1978). The incidence of African Penguins fledging two chicks from one clutch was high in Namibia; between 43.3% and 64.1% of successful attempts produced two fledglings, resulting in 1.43–1.64 fledglings produced per successful attempt. This figure was similar to that obtained at Marcus Island in South Africa's Western Cape region (57.7%, 1.58 fledglings; La Cock *et al.* 1987) but higher than that at St Croix Island in South Africa's Eastern Cape region (12.2%, 1.12 fledglings; Randall 1983).

Boersma (1977) proposed that Galapagos Penguins *S. mendiculus* have an extended breeding season and frequently replace lost clutches as a strategy to overcome limited and unpredictable food supplies. Similarly, Humboldt Penguins *S. humboldti,* which live in a more productive, but unpredictable environment show a high incidence of double brooding, i.e. laying a second clutch after a successful breeding attempt (Paredes *et al.* 2002). The strategy of having as many clutches and raising as many chicks as possible during favourable conditions most likely also apply to African Penguins in Namibia, which breed in the highly variable northern Benguela upwelling system. African Penguins may lay replacement clutches in the event of breeding failure and are able to lay second clutches after chicks are fledged successfully in the same breeding season (Randall 1983, La Cock & Cooper 1988). At Halifax Island, for example, penguin S06218 moulted during March 2002 and was noted incubating eggs in June 2002. Two healthy chicks fledged in September 2002. The same penguin was seen incubating eggs again in October 2002 and two more healthy chicks fledged in February 2003. The bird subsequently moulted during March 2003. Because nests rather than individual pairs were monitored, the incidence of second clutches and their success were not measured for breeding localities in Namibia, and the number of chicks fledged per pair per year

could therefore not be determined. At Marcus Island, the number of fledglings produced per breeding pair increased from an average of 0.49 to 0.63 per year when replacement and second clutches were taken into account (La Cock & Cooper 1988). It is vital that the incidence of this is ascertained for the Namibian population too.

In Magellanic Penguins *S. magellanicus*, more than three quarters of nest failures were found to occur during incubation and early chick rearing (Boersma *et al.* 1990, Boersma & Stokes 1995). In this study, 57.8% of monitored nests survived incubation. In addition, 21.3% of all chicks died within two weeks after hatching; only 5.8% of all chicks died at the age of 40 days or older. Common causes of breeding failure in African Penguins include egg infertility, human disturbance, accidental crushing by a parent or during a burrow collapse, starvation, heat stress, nest flooding, drowning, gull predation, disappearance of a mate, parents moulting while breeding, infestation by endoparasites, and eggs or small chicks rolling out of the nest and not being retrieved (Siegfried 1977, Randall 1983, Duffy *et al.* 1984, Wilson 1985, Crawford *et al.* 1986, Randall *et al.* 1986, La Cock 1988, Seddon & van Heezik 1991, Crawford & Dyer 1995, pers. obs). Nest contents tend to be susceptible to different causes of mortality at different stages of the nesting cycle (Randall 1983, Seddon & van Heezik 1991, Renner & Davis 2001). In this study, the contents of nests frequently disappeared in between visits. In such cases it was not possible to ascertain whether nest contents had been predated by Kelp Gulls or whether they had been scavenged subsequent to abandonment or death. Causes of mortality could, therefore, not be adequately quantified. However, mortality of eggs and small chicks appeared to be mostly due to desertion, predation, exposure or drowning; that of large chicks appeared to be mainly due to starvation or heat stress.

Factors affecting nest success

Many studies have focused on spatial and temporal patterns of breeding success in seabirds. Penguin breeding success has been shown to differ between localities (Fortescue 1999, Crawford *et al.* 2000, Yorio *et al.* 2001), between years (Boersma *et al.* 1990, Dann & Cullen 1990, Frere *et al.* 1998, Crawford *et al.* 2000) and with the timing of breeding (Randall 1983, Wilson 1985, Chiaradia & Kerry 1999, Renner & Davis 2001). Success may also differ between habitats (Frost *et al.* 1976, Murison 1998, Stokes & Boersma 1991, 1998,

Paredes & Zavalaga 2001, Kemper *et al.* submitted 1), between nests positioned centrally or peripherally in colonies (Oelke 1975, Gochfeld 1980), with colony size (Oelke 1975, van Heezik *et al.* 1995) and with nesting density (Siegfried 1977, Scolaro 1990, Stokes & Boersma 2000).

