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Moult phenology and the influence of breeding activity in adult African penguins Spheniscus demersus at Allwetterzoo Münster, Germany

Friederike Schmitz and Philipp Wagner

Allwetterzoo Münster, Westfälischer Zoologischer Garten Münster GmbH, Münster, Germany

Correspondence: Friederike Schmitz, e-mail; f.schmitz1@outlook.com

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Abstract

Observations of ex-situ populations represent valuable resources for comparing data of captive and free-ranging populations and provide useful information to enhance species management and welfare. In this study, the African penguin Spheniscus demersus, listed as Endangered by the IUCN, serves as a model to evaluate adult moult phenology at Allwetterzoo Münster, Germany between 2018 and 2022. Further, the impact of an altered breeding cycle on the timing of moult was assessed. Moult was highly synchronistic within the ex-situ colony and comparable with moult seasonality of colonies in the wild. Here, timing of moult seems to be strongly dictated by breeding schedule. However, while moult synchrony at Allwetterzoo was positively influenced by breeding synchrony, timing of moult might be more affected by individual (sex, age and breeding activity) and seasonal variables, than by the timing of breeding. Nevertheless, the data indicate the relevance of exhibiting nesting behaviour for moulting, with both events representing sensitive key drivers of the annual cycle in African penguins under human care.

Background

The African penguin *Spheniscus demersus* is one of 18 extant penguin species (del Hoyo 2020) and the only one endemic to southern Africa. Since 2010 it has been listed as Endangered on the Red List of the International Union for Conservation of Nature (IUCN) (BirdLife International 2020). Populations are rapidly decreasing, which increases the importance of ex-situ management activities for ensuring the long-term survival of the species. In Europe, the captive population is managed by the European Association of Zoos and Aquaria (EAZA), which established the African penguin EAZA Ex-situ Programme (EEP) to preserve a sustainable population under human care. The program now includes around 2,000 animals spread over 60 facilities (EAZA 2021; Species360 2022).

Breeding and moult

African penguins spend most of their lives at sea and only come ashore for two important phases of their annual cycle: to reproduce and rear chicks, and to moult (Williams 1995).

African penguins are colony breeders, with courtship behaviour in penguins stimulated by conspecifics (Gailey-Phipps 1978; Marshall et al. 2016). Reproduction can theoretically occur in any month of the year, however there might be colony-specific peaks (e.g. Gailey-Phipps 1978; Kemper et al. 2007; Salleh et al. 2019; Wilson 1985; Wolfaardt et al. 2009a) and a low point during the adult moult season (Kemper 2006; Otsuka et al. 2004; Wolfaardt et al. 2009a).

Feathers deteriorate with time and need to be restored to guarantee functionality (Payne 1972). Penguins are special in renewing their plumage over a relatively short time (Williams 1995). Generally, African penguins moult annually, and even

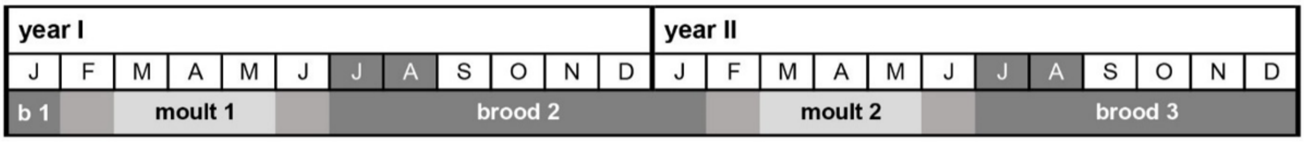

Figure 1. Schematic breeding–moult-cycle in adult African penguins at Allwetterzoo before 2016, including breeding season with two possible clutches (dark grey) and moulting season (light grey) in consecutive years

though they might moult throughout the year, moult season is often synchronised within a colony, with distinctive peaks. In South Africa, most adults moult in spring and summer (e.g. Crawford et al. 1999, 2006; Randall and Randall 1981; Underhill and Crawford 1999; Wolfaardt et al. 2009b) and in Namibia additionally in autumn (Crawford et al. 2006; Kemper et al. 2008). In captivity, moult often occurs in the summer months (AZA Penguin TAG 2014; Bennett 1991; Gailey-Phipps 1978; Golembeski et al. 2020).

Breeding and moult at Allwetterzoo

At Allwetterzoo appropriate nesting options are only provided for a limited time during the year. Thereby effective management is achieved, with a very defined breeding season. When mating interest increases within the colony, breeding is initiated by presenting artificial nests and nesting materials. Within a couple of weeks, pairs synchronously lay clutches and start incubation. Some pairs might lay eggs much later (e.g. when the other pairs are already rearing chicks). Those clutches are removed, being too late for the breeding season. After an incubation phase of 38–41 days (Rand 1960; Ross 1971), chicks hatch. At approximately 50 days of age fledglings are taken off-exhibit and learn to eat fish, which is called ‘fish school’. At the same time, the artificial nests are removed and breeding season is finished.

From 1985 to 2015 (n=31), onset of breeding season (characterised by the mean laying date of incubated eggs of first clutches per season) started in July (51.6%) or August (38.7%) and rarely in September (6.5%) or October (3.2%). Even though there are no records of the moult phenology, according to zookeepers' observations penguins at Allwetterzoo moulted annually in spring (Figure 1). The colony moulted synchronously after brood (postnuptial), with the last animals moulting in June, shortly before the beginning of the next breeding season.

