Reproductive success delays moult phenology in a polar mammal

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Animals can respond to dynamic environments through phenological plasticity of life history events; however, changes in one part of the annual cycle can diminish the success of subsequent life history events. Our aims were to determine the associations between reproduction and moult phenology across years and to quantify phenological plasticity across varying environmental conditions. We conducted demographic surveys of 4,252 flipper-tagged Weddell seals (Leptonychotes weddellii) in the Ross Sea, Antarctica during four austral summers. At each sighting, seals were assigned a moult code based on the visible presence of new fur and the start date of each animal’s moult was back-calculated. Reproductive success and parturition dates were obtained for the breeding season prior to and following the moult. We found that successful reproduction delayed moult by 16 days relative to non-parturient females. Phenology of the intervening moult was indicative of previous reproductive dynamics but not predictive of subsequent reproductive outcomes. Across years, moult phenology varied by about two weeks and covaried strongly with sea ice break-out timing for all reproductive categories. Our findings suggest these polar mammals have some flexibility within the annual cycle that allows adjustment of moult phenology to fluctuating environmental conditions without compromising future reproductive success.
level or in a limited number of captive animals. Thus, the drivers and consequences of moult duration and phenology in individuals are unclear.

In this study, we use free-ranging Weddell seals as a model species to evaluate the moult as an intermediate life history event between two reproduction events. Specifically, we address three aims: (1) to describe the duration and phenology of the moult across age, sex, reproductive categories, and environmental conditions; (2) to analyse the relationship between reproductive phenology (October–November, Year 1) and subsequent mouthing phenology (January–March, Year 1) in parturient females; and (3) to understand the relationship between mouling phenology and reproductive outcomes in the following season (October–November, Year 2). As the most southern breeding mammal, Weddell seals have highly constrained annual cycles and serve as a useful model for understanding mammalian moult cycles. Further, the ages and reproductive histories of most individuals are known due to a 45-year demographic study38,39.

**Methods**

Research activities were approved by National Marine Fisheries Service Marine Mammal permit #17411, University of Alaska IACUC protocols #419971 and #854089 and the Antarctic Conservation Act permit #2014-003 and were carried out in accordance with guidelines for handling marine mammals.

**Field methods.** In 2013–2017, we conducted semi-weekly surveys of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica (77°S, 165°E). Each seal was approached and its flipper tag identification number, age class, and sex were recorded along with a qualitative moult code based on the visible presence of new fur (Fig. 1): code 0 - moult had not begun, no new fur visible; code 1 - head moulted and/or a thin stripe of new fur visible along the spine; code 2 - head completely moulted and connected to a wide dorsal stripe of new fur remaining laterally between the front and rear flippers; code 3 - only small patches of unmoulted fur remained laterally between the front and rear flippers; and code 4 - fully moulted, no old fur visible. If the moult code could not be assigned because the animal was wet, covered in snow, or laying so that dorsal pelage was not visible, moult state was noted as unknown. Ages and sexes were obtained for tagged individuals based on a long-term demographic study38–40. Year is given as the austral summer each seal was observed moulting (e.g., 2013 is the 2013–14 austral summer season, including October 2013–December 2013 pupping and December 2013–March 2014 moulting) (Table 1). We use sea ice break-out date as a proxy for

| Moul Code 0 | Moul had not begun, no new fur visible. |
| Moul Code 1 | Head was moulted and/or a thin dorsal stripe of new fur was visible. |
| Moul Code 2 | Head was completely moulted and connected to a wide dorsal stripe. |
| Moul Code 3 | Most of the body was moulted aside from small patches of fur remaining laterally between the front and rear flippers. |
| Moul Code 4 | Fully moulted, with no old fur visible. |

Figure 1. During surveys, each individual was assigned a moult code: 0 (unmoulted), 1 (head or dorsal stripe moulted), 2 (head and wide dorsal stripe moulted), 3 (flank starting to moult), or 4 (completely moulted).
Due to logistical constraints in 2013, pupping quartiles calculations were modified slightly (see methods). Because male breeding behavior is difficult to assess, we did not attempt to link breeding and moulting phenology.

Categorized females who did not give birth (Attendant Juvenile Females, Attendant Non-Parturients) or who were not observed during the reproductive season (Non-Attendant Adult Females, Non-Attendant Juvenile Females).

