

Chapter 14

Effect of age and breeding status on molt phenology of adult African Penguins *Spheniscus demersus* in Namibia

Jessica Kemper^{1,2*}, Jean-Paul Roux³ and Les G. Underhill¹

¹ Avian Demography Unit, Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa

² African Penguin Conservation Project, c/o Lüderitz Marine Research, Ministry of Fisheries and Marine Resources, P.O. 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 described the seasonality of molt of African Penguins *Spheniscus demersus* in adult plumage in Namibia and used information derived from banded penguins to examine the relationship between age, breeding status and timing of molt of adult African Penguins in Namibia. Molt seasonality was bimodal with a primary molt peak in the austral autumn and a secondary molt peak in mid-summer. Penguins younger than four year, and therefore unlikely to be sexually mature, molted in early January, at the same time as juvenile penguins. Birds aged between four and six years molted either early or late and were likely to be individuals making the transition from non-breeder to breeder. Penguins older than six years,

considered to be breeders, molted, on average, in early May. The majority of penguins which had been recorded breeding during the 12 months preceding and following molt, molted between March and May. Summer breeding in Namibia appears to force breeders to delay molt until autumn. There was individual variation in molt seasonality which could not be explained by age alone. Estimates of the proportion of potential breeders in the population derived from molt phenology and from the molt histories of banded, known-aged individuals were likely to be underestimates and suggested that a high proportion of adults of breeding age defer breeding.

Keywords: seabird, molt, seasonality, demography, age, breeding activity

Introduction

Juvenile African Penguins *Spheniscus demersus* attain their characteristic black and white banded adult plumage when they undergo their first molt after fledging at between 12 and 23 months of age (Kemper and Roux 2005). Thereafter, they molt annually; the feather shedding phase lasts about two weeks (Randall and Randall 1981). Although some penguins begin to breed during their third year, the majority begin to breed during their fourth to sixth years (Whittington et al. 2005). The sum of two-weekly counts of molting penguins in adult plumage has been used to obtain estimates of adult population size attached to a particular locality or region (Randall et al. 1986, Crawford and Boonstra 1994, Crawford et al. 1999, 2000, Kemper et al. 2001, 2007). Because sexually mature penguins cannot be distinguished visually from immature penguins, estimates of breeding populations can currently only be obtained through counts of active nests at the time of peak breeding activity (Crawford et al. 1990, 1999, 2000, Crawford and Boonstra 1994, Kemper et al. 2001). However, at most African Penguin localities the breeding season is protracted (Wilson 1985, Kemper and

Roux 2005), breeding is not well synchronized (Kemper 2006) and even at the time of peak breeding activity, only part of the breeding adults associated with a locality may actually be breeding (Kemper et al. 2007). In addition, not all mature adult penguins necessarily breed each year (Randall and Randall 1981, Randall et al. 1986, Whittington et al. 1996, Kemper 2006) and the annual peak count of breeding adults is thus likely to provide an underestimate of the size of the breeding population.

Here we describe the seasonality of molt of African Penguins in adult plumage in Namibia. We use information derived from banded penguins to examine the relationship between age and timing of molt of adult African Penguins in Namibia, the influence of breeding activities on the timing of molt, and assess whether the duration of the interval between successive molts varies with age. Given the difficulties of estimating the size of the breeding population belonging to a locality, an understanding of the factors determining adult molt phenology might provide the means to separately estimate numbers of breeders and non-breeders within a population.

Methods

Molt seasonality

Within this study, the most sensible biological definition of a year runs between the beginning of September of one year and the end of August the following year, because the fewest birds molt between July and September. Seasons are austral.

Counts of molting penguins in adult plumage were made until 31 August 2005 and followed the protocol proposed by Randall et al. (1986). At Mercury Island (25°43'S 14°50'E), counts were made weekly between October 1991 and May 1996, with a lack of data between May 1993 and March 1994. After May 1996, counts were done every two weeks. At Ichaboe Island (26°17'S, 14°56'E), counts were made two-weekly from May 1992. Counts at Halifax (26°37'S, 15°04'E) and Possession (27°01'S, 15°12'E) Islands were made from July and June 1996 respectively. Counts at Halifax Island during 1996 were irregular. For each island, actual counts were interpolated linearly to yield estimated daily numbers of molting penguins for each day of the year, following Underhill and Crawford (1999). Daily totals were scaled by dividing by the sum of molting penguins in each year and then averaged across years to establish an average seasonal molt pattern for each island.

Adult molt patterns were described using Bhattacharya's (1967) method, which allows the splitting of composite distributions into separate normal distributions. Gaussian curves were fitted to average seasonal molt patterns to define mean molt dates, provide a measure of synchrony and to provide an estimate of the contribution of each component to the whole season. To allow comparison of African Penguin adult molt seasonality with other localities for which it has been described, the number of penguins molting in every half month and per month was calculated as a percentage of the total number of penguins molting during that period.