For many decades, until 2016, the colony at Allwetterzoo presented a well-synchronised breeding–moult routine. Due to a research project to determine whether animals in the EEP are of hybrid ancestry of different Spheniscus species (EAZA 2017, 2018, 2019), Allwetterzoo was given the recommendation not to breed in 2016 and 2017. Even though nesting options were not presented, the penguins built natural nests and laid eggs. Based on data from 2018–2022 (Schmitz unpublished data), there was theoretically an average of three eggs/two clutches per pair per year, which were removed. In both years, zookeepers noticed a shift in the formerly scheduled annual cycle. Moulting behaviour became less synchronised with more animals presented ‘abnormal’ moulting such as partial or arrested moult (Austin 2016; AZA Penguin TAG 2014; Golembeski et al. 2020).

Moult phenology in 2018

The purpose of this study was to observe and describe the general adult moult phenology at Allwetterzoo. In spring 2018, when data collection had already started, the EEP gave a recommendation to breed and shortly after, a breeding season started in March.

Influence of early breeding on moult

Moulting is a complex process and initiation is influenced by an interplay of different factors (Payne 1972). Environmental cues such as season, photoperiod and food availability seem to be associated with moulting (AZA Penguin TAG 2014; Crawford et al. 2006; Otsuka et al. 1998, 2004; Vaucoulon et al. 1985). Besides, moult schedules are affected by individual elements, like age, sex and reproductive condition, which in turn influence nutritional and hormonal levels (Groscolas et al. 1986; Kemper et al. 2008; Kojima 1978; Otsuka et al. 1998, 2004; Scholten 1989). In the wild, timing of moult is often determined by breeding activities, which coincide with food accessibility near the colony (Crawford et al. 1999; Randall and Randall 1981; Wilson 1985).

A moult season in summer has disadvantages due to higher temperatures and increased mosquito risk. African penguins can tolerate a range of temperatures, but show signs of heat stress at $\geq$22°C (Frost et al. 1976; Welman and Pichegru 2022). Physiological stress can affect the immune system, making animals susceptible to diseases like avian malaria, to which captive penguins are vulnerable (Bennett et al. 1993). The disease is borne by mosquitos and considered one of the most important causes of mortality in penguins kept in outdoor exhibits (Stoskopf and Beier 1979; Wallace 2015). Even though animals of all ages may show clinical signs, naive birds like juveniles are at higher risk. In addition, situations causing distress like chick rearing or moult may increase susceptibility (AZA Penguin TAG 2014; Hernandez-Colina et al. 2021; Wallace 2015). Penguins are potentially vulnerable in summer (Cranfield et al. 1994; Hernandez-Colina et al. 2021) when mosquito density is high (Lalubin et al. 2013; Schoener et al. 2017). Therefore, it would be beneficial if the timing of breeding and moulting could be influenced in captivity. At Allwetterzoo, a brood in autumn for example would minimise avian malaria risk for vulnerable juveniles, which would be reintroduced to the colony after ‘fish school’ during late winter/spring. A moulting season in spring, instead of summer, would reduce heat stress for adults and the risk of moulting in months where mosquito contact is highly probable.

The penguins at Allwetterzoo are kept in an outdoor enclosure. They experience a natural daylight cycle and seasonal changes throughout the year. The colony is scatter-fed ad libitum, facilitating appropriate mass increase prior to moult. Most of the factors that may trigger moult cannot be altered. However, literature describes individual plasticity in the timing of moulting in penguins and an effect of reproduction (Cooper 1978; Otsuka et al. 1998, 2004; Randall and Randall 1981; Wolfaardt et al. 2009a, b). Hence, the specific breeding approach at Allwetterzoo with defined nesting period might represent a possibility to alter the moult cycle. Therefore, the second part of this study is focused on the influence of an earlier breeding season on the timing of corresponding postnuptial moult.

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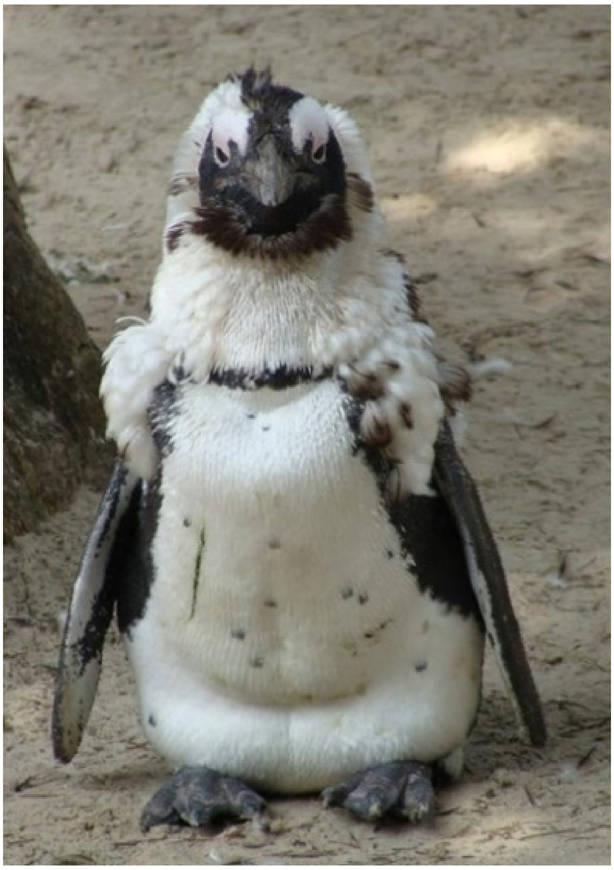

Figure 2. Adult African penguin *Spheniscus demersus* in the feather-shedding phase of moult.

Actions

Animals and housing

The African penguins at Allwetterzoo have been bred in captivity, with animals hatched in Münster or at facilities within Europe. In this study, only adults were analysed, considered as birds in adult plumage and with an age ranging from two to nearly 40 years. During the study period (2018–2022) the colony size varied from 46 to 53 adults. All penguins have a house number and can be individually identified. The outdoor enclosure has a land area (100 m^2) and a freshwater pool (65 m^2), in which the penguins were scatter-fed at least twice a day.