Using methods described in Beltran42. Using the pupping date distribution for new-borns to estimate the quantiles of pupping dates for each year, we categorized attendant parturient females as Early-, Mid-, or Late-Parturients (Table 2, Fig. 2). Alternatively, we estimated moult initiation dates for each year and reproductive category. Significant differences in moult initiation dates among years (by row, within a reproductive category) are denoted with Roman numerals ($\alpha$ level = 0.05). *In 2013, the United States government shut down delayed the Weddell seal research program by several weeks, and pup tagging began only after 50% of the pups were born; as a result, the dates of the earlier quartiles are not known (see methods). **Date when 7-day running mean of ice concentration falls below 50%. See Beltran for details. ***Colony attendance proportions for the following year.

** Table 1. Information about moult surveys during 2013–2016, including quartiles for pupping dates and mean ± standard deviation moult initiation dates for each year and reproductive category.**

| Sighting Metadata | 2013 | 2014 | 2015 | 2016 |
|-------------------|------|------|------|------|
| # Sightings       | 1810 | 1470 | 2212 | 3423 |
| # Seals           | 1038 | 866  | 937  | 1411 |
| # Survey Days     | 19   | 10   | 11   | 26   |
| First Moult Survey Date | Jan 13 | Jan 17 | Jan 18 | Jan 18 |
| Last Moult Survey Date | Feb 13 | Feb 14 | Feb 15 | Mar 8 |
| Pupping Quartiles |      |      |      |      |
| Minimum           | *    | Oct 11 | Oct 13 | Oct 14 |
| 25th percentile   | *    | Oct 22 | Oct 22 | Oct 24 |
| Median            | Oct 29 | Oct 26 | Oct 27 | Oct 28 |
| 75th percentile   | Nov 02 | Oct 30 | Oct 30 | Nov 02 |
| Maximum           | Nov 15 | Nov 26 | Nov 13 | Nov 19 |
| Moult Initiation Dates |      |      |      |      |
| Attendant Non-Parturient | Dec 28 ± 11.9i | Jan 05 ± 10.7ii | Jan 07 ± 9.9ii | Jan 12 ± 9.8iii |
| Non-Attendant Juvenile Females | Jan 06 ± 11.6i | Jan 07 ± 13.7i | Jan 11 ± 9.7i | Jan 17 ± 12.1i |
| Attendant Juvenile Females | Jan 04 ± 11.3i | Jan 11 ± 6.7i | Jan 15 ± 8.3ii | Jan 15 ± 14.6i |
| Non-Attendant Adult Females | Jan 07 ± 14.5i | Jan 11 ± 11.8i | Jan 17 ± 11.7i | Jan 19 ± 9.6i |
| Attendant Parturient | Jan 19 ± 8.4i | Jan 15 ± 11.1i | Jan 18 ± 9.2i | Jan 29 ± 13.2i |
| Males             | Jan 09 ± 13.1i | Jan 13 ± 10.6i | Jan 16 ± 8.1ii | Jan 24 ± 12.9ii |
| Ice break-out date** | Jan 14 | Jan 14 | Jan 02 | Feb 04 |
| Colony attendance*** |      |      |      |      |
| Attendant Non-Parturient | 22%  | 22%  | 18%  | 25%  |
| Non-Attendant Parous | 10%  | 6%   | 22%  | 20%  |
| Attendant Parturient | 68%  | 72%  | 60%  | 55%  |

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Although an existing R package “moult”43 is available for analyses of moult dynamics, it does not allow for individual random effects in moult duration. Therefore, we developed custom functions in R (R Development Core Team 2017, version 3.3.2) to estimate the duration of moult based on subsequent sightings of a series of moult codes in each individual. Moult stage durations $\tau_n$ were calculated as the amount of time that passed between the observed moult stage ($n$) and the moult stages preceding ($n−1$) and following ($n+1$), using a midpoint approach (see Fig. 3). The moult codes 0, 1, 2, 3, and 4 represent each of the five stages and were used to calculate moult durations $\tau_n$ for codes $n = 1, 2, 3$ as follows:

$$\tau_n = \left( \frac{First_{n+1} + Last_n}{2} \right) - \left( \frac{First_n + Last_{n-1}}{2} \right)$$