Age and timing of molt

Between November 1986 and July 2001, 9,292 penguins were banded in Namibia. Of these, 8,327 penguins were banded as chicks, just prior to fledging, 467 were banded in juvenile plumage and 474 were banded as adults. Age at banding was not recorded for an additional 24 individuals. Penguins were banded at Mercury, Ichaboe and Possession Islands since 1986, and at Halifax Island since 1990. Methods to determine fledging date and age as well as definitions for adjustments for molt records to correspond to the mid-

Table 1: Adjustments made to breeding records of banded African Penguins in Namibia, where date of egg-laying was not known. For nests with two chicks, the breeding stage of the older chick was used for the adjustment. Date of egg-laying was known for an additional 34 (12.78%) breeding records

Observed breeding stage	Number of cases (% of all cases)	Estimated age (days) since beginning of incubation	No. of days backdated per record
Incubation	151 (56.77)	1–38	19
Small downy chick	22 (8.27)	39–48	43
Medium downy chick	15 (5.64)	49–58	53
Large downy chick	14 (5.26)	59–78	68
¼ shed chick	1 (0.38)	79–88	83
½ shed chick	3 (1.13)	89–98	93
¾ shed chick	6 (2.26)	99–108	103
Fully shed chick	20 (7.51)	109–128	118
Total	232 (87.22)		

point of molt follow those described in Kemper and Roux (2005). On average, these adjustments corresponded to 4.8 days (SD = 4.1 days) per record (0.3% of the estimated age at molt). Additional records of 89 molting birds of unknown age (those banded as juvenile or adult birds) were used to estimate the interval between breeding and molt and to calculate the length of the interval between two successive molts.

A weighted moving average algorithm was used to smooth the scatterplot of age against date of molt, similar to that used by Summers et al. (1992) and originally devised by Cleveland (1979). The difference was that molt dates were expressed as vectors in a circle representing the year. Circular statistics (Davis 2002) were used to estimate the circular analogues of the mean and standard deviation of molt at each age. Suppose the *i*th observation was of a penguin aged y_i years which commenced molt on the date (month and day) expressed as angle θ_i (date converted to days since 1 September, and multiplied by 360/365 to express the date in degrees; each month then spans an arc of c. 30°). For each observation, $s_i = \sin \theta_i$ and $c_i = \cos \theta_i$ was calculated. To estimate the circular analogues of the weighted mean and weighted standard deviation of date of molt for penguins aged t years, $w_i = \exp(-(y_i - t)^2)/W$, where $W = \sum \exp(-(y_i - t)^2)$ was first calculated, and then $S = \sum s_i w_i$ and $C = \sum c_i w_i$. Then the mean date of molt for penguins aged t is given by $\phi = \arctan(S/C)$, where the angle ϕ needs to be back-transformed to a date; the circular measure of dispersion is given by $v = (1 - (S^2 + C^2)^{1/2})$ (Davis 2002). The circular measure of spread is close to zero if the molt dates at a given age are closely synchronized, and close to one if the molt dates at a given age are scattered randomly through the year. With this algorithm, the results are not dependent on the date chosen as the starting point of the year, in this case 1 September. Similarly, circular statistics were used to compute the mean date of molt and its spread for age classes of penguins identified from the smoothed trajectory through the scatterplot.

To calculate the interval between breeding and molt and the interval between molt and breeding, records banded birds noted breeding were examined. Some 266 records of birds observed breeding prior to and within a year of molt, and for which detailed descriptions of nest contents were available, were included in the analysis of age at breeding. Breeding records were adjusted to correspond to the estimated beginning of incubation. Average incubation period is 38 days (Williams and Cooper 1984), followed by an average of 83 days between hatching and fledging (Kemper 2006). Egg-laying dates were known for 34 re-sighting records of breeding banded birds. For the other 232 breeding records, dates of egg-laying were back-estimated from time of first detection judged from the approximate age of the nest contents noted in the re-sighting record (Table 1):

- ▶ 19 days were subtracted for incubation records (i.e. assuming mid-incubation at detection)
- ▶ 43 days were subtracted for records of small downy chicks (aged between 1–10 days after hatching)
- ▶ 53 days were subtracted for records of medium downy chicks (aged between 11–20 days)
- ▶ 68 days were subtracted for records of large downy chicks (aged between 21–40 days)
- ▶ 83 days were subtracted for records of ¼ shed chicks (aged between 41–50 days)
- ▶ 93 days were subtracted for records of ½ shed chicks (aged between 51–60 days)
- ▶ 103 days were subtracted for records of ¾ shed chicks (aged between 61–70 days)
- ▶ 118 days were subtracted for records of fully shed chicks (aged older than 70 days)

Interval between molts

The interval between molts was calculated for all banded birds for which successive molts were recorded. For most of these the ages of the birds were known.

Estimates of breeding population size from molt phenology

Banded penguins for which age and molt date were known were classified as potential breeders (i.e. aged ≥ 5 years at molt) or pre-breeders (aged < 5 years at molt). In order to estimate the proportion of breeders molting on any given date, a sine function was fitted. The modeling was done as a generalized linear model with a binomial distribution and logistic link function. This function was applied to daily totals of molting birds in adult plumage at each of the four main breeding localities as well as for all four localities combined.

Results

Molt seasonality

African Penguins in Namibia molted throughout the year (Fig. 1). Except at Possession Island, there was a clear bimodal molt pattern (Fig. 1), with a primary molt peak in autumn (April/May) and a secondary molt peak in mid-summer (December/January) (Table 2). At Possession Island, the molt season was less clearly defined; a large proportion of birds molted during winter.

Summer and autumn peaks were fitted with Gaussian curves (Table 3, Fig. 2). Curves fitted to autumn molt patterns had small standard deviations, indicating that autumn molt was synchronous. Those fitted to summer molt patterns had a large standard deviation, indicating less synchrony. A larger proportion of birds molted in autumn at Mercury Island (0.44) than at Ichaboe (0.42) or Halifax (0.38) Islands. The magnitude of the summer peak in relation to the autumn peak was smallest at Mercury Island, intermediate at Ichaboe and Possession Islands and largest at Halifax Island. Fewer than half the penguins molting at Possession Island, did so in summer and autumn.