Data analysis

Data collection (photographs or notes) took place between 1 January 2018 and 31 December 2022. Data were collected by the same observer (FS). In wild African penguins, the duration of moult is approximately three weeks, with the feather-shedding period (Figure 2) lasting around 13 days (Randall 1983, cited in Randall et al. 1986). The colony was scanned throughout the year. Pre-moulting penguins can be reliably identified (e.g. significant weight gain, loose plumage) and at this point attempts were made to document the animals' moult process as often as possible. The feather-shedding period can be divided into different stages (Figure 3). It was not possible to record each stage for every penguin. Therefore, a method based on the adjustment rules by Kemper and Roux (2005) was applied. To estimate the date on which the mid-point of the feather-shedding period would fall, days were added or subtracted to the date on which the animals were recorded. For example, when a penguin was observed "shedding a quarter of its plumage" on 12 July the estimated date of the mid-point would be 15 July (Figure 3). Data collection was restricted by work schedule and the number of data points varied among animals (mean 6±2 data points, range 1–13, n=233). Therefore, the individual mean mid-point of the feather-shedding phase (hereafter referred to as 'mid-moult') was calculated in Microsoft Excel (2019). Descriptive statistics include mean±standard deviation (SD). Individual estimates were summed to define percentage of moulters per month and the average moulting date

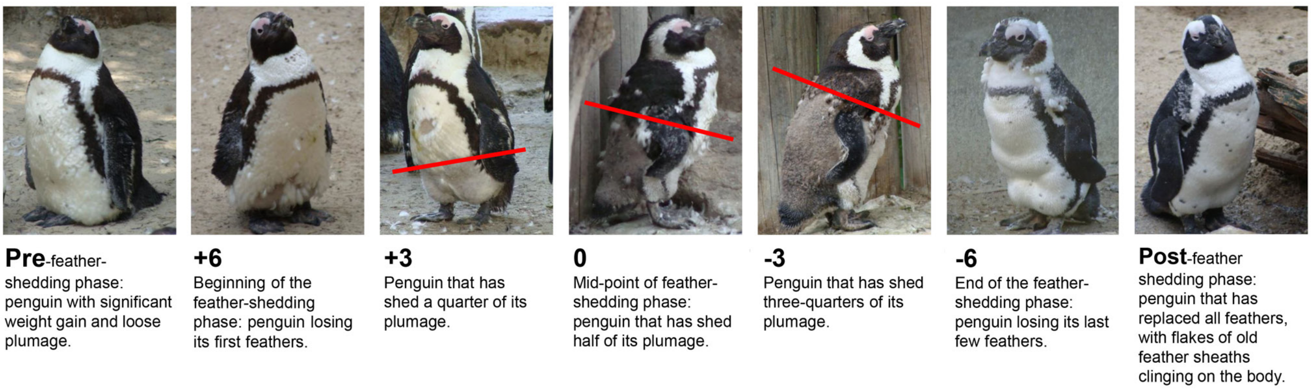

Figure 3. Number of days added to or subtracted from each recorded data point of individual feather-shedding stage (focusing on the torso and head but not wings) to calculate the mid-point of moult (red line for visual support only). If a stage cannot be clearly assigned, the previous stage is selected. Method based on adjustment rules by Kemper and Roux (2005).

of the colony. Moult season was defined as the mid-moult of the first to the last animal within a year. Penguins were classified as outliers and excluded from analysis if their mid-moult occurred more than three months earlier or later than the closest animal's mid-moult. Further, the individual mid-moult dates in consecutive years were compared to see if penguins moult earlier, later or at the same time (characterised as difference in moult≤seven days).

Between 2018 and 2022, pairs were allowed to incubate one clutch per breeding season. Data concerning the timing of breeding refer to the beginning of the breeding season (defined as mean laying date of incubated eggs). Brood A (2018) serves as the baseline value, while broods B (2018/19), C (2019/20) and E (2021/22) started earlier (Table 1). Brood D (2020/21) was initiated at a similar time to brood C and serves as a control.

Moult dates for mated pairs were compared to see if partners moult synchronistically. Pair synchrony was defined as the individual mid-moult being within the same three-week period for both animals.

The influence of sex and age at moult on the timing of moult was evaluated. Therefore, penguins were assigned to age categories, ranging from animals <5 years ('5') to >30 years ('30+') of age. By comparing moult dates of non-breeders (unpaired animals/mated penguins not nesting), and both unsuccessful (animals in pairs, which presented nesting behaviours for several weeks without laying eggs) and successful (animals in pairs incubating eggs or rearing chicks) breeders, only the effect of 'breeding success' on moult was assessed.

In broods D and E, the Allwetterzoo decided to rear only two chicks (selected pairs were allowed to incubate one egg, while the other pairs had their eggs replaced with dummy eggs). Consequently the maximum number of pairs with possible chicks decreased to two.

The average duration of the feather-loss stages was calculated. In addition, the length of the shedding period was assessed by using perfect moulters, birds for which the last pre-moult day and the first day of the feather replacement period ('+6') was documented, as well as their last day ('−6') and the first day of the post-moult phase.

Penguins with eggs were examined to calculate the mean interval between onset of brood to mid-point of moult season (I-bm) and mid-point of moult season to first eggs after moult, before next brood (I-m1st). If there were two eggs per clutch, the mean laying date was used. The average time between two consecutive moult periods (I-mm) was also calculated.

