



EFFECT OF AGE AND BREEDING STATUS ON MOLT PHENOLOGY OF ADULT AFRICAN PENGUINS (*SPHENISCUS DEMERSUS*) IN NAMIBIA

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ABSTRACT.—We analyzed the seasonality of molt of African Penguins (*Spheniscus demersus*) in adult plumage and used information derived from banded individuals to examine the relationship between age, breeding status, and timing of molt in Namibia. Molt seasonality was bimodal, with a major molt peak in the austral autumn and a minor peak in midsummer. African Penguins younger than four years—and, therefore, unlikely to be sexually mature—molted in early January, at the same time as juvenile African Penguins. Birds aged between four and six years molted either in summer or autumn and were likely to be individuals making the transition from nonbreeder to breeder. African Penguins older than six years, considered to be breeders, molted, on average, in early May. Most birds that had been recorded breeding within 12 months of 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 that we could not explain 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-age individuals were likely to be underestimates and suggested that some adults of breeding age defer breeding. Received 10 December 2006, accepted 25 February 2008.

Key words: African Penguin, age, breeding activity, demography, molt, seabird, seasonality, *Spheniscus demersus*.

Efectos de la Edad y del Estatus Reproductivo sobre la Fenología de la Muda de Adultos de *Spheniscus demersus* en Namibia

RESUMEN.—Analizamos la estacionalidad de la muda de los plumajes adultos en *Spheniscus demersus* y usamos información derivada de individuos anillados para examinar la relación entre la edad, el estatus reproductivo y el momento en que tiene lugar la muda en Namibia. La estacionalidad de la muda fue bimodal, con un gran pico en el otoño austral y un pico menor a mediados del verano. Los individuos de *S. demersus* de menos de cuatro años de edad —y, por lo tanto, con poca probabilidad de estar sexualmente maduros—mudaron a principios de enero, al mismo tiempo que los juveniles. Las aves con edades de entre cuatro y seis años mudaron ya sea en verano u otoño, y en general fueron individuos en la transición de no reproductivos a reproductivos. Los individuos de más de seis años de edad, considerados como reproductivos, mudaron en promedio a principios de mayo. La mayoría de las aves que se habían registrado criando a menos de 12 meses de la muda, mudaron entre marzo y mayo. La cría de verano en Namibia parece forzar a las aves reproductivas a demorar la muda hasta el otoño. Hubo variación entre los individuos en la estacionalidad de la muda que no pudimos explicar considerando sólo la edad. Las estimaciones de la proporción de aves reproductivas potenciales en la población, calculadas a partir de la fenología de la muda y de las historias de muda de individuos anillados de edades conocidas, fueron probablemente subestimadas y sugirieron que algunos adultos en edad reproductiva aplazaron la reproducción.

IN MOST BIRDS, reproductive activities and migration must be precisely timed to correspond to optimal windows of food availability and climate. Breeding and molting are energetically costly activities, and usually there is little overlap between the two (e.g., Payne 1972), with some notable exceptions (Monteiro and Furness 1996). Molt schedules and timing seem to be more flexible elements of the

life cycle and have been described as a buffer in the annual cycle (Helm and Gwinner 2006). During the shedding phase of molt, African Penguins (*Spheniscus demersus*) remain ashore and fast (Cooper 1978). The energetic requirements for the fast and the entire plumage replacement render penguins dependent on high food availability at the time of molt. This is likely to result in conflict in

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energy and time allocation between breeding and molting. 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 nonbreeding phase (Boersma 1975, Randall and Randall 1981, Dann et al. 1992). Penguins are, therefore, potentially useful for studying the interactions between age, transition to sexual maturity, breeding status, and molt cycles.

African Penguins breed throughout the year (Wilson 1985), and chicks are fledged in all seasons. Here, we define “juveniles” as fledged individuals characterized by their gray to gray-brown plumage above and fading into white underparts. Juveniles undergo molt (referred to here as “juvenile molt”) in spring and summer between the ages of 12 and 23 months. The wide range of ages at juvenile molt could be explained by the combination of several constraints: a minimum age of about one year; a seasonal pattern of molt, possibly mediated by photoperiod (and food availability); and a maximum age, determined by plumage wear (Kemper and Roux 2005). During juvenile molt, they attain their characteristic black and white banded adult plumage (Kemper and Roux 2005) and become visually indistinguishable from sexually mature adults (see Fig. 3A). After attaining their adult plumage, African Penguins molt annually (referred to here as “adult molt”); the feather-shedding phase lasts 12.7 ± 1.4 days (Randall and Randall 1981, Randall et al. 1986). Although some African Penguins begin to breed during their third year, most begin to breed during their fourth to sixth years (Whittington et al. 2005; see Fig. 3A).