Age and timing of molt

Between August 1992 and October 2003, 757 penguins banded as chicks at the four Namibian islands were later recorded during adult molt. Of these known-age penguins, 598 were recorded molting once, 131 recorded twice, 23 recorded three times, five recorded four times and two recorded five times, a total of 959 molt records. Of birds banded in juvenile or adult plumage, 89 birds were subsequently recorded molting. Of these, molt was recorded once in 72 individuals, twice in 13 individuals, three times in one individual, four times in two individuals and five times in one individual. This yielded a total of 114 records. Observations of individuals molting more than once were not necessarily made in successive years. The youngest age at which a bird was recorded to undergo its first adult molt was 1.8 years at

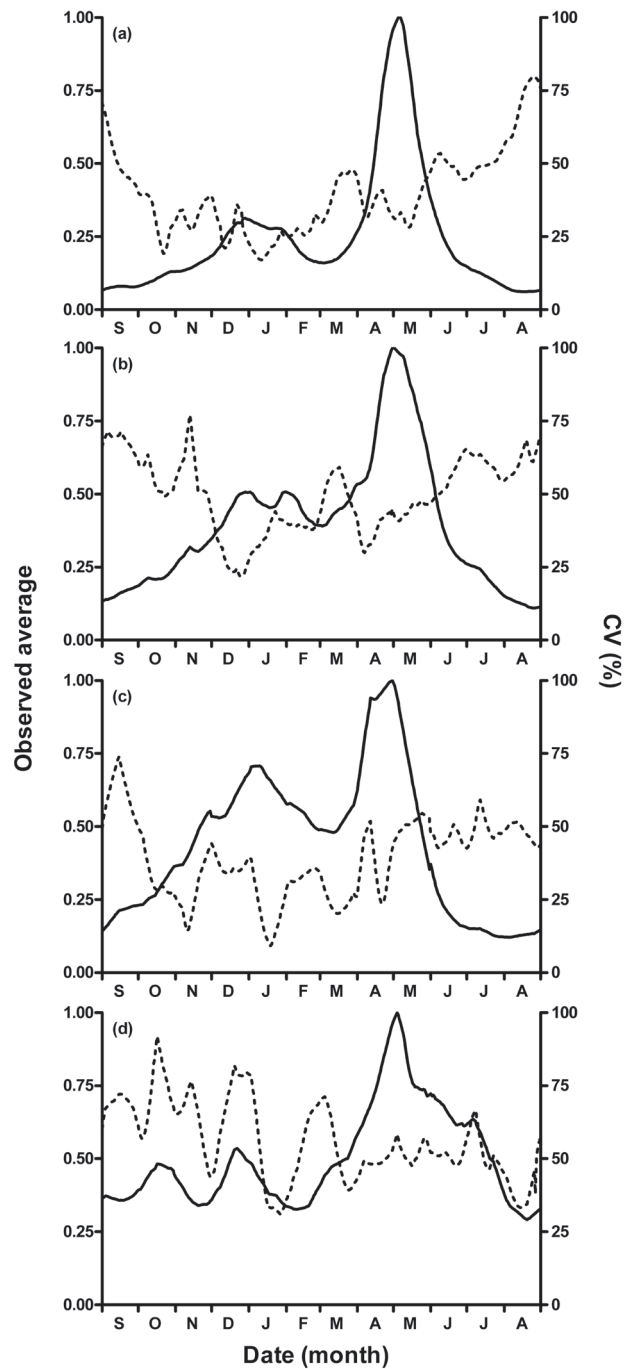


Figure 1: Standardized, average seasonal molt patterns of African Penguins in adult plumage (solid line) and associated coefficients of variation (dashed line) at the four main breeding localities in Namibia: (a) Mercury, (b) Ichaboe, (c) Halifax and (d) Possession Islands

Table 2: Average peak half month or month of molt (% contribution to annual total) of African Penguins in adult plumage at the four main breeding localities in Namibia. FH = first half, SH = second half

Period		Mercury	Ichaboe	Halifax	Possession
Half month	Summer	SH December (5.05%)	SH December (5.30%)	FH January (6.44%)	SH December (5.00%)
	Autumn	FH May (13.54%)	FH May (9.53%)	SH April (9.88%)	FH May (7.04%)
Month	Summer	January (9.60%)	January (9.84%)	January (12.43%)	December (8.72%)
	Autumn	May (22.63%)	May (17.69%)	April (17.79%)	May (13.17%)

