Chapter 8

The African Penguin *Spheniscus demersus*: population estimates, trends, adult survival and age structure from molt and nest counts

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We used serial counts of molting adult individual African Penguins *Spheniscus demersus* and counts of active nests at peak breeding at the four main breeding localities in Namibia to assess population estimates and trends of this discrete, regional population of African Penguins. These localities accounted for 96% of the Namibian penguin population between the early to mid 1990s and 2004. Between 1996 and 2004, the number of individuals in adult plumage decreased by 2.4% per year; numbers of peak active nests declined by 2.5% per year between 1990 and 2004. Since 1956, when Namibia supported c. 100,000 African Penguins, a third of the global population at the time, the regional population declined by 75% to fewer than 25,000 adult individuals in 2004, which contributed 12.8% to the global population in 2001. The rapid decline was mainly due to a population crash at Possession Island. The mean observed annual survival rate of penguins in adult plumage between 1997 and 2004 was 0.83. We constructed an age structure based on observed annual survival rates. From this, we determined that an average of 62.1% of all individuals in adult plumage in Namibia were five years or older and constituted the potential breeding population. Counts of active nests at peak breeding provided a poor proxy for breeding population estimates. Those based on serial molt counts appeared to be more accurate, provided the exact duration of the feather-shedding phase of molt is ascertained.

Keywords: seabird, census, demography, survival, age structure

The breeding range of African Penguins *Spheniscus demersus* can be divided into three breeding centers, consisting of Namibia and the Western and Eastern Cape regions in South Africa (Whittington et al. 2005a). At the start of the 21st century, African Penguins in Namibia probably bred on 14 islands and 2 mainland sites (Kemper 2006); by 2004, breeding had ceased on 6 islands. Banding studies have shown that there is some movement, particularly of young birds, between localities within Namibia (Whittington et al. 2005a, Kemper and Roux 2005). However, emigration of young birds from Namibia to South Africa is uncommon (Whittington et al. 2005b), and permanent immigration from South Africa to Namibia is rare (Whittington et al. 2005b). Namibia can therefore be considered as supporting a discrete regional population of African Penguins.

Early reports speak of hundreds of thousands of penguins breeding at a number of islands in Namibia (e.g. Eden 1846, Morrell 1844 in Shelton et al. 1984, Shaughnessy 1984, Kinahan 1990, 1992). In the 1950s, when the first thorough surveys of penguin populations were done, Namibia supported c. 100,000 adult penguins (Rand 1963, Crawford et al. 1995a). This is the earliest available population estimate, and probably already represented a major decline from the middle of the 19th century. During the second half of the 20th century, the Namibian population declined by c.72% (Kemper et al. 2001) and by the early 1990s only Mercury (25°43'S 14°50'E) and Ichaboe (26°17'S 14°56'E) Islands supported more than 1,000 breeding pairs (Crawford et al. 1995a).

The wind-driven Lüderitz upwelling cell, which divides the northern and southern Benguela regions (van der Lingen et al. 2006), constitutes an oceanographic barrier to most pelagic fish stocks (Boyer and Hampton 2001). This, together with the effects of the considerable variability that characterizes the northern Benguela marine ecosystem (Roux 2003) on prey distribution and abundance, and the depleted status of the main commercial pelagic fish stocks in the northern Benguela, are thought to be the major determinants of the

observed differences in penguin population trends between Namibia and South Africa (Kemper et al. 2001).

African Penguins in Namibia breed throughout the year (Kemper 2006). After fledging, they spend most of their time at sea until they return to land to molt, aged 12 to 23 months (Kemper and Roux 2005), into adult plumage for the first time. After this juvenile molt, they are indistinguishable from adults but are not necessarily sexually mature. Age at first breeding averages five years and ranges between two and eight years (Crawford et al. 1999, Whittington et al. 2005c). Molt in the adult African Penguin takes place annually (Randall and Randall 1981, Kemper 2006). Serial molt counts can therefore be used to estimate the population size of birds in adult plumage each year (Randall et al. 1986, Crawford and Boonstra 1994, Crawford et al. 1999, 2000, Kemper et al. 2001). However, because a given population of adult African Penguins will include non-breeders, peak counts of active nests have been used extensively to estimate the size of the breeding population (Shelton et al. 1984, Crawford et al. 1990, 1995a, 1995b, 2001, Crawford and Boonstra 1994, Kemper et al. 2001).