Analytical methods. Estimating moult stage durations. Although an existing R package “moult”43 is available for analyses of moult dynamics, it does not allow for individual random effects in moult duration. Therefore, we developed custom functions in R (R Development Core Team 2017, version 3.3.2) to estimate the duration of moult based on subsequent sightings of a series of moult codes in each individual. Moult stage durations $\tau_n$ were calculated as the amount of time that passed between the observed moult stage ($n$) and the moult stages preceding ($n−1$) and following ($n+1$), using a midpoint approach (see Fig. 3). The moult codes 0, 1, 2, 3, and 4 represent each of the five stages and were used to calculate moult durations $\tau_n$ for codes $n = 1, 2, 3$ as follows:

$$\tau_n = \left( \frac{First_{n+1} + Last_n}{2} \right) - \left( \frac{First_n + Last_{n-1}}{2} \right)$$

(1)
where \( \text{First} \) is the first sighting in a given moult code \( n \), and \( \text{Last} \) is the last sighting in a given moult code \( n \). For instance, the moult stage 1 duration \( \tau_1 \) is the difference between [the temporal midpoint of the first code 2 sighting and the last code 1 sighting] and [the temporal midpoint of the first code 1 sighting and the last code 0 sighting during the Jan/Feb moult season]. Stage durations were calculated for all seals that were observed in three consecutive moult codes (e.g. codes 0, 1, 2 in the case of \( \tau_1 \)), and the distributions of those durations was tested for normality using Lilliefors tests. Moult stage durations did not differ across years, sexes, or reproductive histories (unpaired t-test, \( p > 0.05 \) for each stage); thus, data were combined to calculate the mean and standard deviation \( \tau_n \) for the duration of each stage. Total moult duration \( \Theta \) was then calculated by summing \( \tau_1, \tau_2, \) and \( \tau_3 \) (Fig. 3).

We acknowledge that the existence of a negative co-variance between the duration of \( \tau_n \) and \( \tau_{n+1} \) results in a conservative estimate of \( \Theta \). Moult duration values are presented as mean \( \mu \) ± standard deviation \( \sigma \) (see Supplemental Materials for \( \sigma \) equations).

**Estimating moult initiation dates.** Of the 4252 unique seal-year combinations that were observed during the study, 1208 were observed in both moult codes 0 and 1 (i.e., beginning of moult was known to occur between two set dates. For these individuals, we estimated the moult initiation date as the temporal midpoint between the last code 0 sighting and the first code 1 sighting). Of the remaining individuals, 681 were first observed in moult code 1, 681 in moult code 2, 444 in moult code 3, and 749 in moult code 4. To include the animals in our moult phenology analysis that had not been observed at moult initiation, we back-calculated moult initiation dates for each remaining animal based on their moult code \( k \) at first sighting \( \text{First}_k \). Estimating the beginning of a stage required that we first estimate the mean difference \( \Delta_k \) between [the midpoint of the first code \( n + 1 \) sighting and the last code \( n \) sighting] and [the subsequent code \( n \) sighting] (Fig. 3), using:

\[
\Delta_n = \text{First}_n - \left( \frac{\text{First}_{n+1} + \text{Last}_n}{2} \right)
\]

for all seals that were observed in two consecutive moult codes (e.g. codes 0, 1 to calculate \( \Delta_1 \)). Using a Lilliefors test, the \( \Delta_n \) distributions were found to be normal. This resulted in average difference \( \Delta_n \) values of 5.4 ± 3.9

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**Table 2.** Details of reproductive categories assigned to each female during the period preceding each moult.

| Reproductive Category | Gave birth? | Attended colony? | Details |
|-----------------------|------------|-----------------|---------|
| Early-Parturient      | Y          | Y               | Gave birth before the 25th percentile of the pupping distribution. |
| Mid-Parturient        | Y          | Y               | Gave birth between (or on) the 25th and 75th percentile of the pupping distribution. |
| Late-Parturient       | Y          | Y               | Gave birth after the 75th percentile of the pupping distribution. |
| Attendant Juvenile Female | N         | Y               | Seen during the breeding season without a pup and never recorded with a pup in any previous year (i.e., no pups produced yet in life). |
| Attendant Non-Parturient | N        | Y               | Seen during the breeding season without a pup but recorded with a pup in any previous year. |
| Non-Attendant Adult Female | N*        | N               | Not seen during the breeding season but recorded with a pup in previous years. |
| Non-Attendant Juvenile Female | N*     | N               | Not seen during the breeding season and never recorded with a pup in previous years. |