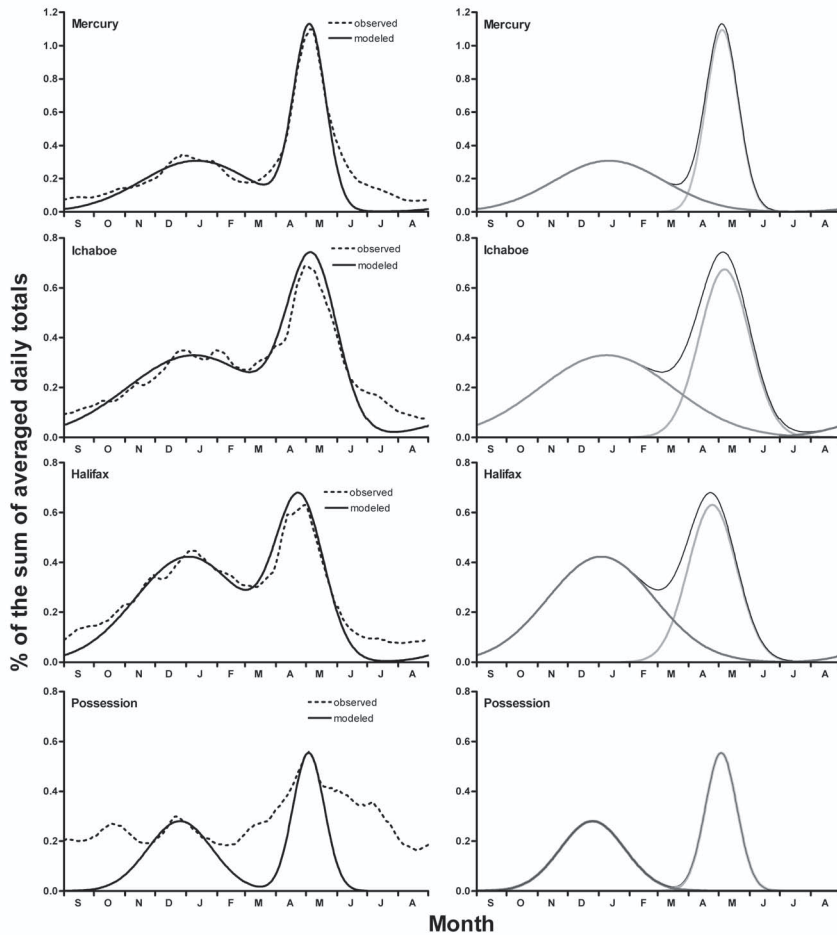


Figure 2: Gaussian curves fitted to describe standardized, average seasonal molt patterns of African Penguins in adult plumage at the four main breeding localities in Namibia. Graphs on the left show smoothed observed and modeled molt patterns; graphs on the right show how modeled patterns were derived from splitting composite distributions into separate normal distributions. Observed molt patterns come from Fig. 1

molt. The oldest bird recorded molting was nearly 17 years old.

Young birds generally molted earlier in the year than older birds (Figs. 3a and 3b). The circular dispersion of molt dates varied with age (Fig. 3c). Birds aged two to three years showed little dispersion of molt dates (range = 0.21 to 0.32). Dispersion increased to a maximum of 0.99 at age 4.8 years, indicating a random pattern of molt dates at this age. The

dispersion then decreased to 0.17 at age 7.7 years, with secondary dispersion peaks of 0.74 and 0.49 at ages 6.05 years and 7.1 years respectively. Dispersion of molt dates in birds older than eight years remained small, ranging between 0.24 and 0.46. Minor dispersion peaks at ages greater than 10 years are attributable to small sample sizes. Adult molt was recorded for 502 banded penguins younger than four years; using circular statistics, their mean molt date was

Table 3: Summary of observed and modeled parameters (using Bhattacharya's method) describing adult molt seasonality of African Penguins at the four main breeding localities in Namibia

Curve		Mercury 1994–2004	Ichaboe 1992–2004	Halifax 1997–2004	Possession 1996–2004
Summer					
Mean molt date	Observed	29 December	31 January	10 January	22 December
	Modeled (SD)	12 January (54.9)	9 January (66.6)	4 January (53.2)	25 December (32.1)
Proportion of observed total		0.42	0.55	0.56	0.22
Autumn					
Mean molt date	Observed	5 May	30 April	30 April	4 May
	Modeled (SD)	5 May (16.1)	7 May (25.0)	25 April (24.2)	4 May (15.8)
Proportion of observed total		0.44	0.42	0.38	0.21
Total					
Proportion of observed total		0.86	0.97	0.94	0.43
Measure of fit		0.93	0.93	0.93	0.28
Ratio of summer to autumn peak heights	Observed	0.31	0.51	0.71	0.54
	Modeled	0.28	0.49	0.67	0.50