Here we present estimates of population size and trends of penguins in adult plumage using molt counts as well as of breeding populations from counts of active nests at peak breeding, at the four most important breeding localities in Namibia for the period spanning the early to mid 1990s to 2004. Using population estimates and annual observed adult survival rates, we develop an age structure for the Namibian African Penguin population.

Methods

The four breeding localities (Mercury, Ichaboe, Halifax (26°37'S 15°04'E) and Possession (27°01'S 15°12'E) Islands) for which serial two-weekly molt counts and monthly active nest counts are available, account for c. 96% of Namibia's penguin population (Crawford et al. 1995a, Kemper et al. 2001). Other penguin breeding localities in Namibia are difficult to access, and were only visited and surveyed opportunistically, so that detailed studies are not feasible. These localities are not included in the analyses of trends. Annual estimates of numbers of penguins in adult plumage at each breeding locality were calculated from molt counts (Randall et al. 1986). Daily estimates of molting birds were obtained by interpolating linearly between actual counts (Underhill and Crawford 1999). The daily estimates for the period September to August were summed annually, because the fewest birds molt between July and September (Kemper 2006). This total was divided by 12.7, the average duration of the feather-shedding phase of molt previously calculated for 45 individuals (Randall 1983), to estimate the number of penguins which molted (Underhill and Crawford 1999).

Counts of active nests (i.e. those containing eggs or chicks) were conducted monthly at Mercury (since 1994), Ichaboe (since 1992) and Halifax Islands (since 1996) and every two weeks at Possession Island (since 1996). Counts between 1990 and 1993 at Mercury Island, in 1990 at Ichaboe Island and between 1990 and 1995 at Halifax and Possession Islands, were single annual counts, conducted as close as possible to the time of peak breeding activity. Data for 1991 are lacking for all four islands. Where multiple counts were available per year, the largest active nest count between May and April of the next year was used as an indication of the breeding population size at each island. Estimates obtained from peak active nests assume that breeding synchrony at a particular locality is high and that it does not vary over time, producing comparable annual estimates and reliable trends.

Exponential curves were fitted by least-squares regression to estimate population trends based on molt and nest counts at each of the four islands, as well as for all islands combined. The observed exponential rate of population change was expressed as a percentage, $\bar{r}$, following the notation of Caughley (1980). Only statistically significant trends are reported.

Additional counts of active nests (Rand 1963, Shelton et al. 1984, Crawford et al. 1990, 1995a) were used to calculate long-term trends for the Namibian penguin population. Counts from 1956 and 1967 were based on aerial surveys, while later counts were from ground surveys and may include extrapolations from partial nest counts and counts of active nest sites, i.e. nests which are empty but have an adult defending it or contain evidence of nesting material. Methods differed between localities and were done at different times of the year. Population trends based on breeding population estimates for 1956–1990 were calculated in addition to 1956–2004 trends because of differences in census methods after 1990.

The number of juvenile penguins molting into adult plumage provide an estimate of the recruitment of penguins into the adult population each year. The number of juvenile individuals molting into adult plumage each year, estimated from molt counts in the same way as the number of individuals in adult plumage, were taken from Kemper (2006) and Roux et al. (submitted). The annual survival rate of penguins in adult plumage between successive years was estimated as the ratio of the number of adult penguins in one year to the sum of adult and juvenile penguins of the previous year. Using records of banded individuals for which fledging and juvenile molt dates were known, Kemper and Roux (2005) showed that the time of the year during which a penguin fledged dictated its age at molt into adult plumage. Following this, between 93.8% and 96.6% of recruits were found to have fledged during the year prior to the year they molted in, with the remaining recruits having fledged during the year preceding that one (Kemper 2006). An age structure of the Namibian adult penguin population was built using estimates of the two age classes, recruits and penguins in adult plumage, assuming that the observed annual adult survival rates apply to all age classes in adult plumage

Results

Based on molt counts, the population of adult penguins at the four most important breeding localities in Namibia showed an exponential rate of decrease ($\bar{r}$) of 2.4% per year between 1996 and 2004, a decrease of c. 5,600 birds (Table 1, Fig. 1a). Mercury Island supported the largest number of penguins (Fig. 1b). The adult population increased sharply at Mercury Island between the early 1990s and 1996, but has subsequently declined at a rate of 3.7% per annum (Table 1). Ichaboe Island sustained the second-largest penguin population in Namibia (Fig. 1c). The population there remained relatively stable during the early 1990s; since 1995 it has decreased. Between 1995 and 2004, adult penguin numbers decreased by nearly 40%, at 3.7% per year (Table 1). The decrease was most notable between 1995 and 1997. The population at Halifax Island increased between 1996 and 2004 (Fig. 1d), at a rate of 8.9% per year (Table 1). In contrast, numbers of penguins on Possession Island steadily declined during the same period at a rate of 8.0% per year (Table 1, Fig. 1e).