*Given that there are no known pupping colonies near our study site, we assume that Non-Attendant individuals skipped pupping and temporarily emigrated, as described by Chambert, *et al.*88.
days ($n = 347$ animals) for $\Delta_1$, $4.5 \pm 2.9$ days ($n = 347$ animals) for $\Delta_2$, $4.3 \pm 2.9$ days ($n = 226$ animals) for $\Delta_3$, $5.1 \pm 3.7$ days ($n = 213$ animals) for $\Delta_4$ (Table 3). Finally, to back-calculate an initiation date for each animal based on their moult code $k$ at first sighting $\text{First}_k$, we subtracted the difference value $\Delta_k$ and the sum of the stage durations $\tau_n$ for each moult stage $n$ in which the animal was not observed:

$$\text{Initiation Date } \text{First}_k = \text{First}_k - \Delta_k - \sum_{n=1}^{k-1} \tau_n$$ (3)

To control for inter-annual variation in moult timing, individuals were assigned to moult categories based on the moult initiation date relative to the initiation dates of the other animals in the year of sighting:

- “Early-Moulters”, who initiated moulting before the 25th percentile of the moult initiation dates;
- “Middle-Moulters”, who initiated moulting between (or on) the 25th and 75th percentile of the moult initiation dates; or
- “Late-Moulters”, who initiated moult after the 75th percentile of the moult initiation dates.

**Drivers of moult phenology.** To evaluate relationships between moult phenology and sex, year, and reproductive category, we constructed biologically plausible models and then selected the best models using an information-theoretic approach (Table S4). Mixed-effects models were constructed using the package lme4 and selected using AIC$^{44,45}$ in R (R Core Team 2017). The global model was $\text{Date_init} \sim \text{Repro_cat} \ast \text{Year} \ast \text{Age} + (1|\text{ID})$ where $1|\text{ID}$ is the random effect of individual and Repro_cat is a combined sex/reproductive history category that includes males and females. Age differed by reproductive category (mean ages for Juvenile Females = 4.45 years old (yo), Males = 8.73 yo, Attendant Parturients = 14.03 yo, Attendant Non-Parturient = 15.12 yo; ANOVA, Tukey HSD post-hoc, $p < 0.05$ for all, except Attendant Parturients:Attendant Non-Parturient $p > 0.05$). However, the model AIC was higher when Age was included in the global model (Table S4); as a result, all ages within a single reproductive category were combined for the remaining analyses. For parturient females, the relationship between Year 2 pup birth date and Year 1 pup birth date (with and without the added factor of Year 2 moult initiation date) was also examined using a linear mixed-effects model with year as a fixed effect and individual as a random effect using the package lme4 in R. Finally, a multinomial logistic regression of Year 2 reproductive success as a function of Year 1 reproductive category plus Year 1 moult category was examined using the package mgcv in R.

**Interactions between pupping success/phenology and moult phenology.** For sexually mature females, we calculated three sets of transition probabilities:

1) From all Year 1 pupping categories into each mouling category (Table S1; transition probabilities 26% Early-Moulters, 48% Mid-Moulters, and 26% Late-Moulters).
2) From all Year 1 mouling categories into Year 2 pupping categories (Table S2; expected transition probabilities 24% Attendant Non-Parturient, 16% Attendant Early-Parturients, 32% Attendant Mid-Parturients, 17% Attendant Late-Parturients, 12% Non-Attendant Adult Females).
3) From all from Year 1 pupping categories into Year 2 pupping categories (Table S3; expected transition probabilities 22% Attendant Non-Parturient, 16% Attendant Early-Parturients, 31% Attendant...
Table 3. Parameter values used to estimate moult duration and moult initiation dates for all ages and sexes combined.

Mid-Parturients, 16% Attendant Late-Parturients, 14% Non-Attendant Adult Females).

These “expected” transition probabilities (null hypothesis; seals transition from one category to another with equal probabilities) were compared against the “observed” transition probabilities using a Markov simulation on 10,000 multinomial draws. P-values were adjusted to account for table-wide Type I errors using a Bonferonni-type correction (see Supplemental Material).

Results

Demography of moulting animals. Survey frequencies and counts for each study year are provided in Table 1. We observed 2% of all animals during all four study years, 11% during three years, 25% during two years, and all other animals during only one study year (62%). Tagged animals (all ages and sexes) were observed an average of 2.1 ± 1.4 times within a moult season (minimum 1, maximum 15, median 2, mode 1). Of the 4252 seals seen during the moult, 63% of animals had been seen during the lactation period several weeks earlier. For females, the composition of Juvenile Females, Attendant Parturients, and Attendant Non-Parturients seen during the moult period stayed relatively consistent within and across years, averaging 23%, 51%, and 26%, respectively.