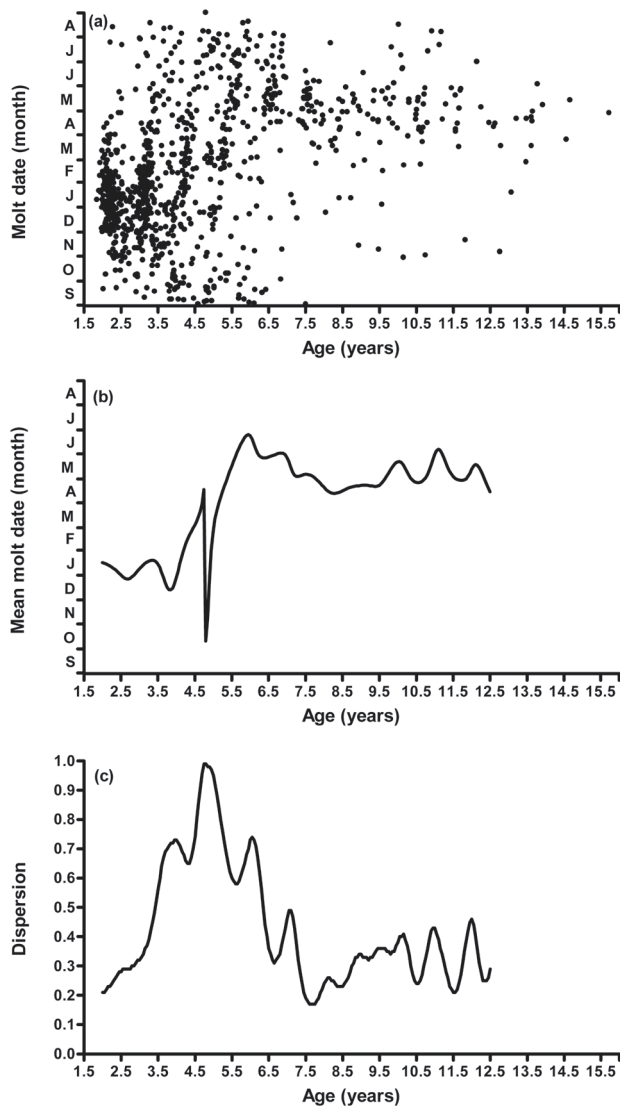


Figure 3: Relationship between age and date of molt of African Penguins in adult plumage in Namibia using (a) molt records derived from banded individuals, (b) mean molt date calculated from molt records from banded individuals and (c) dispersion (see text). The year runs from 1 September to 31 August

8 January with circular dispersion of 0.38. Between the ages of four and six years, the mean molt date for 240 individuals was 8 April. However the circular dispersion was large, 0.84, indicating that the starting dates of molt for this age group were spread through the year. The mean molt date for 217 penguins aged six years and older was 5 May, circular dispersion 0.37. Penguins aged five and six years, which were assumed to have recently reached sexual maturity, molted later in the year (mean = 28 May, but with a relatively large circular dispersion of 0.73, $n = 109$) than penguins aged 10 years or older (mean = 2 May, with a relatively small circular dispersion of 0.36, $n = 62$).

The interval between the estimated egg-laying date within 12 months of molt and the estimated date of start of molt was available for 135 penguins, with a mean interval of 191 days ($SD = 66$) and an interval range of 19 and 350 days (Fig. 4a). Some 92 birds (68%) which bred during the preceding 12 months, molted between March and the end of May. For 131 penguins, the period between mid-molt and the beginning of egg-laying within 12 months of molt averaged 123 days ($SD = 60$ days), and ranged between 22 and 350 days (Fig. 4b).

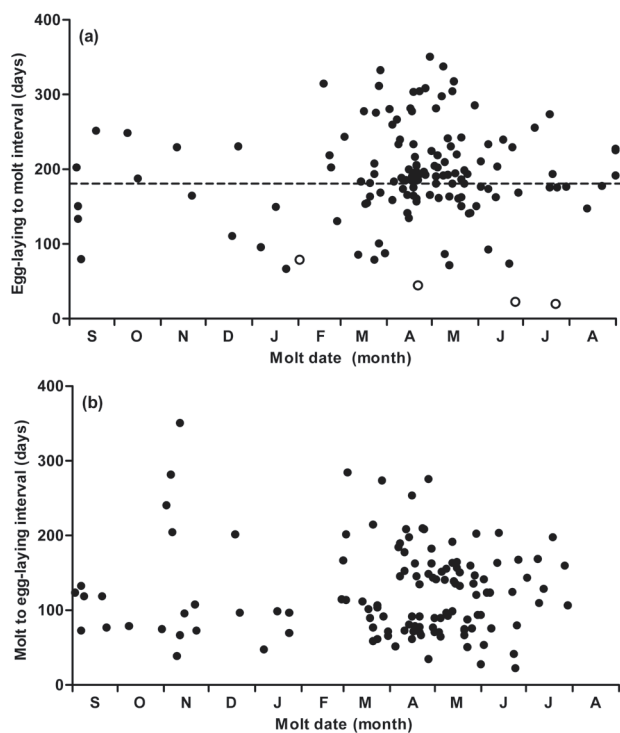


Figure 4: Intervals between (a) observed egg-laying and molt and (b) molt and observed egg-laying within 12 months of molt of banded African Penguins in Namibia. Open circles represent individuals molting while breeding. Dotted line shows interval limit below which it is unlikely for a breeding attempt to be successful before molt

Altogether 86 birds (66%) which bred during the 12 months following molt, molted between March and the end of May. Additional, intermediary breeding attempts may have been missed; consequently, mean interval durations are likely to be overestimates. In a few cases, breeding was recorded during or just before molt in banded penguins (Fig. 4a).

Interval between molts

Some 117 individuals provided 137 records of intervals between successive molts. The shortest interval between two molts recorded was 280 days. From this observed interval, $(280 \times 2) - 1 = 559$ days is assumed to be the shortest possible interval in which a bird could molt for a second time. The longest possible molt interval was observed to be 557 days. Records of molt intervals between 558 and 730 days (= two years) were assumed to have involved an unobserved molt and were not included; there were 10 such observations. Mean molt interval was 366.9 days ($SD = 49.2$ days) with a median date of 360 days, and lower and upper quartile intervals of 339.0 and 387.8 days respectively. The 17 molt intervals equaling or longer than 400 days were from birds younger than eight years, with long (>480 days) and short molt intervals (<315 days) confined to birds younger than 6.5 years (Fig. 5); these records inflated the standard deviation. One bird was recorded molting in five successive years, with a mean interval between successive molts of 373 days ($SD = 27.1$ days), and a range of 344 to 401 days.

Molt dates for the seven individuals banded as chicks and the individual banded at age <2 years, for which molt was recorded more than three times show that younger birds tended to molt earlier than older birds, but that there was some individual variation (Fig. 6).