Data

Moult phenology in 2018

In 2018, two animals were excluded from analysis: male 298 that moulted far out of peak season in February (defined as an outlier) and female 212 that did not moult at all (Table 1). Data of 45 African penguins presented well-synchronised adult moult behaviour with a peak in August 2018 and a moult season of less than two and a half months (Figure 4, Table 1).

Influence of early breeding on moult

The beginning of breeding season A was in March (Table 1). The following brood B started over two months earlier in January. Onset of breeding seasons C and E were in November, therefore four to almost five months earlier compared to brood A.

Female 212 moulted out of peak season in January 2019. Male 106 did not moult in 2020, male 242 did not moult in 2021 and male 298 had his mid-moult in the beginning of January 2023, when data collection was already completed (Table 1). Therefore, these animals were excluded during analysis in the corresponding years. Further, one female was photographed pre- and post-moult but not during her shedding phase. The bird moulted between 29 May and 12 June 2022 and the mid-point of that period was used in the calculation.

Data shows a synchronised moult phenology (Figure 4, Table 1) with a peak in August (2019) and July (2020, 2022) and with all seasons being broader in contrast to 2018. Based on an annual

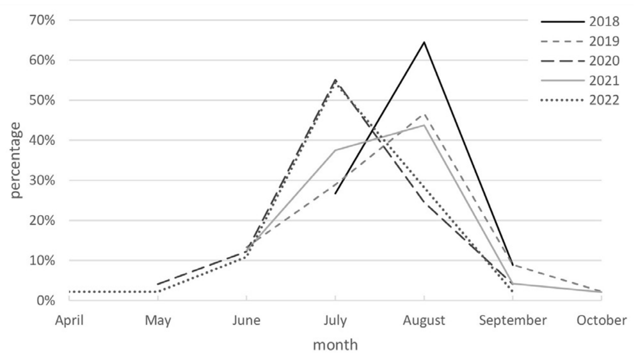

Figure 4. Moult phenology with percentage of adult African penguins moulting per month in 2018 (n=45), 2019 (n=45), 2020 (n=49), 2021 (n=48) and 2022 (n=46)

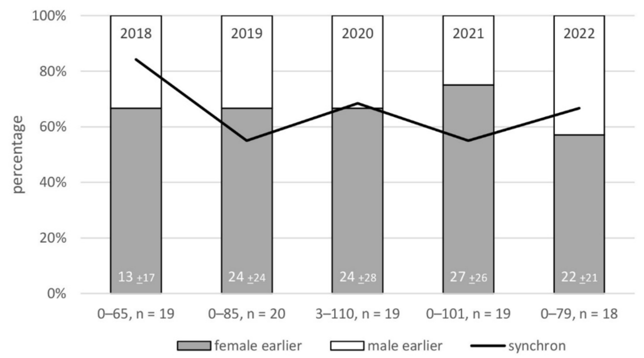

Figure 5. Pair synchrony (defined as the individual mid-moult being within the same three-week period for both animals, black line) and female-male ratio in pairs in which the partners moulted differently. Values within the bars indicate average difference in time (days±SD) between mates (below: range and number of pairs).

Table 1. Breeding season, egg-laying phase, animals observed, moult season and intervals. Documentation from 1 January 2018 to 31 December 2022 with all data included to the best of the authors' knowledge

	A	B	C	D	E	F
Breeding season	2018	2018/19	2019/20	2020/21	2021/22	2022/23
Brood	initial state	earlier brood I	earlier brood II	control	earlier brood III	
Onset of brood [date±SD]	25 Mar 2018±5 n=38	15 Jan 2019±6 n=37	26 Nov 2019±5 n=33	22 Nov 2020±12 n=36	01 Nov 2021±7 n=34	
Onset of brood shifted compared to previous brood [d]		-69	–50	–4	–21	
Onset of brood shifted compared to brood2018 [d]			–119		–144	
Nest opening [date] duration [d]	01 Mar 8–19 Jun 2018 110	25 Dec 18–21 Apr 2019 117	05 Nov 19–03 Mar 2020 119	03 Nov 20–24 Jan 2021 82	16 Oct 21–18 Jan 2022 94	15 Oct 2022 – >> ---
Egg-laying phase	2018	2018/19	2019/20	2020/21	2021/22	2022/23
Eggs after moult before brood [date]	<< –19 Feb 2018	26 Oct 18–15 Dec 2018	25 Oct 19–03 Nov 2019	14 Oct 20–03 Nov 20	---	05 Oct 2022–10 Oct 2022
Eggs within brood [date]	18 Mar 18–10 Apr 2018	24 Dec 18–23 Jan 2019	17 Nov 19–08 Dec 2019	08 Nov 20–16 Dec 2020	19 Oct 21–16 Nov 2021	20 Oct 2022–19 Nov 2022
Eggs too late for brood [date]	---	19 Feb 19–04 Apr 2019	23 Dec 19–15 Feb 2020	06 Jan 21–20 Jan 2021	03 Dec 21–13 Jan 2022	~19 Dec 2022– >>
Eggs after brood before moult [date]	---	23 Apr 19–09 May 19	03 Mar 20–16 Apr 2020	31 Jan 21–20 May 2021	24 Jan 22–04 May 2022	
Animals observed	2018	2019	2020	2021	2022	
Adult penguins	47 (25.22)	46 (24.22)	50 (25.25)	49 (26.23)	47 (25.22)	
Birds not moulting [sex "house-number"]	0.1 "212"		1.0 "106"	1.0 "242"	1.0 "298"	
Birds excluded (outliers) mid-moult [date]	1.0 "298" 15 Feb 2018	0.1 "212" 10 Jan 2019				
Moult season	2018	2019	2020	2021	2022	
Mid-point of moult season (m) [date±SD]	10 Aug 2018±15 n=45	02 Aug 2019±28 n=45	20 Jul 2020±24 n=49	30 Jul 2021±27 n=48	18 Jul 2022±27 n=46	
m shifted compared to previous m [d±SD], range		−8±24 −48–±87, n=44	−7±16 −59–±32, n=42	15±21 −21–±94, n=45	−5±11 −36–±22, n=42	
m shifted compared to m2018 [d±SD], range			−18±18 −52–±29, n=41		−11±18 −42–±20, n=34	
Moult period [date] duration [d]	12 Jul 2018–22 Sep 2018 72	09 Jun 19–14 Oct 2019 127	29 May 20–19 Sep 2020 113	05 Jun 21–10 Oct 2021 127	23 Apr 22–14 Sep 2022 144	
Mean age at moult [y±SD]	15±8	16±8	14±8	14±8	14±8	
Intervals	2018	2019	2020	2021	2022	
Onset of brood to mid-point of moult season (I-bm) [d±SD], range	140±16 112–184, n=38	196±27 145–273, n=39	239±20 183–293, n=35	255±27 214–334, n=35	262±20 216–294, n=34	
Mid-point of moult season to first eggs after moult, before next brood (I-m1st) [d±SD], range	96±17 62–116, n=9	98±26 62–129, n=8	97±14 76–118, n=12	---	84±12 68–93, n=4	
Mid-point of moult season to mid-point of moult season (I-mm) [d±SD], range	357±24 317–452, n=44	358±16 306–397, n=42	380±21 344–459, n=45	360±11 329–387, n=42		

