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Of squeezers and skippers: factors determining the age at moult of immature African Penguins *Spheniscus demersus* in Namibia

JESSICA KEMPER[1,2*] & JEAN-PAUL ROUX[3]
[1]*Avian Demography Unit, University of Cape Town, Rondebosch 7701, Cape Town, South Africa*
[2]*African Penguin Conservation Project, c/o Ministry of Fisheries and Marine Resources, PO Box 394, Lüderitz, Namibia*
[3]*Ministry of Fisheries and Marine Resources, PO Box 394, Lüderitz, Namibia*

We used banding and resighting records of 391 African Penguins *Spheniscus demersus* banded as chicks and later resighted during immature moult to explain the roles of date of fledging and age at moult in determining the season of moult and its timing within the season. Breeding was continuous, but immature moult occurred mainly during spring and summer. Age at immature moult extended over 11 months, from 12 to 23 months after hatching. Birds that fledged during summer and early autumn generally moulted during the next moult season (squeezers), whereas birds that fledged in late autumn, winter and spring skipped the next moult season to moult only the following season (skippers). There was a significant relationship between age at moult and moult date, with young birds moulting later in the season than older birds. The age at moult of immature birds appears to be constrained by minimum age, moult seasonality and plumage wear. Birds that fledged over nearly 2 years moult during one season. Counts of moulting immature African Penguins have not been used to estimate year-class strength and post-fledging survival owing to the wide range of ages at immature moult. Our results provide the means of assigning recruits to specific age groups.

The African Penguin *Spheniscus demersus* breeds along the southern African coast, between Hollamsbird Island, Namibia (24°38′S, 14°31′E), and Bird Island, Algoa Bay, South Africa (33°50′S, 26°17′E) (Crawford & Whittington 1997). African Penguins fledge once all down has been replaced by a grey and white, immature plumage, which lacks the adult black and white banded pattern and the characteristic head coloration pattern. After fledging, the Penguins spend most of their time at sea until they return to land for moulting when they acquire their first adult plumage. During this time, the worn plumage becomes a mottled brown. Some immature birds undergo a partial head moult at sea (Ryan *et al.* 1987). Once immature Penguins have moulted, they are indistinguishable from adults although they generally do not breed until they are 3 years or older (Crawford *et al.* 1999, Whittington *et al.* in press).

Moult in the adult African Penguin takes place at yearly intervals (Randall & Randall 1981). Serial moult counts can therefore be used to estimate the population size of adult-plumaged birds each year (Randall *et al.* 1986, Underhill & Crawford 1999, Crawford *et al.* 2000, Kemper *et al.* 2001). Counts of moulting immature birds have been used to monitor trends in numbers at some colonies (Crawford *et al.* 1995, 1999, 2000). Although immature survival is a key component in understanding the population dynamics of long-lived seabirds, including the African Penguin, estimates of immature survival have thus far only been obtained from banding and resighting records. Immature Penguins have been found to moult at ages between 12 and 22 months (Randall 1989). Therefore, counts of immature moulting birds cannot be related directly to post-fledging survival or year-class strength, defined here as the contribution of a given year class to recruitment into the adult population. The aims of this study are to examine the age at moult of immature African Penguins in Namibia, and to determine the factors that underlie its interindividual variability and the phenology of the immature moult cycle. The understanding of these factors could provide a

*Corresponding author.
Email: Spheniscus03@yahoo.co.uk

tool for interpreting counts of moulting immature Penguins in terms of year-class strength, immature survival and recruitment.