Series of biweekly (i.e., every two weeks) counts of molting African Penguins in adult plumage have been used to obtain estimates of adult population size in particular localities or regions (Randall et al. 1986; Crawford and Boonstra 1994; Crawford et al. 1999, 2000; Kemper et al. 2001; Kemper 2006). Because sexually immature and mature African Penguins are indistinguishable, estimates of breeding populations can currently be obtained only 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 2006). In addition, not all sexually mature adult African Penguins breed each year (Randall and Randall 1981, Randall et al. 1986, Whittington et al. 1996, Kemper 2006), so the annual peak count of breeding adults underestimates the size of the breeding population.

Here, we analyze the seasonality of molt of African Penguins in adult plumage in Namibia. We use information derived from banded individuals to examine the relationship between age, breeding activities, and timing of molt of adult African Penguins in Namibia and assess whether the duration of the interval between successive molts varies with age. Using our results, we propose a method of estimating the proportion of sexually mature adults using serial molt counts.

METHODS

Molt seasonality.—For the present study, the most sensible biological definition of a year runs between the beginning of September

of one year and the end of August of the following year, because the fewest birds molt between July and September. Seasons are austral.

Counts of molting African 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 biweekly 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, we linearly interpolated actual counts to estimate daily numbers of molting African Penguins for each day of the year, following Underhill and Crawford (1999). We scaled daily totals by dividing by the sum of molting African Penguins in each year and averaged these across years to establish an average seasonal molt phenology for each island.

We described adult molt phenology using Bhattacharya's (1967) method, which allows the splitting of composite distributions into separate normal (Gaussian) distributions (Sparre and Venema 1992, Carmona et al. 1995). We used the parameter estimates thus obtained to fit Gaussian curves to average seasonal molt patterns to calculate mean molt dates within a molt distribution, thus providing a measure of synchrony and an estimate of the contribution of each Gaussian component to the whole year (through summing the distributions). We used the following expression of a Gaussian curve: $F = a \cdot \exp(-(x - b)^2 / 2c^2)$ where F = frequency of molting birds as a function of the date (x), a = the mode (maximum frequency), b = date of the mode (equivalent to the mean date of the distribution), and c = standard deviation (in days) of the molt dates used as a measure of synchrony. To allow comparison of adult molt seasonality of African Penguins in the study area with that in other localities for which it has been described, we calculated the number of individuals molting in every half month and per month as a percentage of the total number of birds molting during the year.

Age and timing of molt.—Between November 1986 and July 2001, 9,292 African Penguins were banded in Namibia. Of these, 8,327 were banded as chicks, just before fledging, 467 were banded in juvenal plumage, and 474 were banded in adult plumage. Age at banding was not recorded for an additional 24 individuals. African Penguins were banded at Mercury, Ichaboe, and Possession islands since 1986, and at Halifax Island since 1990. Methods to determine fledging date and age of individuals banded as chicks, as well as definitions for adjustments of molt records to correspond to the midpoint of molt, follow those described in Kemper and Roux (2005). On average, these adjustments corresponded to 4.8 ± 4.1 (SD) days per record (0.3% of the estimated age at molt). We added records of 89 molting African Penguins of unknown age (those banded in juvenal or adult plumage) to estimate the interval between breeding and molt and to calculate the interval between two successive molts.

We used a weighted moving average algorithm, similar to that used by Summers et al. (1992) and originally devised by Cleveland (1979), to smooth the scatterplot of age against date of molt. Our algorithm differed in that molt dates were expressed as

vectors in a circle representing the year. We used circular statistics (Davis 2002) to estimate the circular analogues of the mean and standard deviation of molt at each age. Suppose that the i th observation was of an individual aged y_i years that was in midmolt 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 $\sim 30^\circ$). For each observation, we calculated $s_i = \sin \theta_i$ and $c_i = \cos \theta_i$. To estimate the circular analogues of the weighted mean and weighted standard deviation of date of molt for individuals aged t years, $w_i = \exp((y_i - t)^2)/W$; we first calculated $W = \sum \exp((y_i - t)^2)$, and then $S = \sum s_i w_i$ and $C = \sum c_i w_i$. Then the mean date of molt for birds aged t is given by $\varphi = \arctan(S/C)$, where the angle φ needs to be back-transformed to a date; the circular measure of dispersion is given by $\nu = (1 - (S^2 + C^2)^{1/2})$ (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, we used circular statistics to compute the mean date of molt and its spread for age classes of African Penguins identified from the smoothed trajectory through the scatterplot.