Between 1990 and 2004, the total number of active nests at peak breeding at the four islands fluctuated between a maximum of 7,781 nests in 1993 and a minimum of 4,015 nests in 2004 (Fig. 2a). Since 1990, numbers of peak annual active nests decreased by 2.5% per year (Table 1). Trend slopes did not differ between total number of peak active

Table 1: Population trends of African Penguins at the four main breeding colonies in Namibia obtained from counts of molting birds and peak annual number of active nests. Observed rates of population change ($\bar{r}$), correlation coefficients (r) and probability values (P) are shown. Only significant trends are reported

Breeding locality	Adult population trend					Breeding population trend				
	Years	n	$\bar{r}$	r	P	Years	n	$\bar{r}$	r	P
Mercury	1996–2004	9	−0.037	−0.91	<0.001					
Ichaboe	1995–2004	10	−0.037	−0.78	<0.01					
Halifax	1996–2004	9	0.090	0.85	<0.01	1996–2004	9	0.051	0.75	<0.05
Possession	1996–2004	9	−0.080	−0.89	<0.01	1990–2004*	14	−0.049	−0.87	<0.001
Total	1996–2004	9	−0.023	−0.87	<0.01	1990–2004*	14	−0.025	−0.66	<0.05
Total since 1956**						1956–1990	7	−0.056	−0.87	<0.05
						1956–2004	20	−0.030	−0.74	<0.001

*no count for 1991
**includes all breeding localities in Namibia

nests and total number of individuals in adult plumage for the years 1996 to 2004. In 2004, the other breeding localities in Namibia supplied about 180 to 250 additional active nests; these contributed between 3.3% and 4.5% to the total population (Kemper 2006). Between 1956 and 1990, the number of peak active nests at the four main breeding localities decreased at an observed exponential rate of 5.6% per year; between 1956 and 2004, numbers declined at 3.0% per year (Table 1, Figs. 3a and 3b) However, trends calculated between 1956 and 2004 must be viewed with caution as few counts are available between 1956 and 1990. This biases the trend towards counts done after 1990.

At Mercury Island, numbers of active nests at peak breeding dropped by 42.1% between 1993 and 1994 (Fig. 2b). Numbers then increased between 1994 and 1999 at 7.5% per year (Table 1). Between 2002 and 2004, peak annual nest counts have dropped by 41.2%. At Ichaboe Island, numbers of active nests at peak breeding increased in the early 1990s, and declined after 1994 at 7.3% per year (Table 1, Fig. 2c). This trend was not significant. The number of active nests at peak breeding during 2004 was the lowest count between 1990 and 2004. Peak numbers of active nests at Halifax Island decreased until the mid-1990s but increased at 5.1% per year since 1996 (Table 1, Fig. 2d). At Possession Island, numbers decreased steadily between 1990 and 2004 at a rate of 4.9% per year (Table 1, Fig. 2e).

Trends of adult individuals and active nests appeared to be consistent for all four islands. There was no significant difference in trend slopes for the number of adult birds and active nests from 1995 to 2004 at Mercury Island. At Ichaboe Island, the observed annual rate of decline for adult birds was twice that of peak active nests between 1995 and 2004, but the difference in rates was not significant. At Halifax Island the adult population increased more rapidly than the numbers of active nests at peak breeding, although this trend was again not significant. However, at Possession Island the adult population decreased significantly more rapidly than the number of nests at peak breeding ($F = 5.01$, $n = 18$, $P = 0.04$) between 1996 and 2004.