METHODS

Between May 1991 and April 2002, 6237 African Penguin chicks, from the early stages of down-shedding to the completely feathered stage, were banded prior to fledging in Namibia: at Mercury Island (25°43′S, 14°50′E) since 1992; Ichaboe Island (26°17′S, 14°56′E) since 1991; Halifax Island (26°37′S, 15°04′E) since 1997; and Possession Island (27°01′S, 15°12′E) since 1991. These islands support 97% of the Namibian African Penguin population (Kemper *et al.* 2001). Most birds, for which the exact fledging dates were not known, were banded as fully feathered chicks. For these, the day after the last resighting of the bird, or the day after banding if the bird was not resighted before fledging, was assumed to be the fledging date. For chicks originating from monitored nests, the fledging date was known. The average age at fledging of 585 chicks monitored between hatching and fledging in Namibia (± se) was 84 days (± 0.4) (J.K. pers. obs.). This was used as the age of all fledglings in the dataset. Systematic searches for banded Penguins were made at these localities in recent years. The numbers stamped on Penguin bands are large enough to be read in the field with binoculars or a spotting scope without having to recapture the bird. Data were partly obtained from the South African Bird Ringing Unit, SAFRING, and were supplemented with data collected by J.K. and island personnel from the Ministry of Fisheries and Marine Resources, Namibia. Records involving rehabilitated birds were not included because rehabilitation has been reported to alter the moult cycle in the African Penguin (Wolfaardt & Nel 2003). In most cases, mass at banding was also recorded.

The duration of moult for both adult and immature African Penguins is approximately 3 weeks (Randall & Randall 1981), with the feather-shedding and replacement stage of moult lasting on average 12.7 days (Randall 1989). During moult, Penguins are confined to land, usually to one of the breeding localities. The date at the mid-point of the feather-shedding phase of the immature moult was chosen to calculate the age at moult. Immature birds were recorded at different stages of moult, from the time they returned to land after fattening at sea to the end of the feather replacement phase. For birds for which the mid-moult point was not observed, moult dates were adjusted to correspond to the mid-point of the feather-shedding period as follows:

(1) Ten days were added for birds that had returned from sea and were showing signs of feathers loosening, but not yet shedding (23.8% of cases).
(2) Six days were added to the moult date of birds shedding their first feathers (2.3%).
(3) Three days were added for birds that had shed a quarter of their feathers (4.8%).
(4) Three days were subtracted for birds that had shed three-quarters of their feathers (23.0%).
(5) Six days were subtracted for birds that were shedding their last few feathers (9.0%).
(6) Ten days were subtracted for birds with completely replaced plumage (12.5%). These birds still had flakes of moulted feather sheaths on their bodies, distinguishing them from birds that moulted some days or weeks ago.

On average, these adjustments corresponded to 5.1 days (± 0.2) per record (1.1% of the estimated age at moult) and made no difference to the final conclusions. To investigate seasonal patterns, seasons were defined as: summer = January–March, autumn = April–June, winter = July–September and spring = October–December. Means are given ± se and first and last quartiles (Q_1 and Q_3) were computed.

RESULTS

Of the 6237 fledglings banded at the four main Namibian breeding localities, 391, excluding rehabilitated birds, were resighted in Namibia during immature moult; 49% of these did not moult at their natal colonies. Of those moulting elsewhere, 69% moulted at a locality north of their natal one.

Although there is an increase in fledging activity in January and February, Penguins in the sample fledged throughout the year (Fig. 1a). Nearly two-thirds of the birds fledged during spring (20.0%) and summer (45.0%), with 16.6% of birds fledging during autumn and 18.4% during winter. Moult was far more seasonal than fledging, with 93.1% of immature Penguins moulting during spring (43.7%) and summer (49.4%) (Fig. 1b). The mean moult date was 6 January (± 2.5 days), and median moult day was 3 January. Only 4.3% of the birds moulted during autumn and 2.6% during winter. The proportions of fledglings and moulters differed significantly between seasons ($\chi^2 = 110.49$, $df = 3$, $P < 0.0001$). The results are consistent with the fledging and moulting seasonality patterns for the entire Namibian