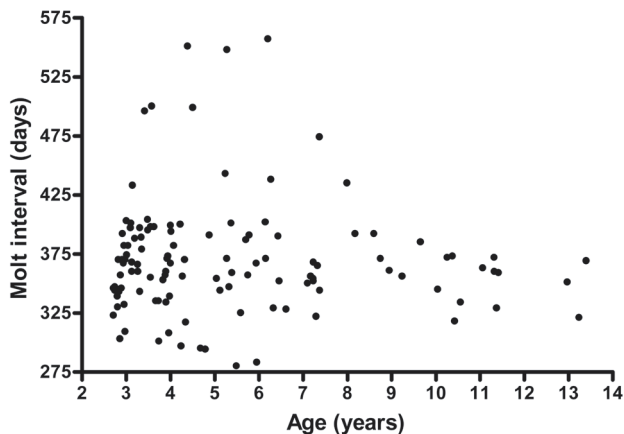


Figure 5: Relationship between age at successive molt and the length of the interval between molts from records of banded adult African Penguins in Namibia

Estimates of breeding population size from molt phenology

The number of potential breeders and pre-breeders for which both age and calendar date of mid-molt was known was 959. Based on this sample, the generalized linear model estimated that the logit of the proportion of potential breeders was:

$$y(\theta) = -0.6297 - 1.939 \sin \theta + 0.367 \cos \theta,$$

where θ is the day since 1 September converted to an angle between 0° and 360° (where the model accounted for 27.4% of the deviance, and the standard errors, t -values, and P -values associated with the regression coefficients were 0.093, -6.77 $P < 0.001$ for the constant; 0.125, -15.5 , $P < 0.001$ for the sine term; and 0.124, 2.95, $P = 0.003$ for the cosine term). The estimated proportion of potential breeders, p , is then given by

$$p = \exp(y(\theta)) / (1 + \exp(y(\theta))).$$

Applying this equation to the seasonal molt pattern of each of the four islands, the estimated proportion of penguins aged ≥ 5 years ranged from 0.27 (Halifax Island 2004) to 0.56 (Possession Island 2000). On average, between 37% and 48% of the adult penguin population in Namibia was estimated to be five years or older (Table 4).

Discussion

Molt seasonality

In Namibia, the molt season of penguins in adult plumage was bimodal, with a primary molt peak during autumn and a secondary peak during summer, at the same time as the juvenile molt peak (Kemper and Roux 2005, Kemper 2006). The timing and synchrony of molt varied slightly between islands and years, with the molt season at Possession Island being less clearly defined than at the other three islands.

Molt season patterns of African Penguins in Namibia differed from those in South Africa. At all South African breeding localities for which data are available, molt of adult penguins is monomodal, well synchronized and generally coincides with juvenile molt. At Robben Island ($33^\circ 48' S$, $18^\circ 22' E$), approximately 25% of adult penguins molt during the first half of December (Underhill and Crawford 1999, Hemming 2001). Peak molt at Dassen Island ($33^\circ 25' S$, $18^\circ 05' E$) is between November and January (Wolfaardt and

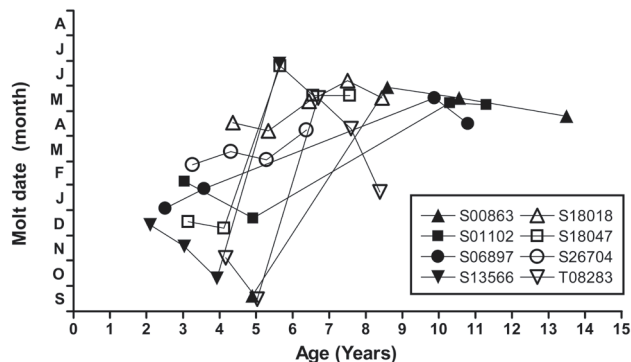


Figure 6: Individual molt histories of African Penguins banded as chicks in Namibia, which were subsequently recorded molting four or more times. Molt was not necessarily observed in successive years

Nel 2003), with nearly 30% of adult penguins molting there during December (Crawford et al. 2006), while 30% of birds molt at the Lambert's Bay islands ($33^\circ 05' S$, $17^\circ 57' E$) about a month earlier (Wilson 1985, Crawford et al. 2006). At St Croix Island ($33^\circ 47' S$, $25^\circ 46' E$), peak molt is during November (Randall and Randall 1981), at The Boulders ($34^\circ 11' S$, $18^\circ 27' E$) in late November to December (Hemming 2001) and at Stony Point ($34^\circ 22' S$, $18^\circ 54' E$) in late November (Hemming 2001).

Age and timing of molt

In Namibia, adult penguins younger than four years molt in early January, at the same time as juvenile penguins, i.e. first-time molters (Kemper and Roux 2005). Birds older than six years molt, on average, in early May, a difference of four months later. For birds between four and six years, molt tends to be either early, in the January peak with the juvenile penguins, or late, in the May peak with the breeding adults. These are likely to be individuals making the transition from non-breeder to breeder. However, while younger birds tend to molt earlier than older birds, there is individual variation, which cannot be explained only by age.

The high energy demands during molt are thought to be incompatible with those of chick-rearing (Payne 1972), and molt in penguins therefore takes place during the non-breeding phase (Boersma 1975, Randall and Randall 1981, Dann et al. 1992). African Penguins breed throughout the year (Wilson 1985). In Namibia, a wave of egg-laying during late June and July is followed by a second, often larger, wave during October and November (Kemper 2006). Successful chicks from the second wave fledge during January and February, extending into March (Kemper 2006). Taking a pre- and post-molt fattening period at sea of approximately 30–40 days each into account (Randall and Randall 1981), this leaves a relatively narrow window (April and May) for breeding birds to molt in before the beginning of the next breeding wave. Here, the majority of birds, which had been recorded breeding during the 12 months preceding and following molt, molted between March and May.