There was a positive, significant relationship between estimates of adult birds and numbers of active nests at peak breeding at Ichaboe Island ($r = 0.83$, $n = 13$, $P < 0.001$) and at Possession Island ($r = 0.89$, $n = 9$, $P < 0.01$). Relationships were not significant at Mercury or Halifax Islands, nor were they for all four islands combined.
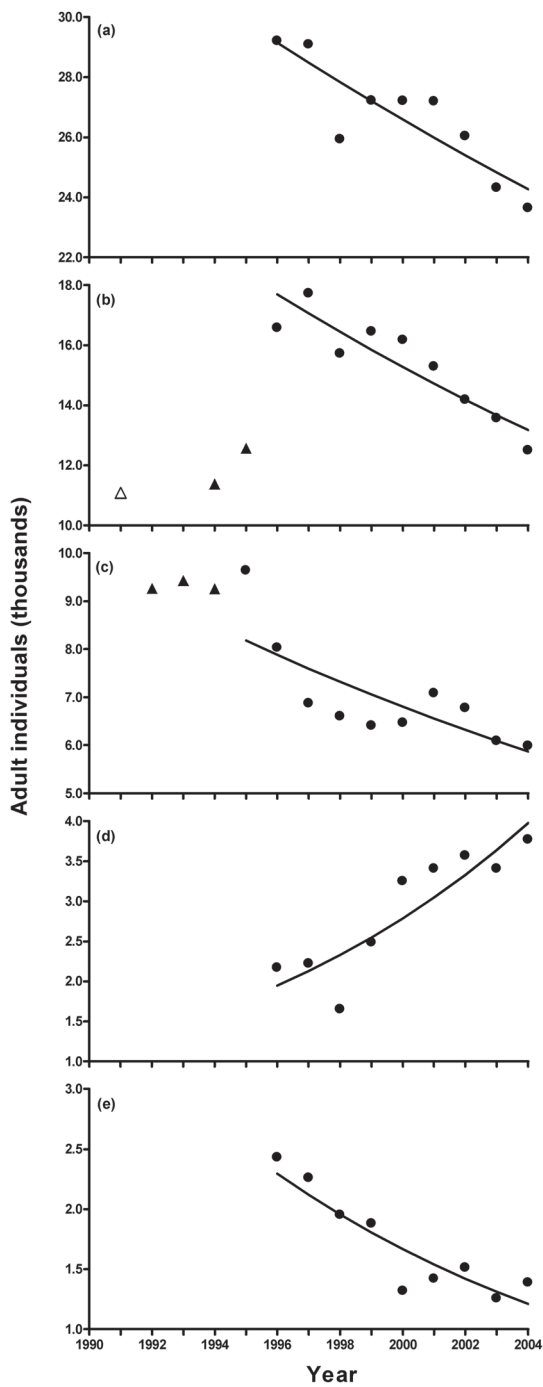
The ratio of the number of penguins in adult plumage to the number of active nests at peak breeding differed between islands and years (Fig. 4). Between 1996 and 2004, ratios ranged from 3.97 and 5.89, with a mean of 4.89 (SD = 0.62) and a median of 4.84 for all four islands combined. Mercury and Halifax Islands had consistently higher ratios (mean = 5.64 (0.79) and 5.91 (1.53) respectively) than Ichaboe (mean = 3.77 (1.11)) and Possession Islands (mean = 3.92 (0.53)). Ratios were particularly high for Halifax Island (9.10) in 2000 and for Ichaboe Island (6.93) in 2004 and especially low for Mercury Island (4.10) in 2002. At Possession Island the ratio decreased steadily with time.
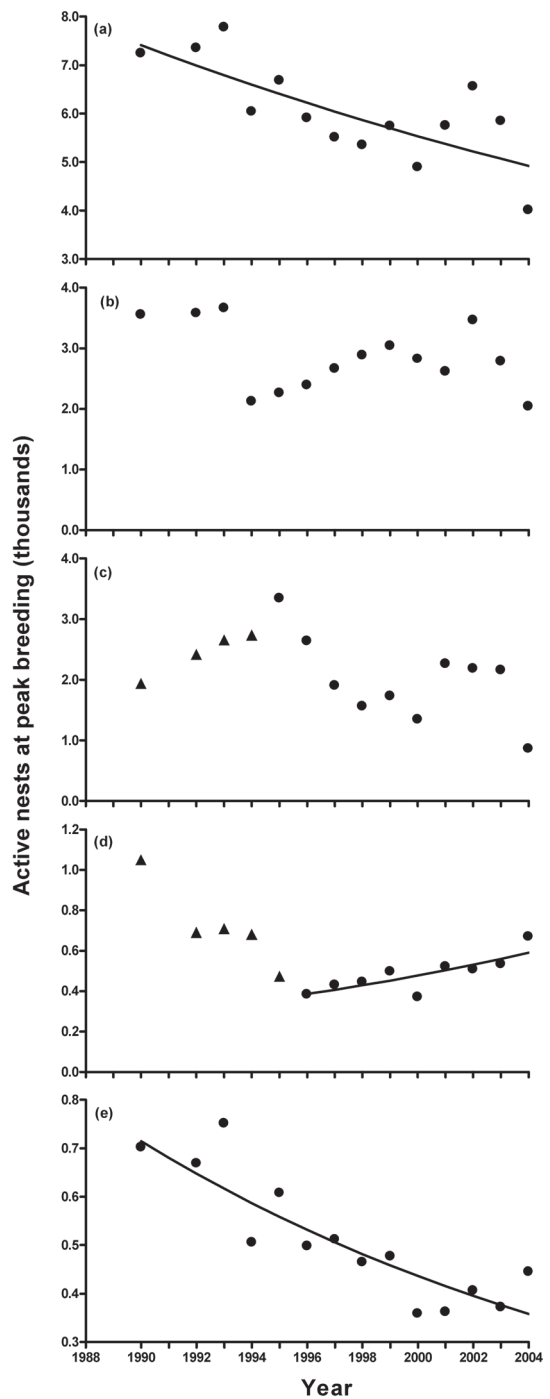