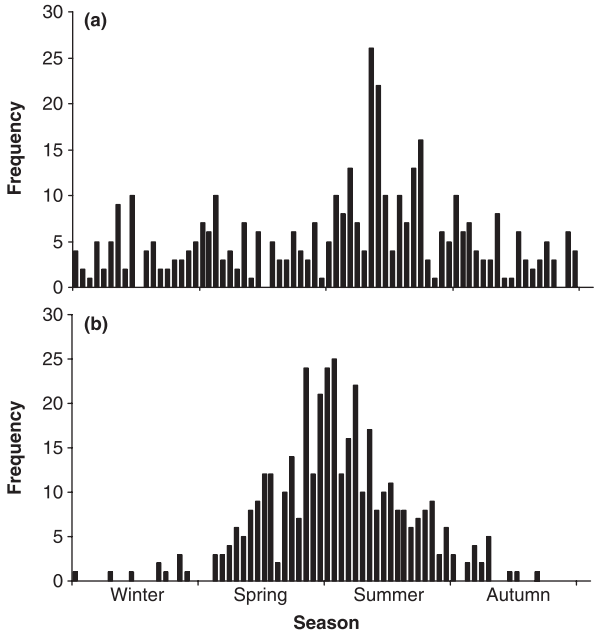

Figure 1. Seasonality of (a) fledging and (b) moulting of 391 African Penguins grouped in periods of 5 days starting on 1 July (beginning of winter).

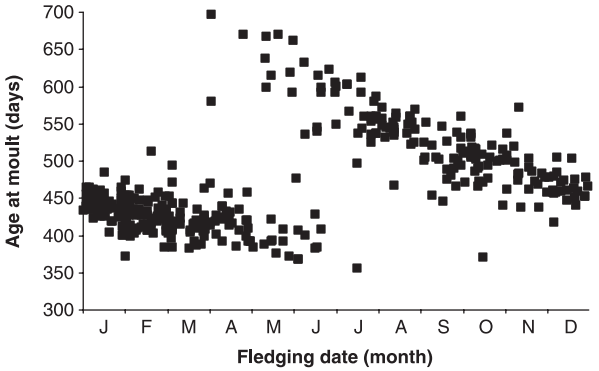

Figure 2. Relationship between fledging date and age at immature moult.

population. Proportions of moulters in each season did not differ between our sample and the total immature moulters (n = 28 315) monitored on all four islands over six seasons, between 1997 and 2003 (χ^2 = 1.85, df = 3, P > 0.5).

Immature Penguins in the sample moulted between the ages of 12 and 23 months (Fig. 2, Table 1). The mean age at moult was 15.4 months. Only 16 Penguins (4.1%) in the sample were older than 600 days at moult and only one Penguin (0.3%) was younger than 365 days at moult.

All but one Penguin which fledged during winter skipped the next moult season and moulted the following year (Fig. 3a). This bird squeezed into the next moult season and is the youngest bird in the dataset (moulting on 15 April, aged 356 days). All Penguins fledged during spring skipped the next moult season to moult in the following season (Fig. 3b). Spring-fledged birds were on average younger at moult than winter-fledged birds (df = 130, t = 8.76, P < 0.0001). All birds fledged during summer moulted during the next moult season (Fig. 3c). Penguins fledged during summer were 53 days younger on average than spring-fledged birds (df = 111, t = 13.91, P < 0.0001). Birds fledged in autumn followed a bimodal age distribution at moult (Fig. 3d): they were either relatively young or relatively old at first moult. This indicates that they either moulted in the coming moult season or skipped a season to moult only during the following season. Birds fledged during April generally still moulted roughly a year later (Fig. 2). Only three out of 29 individuals skipped that moult season and only moulted during the following moult season. Of the 36 birds fledged during May and June, 20 squeezed into the next moult season. Sixteen birds skipped that season to moult in the following moult season.

There was a significant relationship between age at moult and moult date, with young birds generally moulting later in the season than older birds (r^2 = 0.256, df = 390, F = 133.57, P < 0.0001). Figure 4

Table 1. Age at moult per season of fledging. Squeezers and skippers were separated in autumn-fledged birds.