We examined 266 records of banded African Penguins that bred before and within a year of molt, and for which detailed descriptions of nest contents were available, to calculate the interval between breeding and molt and the interval between molt and breeding. We adjusted breeding records to correspond to the estimated beginning of incubation to indicate the onset of breeding. 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 resighting records of breeding banded birds. For the other 232 breeding records, we back-estimated dates of egg laying from time of first detection as judged from the approximate age of the nest contents noted in the resighting record, following Kemper and Roux (2005) as detailed in Table 1.

Interval between molts.—We calculated the interval between molts for 117 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.—We classified as potential breeders (aged ≥ 5 years at molt) or pre-breeders (aged < 5 years at molt) those banded individuals for which we knew both age and date of molt. To estimate the proportion of breeders molting on any given date, we fitted a sine function. The modeling was done as a generalized linear model with a binomial distribution and logistic link function. We applied this function 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 at any time of the year, but with a clear minimum in August–September at all localities (Fig. 1). With the exception of Possession Island, a bimodal molt seasonality was evident, with a major peak in autumn (April–May) and a minor peak in summer (December–January) (Table 2 and Fig. 1). At Possession Island, molt seasonality was less clearly defined; a large proportion of birds molted during winter.

We fitted Gaussian curves to the summer and autumn peaks (Table 3 and Fig. 2). Curves fitted to autumn molt patterns had small standard deviations (range: 15.8–25.0 days), which indicates that autumn molt was well synchronized. Those fitted to summer molt patterns had a large standard deviation (range: 32.1–66.6 days), which indicates 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 difference between the summer and autumn peak values was greatest at Mercury Island, intermediate at Ichaboe and Possession islands, and smallest at Halifax Island. Fewer than half the African Penguins molting at Possession Island did so in summer and autumn.

Age and timing of molt.—Between August 1992 and October 2003, 757 African Penguins banded as chicks at the four Namibian islands were later recorded during adult molt. Of these known-age individuals, 598 were recorded molting once, 131 recorded twice, 23 recorded three times, 5 recorded four times, and 2 recorded five times, for a total of 959 molt records. Of birds banded in juvenal or adult plumage, 89 were subsequently recorded molting. Of these,

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 (and percentage of all cases)		Estimated age (days) since beginning of incubation	Number 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
Quarter-shed chick	1	(0.38)	79–88	83
Half-shed chick	3	(1.13)	89–98	93
Three-quarters-shed chick	6	(2.26)	99–108	103
Fully shed chick	20	(7.51)	109–128	118
Total	232	(87.22)		