cycle, the colony's mid-moult shifted a few days forward in the year compared to the previous moult. Most penguins moulted earlier in 2019 (59%) and 2020 (45%) while the majority in 2022 moulted at the same time (48%).

The beginning of control brood D was comparable to breeding season C (Table 1). In 2021, the penguins more frequently moulted in August (Figure 4) with the mean mid-moult just in July (Table 1). In contrast to 2020, the colony's mid-moult shifted backward in the year and more penguins moulted later (67%).

The degree of pair synchrony changed over the years with females in nonsynchronous pairs moulting earlier (Figure 5). The average difference in time between the partners moulting was similar in 2019 to 2022 but greater compared to 2018.

Between 2018 and 2022, two animals were recorded moulting once, five recorded twice, 12 three times, 5 four times and 33 five times (n=233). Overall, females moulted slightly earlier than males (Figure 6a) and younger animals earlier in the season (Figure 6b). There was no difference between unsuccessful and successful breeders (Figure 6c). However, non-breeders (13 July±35 days, mean age at moult 10±10 years, median 3 years, n=27) moulted earlier compared to breeders in general (30 July±24 days, mean age at moult 15±7 years, median 16 years, n=206). Within the younger age category (5 years), non-breeding animals (21 June±27 days, mean age at moult 3±0.6 years, median 3 years, n=15) moulted earlier compared to breeders (9 July±15 days, mean age at moult 4±0.8 years, median 4 years, n=20). However, young non-breeders moulted later than juveniles (12 June±18 days, mean age at moult 1±0.1 years, median 1 year, n=13; 2019–2022, Schmitz unpublished data).

The feather-loss phase lasted on average 9±2 days (n=67, Figure 7a), which corresponds to the sum of the average days per shedding stage (Figure 7b). There was neither a sex nor an age influence. However, in over 80% of the cases in which the replacement phase lasted thirteen days or longer, the animals were older (>20 years).

The interval between successive moults (I-mm) was similar in all years, except between moult 2020 and 2021, where it was longer (Table 1). Two males skipped their moult and the inter-moult period lasted extremely long (male 106 I-mm2019-2021: 624 days, age at moult: 27 years; male 242 I-mm2020-2022: 659 days, age at moult: 19 years). The mean moult interval for all birds and years was 364±21 days (range 306 to 459 days, n=173).

The interval between breeding and subsequent moult (I-bm) increased with time (Table 1). Between 2018 and 2022, 19 individuals laid eggs after moulting before the next brood (I-m1st) (Table 1). The corresponding mean period was 95±18 days, ranging from 62 to 129 days (n=33). A model of the annual breeding–moult cycle is shown in Figure 8.

Consequences

Moult phenology in 2018

The African penguin colony at Allwetterzoo is a good model to study moult behaviour related to breeding conditions. The observations show that the moult season was concentrated in summer months which is comparable to the timing of moult in in-situ and other ex-situ populations. There was high intra-colony and intra-pair synchrony. The cause of restoration in synchrony after an interruption in breeding in 2016 and 2017 is difficult to identify. External factors such as mean temperature (°C) and sum of sunshine (hr) per month were similar in 2016 to 2018, with peaks in spring/summer (WetterKontor n.d.). However, the only difference in husbandry compared to previous years was the breeding season, including nesting behaviour and egg incubation.