In this study the egg-laying date was the most important determinant of nest success, defined as a nest producing at least one fledgling. At Mercury, Ichaboe and Halifax Islands, the probability of success was highest for nests initiated at the end of October. The probability of success at Possession Island was highest about one month earlier. At Mercury, Ichaboe and Possession Islands, peak breeding activities roughly coincided with the period of maximum probability of nest success. However, at Halifax Island, the timing of the primary incubation peak (July) corresponded to the time when the modelled nest survival probability was less than half the maximum. Poorly-timed breeding is probably the key factor responsible for the poor breeding success at Halifax Island compared to the other three localities.

For most of the year, cool coastal conditions moderate air temperature, and even during mid-summer, daily temperatures seldom exceed 25°C (Pallett 1995). However, between May and October, high pressure systems over the interior of southern Africa lead to occasional spells of strong and hot desert winds. These "east wind" conditions may last from one to several days and can be accompanied by temperatures reaching 40°C, resulting in large-scale abandonment of nests (Kemper *et al.* submitted 1). Nests initiated after October are less likely to be subject to east wind conditions.

At all four islands, the optimum time for egg-laying roughly coincided with the initiation of breeding activities by Kelp Gulls. Kelp Gull predation has not been quantified in this study, but most predation is of eggs, young (<0.5 kg) and unhealthy chicks (pers. obs). Predation of eggs and small chicks by Kelp Gulls generally occurs when nests are not properly guarded by a parent. This often happens when Kelp Gulls create a disturbance, causing a penguin to lift off its nest or in extreme cases, flee, leaving nest contents exposed. Disturbance by Kelp Gulls tends to increase as their chicks hatch and become mobile in early to mid-December (pers. obs) and is high until their chicks are able to fly (mid- to late January). Such disturbance is usually caused by fighting gulls protecting their young through noisy aerial attacks; this can be greatly exacerbated by human presence. Penguin eggs laid at the end of October would hatch exactly at the time when the threat of predation by Kelp Gulls is great-

Table 6: Estimates of breeding success, in terms of the number of chicks fledged, for African Penguins at localities in South Africa

Breeding locality	Position	Nest type	Number of fledglings produced per:			Reference
			nesting attempt	pair	pair/year	
Marcus and Jutten	33°03'S 17°58'E, 33°05'S 17°57'E		0.15–0.55			Adams *et al.* 1992
Marcus					0.49–0.63	La Cock *et al.* 1987, La Cock & Cooper 1988
Dassen	33°25'S 18°05'E	Burrows	0.67			Frost *et al.* 1976
		Under rocks	0.51			Frost *et al.* 1976
		Exposed	0.37			Frost *et al.* 1976
				0.58–0.62		Wolfaardt & Nel 2003
			c. 0.8			Whittington *et al.* 2000
Robben	33°48'S 18°22'E		0.4–0.6			Crawford *et al.* 1995
					0.32–0.65	Crawford *et al.* 1999, 2000
					0.8	Whittington *et al.* 2000
					0.46–0.73	Crawford *et al.* 2006b
The Boulders	34°11'S 18°27'E			0.61		Crawford *et al.* 2000
			0.65			Whittington *et al.* 2000
Stony Point	34°22'S 18°54'E		0.11–0.39			Whittington *et al.* 1996
St Croix	33°47'S 25°46'E				0.38	Randall 1983

est. Kelp Gulls occur in relatively small numbers at Mercury and Ichaboe Islands and the threat of gull predation at these localities is modest. At Halifax Island, large numbers of Kelp Gulls pose a significant predation threat. Breeding during July, at a time of year not considered optimal in other respects, but when predation risk is minimal, may therefore be beneficial at this particular locality. At Possession Island, optimal nest initiation is a month earlier than at Mercury and Ichaboe islands, and by mid-December most penguin chicks are probably too large to be predated.

The timing of egg-laying may be particularly important for strictly seasonal penguins, such as Magellanic Penguins which do not produce replacement clutches or second clutches (Boersma et al. 1990). However, even for species such as African Penguins, which have an extended breeding season and can produce several clutches per year, there appears to be an optimum period for egg-laying, albeit that the timing thereof is less restricted or synchronous than for more seasonal species. Whereas the seemingly poorly-timed incubation peak in July at Halifax Island may decrease the probability of being successful during that period, this strategy may ultimately increase the likelihood of individuals maximizing their annual breeding success through increasing their chances of raising a second clutch later in the year. Inter-annual differences in breeding success probability were more pronounced than inter-island differences. This shows that inter-annual environmental variability acts at a regional rather than at a local scale.