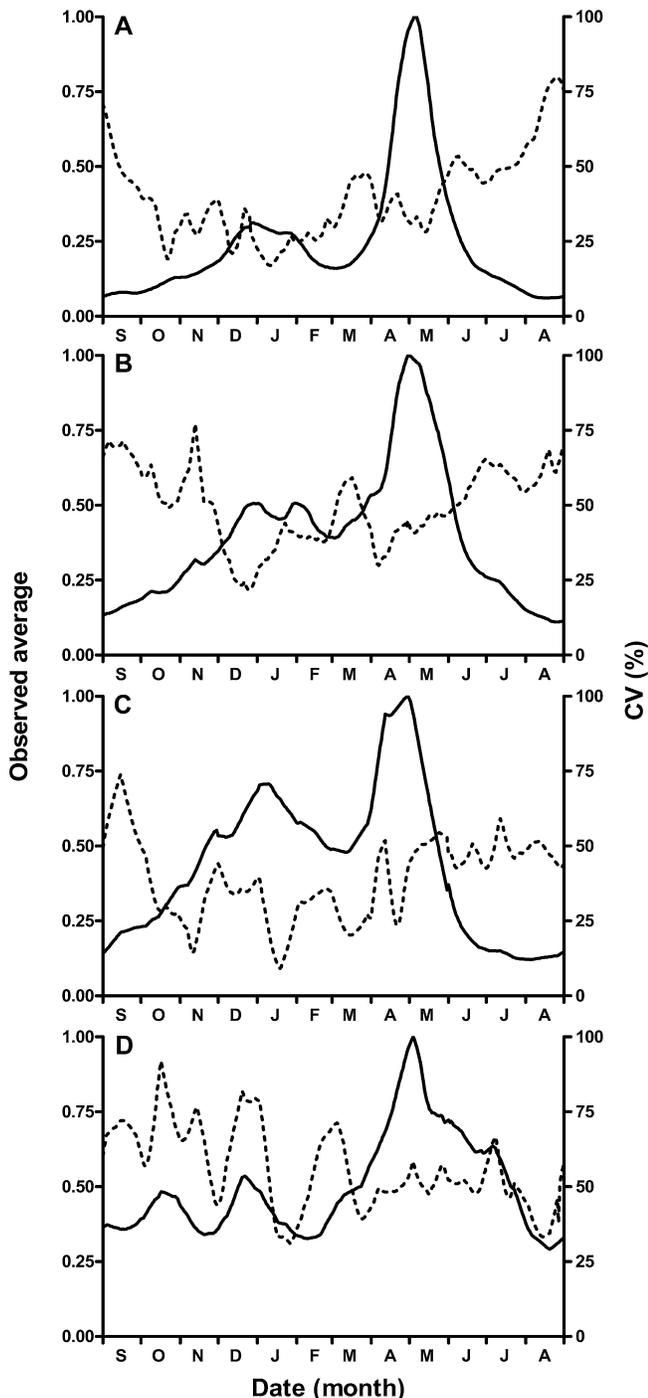


FIG. 1. Standardized, average seasonal molt patterns of African Penguins in adult plumage (solid line) and associated coefficients of variation (dashed line) at the four main breeding localities in Namibia: (A) Mercury, (B) Ichaboe, (C) Halifax, and (D) Possession islands.

molt was recorded once in 72 individuals, twice in 13 individuals, three times in 1 individual, four times in 2 individuals, and five times in 1 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 undergoing its first adult molt was 1.8 years. The oldest bird recorded molting was nearly 17 years old.

Young birds generally molted earlier in the year than older birds, with a concentration of molt dates in December–January (Fig. 3B, C). The circular dispersion of molt dates varied with age (Fig. 3D). Birds aged two to three years showed little dispersion of molt dates (range: 0.21–0.32). Dispersion increased to a maximum of 0.99 at age 4.8 years, which indicates a random pattern of molt dates at this age. The dispersion then decreased to 0.17 at age 7.70 years, with secondary dispersion peaks of 0.74 and 0.49 at ages 6.05 years and 7.10 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 >10 years are attributable to small sample sizes. Adult molt was recorded for 502 banded African Penguins younger than four years; using circular statistics, their mean molt date was 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 African Penguins aged six years and older was 5 May, circular dispersion 0.37. African Penguins aged five and six years, which we 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 African Penguins aged ≥ 10 years (mean = 2 May, with a relatively small circular dispersion of 0.36; $n = 62$).

The interval between the onset of breeding within 12 months of molt and the estimated date of midmolt for 135 birds averaged 191 ± 66 (SD) days (range: 19–350 days; Fig. 4A). Ninety-two birds (68%) in this sample molted between March and the end of May. The interval between midmolt and the beginning of egg laying, within 12 months following molt, for 131 birds averaged 123 ± 60 days (range: 22–350 days; Fig. 4B). Altogether, 86 birds (66%) in this sample molted between March and the end of May. Some 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 individuals (Fig. 4A).

Interval between molts.—A total of 117 individuals provided 137 records of intervals between successive molts. The shortest recorded interval between two molts was 280 days. From this observed interval, we assumed $(280 \times 2) - 1 = 559$ days to be the longest possible interval between successive molts. The longest recorded interval was 557 days. Following this assumption, we suspected that the 10 records of molt intervals between 560 and 730 days may have involved an unobserved molt, so we did not include these in the analysis. Mean molt interval was 366.9 ± 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 ≥ 400 days were from birds younger than eight years, with long (>480 days) and short (<315 days) molt intervals 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 ± 27.1 days and a range of 344–401 days.

For seven individuals banded as chicks and one individual banded in juvenal plumage, molt was recorded more than three

TABLE 2. Average peak half-month or month of molt (percent 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%)

times. These molt dates show that younger birds tended to molt earlier than older birds. There was some individual variation (Fig. 6). The molt dates of these few birds match the pattern observed in Figure 3B and illustrate the change from summer to autumn molt with age within individuals.

Estimates of breeding population size from molt phenology.—

Both age and calendar date of midmolt were known for 959 individuals. On the basis of 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 , and $P < 0.001$ for the constant; 0.125, -15.5 , and $P < 0.001$ for the sine term; and 0.124, 2.95, and $P = 0.003$ 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 African Penguins aged ≥ 5 years ranged from 0.27 (Halifax Island, 2004) to 0.56 (Possession Island, 2000). On average, we estimated that between 37% and 48% of the African Penguin population in adult plumage in Namibia was five years or older (Table 4).

DISCUSSION

In Namibia, molt seasonality of African Penguins in adult plumage was bimodal, with a major peak during autumn and a minor 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 seasonality at Possession Island being less clearly defined than that at the other three islands.

Adult-plumaged African Penguins younger than four years molt in early January, at the same time as juvenile African Penguins (Kemper and Roux 2005). Birds older than six years molt, on average, four months later in early May. For birds between four and six years, molt tends to be either early, in the January peak with the juvenile African Penguins, or late, in the May peak with the breeding adults. These are likely to be individuals making the transition from nonbreeder to breeder, this transition coinciding with a marked peak in dispersion of molt dates around age five (Fig. 3D). However, although younger birds tend to molt earlier than older birds, there is individual variation, which cannot be explained by age alone.