In penguins, timing of moult may vary e.g. a breeding stop can initiate moult (Crawford et al. 2006; Underhill and Crawford 1999) whereas delayed breeding may postpone onset of moult (Landowski 1967; Otsuka et al. 1998, 2004; Randall and Randall 1981). When African penguins lose their egg, they might replace it (Crawford et al. 1999; Hockey 2001; La Cock and Cooper 1988; Leloup 1982; Wolfaardt et al. 2008) after approximately one and a half months on average (Randall and Randall 1981; Schmitz unpublished data). These animals can show a different moult timing compared to conspecifics. Therefore, moult synchrony

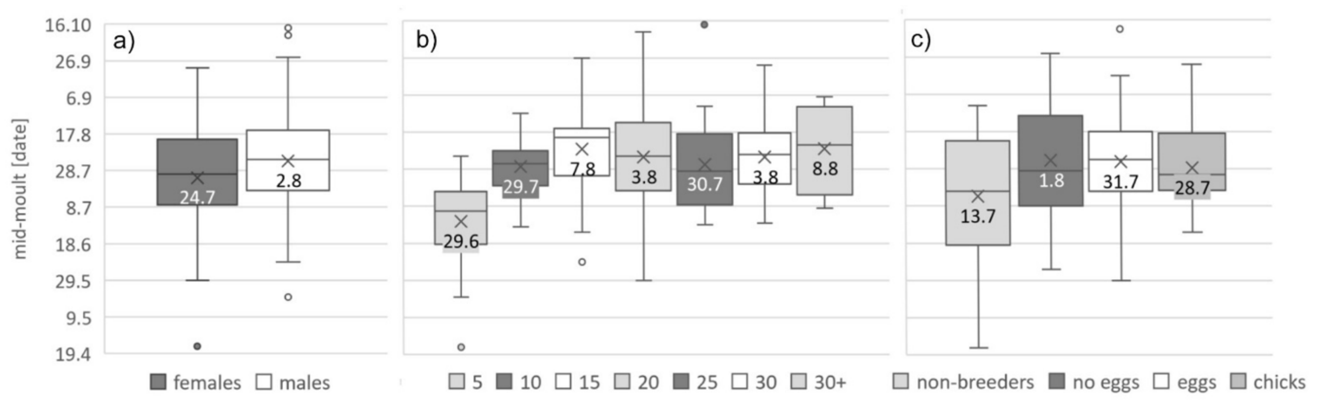

Figure 6. a) Mean moult dates in females (SD±25 days, mean age at moult 15±8 years, n=112) and males (SD±26 days, mean age at moult 14±7 years, n=121); b) Mean moult dates in relation to age at moult: 5:<5 years (SD±23 days, n=36), 10:>5<("needs to be greater-equal")10 years (SD±15 days, n=39), 15:>10<("needs to be greater-equal")15 years (SD±21 days, n=41), 20:>15<"needs to be greater-equal"20 years (SD±27 days, n=70), 25:>20<("needs to be greater-equal")25 years (SD±24 days, n=30), 30:>25<("needs to be greater-equal")30 years (SD±22 days, n=13), 30+:>30 years (SD±25 days, n=4)15 years (SD±21 days, n=41), 20:>15<20 years (SD±27 days, n=70), 25:>20<25 years (SD±24 days, n=30), 30:>25<30 years (SD±22 days, n=13), 30+:>30 years (SD±25 days, n=4)

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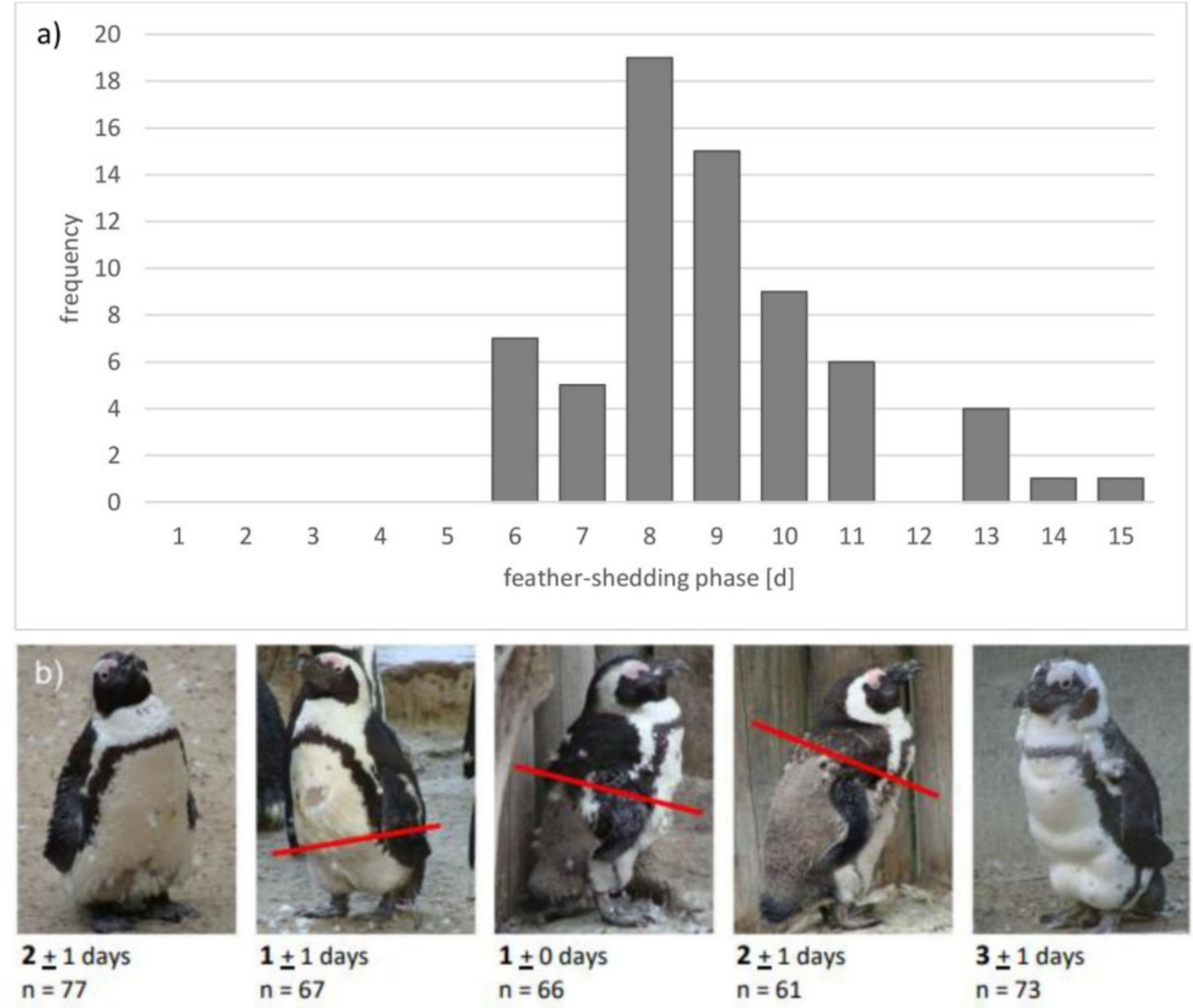