		Age at moult (days)				
Fledging season	n	Mean ± se	Median	Range	Q_1	Q_3
Winter	72	537 ± 5.0	543	356–613	521	560
Spring	78	483 ± 3.5	481	371–572	462	505
Summer	176	430 ± 21.3	430	373–513	415	443
Autumn (squeezers)	46	411 ± 3.8	410	368–477	393	425
Autumn (skippers)	19	616 ± 10.6	616	536–697	593	650
Total	391	467 ± 3.2	450	356–697	422	505

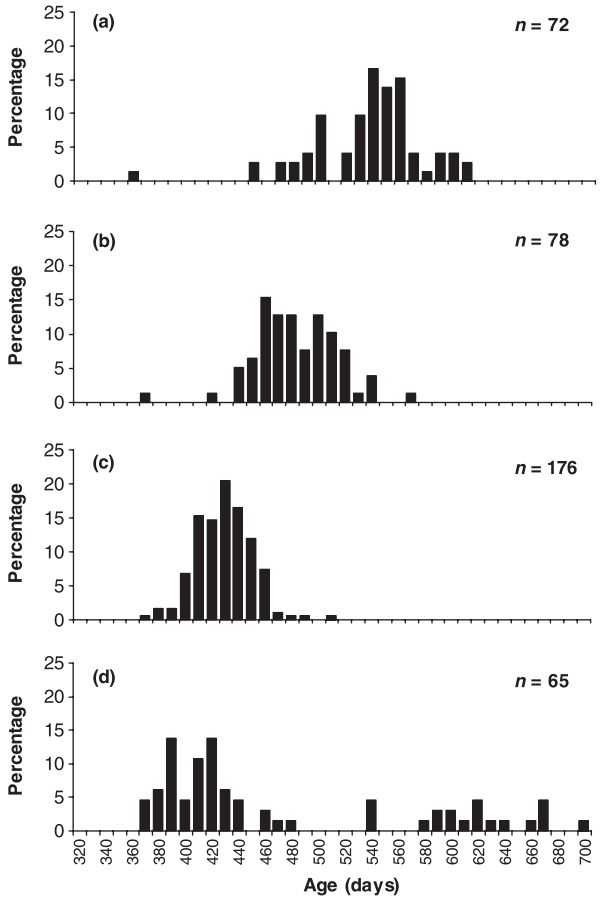

Figure 3. Age distribution at immature moult for African Penguins fledged during (a) winter, (b) spring, (c) summer and (d) autumn (grouped in age classes of 10 days).

shows the age frequency distribution of birds moulting before and after the median moult date of 3 January. Birds of all ages moulted before 3 January. Age in this group ranged from 371 to 697 days (n = 197, mean = 501 ± 4.7 days). Birds moulting after 3 January were almost exclusively young birds, ranging in age from 356 to 572 days (n = 194, mean = 433 ± 2.4 days). Birds moulting after 3 January were significantly younger than those moulting before 3 January (df = 290, t = 12.77, P < 0.0001).

Mass at banding was available for 219 Penguins and ranged from 1750 to 4000 g (mean = 2758 ± 26.0 g). There was no difference in mass at fledging between seasons (df = 218, F = 0.77, P = 0.512). Overall, mass at fledging did not influence date of moult (r^2 = 0.0093, df = 218, F = 2.04, P = 0.154) nor age at moult (r^2 = 0.0024, df = 218, F = 0.53, P = 0.467). Between 25 April and 25 July, the period of greatest overlap of squeezers and skippers, 57

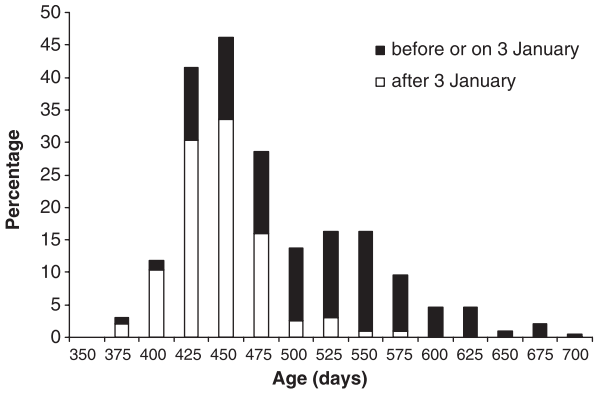

Figure 4. Age distribution of immature African Penguins moulting before and after the median moult date of 3 January.

birds fledged (Fig. 2). For 33 of those, mass was recorded. Fledging mass did not determine whether a bird squeezed or skipped (r^2 = 0.0221, df = 33, F = 0.72, P = 0.401).