By contrast, at all South African breeding localities for which data are available, molt of African Penguins in adult plumage is

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 split into summer and autumn Gaussian components.

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

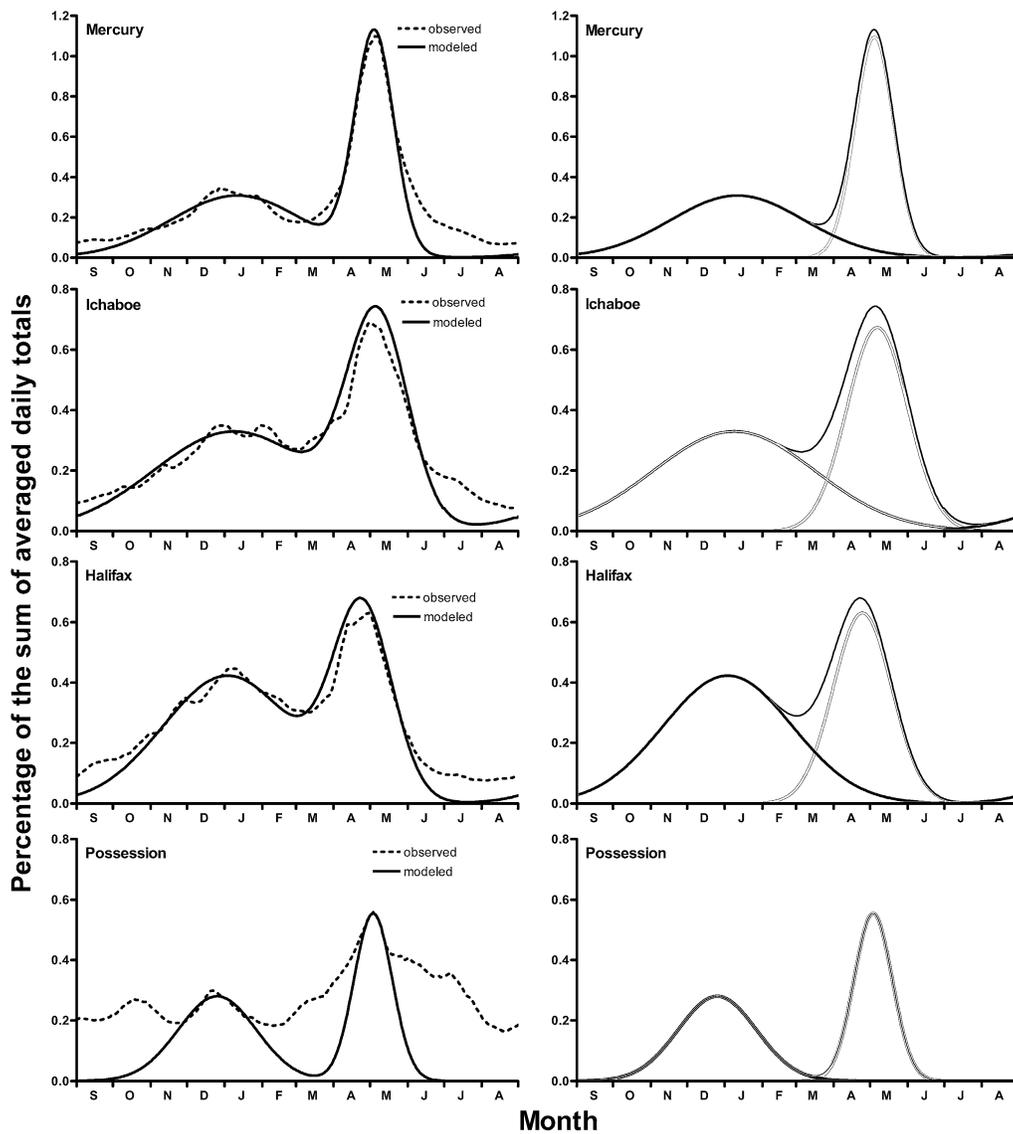


FIG. 2. Gaussian curves fitted to describe standardized, average seasonal molt phenology of African Penguins in adult plumage at the four main breeding localities in Namibia. Graphs on the left show smoothed observed and modeled molt patterns; graphs on the right show how modeled patterns were derived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

monomodal, is well synchronized around a summer peak (between November and January), and coincides with the juvenile molt season (Randall and Randall 1981, Wilson 1985, Underhill and Crawford 1999, Hemming 2001, Wolfaardt and Nel 2003, Crawford et al. 2006). Hence, molt seasonality in South Africa does not appear to be influenced by age.