Further key variables of nesting success were vulnerability to flooding, the location of the nest within a colony and nest type. Although flooding occurred infrequently, flooded nests rarely succeeded, unless flooding took place when the chick was already at the feather-shedding stage. Breeding success in centrally-located nests was found to be higher than in peripheral nests. Central nests tend to be less exposed to disturbance caused by gulls or humans, and gulls were more likely to steal unguarded eggs at the edge of a colony than in the centre (pers. obs). Breeding success was marginally higher in isolated nests than in colony edge nests. Penguins nesting colonially tend to be more unsettled than isolated breeders, constantly defending their nest sites (and their nesting material) from neighbouring breeders and penguins walking past their nests. Kelp Gulls appear to be more attracted to colonies than to isolated nests, perhaps because colonially-breeding penguins tend to inadvertently expose their nest contents more often than solitary breeders (pers. obs). Nest type was another important determinant of breeding success at African Penguin breeding localities in Namibia, with protected nests faring better than exposed nests.

Breeding success in long-lived seabirds has been found to increase with the age of partners and the length of time they have bred together (Pugesek & Diem 1983, Bradley et al. 1995, Daunt et al. 2001), particularly during years with poor breeding conditions (Murphy et al. 1992). The relationship between parental quality, age or experience and nest choice was not investigated in this study, and it is possible that differences in both breeding success and nest site characteristics were influenced by pair quality.

Although breeding success at the Namibian breeding localities compared favourably with estimates obtained from South African localities, these figures appear to be insufficient to keep the African Penguin population in Namibia stable. Nest sites providing shade and protection from predators are in short supply at most breeding localities in Namibia. The arid, windy conditions prevailing at most localities make the planting of additional bushes infeasible and the deployment of artificial burrows at these localities to further boost breeding success should be considered. At localities such as Ichaboe Island, drainage channels should be maintained to encourage water run-off during rainstorms and minimize flooding of nests. In addition, measures to deter Kelp Gulls from nesting at breeding localities, particularly at Halifax and Possession Islands, should be considered.

References

Adams, N.J., Seddon, P.J. & van Heezik, Y.M. 1992. Monitoring of seabirds in the Benguela Upwelling System: can seabirds be used as indicators and predictors of change in the marine environment? *S. Afr. J. Mar. Sci.* 12: 959–974.

Boersma, P.D. 1977. An ecological and behavioural study of the Galápagos Penguin. *Living Bird* 15: 43–93.

Boersma, P.D. & Stokes, D.L. 1995. Mortality patterns, hatching asynchrony, and size asymmetry in Magellanic Penguin *Spheniscus magellanicus* chicks. In Dann, P., Norman, I. & Reilly, P. (eds) *The penguins: ecology and management*: 3–25. Chipping Norton, Australia: Surrey Beatty & Sons.

Boersma, P.D., Stokes, D.L. & Yorio, P.M. 1990. Reproductive variability and historical change of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. In Davis, L.S. & Darby, J.T. (eds) *Penguin Biology*: 15–43. San Diego, CA: Academic Press.

Bradley, J.S., Wooller, R.D., Skira, I.J. & Serventy, D.L. 1990. The influence of mate retention and divorce upon reproductive success in short-tailed shearwater *Puffinus tenuirostris*. *J. Anim. Ecol.* 59: 487–496.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information–theoretic approach*. 2nd edn. New York: Springer.

Chiaradia, A.F. & Kerry, K.R. 1999. Daily nest attendance and breeding performance in the Little Penguin *Eudyptula minor* at Phillip Island, Australia. *Mar. Ornithol.* 27: 13–20.

Cooper, J. 1980. Breeding biology of the Jackass Penguin with special reference to its conservation. In Johnson, D.N. (ed.) *Proceedings of the 4th Pan-African Ornithological Congress*: 227–231. Johannesburg, South Africa: Southern African Ornithological Society.

Cordes, I., Crawford, R.J.M., Williams, A.J. & Dyer, B.M. 1999. Decrease of African Penguins at the Possession Island group, 1956–1995: contrasting trends for colonial and solitary breeders. *Mar. Ornithol.* 27: 129–138.