DISCUSSION

The African Penguin has a poorly defined breeding season, although there are breeding peaks specific to breeding localities or regions (Randall & Randall 1981, La Cock *et al.* 1987, Crawford *et al.* 1995, Whittington *et al.* 1996). A high incidence of breeding failure leads to clutch replacement and in some cases a second clutch is laid after successful breeding (Randall & Randall 1981). This results in chicks being fledged throughout the year (Wilson 1985). By contrast, immature moult is seasonal and is centred around mid-summer throughout the species' range (Wilson 1985, Randall *et al.* 1986, Randall 1989, Underhill & Crawford 1999, Crawford *et al.* in press). Therefore, immature African Penguins, which fledge throughout the year but moult only during part of the year, cannot moult at a specific age, unlike adult Penguins which moult at yearly intervals. As a consequence, chicks fledged during any given 12-month period will moult during two different moult seasons.

In our sample, Penguins moulted at ages from 12 to 23 months, a range of 11 months. These results agree with those obtained by Randall (1989) for Bird Island, Algoa Bay, South Africa, where the age at first moult was between 12 and 22 months.

Our results suggest that the main factor that determines in which season an immature Penguin will moult is its age at the next moult season. If it reaches a minimum age of about a year by the end

of the next moult season, it will squeeze in a moult. However, if the bird is younger than that, it will only moult in the following season, when it will be much older, i.e. a skipper. Therefore, in any given moult season, the youngest birds are those fledged during the previous summer as well as some of the birds fledged during the previous autumn. Conversely, the oldest birds are the ones fledged during the winter preceding the last moult season as well as some birds fledged during that autumn.

Within a moult season, the youngest birds (squeezers) moulted mainly during the second half of the season, whereas all the birds older than 572 days (skippers) moulted in the first half of the season. This seemingly counterintuitive result of the youngest birds moulting later in the season is explained by the interaction between two constraints facing an immature bird about to moult: the minimum age required and the seasonality of the moulting cycle. This result implies that differences in the relative proportions of skippers and squeezers in a population will influence the phenology of the moult cycle. At Robben Island (33°48′S, 18°23′E), South Africa, most immature Penguins moult between November and January, as found in this study, but there is a secondary peak in February and March (Underhill & Crawford 1999). These authors attributed this late secondary moult peak to replacement clutches. However, following our findings it is likely that the birds moulting late in the season would in fact be younger birds originating from the beginning of the past breeding season, whereas the main moult peak would consist of birds from the preceding season.

In their study of immature Penguins displaying adult head plumage patterns, Ryan *et al.* (1987) concluded that immature head moult is a signal of social status, reducing aggression from adults and acceptance into adult feeding groups. Because of the potentially high cost of replacing feathers at sea, only the fittest immature birds are thought to be able to afford it. During the 2003/04 immature moult season on Halifax Island, nine of ten moulting immature birds with adult head plumage patterns completed their moult before 30 November (J.K. pers. obs.), suggesting that these were old birds. There seems to be a smaller proportion of immature birds displaying head moult in Namibia than in South Africa (Ryan *et al.* 1987, J.K. pers. obs.). This agrees with the likelihood that immature moulters might, on average, be older in South Africa than in Namibia. Thus, the occurrence of adult head moult could be a function of age.