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). A breeding-success study of African Penguins in Namibia, during which the fates of 2,780 nesting attempts were followed between 1996 and 2004, revealed that egg laying date was the most important determinant of nest success. Nests initiated at the end of October at Mercury, Ichaboe, and

Halifax islands, and about one month earlier at Possession Island, had a higher probability of survival than at any other time of the year (Kemper 2006). Successful chicks from nests initiated during October and November fledge during January and February, extending into March (Kemper 2006). Taking a pre- and postmolt fattening period at sea of approximately 30–40 days each into account (Randall and Randall 1981) leaves a relatively narrow window (April and May) for breeding birds in Namibia to molt before the next breeding wave begins. Here, most of the birds that were recorded breeding during the 12 months preceding and the 12 months following molt molted between March and May. By contrast, in the Western Cape, South Africa, peak breeding is primarily during autumn and winter (Cooper 1978; Randall and

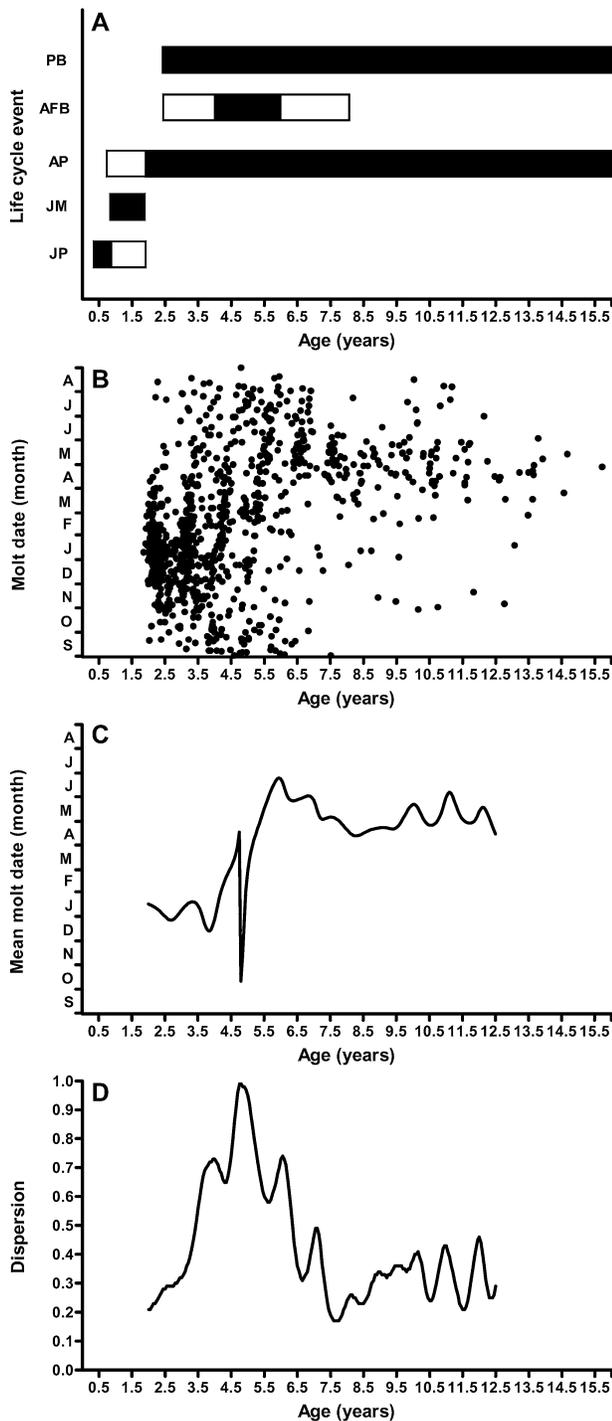


FIG. 3. Relationship between age and date of molt of African Penguins in adult plumage in Namibia. (A) Chronology of the main events in the life cycle show the correspondence with timing and variability of molt; white bars indicate range, and black bars indicate the majority of the birds; JP = juvenal plumage phase, JM = juvenile molt, AP = adult plumage phase, AFB = age at first breeding, and PB = potential breeders. (B) Molt records derived from banded individuals. (C) Mean molt date calculated from molt records from banded individuals. (D) Dispersion (see text). The year runs from 1 September to 31 August.