Crawford, R.J.M. & Dyer, B.M. 1995. Responses by four seabird species to a fluctuating availability of Cape Anchovy *Engraulis capensis* off South Africa. *Ibis* 137: 329–339.

Crawford, R.J.M., Cruickshank, R.A., Shelton, P.A. & Kruger, I. 1985. Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system. *S. Afr. J. Mar. Sci.* 3: 215–228.

Crawford, R.J.M., Williams, A.J. & Crawford, P.B. 1986. A note on mortality of seabirds off western southern Africa, October 1985 – February 1986. *S. Afr. J. Mar. Sci.* 4: 119–123.

Crawford, R.J.M., Ryan, P.G. & Williams, A.J. 1991. Seabird consumption and production in the Benguela and Western Agulhas Ecosystems. *S. Afr. J. Mar. Sci.* 11: 357–375.

Crawford, R.J.M., Shannon, L.J. & Whittington, P.A. 1999. Population dynamics of the African Penguin *Spheniscus demersus* at Robben Island, South Africa. *Mar. Ornithol.* 27: 139–147.

Crawford, R.J.M., Shannon, L.J., Whittington, P.A. & Murison, G. 2000. Factors influencing growth of the African Penguin colony at Boulders, South Africa, 1985–1999. *S. Afr. J. Mar. Sci.* 22: 111–119.

Crawford, R.J.M., Hemming, M., Kemper, J., Klages, N.T.W., Randall, R.M., Underhill, L.G., Venter, A.D., Ward, V.L. &

Wolfaardt, A.C. 2006a. Molt of the African Penguin, *Spheniscus demersus*, in relation to its breeding season and food availability. *Acta Zoologica Sinica* 52: S444–S447.

Crawford, R.J.M., Barham, P.J., Underhill, L.G., Shannon, L.J., Coetzee, J.C., Dyer, B.M., Leshoro, T.M. & Upfold, L. 2006b. The influence of food availability on breeding success of African Penguins *Spheniscus demersus* at Robben Island, South Africa. *Biol. Conserv.* 132: 119–125.

Cruickshank, R.A., Hampton, I. & Armstrong, M.J. 1990. The origin and movements of juvenile Anchovy in the Orange River region as deduced from acoustic surveys. *S. Afr. J. Mar. Sci.* 9: 101–114.

Dann, P. & Cullen, J.M. 1990. Survival, patterns of reproduction, and lifetime reproductive output in Little Blue Penguins (*Eudyptula minor*) on Phillip Island, Victoria, Australia. In Davis, L.S. & Darby, J.T. (eds) *Penguin Biology*: 63–84. San Diego, CA: Academic Press.

Daunt, F., Monaghan, P., Wanless, S., Harris, M.P. & Griffiths, R. 2001. Sons and daughters: age-specific differences in parental rearing capacities. *Funct. Ecol.* 15: 211–216.

Dobson, A.J. 2002. *An introduction to generalized linear models*. 2nd edn. Boca Raton: Chapman & Hall/CRC.

Duffy, D.C. & La Cock, G.D. 1985. Partitioning of nesting space among seabirds of the Benguela upwelling region. *Ostrich* 56: 186–201.

Duffy, D.C., Berruti, A., Randall, R.M. & Cooper, J. 1984. Effects of the 1982–83 warm water event on the breeding of South African seabirds. *S. Afr. J. Sci.* 80: 65–69.

Fortescue, M. 1999. Temporal and spatial variation in breeding success of the Little Penguin *Eudyptula minor* on the east coast of Australia. *Mar. Ornithol.* 27: 21–28.

Frere, E., Gandini, P. & Boersma, P.D. 1998. The breeding ecology of Magellanic Penguins at Cabo Vírgenes, Argentina: what factors determine reproductive success? *Colon. Waterbirds* 21: 205–210.

Frost, P.G.H., Siegfried, W.R. & Cooper, J. 1976. Conservation of the Jackass Penguin (*Spheniscus demersus* (L.)). *Biol. Conserv.* 9: 79–99.

GenStat Committee. 2005. *The Guide to GenStat® Release 8 – Part 2: Statistics*. Hemel Hempstead: VSN International.

Gochfeld, M. 1980. Timing of breeding and chick mortality in central and peripheral nests of Magellanic Penguins. *Auk* 97: 191–193.