The observed annual survival rate of penguins in adult plumage between 1997 and 2004 ranged from 0.78 in 1998 to 0.89 in 1999, with a mean rate of 0.83 over eight years (SD = 0.04) (Fig. 5). From the age structure (Fig. 6) based on these survival rates, it is estimated that between 59.0% and 66.0% of all individuals in adult plumage were five years or older for the years 1999 to 2004, with a mean percentage of 62.1% (SD = 2.9%). These are considered to constitute the breeding population. Adult penguins between two and four years old were considered here to be sexually immature birds in adult plumage or "pre-breeders". Numbers of pre-breeders decreased by 24.4%, or 2,657 individuals, between 2001 and 2003. Numbers of penguins of breeding age also declined, particularly between 2002 and 2004, when nearly 1,600 birds (9.5%) were lost from the breeding population (Fig. 7). Between 1999 and 2004, estimates for the breeding population were positively related to peak active nest counts ($r = 0.94$, $n = 6$, $P < 0.01$) (Fig. 8). Annual peak active nest numbers consistently underestimated the number of breeding pairs (i.e. half the potential breeding population) by between 21.4% and 46.8%, and on average by 32.2% (SD = 9.1%). On average, the number of individuals aged five years or older was 3.0 times greater than the peak annual active nest count.
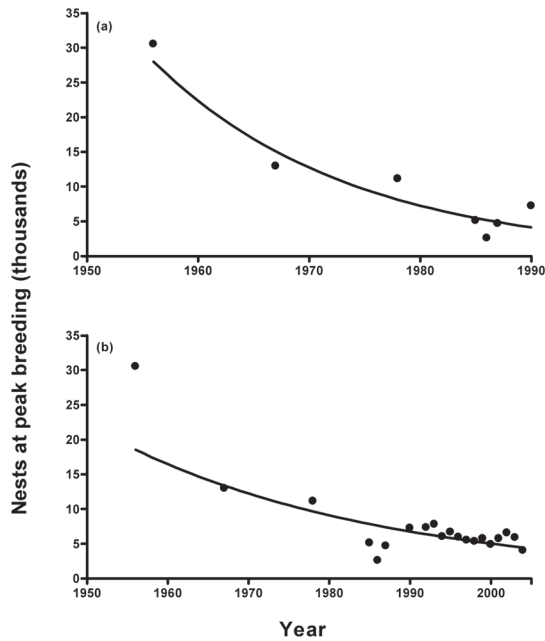
Discussion