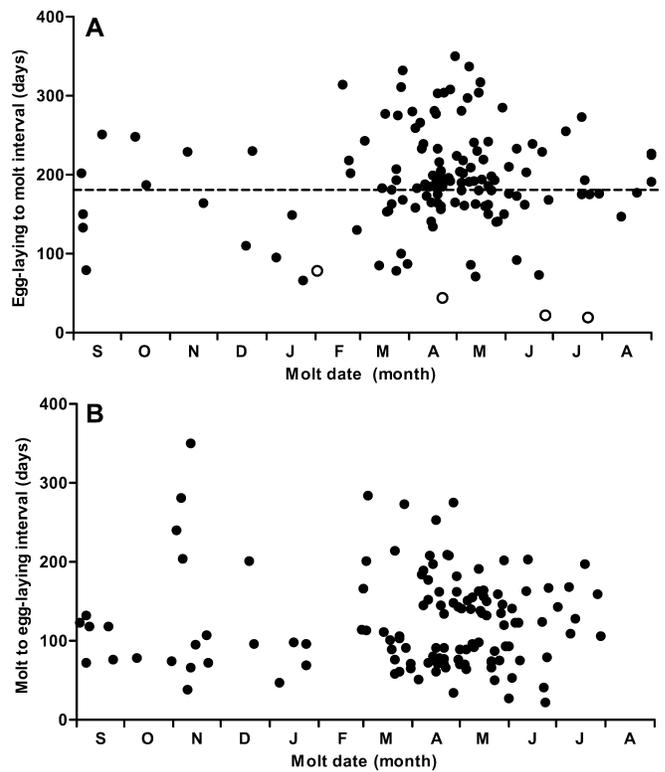


FIG. 4. Intervals between (A) egg laying and molt (open circles represent individuals molting while breeding, and dotted line shows interval limit below which it is unlikely for a breeding attempt to be successful before molt) and (B) molt and egg laying within 12 months of molt of banded African Penguins in Namibia.

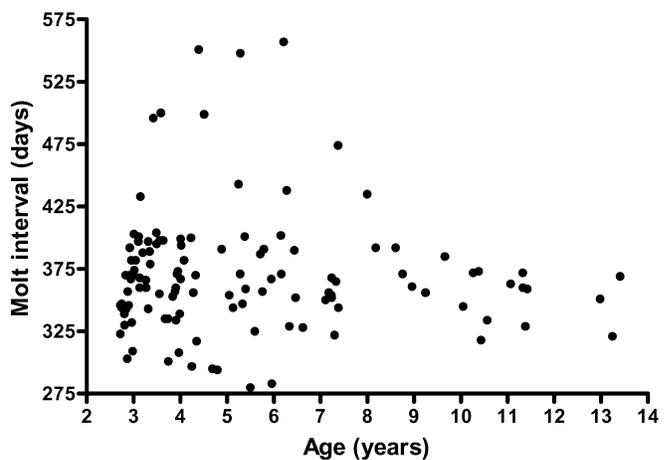


FIG. 5. Relationship between age at successive molt and the length of the interval between molts from records of banded adult African Penguins in Namibia.

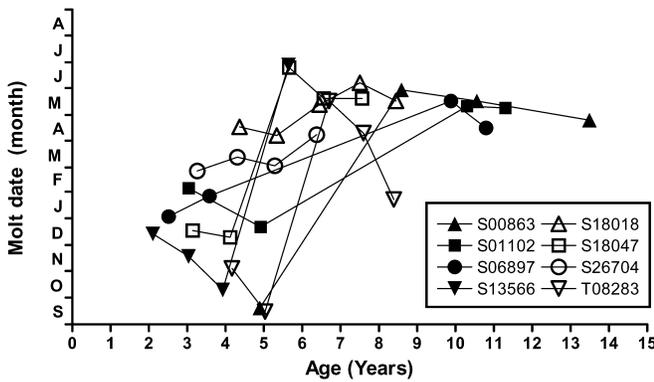


FIG. 6. Individual molt histories of African Penguins, banded as chicks in Namibia, that were subsequently recorded molting four or more times. Molt was not necessarily observed in successive years.

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). The timing of breeding at these localities allows most birds to molt during summer.

Like juvenile African Penguins, sexually immature individuals (and perhaps sexually mature individuals that have not 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 breeding activities.

Birds molting earlier than 150 days after egg laying were most likely to be failed breeders, because a successful breeding attempt

takes ~120 days (Kemper 2006) and an additional 30–40 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 a failed attempt or second clutch after a successful first attempt) was not recorded before molt. Randall and Randall (1981) found that long molt intervals at St. Croix Island were the result of extended breeding activities, whereby individuals would delay molt until the chicks had fledged. In that case, molt the following year was at the usual time, resulting in short molt intervals.

African Penguins aged five years, and thus considered young breeders, molted 24 days later, on average, than experienced breeders aged ≥ 10 years. This tendency may be the result of young and inexperienced breeders taking longer to initiate a breeding attempt or to fledge their chicks (e.g., Coulson 1966, De Forest and Gaston 1996, Daunt et al. 2001). Alternatively, they could be more prone to 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.