Although mass at fledging probably influences survival (Randall & Randall 1981), it did not influence age at moult, date of moult nor which moult season a bird would moult in. Mass during the moult season, not at fledging, might be more important in determining whether an autumn-fledged bird squeezes or skips.

Within the genus *Spheniscus*, only the Magellanic Penguin *Spheniscus magellanicus* has a well-defined breeding season. Moult of immature birds takes place in January and February and is well synchronized (Boersma *et al.* 1990). The timing of breeding of the Galapagos Penguin *Spheniscus mendiculus* is erratic and unpredictable (Boersma 1977, 1978). Moult generally takes place prior to, and during, breeding (Boersma 1977), but information on immature moult synchrony and age at immature moult is lacking. The Humboldt Penguin *Spheniscus humboldti* breeds throughout the year (Cheney 1998). The moult of immature birds in the wild is poorly documented. Captive immature Humboldt Penguins showed a similar moulting pattern to that observed here (Kojima 1978, Scholten 1989). Chicks hatched in spring moulted in the following year, aged just over 1 year. Chicks hatched in winter either moulted during the next summer or moulted only in the following summer. Age at immature moult ranged from 7 months to over 18 months after hatching.

Only 12 Penguins in our sample moulted when older than 20 months. By that time the plumage tends to be badly worn, and prone to a loss of waterproofing. This, in turn, would cause the bird to starve, because it is no longer able to spend long periods at sea building up fat reserves for the moult. All old birds, including those older than 20 months, moulted during the first half of the moult season. No birds older than 572 days (or almost 19 months) moulted during the second half of the moult season. This pattern implies that by then all old birds had moulted, or that any birds older than 19 months, which had not moulted during the first half of the moult season, did not survive.

If worn plumage limits maximum age at first moult it is possible that skippers have a lower chance of survival if their plumage becomes too worn before moult. If so, autumn-fledged skippers are more likely to have a lower probability of survival into adult plumage than birds fledged in any other season. One Penguin, hatched on Halifax Island on 23 June 2000, illustrates this point. It was found with very worn plumage and close to starvation on 29 January 2002,

aged 19 months. It is probable that the bird was unable to fatten up for moult owing to lack of insulation. The Penguin was subsequently taken in for rehabilitation and finally moulted in captivity in April 2002, aged 22 months. It is unlikely that it would have survived in the wild. Plumage wear constrains the maximum possible age (of about 22 months) at which an immature Penguin can moult.

Randall *et al.* (1986) found that the incidence of immature birds moulting at localities other than their natal ones was minimal. Crawford *et al.* (2000), by contrast, suggested that young birds, free from breeding constraints, have the flexibility to move from their natal locality to places where feeding conditions are more favourable. This may indeed be the case, with food quality and abundance considered better at the northern Penguin breeding localities in Namibia (Crawford *et al.* 2001). Although the moulting of immature Penguins banded as chicks in Namibia at localities outside Namibia was not investigated in this study, it is likely to be infrequent as Randall *et al.* (1987) and Whittington (2002) reported minimal movement of young birds from Namibia to other regions. The interpretation of immature moult counts might therefore not be accurate for individual colonies or localities, but nevertheless will be valid at a regional scale.

As breeding is continuous, discrete year classes cannot be empirically defined. In addition, estimates of yearly recruitment could not be made, because birds produced over nearly 2 years of breeding moult during one season. Our results explain the relative role of factors such as date of fledging and age in the determination of the season of moult and its timing within the season, and provide the means of assigning recruits to specific age groups.

P.A. Bartlett, Y.J. Chesselet, I.G. Cordes, G.J.G. Hofmeyr, J.A.C. James, R. Jones, N.N. Uhongora and S. Wepener banded and resighted African Penguins on the Namibian islands. D. Oschadleus extracted banding details from the SAFRING database. L.G. Underhill, P.G. Ryan and an anonymous reviewer commented on earlier drafts. J.K. acknowledges financial support from the Namibia Nature Foundation, the New England Aquarium, Total Namibia, the Des and Jen Bartlett Fund and F. Kemper.

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