It is evident from anecdotal information that the penguin population in Namibia declined sharply between the early descriptions made by whalers, sealers and guano collectors in the nineteenth century (Eden 1846, Shaughnessy 1984, Shelton et al. 1984, Kinahan 1990, 1992) and the commencement of quantitative records in the 1950s (Rand 1963). Census data prior to 1990 need to be interpreted with caution, because the variety of census methods used up to then may not be comparable with more recent, standardized counts and because few counts were made between 1956 and 1990. However, the overall trend during this period was overwhelmingly downwards. Since 1956, when nearly 100,000 adult penguins were estimated, contributing about one third of the global population (Crawford et al. 1995a), the Namibian population declined by 75% to fewer than 25,000 adult individuals estimated from molt counts in 2004. This

Figure 1: Numbers of African Penguins in adult plumage estimated from molt counts between 1991 and 2004 in Namibia at (a) the four main breeding localities combined, (b) Mercury Island, (c) Ichaboe Island, (d) Halifax Island, (e) Possession Island. Estimates represented by closed triangles were not included in the trend analysis. Open triangle: estimate calculated from 1 May 1991 to 30 April 1992
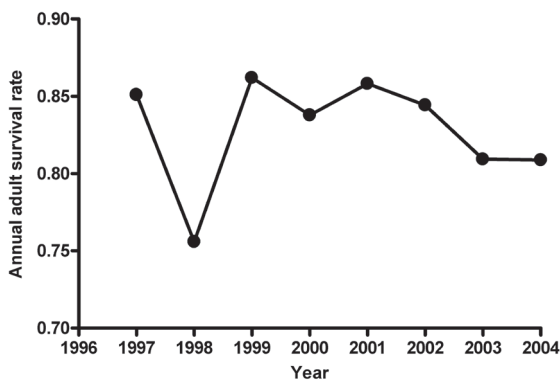
Figure 2: Annual peak counts of active nests of African Penguins between 1990 and 2004 at (a) the four breeding localities combined, (b) Mercury Island, (c) Ichaboe Island, (d) Halifax Island and (e) Possession Island. Estimates represented by closed triangles were not included in the trend analysis
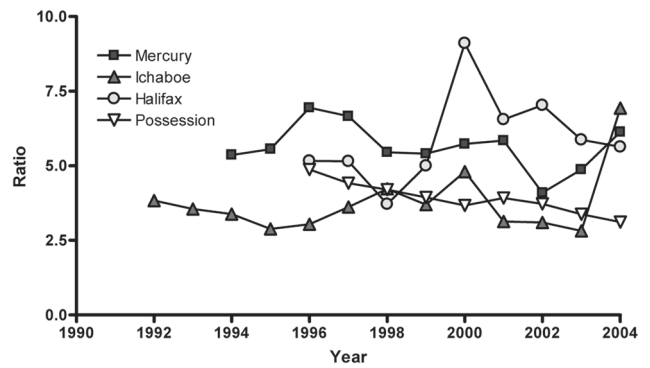
Figure 3: Annual peak counts of active nests of African Penguins in Namibia (a) 1956–1990, (b) 1956–2004

accounted for 12.8% in terms of the global population estimated in 2001 (du Toit et al. 2003, Kemper in press). The rapid decline was mainly due to a population crash at Possession Island. During the 1950s, Possession Island supported c. 46,000 adult individuals (Rand 1963), and was the largest colony in Namibia. Subsequently, the island lost nearly 97% of its penguins and in 2004 was the least important of the four main breeding localities in Namibia. Although the rate of decrease in Namibia slowed after 1990, penguin numbers continued to decline by between 2.3% and 2.5% per year. If current trends persist, the population is expected to halve within the next 30 years.

The small number of penguins at Mercury Island between 1991 and 1994 could be the consequence of disturbance caused by a seal chasing program implemented there between 1989 and 1993, after seals had displaced a number of seabirds, including penguins, between 1978 and 1989 (Crawford et al. 1989, 1994). This explanation does not, however, agree with the large number of active nests at Mercury Island during the early 1990s. It is likely, though, that numbers of nest sites, i.e. nests void of eggs or chicks, but containing nesting material or defended by an adult bird

Figure 4: Annual ratios between the estimated number of African Penguins in adult plumage and the peak count of active nests at four breeding localities in Namibia

(Crawford et al. 1995a), rather than active nests were counted before 1994, leading to inflated counts. Until 1994 at Mercury and Ichaboe Islands, and until 1996 at Halifax and Possession Islands, the timing of nest counts and the definition of active nests were not well standardized.