Evidence of deferred molt attributable 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). Humboldt Penguins (*S. humboldti*) in adult plumage in Chile molt in February after fledging chicks in January, about a month later than juvenile individuals (Simeone et al. 2002). Nonbreeding Galapagos Penguins (*S. mendiculus*) molted before breeding adults when food was plentiful (Boersma 1977). Reilly and Balmford (1975) reported a Little Penguin (*Eudyptula minor*) molting late at Phillip Island, Australia, after having twice bred successfully in that season.

An overlap in breeding season and optimal molt season might lead to lower breeding success. Second clutches and replacement clutches will have less chance of success if the parent is already delaying molt. In Namibia, molting African Penguins simultaneously incubating eggs or raising chicks are infrequent but possibly more common than in South Africa (A. J. Williams pers. comm.). Given that molting birds are not able to feed but 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 insufficient time to increase fat between its previous breeding attempt and molt.

The mean interval between successive molts calculated for African Penguins at St. Croix Island was 368.3 ± 24.5 days ($n = 152$; Randall and Randall 1981). Our results agree with those of Randall and Randall (1981), the average molt interval being almost exactly one year. The longest molt interval recorded by Randall and Randall (1981) was 444 days, and the longest recorded by Cooper (1978) was 362 days ($n = 11$). Feather wear appears to be a factor limiting the length of the molt interval, 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. The different timing of molt of young (nonbreeding) birds and older (breeding) birds suggests that during the transition from nonbreeder to breeder, molt intervals either become shorter or

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	Four islands 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

(more likely) longer. The transition direction, and whether this happens in a stepwise or a gradual manner, is uncertain and may 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, not attributed to previous breeding success and timing of breeding but rather to food availability, 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 further investigation.

Estimates of breeding population size from molt phenology.—

The phenology of the molt season of African Penguins in adult plumage in Namibia appears to comprise a combination of non-breeding birds molting during summer and breeding birds molting during autumn. A sexually mature bird 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 breed, breeders that have not bred that year, and failed breeders or those that have bred successfully early and have not bred a second time in the season. By contrast, autumn molt was generally highly synchronized and seemed mainly to involve birds that were breeding in mid-summer and were, therefore, forced to delay molt.

Breeding activities may not be synchronized between colonies at a particular breeding locality—for example, at Halifax Island, where breeding activities across the island were less synchronized than within separate colonies there (Kemper 2006). If individuals molting in autumn are breeders delaying molt, molt synchrony patterns at a locality may reflect breeding synchrony patterns. We observed this trend at Halifax Island (J. Kemper pers. obs), where individuals from a particular colony molt at the same time. However, we could not quantify differences in the timing of molt between colonies here, because many individuals tend to molt away from the colonies, usually at the landing beaches.

Mercury Island has a higher proportion of autumn-molting African Penguins than Ichaboe or Halifax islands, which implies 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 have declined dramatically over the past 50 years (Kemper et al. 2001, Kemper 2006), or that it is highly variable and possibly dictated by local (feeding) conditions. Alternatively, poorly synchronized adult molt at Possession Island may result from highly variable timing of breeding activities there (Kemper 2006).

The proportion of African Penguins estimated from banded individuals to be five years or older is similar to that estimated by the proportion 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; the modeled proportion of autumn-molting birds is, therefore, clearly an underestimate. It is likely that estimates based on adult molt phenology are underestimates and that African Penguins of breeding age but molting in spring, summer, or winter account for these discrepancies.

Proportionally few juvenile African Penguins molt at Possession Island (Kemper 2006), which suggests that few young birds are present on the island. Breeding success at Possession Island was higher than that at the other three breeding localities in Namibia (Kemper 2006); this was thought to possibly indicate an older, experienced breeding population there. The poorly defined summer molt peak and the high proportion of adults molting in autumn at Possession Island support this hypothesis. Conversely, the comparatively small proportion of African Penguins molting in autumn at Halifax Island supports findings by Kemper (2006), where 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. 2001, Kemper 2006) could, therefore, be attributable to an influx of young adults. Estimates of the proportion of African Penguins estimated to be five years or older, derived from banding and recapture records and molt phenology in the present study, were lower than those derived from an age structure constructed for the region (Kemper 2006). This could be attributable to potential breeders deferring breeding. If an African Penguin of breeding age does not breed, it could molt during midsummer, 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 indicate that a low proportion of potential breeders in the population actually breed.

The proportion of breeders to nonbreeders 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 African Penguins of breeding age in a population. The reliability of this method could be improved through a better understanding of the relationship between breeding activities and molt phenology—for example, by obtaining accurate breeding histories for banded individuals. In addition, the proportion of potential breeders that defer breeding needs to be ascertained to ensure accurate estimates. We are not aware of similar quantitative studies, and our use of circular statistics to relate age to the timing of molt could be helpful for the analysis of molt in other bird species.

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