Figure 7. a) Duration of the feather-shedding phase based on observations of 67 individuals between 2018 and 2022 and b) average number of days (±SD) per shedding stage

seems to be an expression of breeding synchrony (Kemper 2006; Kemper et al. 2008; Wolfaardt et al. 2009b). In 2018, the colony at Allwetterzoo went through a normal breeding season. In the beginning of March, brood A was triggered by nest-opening and lasted until mid-June (Table 1). There were no clutches between the end of breeding and onset of moult and animals moulted synchronistically. In contrast, in 2016 and 2017 the colony was not supposed to breed and eggs were taken away. There was no defined nesting season and pairs laid eggs very individually. Removing clutches induced replacement, which extended the egg-laying phase. The varying reproductive activities in 2016 and 2017 could likely have resulted in the moulting asynchrony observed. Retrospectively, it would have been better to simulate a breeding season in those years. Nest opening would have caused egg-laying within a certain timeframe and by switching eggs with dummy eggs, animals would have incubated for at least 40 days. All in all, this would have helped to keep up a certain synchrony in egg-laying and presumably in moulting behaviour.

Interestingly, moult season 2018 was synchronistic, but at a very different time compared to the past. This was due to the unusual spring brood, forcing the penguins to postpone their moulting. However, while breeding synchrony was superficially high, there were fewer fertilized eggs (35%) compared to previous broods (2010–2015: range 51–66%), even though number, experience and mean age of breeding pairs was similar. The decrease in fertility rate in 2018 was probably based on the disturbed egg-laying–moult cycle of 2016 and 2017, with a greater number of non-synchronistic pairs (Coulson 2002; Wolfaardt et al. 2009a).

Influence of early breeding on moult

Despite the earlier onset of the breeding season, moult phenology was similar in all years. In theory, the penguins could have moulted in spring and thus returned to their old moulting routine, but the peak moulting season remained in the summer. This emphasises the long-lasting impact of the husbandry decisions of 2016 and 2017 on the colony's annual life-cycle. Further, it suggests a strong influence of seasonal factors on the timing of moult (Otsuka et al. 2004; Wolfaardt et al. 2009a).

In contrast to 2018, moult seasons 2019 to 2022 were broader, indicating a slight decrease in synchrony. Even though pair-moult synchrony varied, the positive influence of breeding activity on moult was confirmed. Being able to nest seems to help the penguins keep a temporal order in their annual behaviour at Allwetterzoo. Further, the results show that following the disturbed years, brood 2018 resulted in a high synchrony in the corresponding moult period. The following moults seemed to positively influence breeding synchrony, visible in the increased egg-fertility rate in subsequent broods (2018/19–2022/23: range 58–79%).

The results show that timing of moult might be influenced by sex, with females moulting slightly before males. In Humboldt penguins *Spheniscus humboldti* in captivity, males tend to moult earlier (Kojima 1978; Otsuka et al. 1998; Scholten 1989). Similar anecdotal observations have been made in wild African penguins, which concides with males returning to the nesting site after moult prior to females (Randall and Randall 1981). Moulting might also be affected by breeding activity (Borboroglu and Boersma 2013; Scholten 1989) but not by breeding success. This was observed in wild African (Randall and Randall 1981) and Adélie penguins *Pygoscelis adeliae* . In captive Humboldt penguins, pairs that fail to care for their juveniles moult earlier after the (theoretical) hatching date compared to pairs rearing offspring (Kojima 1978). Further, moult might be affected by age, with younger adults moulting earlier in the season (Borboroglu and Boersma 2013; Kemper et al. 2008). Kemper et al. (2008) assumed that African penguins younger than four years that are moulting earlier and at a similar time to juveniles transitioning into adult plumage (Kemper and Roux 2005) are probably non-breeders. Those animals are unlikely to be sexually mature, as wild African penguins do not breed until they are on average four years or older (Crawford et al. 1999; Whittington et al. 2005). Even though there was a difference at Allwetterzoo between non-breeders and breeders, the first to moult were mainly younger individuals. Within the younger age category (5 years), non-breeding animals moulted earlier than breeders, confirming the impact of breeding activity on moult. However, young non-breeders moulted later than juveniles, which might indicate the earlier transition of African penguins into potential breeders in captivity (Gailey-Phipps 1978; Leloup 1982; Schmitz personal observation).

Feather-shedding period

The mean duration of the feather-loss period at Allwetterzoo corresponds with data of captive colonies (9 days, Gailey-Phipps 1978). However, it is much shorter compared to African penguins in the wild (13 days, Randall 1983 cited in Randall et al. 1986; Randall and Randall 1981) and those undergoing rehabilitation (16 days, Kemper 2006).