Numbers of adult penguins at Mercury Island increased rapidly between 1995 and 1996, at the same time as numbers of adults and active nests decreased sharply at Ichaboe Island. This coincided with two periods of anomalous environmental conditions. First, extremely low levels of dissolved oxygen in the shelf waters off central Namibia during much of 1994 caused extensive fish mortalities and changes in distribution, with fish stocks moving off-shore, away from the vicinity of penguin breeding localities (Hamukuaya et al. 1998, O'Toole and Bartholomae 1998, Kristmannsson 1999). This was followed in early 1995 by a Benguela Niño, which further impacted on fish abundance and distribution (O'Toole and Bartholomae 1998, Gammelsrød et al. 1998). Since 1996 at Mercury Island and since 1995 at Ichaboe Island, numbers of adult penguins have been declining at the same rate. The impact of these two events appears to be less obvious at Halifax and Possession Islands, but the different census methods (active nests versus nest sites) potentially used before and after 1996 may have masked this effect. The more rapid decrease of adult individuals compared to the number of active nests at Possession Island suggests that Possession Island is experiencing a lack of recruitment of young breeders to the island. Overall, Halifax Island appears to be the only important Namibian penguin breeding locality where numbers of adult individuals and active nests were increasing over the period 1996–2004. This growth was not
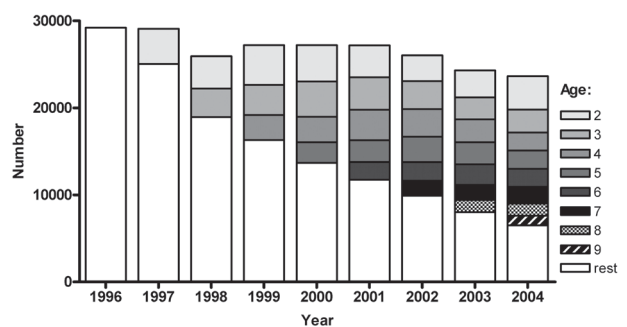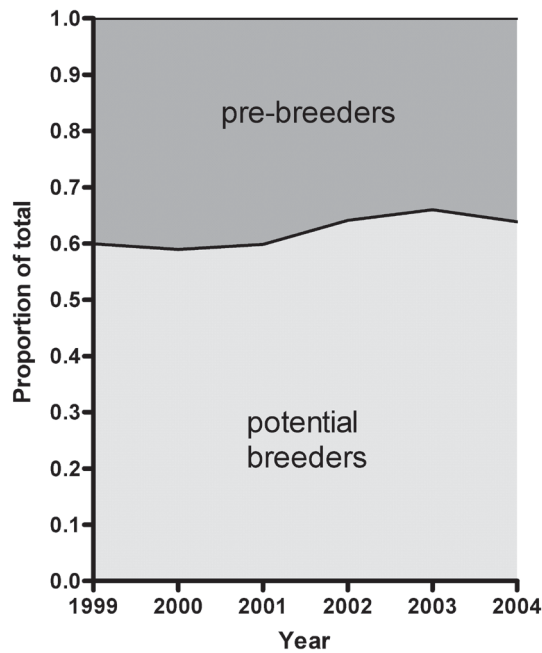

Figure 5: Observed annual survival rate of African Penguins in adult plumage between 1997 and 2004 at four breeding localities in Namibia

Figure 6: Sizes of age classes of African Penguins in adult plumage in Namibia, calculated from the observed annual adult survival rate and based on estimates of penguins in juvenile and adult plumage
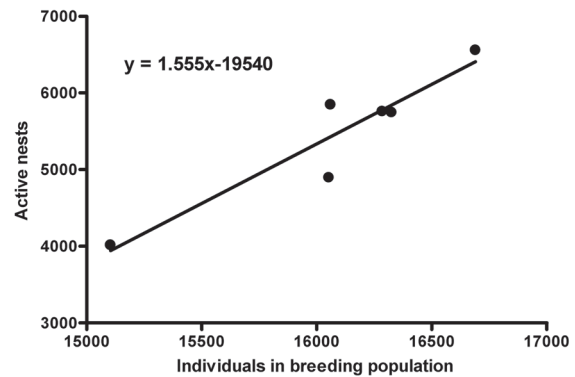
Figure 7: Proportion of pre-breeders (in adult plumage) and potential breeders at the four main breeding localities for African Penguins in Namibia between 1999 and 2004

Figure 8: Relationship between numbers of African Penguins aged five years or older breeding at the four main Namibian breeding localities, estimated from an age structure (see Figure 6), and annual peak counts of active nests at these localities over the period 1999 to 2004

enough to compensate for the losses at the other breeding localities. Before 1999, differences in population trends between localities were ascribed to fish abundance and distribution, with penguins at localities north of Lüderitz taking advantage of accessible non-commercial Pelagic Goby *Sufflogobius bibarbatus* since the collapse of the Sardine *Sardinops sagax* stock in the early 1970s, while those south of Lüderitz were mainly restricted to less nutritious cephalopods (Burger and Cooper 1984, Heath and Randall 1985, Crawford et al. 1985, 1991, Crawford 1998). However, considering the recent decreasing population trends at Ichaboe and Mercury Islands between the mid-1990s and 2004, this pattern seems to have changed.