Hampton, I. 2003. Harvesting the sea. In Molloy, F. & Reinikainen, T. (eds) *Namibia's marine environment*: 31–69. Windhoek, Namibia: Directorate of Environmental Affairs of the Ministry of Environment and Tourism.

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V., Brown & C.J. (eds) 1997. *The atlas of southern African birds. Vol. 1: Non-passerines*. Johannesburg, South Africa: BirdLife South Africa.

Heath, R.G.M. & Randall, R.M. 1985. Growth of Jackass Penguin chicks (*Spheniscus demersus*) hand reared on different diets. *J. Zool., Lond (A)* 205: 91–105.

Kemper, J. 2006. Heading towards extinction? Demography of the African Penguin in Namibia. PhD thesis. University of Cape Town, South Africa.

Kemper, J., Roux, J-P., Bartlett, P.A., Chesselet, Y.J., James, J.A.C., Jones, R., Wepener, S. & Molloy F.J. 2001. Recent population trends of African Penguins *Spheniscus demersus* in Namibia. *S. Afr. J. Mar. Sci.* 23:429–434.

Kemper, J., Roux, J-P. & Underhill, L.G. Submitted 1. Artificial burrows for African Penguins on Halifax Island, Namibia: do they improve breeding success? *Biol. Conserv.*

Kemper, J., Roux, J-P., Bartlett, P.A., Chesselet, Y.J., Delport, J-A., James, J.A.C., Jones, R., Underhill, L.G., Uhongora, N-N. & Wepener, S. Submitted 2. The African Penguin *Spheniscus demersus* in Namibia: population estimates, trends, adult survival and age structure from molt and nest counts. *Auk*.

La Cock, G.D. 1988. Effect of substrate and ambient temperature on burrowing African Penguins. *Wilson Bull.* 100: 131–132.

La Cock, G.D. & Cooper, J. 1988. The breeding frequency of Jackass Penguins on the West Coast of South Africa. *J. Field Orn.* 59: 155–156.

La Cock, G.D., Duffy, D.C. & Cooper, J. 1987. Population dynamics of the African Penguin *Spheniscus demersus* at Marcus Island in the Benguela upwelling ecosystem: 1979–85. *Biol.*

Conserv. 40: 117–126.

Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255–261.

Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87: 456–466.

Murison, G. 1998. Nest site characteristics and breeding success in the African Penguin, *Spheniscus demersus* at Boulders Coastal Park, Simon's Town. BSc Honours thesis, University of Cape Town, South Africa.

Murphy, E.C., Hoover-Miller, A.A., Day, R.H. and Oakley, K.L. 1992. Intra-colony variability during periods of poor reproductive performance at a Glaucous-winged Gull colony. *Condor* 94: 598–607.

Oelke, H. 1975. Breeding behaviour and success in a colony of Adélie Penguins *Pygoscelis adeliae* at Cape Crozier, Antarctica. In Stonehouse, B. (ed.) *The biology of penguins*: 363–395. London: MacMillan.

Pallett, J. (ed.) 1995. *The Sperrgebiet: Namibia's least known wilderness*. Windhoek, Namibia: DRFN and NAMDEB.

Paredes, R. & Zavalaga, C.B. 2001. Nesting sites and nest types as important factors for the conservation of Humboldt penguins (*Spheniscus humboldti*). *Biol. Conserv.* **100**: 199–205.

Paredes, R., Zavalaga, C.B. & Boness, D.J. 2002. Patterns of egg laying and breeding success in Humboldt Penguins (*Spheniscus humboldti*) at Punta San Juan, Peru. *Auk* 119: 244–250.

Pugesek, B.H. & Diem, K.L. 1983. A multivariate study of the relationship of parental age to reproductive success in California Gulls. *Ecology* 64: 829–839.

Randall, R.M. 1983. Biology of the Jackass Penguin *Spheniscus demersus* (L.) at St Croix Island, South Africa. PhD thesis. University of Port Elizabeth, South Africa.

Randall, R.M. & Randall, B.M. 1981. The annual cycle of the Jackass Penguin *Spheniscus demersus* at St Croix Island, South Africa. In Cooper, J. (ed.) *Proceedings of the symposium on birds of the sea and shore*: 427–450. Cape Town, South Africa: African Seabird Group.

Randall, R.M., Randall, B.M. & Erasmus, T. 1986. Rain-related breeding failures in Jackass Penguins. *Gerfaut* 76: 281–288.