Birds molting earlier than 150 days after egg-laying were most likely to be failed breeders, because a successful breeding attempt takes approximately 120 days (Kemper 2006) and an additional 30 to 40 days to fatten up for molt (Randall and Randall 1981). Long intervals between egg-laying and molt may indicate that a subsequent breeding attempt (replacement clutch after nest/chick loss or second clutch after a successful first breeding attempt) was not recorded before molt. Randall and Randall (1981) found that

long molt intervals of up to 444 days at St Croix Island were the result of extended breeding activities, where individuals would delay molt until the chicks had fledged. In that case, molt the following year was at the usual time, resulting in molt intervals as short as 269 days.

Penguins aged five years, and thus considered young breeders, molted on average 24 days later than experienced breeders aged ten years or older. One might expect a tendency for young breeders to molt later than old breeders. Young and inexperienced breeders may take longer to start their breeding attempt or to fledge their chicks (e.g. Coulson 1966, de Forest and Gaston 1996, Daunt et al. 2001). They could be more likely to experience breeding failure (e.g. Pugsek and Diem 1983, Dann and Cullen 1990, Daunt et al. 2001) and might therefore be more likely to lay replacement clutches.

Despite a protracted breeding season, molt of juvenile penguins in Namibia is well synchronized, with a distinct molt peak in mid-summer (Kemper and Roux 2005, Kemper 2006). Like juvenile birds, sexually immature birds (and possibly sexually mature birds which may not have bred during the preceding year) molt mostly in summer, possibly as a result of photoperiodic response in the absence of other constraints (Lofts and Murton 1968, Vaucoulon et al. 1985, Scholten 1989, Otsuka et al. 2004). Summer breeding in Namibia forces breeders to delay their molt until autumn, when they are no longer constrained by summer breeding activities. In the Western Cape, South Africa, peak breeding is primarily during autumn and winter (Cooper 1978, Randall and Randall 1981, Shelton et al. 1984, La Cock et al. 1987, Crawford et al. 1995, 2006, Whittington et al. 1996, Murison 1998, Wolfaardt and Nel 2003). At St Croix Island in the Eastern Cape, breeding starts in summer, but after the end of molt (Randall and Randall 1981). Thus, winter breeding allows most birds to molt during summer there.

Evidence of deferred molt due to breeding has been recorded for Magellanic Penguins *Spheniscus magellanicus*, with breeders molting during March and April after fledging their chicks (Stokes et al. 1998). Adult Humboldt Penguins *S. humboldti* in Chile molt in February after fledging chicks in January, about a month later than juvenile penguins (Simeone et al. 2002). Non-breeding Galapagos Penguins *S. mendiculus* molted before breeding adults when food was plentiful (Boersma 1977). Reilly and Balmford (1975) recounted a Little Penguin molting late at Phillip Island, Australia, after having twice bred successfully in that season.

An overlap in breeding season and optimal molt season could potentially lead to lower breeding success. Second clutches and replacement clutches will have a lower chance of being successful if the parent is already delaying molt. In Namibia, a molting penguin simultaneously incubating eggs or raising chicks is infrequent but possibly more common than in South Africa (A. J. Williams pers. comm.). Since molting birds are not able to feed and live off their fat reserves, it is unlikely that a simultaneous breeding attempt will be successful. Moreover, the survival of the molting bird may become compromised if it has not sufficient time to fatten up between its previous breeding attempt and molt.

Interval between molts

The mean interval between successive molts calculated for African Penguins at St Croix Island, South Africa was 368.3 days (SD = 24.5, $n = 152$) (Randall and Randall 1981). In contrast, Cooper (1978, 1980) calculated 321 days (30, 11) for penguins at Dassen Island. Cooper (1978) concluded that African Penguins do not have an annual molt cycle, but conceded that the general peak molt for the study colony at Dassen Island, South Africa, in 1972 was nearly two months

earlier than that of the previous year. These results agree with those of Randall and Randall (1981), with the average molt interval almost exactly one year. The longest molt interval recorded by Randall and Randall (1981) was 444 days (from a sample of 152) and that found by Cooper (1978) was 362 days (11). Feather wear appears to be a factor limiting the molt interval in juvenile penguins, with a maximum molt interval of 613 days after fledging recorded in banded juvenile African Penguins in Namibia (Kemper and Roux 2005). It is therefore possible that the maximum molt interval of 559 days imposed on this data set caused some particularly long consecutive molt intervals to be missed here.

Intervals between molts may range widely for individuals. If young (non-breeding) birds molt at a different time from older (breeding) birds, it would suggest that during the transition from non-breeder to breeder, molt intervals would change and either become shorter or (more likely) longer. The transition direction and whether this happens in a step-wise or a gradual manner is uncertain, and might depend on the individual or be dictated by environmental conditions. A wide range of consecutive molt intervals was also observed in an individual Laughing Dove *Streptopelia senegalensis* for which primary molt was recorded on eight consecutive occasions (Underhill and Underhill 1997). This variability was not attributed to previous breeding success and timing of breeding, but rather to food availability and demonstrated the plasticity of the circannual molt cycle. In African Penguins, the timing of molt in successive years also appears to be flexible; the role of age- or environment-related variability versus individual variability in determining the timing of molt needs to be investigated further.