The observed annual adult survival rate of 0.83 of African Penguins in Namibia was similar to estimates obtained through mark–recapture studies at localities in South Africa (Randall 1983, La Cock and Hänel 1987, La Cock et al. 1987, Crawford et al. 1995a, Whittington 2002) and substantially higher than an average estimate of 0.76 for Namibia over the same period (Kemper 2006). Reasons for this discrepancy could include increased immigration by individuals from South Africa boosting the observed survival rate, bias related to re-sighting probabilities of banded individuals, or potential negative effects of banding on survival.

The age structure for African Penguins in Namibia was constructed from estimates of penguins in juvenile and adult plumage and by applying the observed annual survival rates. This has not been done before for African Penguins. Our approach was based on serial molt counts and assumed that emigration or immigration did not play an important role in regulating the population size. The age structure enabled an independent estimate of the potential breeding population at the four islands, which accounted for 96% of the Namibian penguin population during the study period. An investigation of age at first breeding showed that African Penguins first breed when between four and five years old, although this varies between localities and years (Whittington et al. 2005c). In Namibia, an estimated 62% of penguins in adult plumage were aged five years or older and constituted the potential breeding population. The sum of the annual peak

numbers of active nests, for the four islands, determined from multiple visits, underestimated the potential breeding population by about a third. Annual peak active nest counts at Halifax Island underestimated peak counts for individual breeding colonies summed over a year by the same factor (Kemper 2006). Serial counts of active nests should be recorded separately for colonies at localities where breeding synchrony is low; annual peak colony counts should therefore yield a more accurate estimate for the breeding population than single peak counts.

Crawford and Boonstra (1994) found that penguins in adult plumage at Robben Island, South Africa, outnumbered the peak active nest count by a ratio of 3.24, during a time when the population there was rapidly increasing. A ratio of 3.2 has subsequently been applied to estimate the total number of adult penguins from nest counts and *vice versa* throughout the range (e.g. Crawford et al. 1995a, 2001, Cordes et al. 1999). While this may be useful for localities where no other ways of assessing population size is possible, it is unlikely that the same factor should apply to all breeding localities because it does not take locality-specific dynamics and age structure into account. Here, the mean ratio was 4.86, considerably higher than 3.24 of Crawford and Boonstra (1994) and varied between localities and years. A large ratio implies that there are comparatively few breeders in the adult population. This suggests that Namibian localities either support fewer individuals of breeding age or that the proportion of penguins of breeding age breeding in a year fluctuates widely between years and localities for some reason, such as lack of food, mate or nest site. Breeding at most localities in Namibia, particularly at Halifax and Possession Islands, is not well synchronized (Kemper 2006), whereas breeding seems well synchronized at Robben Island (Crawford and Boonstra 1994). This is likely to be a key factor contributing to differences in ratios.

A lack of breeding synchrony, together with a prolonged breeding season (Kemper and Roux 2005), possible deferral of breeding and the ability of raising two clutches in a year (Kemper 2006) or relaying after a failed attempt (Randall 1983), implies that counts of active nests at peak breeding provide a poor proxy for breeding population estimates and potentially could lead to gross misinterpretation of trends. Population estimates based on serial molt counts appear to be more accurate than alternative methods. However, this approach depends critically on the duration of the feather-shedding phase of molt; fieldwork is required to focus on variability of this period between breeding colonies and be-

tween years. The current practice, the universal application of a conversion factor of 12.7 days, might prove to be misleading. Although population trends would not change if different feather-shedding intervals are applied, population estimates would vary considerably if the duration was changed (Kemper 2006). This highlights the sensitivity of the molt count census method to estimates of feather-shedding duration. In terms of conservation management planning, it is therefore critical that the feather-shedding duration of molt is investigated more thoroughly.

At localities that are visited rarely, an active nest count at the time of the visit is the only option for obtaining an estimate of the size of the colony. In that case, counting procedures should be standardized to allow comparisons between localities and accurate trend calculations. In addition, the ratio between molt counts of individuals and nest counts needs to be specified for each locality. Interannual changes in the ratio may yield important clues about factors influencing population trends.

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