Renner, M. & Davis, L.S. 2001. Survival analysis of Little Penguin *Eudyptula minor* chicks on Motuara Island, New Zealand. *Ibis* 143: 369–379.

Scolaro, J.A. 1990. Effects of nest density on breeding success in a colony of Magellanic Penguins (*Spheniscus magellanicus*). *Colon. Waterbirds* 13: 41–49.

Seddon, P.J. & van Heezik, Y.M. 1991. Effects of hatching order, sibling asymmetries, and nest site on survival analysis of Jackass Penguin chicks. *Auk* 108: 548–555.

Seddon, P.J. & van Heezik, Y.M. 1993. Behaviour of the Jackass Penguin chick. *Ostrich* 64: 8–12.

Siegfried, W.R. 1977. Packing of Jackass Penguin nests. *S. Afr. J. Sci.* 73: 186–187.

Siegfried, W.R. & Crawford, R.J.M. 1978. Jackass Penguins, eggs and guano: diminishing resources at Dassen Island. *S. Afr. J. Sci.* 74: 389–390.

Stokes, D.L. & Boersma, P.D. 1991. Effects of substrate on the distribution of Magellanic Penguin (*Spheniscus magellanicus*) burrows. *Auk* 108: 923–933.

Stokes, D.L. & Boersma, P.D. 1998. Nest-site characteristics and reproductive success in Magellanic Penguins (*Spheniscus magellanicus*). *Auk* 115: 34–49.

Stokes, D.L. & Boersma, P.D. 2000. Nesting density and reproductive success in a colonial seabird, the Magellanic Penguin. *Ecology* 81: 2878–2891.

Underhill, L.G. submitted. The Mayfield method for estimating nest success: flaws and extensions. *Auk*.

Underhill, L.G. & Parsons, N.J. submitted. Activity patterns of African Black Oystercatchers *Haematopus moquini* on sandy and rocky shores at Koeberg Nuclear Power Station. *Ibis*.

Underhill, L.G., Prys-Jones, R.P., Harrison, J.A. & Martinez, P. 1992. Seasonal patterns of occurrence of Palaearctic migrants in southern Africa using atlas data. *Ibis* 134 Supplement 1: 99–108.

van Heezik, Y.M., Seddon, P.J. & Cooper, J. 1995. Effects of inter-annual and inter-colony variability on counts of King Penguin colonies on Marion Island. In Dann, P., Norman, I. & Reilly, P. (eds) *The penguins: ecology and management*: 96–110. Chipping Norton, Australia: Surrey Beatty & Sons.

Whittington, P.A., Hofmeyr, J.H. & Cooper, J. 1996. Establishment,

growth and conservation of a mainland colony of Jackass Penguins *Spheniscus demersus* at Stony Point, Betty's Bay, South Africa. *Ostrich* 67: 144–150.

Whittington, P., Crawford, R.J.M., Huyser, O., Oschadleus, D., Randall, R., Ryan, P., Shannon, L.J., Wolfaardt, A., Cooper, J., Lacy, R. & Ellis, S. (eds). 2000. *African Penguin population and habitat viability assessment, final report*. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, USA.

Williams, A.J. & Cooper, J. 1984. Aspects of the breeding biology of the Jackass Penguin *Spheniscus demersus*. In Ledger, J.A. (ed.) *Proceedings of the 5th Pan-African Ornithological Congress*: 841–853. Johannesburg, South Africa: Southern African Ornithological Society.

Wilson, R.P. 1985. Seasonality in diet and breeding success of the Jackass Penguin *Spheniscus demersus*. *J. Orn.* 126: 53–62.

Wolfaardt, A.C. & Nel, D.C. 2003. Breeding productivity and annual cycle of rehabilitated African Penguins following oiling. In Nel, D.C. & Whittington, P.A. (eds) *Rehabilitation of oiled African Penguins: a conservation success story*: 18–24. Cape Town, South Africa*:* BirdLife South Africa and the Avian Demography Unit.

Yorio, P., García Borboroglu, P., Potti, J. & Moreno, J. 2001. Breeding biology of Magellanic Penguins *Spheniscus magellanicus* at Golfo San Jorge, Patagonia, Argentina. *Mar. Ornithol.* 29: 75–79.

Zucchini, W. & Adamson, P.T. 1984. *The occurrence and severity of droughts in South Africa*. Water Research Commission Report 91/1/84. Water Research Commission, Pretoria, South Africa.