Estimates of breeding population size from molt phenology

The phenology of the molt season of penguins in adult plumage in Namibia appears to be made up of a combination of non-breeding penguins molting during summer, and breeding birds molting during autumn. A bird which is sexually mature may not breed for a number of reasons, including adverse feeding conditions (e.g. Boersma 1978, Boersma et al. 1990, Cuthbert et al. 2003), the loss of a partner (Giese et al. 2000), or physiological damage after oiling (Wolfaardt and Nel 2003). The lack of synchrony of summer-molting individuals suggests that these include birds too young to

Table 4: Proportion of African Penguins aged five years or older at the four main breeding localities in Namibia and for the four localities combined, estimated from observed seasonal molt patterns derived from molt counts. Daily proportions of molting birds aged five years or older were derived from banded individuals in adult plumage recorded molting

Year	Mercury	Ichaboe	Halifax	Possession	Combined
1992		0.34			
1993		0.38			
1994	0.46	0.42			
1995	0.51	0.50			
1996	0.45	0.49	0.43	0.34	0.45
1997	0.46	0.44	0.44	0.32	0.44
1998	0.47	0.49	0.34	0.45	0.46
1999	0.45	0.44	0.38	0.49	0.44
2000	0.48	0.50	0.39	0.56	0.48
2001	0.51	0.45	0.38	0.52	0.47
2002	0.53	0.47	0.40	0.54	0.49
2003	0.50	0.37	0.34	0.45	0.44
2004	0.46	0.31	0.27	0.39	0.38
Average	0.48	0.43	0.37	0.44	0.45

breed, breeders which have not bred that year, failed breeders or those which have bred successfully early and have not bred a second time in the season. By contrast, autumn molt was generally highly synchronized and suggests that this mainly includes birds which were breeding in mid-summer and were therefore forced to delay molt.

Breeding activities may not be synchronized at a particular breeding locality, for example at Halifax Island, where breeding activities at island scale were less synchronized than at colony scale (Kemper 2006). If individuals molting in autumn are breeders delaying molt, molt synchrony patterns at a locality may be a reflection of breeding synchrony patterns. This trend has been observed at Halifax Island (pers. obs), where individuals from a particular colony molt at the same time. Differences in the timing of molt between colonies could not, however, be quantified here, since many penguins tend to molt away from the breeding colonies, usually at the landing beaches. This is particularly the case on hot days.

Mercury Island has a higher proportion of autumn-molting penguins than Ichaboe or Halifax Islands, implying either a higher proportion of breeding birds there, or a high proportion of birds breeding elsewhere and molting at Mercury Island. The adult molt season at Possession Island differs from that at the other three islands by having a less clearly defined bimodal pattern and a relatively poor model fit. Although there is a distinct autumn peak, there is no clear summer peak and a high proportion of winter- and spring-molting birds. This may indicate that seasonality of molt has collapsed at Possession Island, where numbers of penguins have declined dramatically over the last 50 years (Kemper et al. 2007), or that it is highly variable and possibly dictated by local (feeding) conditions. Alternatively, because penguins are forced to molt and breed at different times and breeding activities influence the timing of molt, poorly synchronized adult molt at Possession Island may be the result of highly variable breeding activities there (Kemper 2006).

The proportion of penguins estimated from banded individuals to be five years or older is similar to that estimated by the proportion of penguins molting in autumn. Possession Island is an exception; there the estimated proportion of birds aged five or older is far higher than the (modeled) proportion of birds molting during autumn. However, model fit at Possession Island, where breeding is less seasonal than at the other three islands, is poor and the modeled proportion of autumn-molting birds therefore clearly an underestimate. Proportions calculated from an age structure (Kemper et al. 2007) were higher. It is likely that estimates based on adult molt phenology are underestimates, and that penguins of breeding age but molting in spring, summer or winter account for these discrepancies.

Proportionally few juvenile penguins molt at Possession Island (Kemper 2006), suggesting the presence of few young birds at the island. Breeding success at Possession Island was found to be high compared to that at the other three breeding localities in Namibia (Kemper 2006); this was thought to be a possible indication of an older, experienced breeding population there. The poorly defined summer molt peak and the high proportion of adults molting in autumn at Possession Island lend support to this hypothesis. Conversely, the comparatively small proportion of penguins molting in autumn at Halifax Island, supports findings by Kemper (2006), where the poor breeding performance was partially attributed to a relatively young, inexperienced breeding population there. The adult population growth observed at Halifax Island (Kemper et al. 2007) could therefore be due to an influx of young adults. Estimates of the proportion of penguins estimated to be five years or older derived from banding and recapture records and molt phenology here

were lower than those derived from an age structure constructed for the region (Kemper et al. 2007). This could be due to potential breeders deferring breeding. If a penguin of breeding age does not breed, it could molt during mid-summer, at the same time as young birds. In that case, estimates of the potential breeding population from molt phenology would underestimate the proportion of potential breeders in the population. The discrepancy could be an indication that a low proportion of potential breeders in the population actually breed.

The proportion of breeders to non-breeders reflects a mix of recruitment, mortality and breeding conditions for a given year, and will not be constant. These results provide the means of using molt counts to estimate numbers of penguins of breeding age in a population. However, the proportion of potential breeders deferring breeding needs to be ascertained to ensure accurate estimates.

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