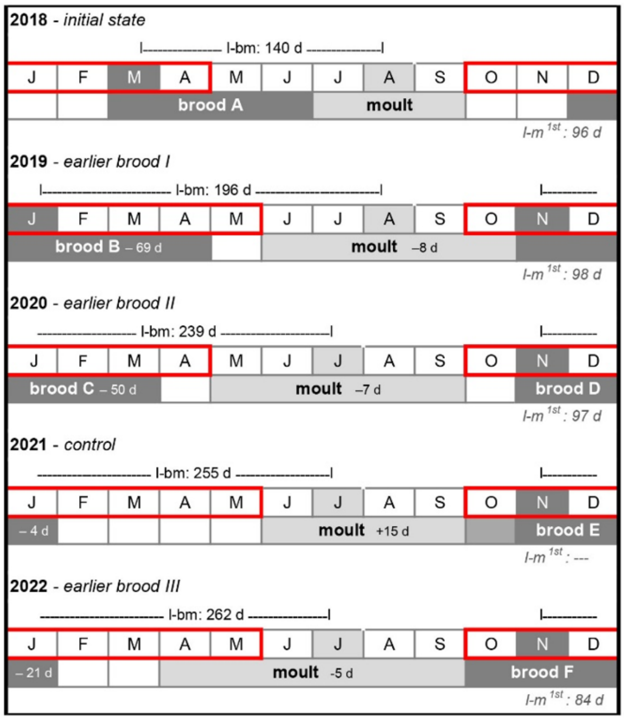

Figure 8. Model of the annual breeding- (dark grey) moult- (light grey) cycle, including months of egg-laying (outlined in red) and relevant intervals (I-bm: time between beginning of brood and moult, and I-m^{1st}: between moult to first eggs after moult, before next brood).

Moulting is a multifactorial process that may be differently affected in captive penguins with presumably better health and nutritional conditions compared to stressed animals (Kemper 2007). On the other hand, varying definitions of the beginning or end of moulting (e.g. Bennett 1991; Cooper 1978; Kemper and Roux 2005; Randall et al. 1986) can lead to different results. A moulting census, conducted approximately every two weeks based on the 13-day shedding period is an accepted method for monitoring wild African penguin populations (Crawford and Boonstra 1994; Crawford et al. 1995, 1999, 2000; Kemper et al. 2001; Randall et al. 1986). However, the method is sensitive to the duration of the replacement phase, which must be taken into account.

Intervals

Theoretically, the earlier beginning of the breeding season should have shifted the onset of the moult. However, while breeding season B started two and a half months earlier compared to brood A, and breeding season E almost five months, the colony's corresponding mid-moult slightly changed. The hypothesis that shifting the breeding period would shift the moult season could not be confirmed. The interval between brood and moult even

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increased with time, indicating no clear relationship.

In African penguins, the mean time between two successive moults is about one year, ranging between 349 and 375 days (Bennett 1991; Kemper et al. 2008; Randall and Randall 1981; Wolfaardt et al. 2009a). Even though there were year-to-year and individual variations at Allwetterzoo the mean moult interval was indeed one year.

Some pairs started having clutches after moult before the subsequent breeding season. In wild African penguins the interval between the end of moult and the next breeding attempt (I-mend1st) is mainly limited by two factors: the time to recovery after moult (approximately six weeks, Randall and Randall 1981) and the period from returning to the colony to first clutch, which takes about three weeks (Hockey 2001; Rand 1960; Randall and Randall 1981; Wilson 1985). In captivity where food is plentiful, it could be assumed that animals need less time to regain their body mass. At Allwetterzoo, the moult-to-egg-laying interval refers to the time between mid-moult to first clutch after moult (I-m1st) and therefore some days must be subtracted. A mean interval of about three months is longer than expected but comparable to captive (Bennett 1991; Gailey-Phipps 1978) and free-ranging (Kemper et al. 2008; Wolfaardt et al. 2009a) populations. The results suggest that in human care nutritional status might not be the main factor determining onset of the egg-laying phase (Otsuka et al. 2004). Interestingly, between 2018 and 2022, penguins always started having their first clutches after moult in October (Table 1). Therefore, exogenous cues which work on internal factors seem to be mainly responsible.

Breeding season versus reproductive period

The interval between consecutive moults was comparable as was the period between moult and egg-laying after moult. There was a small shift in moult season but moult was not decisively affected by timing of the breeding season. Endogenous and exogenous factors influence moult and breeding activity, visible in the consistent first-eggs-after-moult interval. It is not clear why the same factors do not seem to affect the breeding-moult phase.

During the study period, the colony laid eggs throughout the year, except during peak moult season. ‘Wild’ eggs are considered those laid outside nesting season and are removed to avoid incubation. In 2018, no wild eggs were found after breeding, therefore, the last eggs of the season laid in mid-April were considered. In 2020, the penguins had eggs after breeding/before moulting until mid-April, and in 2019, 2021 and 2022 until the beginning of/mid-May (Table 1). Considering these dates as ‘end of reproductivity before moult’ would explain why there was no detectable influence of an earlier breeding season on moult. For the penguin colony there was simply no shift in breeding season. Even though brood B, C and E started earlier, and therefore all seasons ended sooner, the animals had their normal reproductive period which starts in autumn (October: first eggs after moult, before breeding) and may last until spring (April/May: last eggs after breeding, before moult) (Figure 8). The modification to the onset of the breeding season was within this reproductive time window and did not alter the timing of breeding activity within the colony.

Conclusion

This study illustrates the relevance of nesting behaviour on moult phenology of African penguins in captivity. The results indicate that while moult synchrony is positively influenced by breeding synchrony, timing of moult might be more affected by individual and exogenous cues. On the other hand, breeding activity might suppress moult but moult might be triggered by reproductive inactivity (to synchronise the two behaviours). Nevertheless, both events represent sensitive key factors in the annual cycle of captive African penguins and the role of environmental, individual or even social signals (Palmer 1972) needs to be investigated further.

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