Moult duration. Moult stage durations were 10.2 ± 5.3 days for \( \tau_1 \) (stage 1), 9.4 ± 4.0 days for \( \tau_2 \) (stage 2), and 9.6 ± 3.8 days for \( \tau_3 \) (stage 3) (Table 3). Using these average stage durations, the entire visible moult duration \( T \) was 29.2 ± 7.7 days for Weddell seals. Using Equation 5, animals first seen in moult had an average moult duration of 7.7 days (mean ± standard deviation) days for Weddell seals. Using Equation 5, animals first seen in moult had an average moult duration of 7.7 days ± 5.3 days for \( \tau_1 \), 9.4 ± 4.0 days for \( \tau_2 \), and 9.6 ± 3.8 days for \( \tau_3 \) (Table 3). Using these average stage durations, the entire visible moult duration \( T \) was 29.2 ± 7.7 days (mean ± standard deviation) days for Weddell seals. Using Equation 5, animals first seen in moult had an average moult duration of 7.7 days ± 5.3 days for \( \tau_1 \), 9.4 ± 4.0 days for \( \tau_2 \), and 9.6 ± 3.8 days for \( \tau_3 \) (Table 3).

Links between pupping phenology and moult initiation dates. Moult initiation date ranged from Dec 09 to Feb 28 with a mean start date of January 15 ± 13.5 (SD) days, although the variance was generally smaller within each reproductive category. Based on the lowest AIC value and Akaike weight, the best mixed-effects model included the interaction between Repro_cat and Year (Table S4). Thus, the wide range (81 days) of moult initiation dates likely resulted from influences of year and reproductive categories.

The resulting transition probabilities from pupping categories to mouling categories in each year are provided in Table S1. Attendant Non-Parturients had the earliest average moult initiation dates (range December 28 to January 12 across study years) followed by Juvenile Females (January 04 to January 15), Males (January 09 to January 24), and females that had given birth (Attendant Parturients; January 15 to January 29) (Fig. 4). Given that eight of fifteen transition outcomes differ significantly from expected, the data strongly suggest that moult phenology is not independent from pupping phenology in a given year (Table S1) (Fig. 5). Specifically, the Early-Moult category is more likely to be comprised of Attendant Non-Parturients (28% greater than expected) than Attendant Early-, Mid-, or Late- Parturients (13%, 13%, and 15% less than expected, respectively). Animals in the Mid-Moult category were disproportionately composed of animals that had been Non-Attendant during the previous pupping period (14% greater than expected). Animals that pupped contributed significantly more than expected to the Late-Moult category, with Attendant Late-Parturients (46%) contributing more than Attendant Mid-Parturients (39%), or Attendant Early-Parturients (36%). For Attendant Parturients, the moult initiation date was significantly related to when the pup was born (linear mixed effects model, \( R^2 = 0.24 \)). Thus, moult phenology is delayed in Attendant Parturients relative to Attendant Non-Parturients, and there is a direct relationship between date of pupping and moult onset.

Inter-annual variation in ice dynamics, moult phenology, and colony attendance. Among study years, the moult was earliest in 2013 (mean moult initiation date January 08 ± 13 days) and latest in 2016 (January 22 ± 14 days) with moult onset during the two intermediate years occurring in between (January 11 ± 11 days

| Parameter | Moult duration (mean ± SD) | Number of Individuals |
|-----------|-----------------|-----------------|
| \( \tau_1 \), duration of moult stage 1 | 10.2 ± 5.3 days | 70 |
| \( \tau_2 \) | 9.4 ± 4.0 days | 73 |
| \( \tau_3 \) | 9.6 ± 3.8 days | 50 |
| \( T \), duration of entire moult | 29.2 ± 7.7 days | |

\( \Delta_{\tau_j} \), difference between first sighting at stage \( \tau_j \) and previous midpoint

| \( \Delta_1 \) | 5.4 ± 3.9 days | 347 |
| \( \Delta_2 \) | 4.5 ± 2.9 days | 347 |
| \( \Delta_3 \) | 4.3 ± 2.9 days | 226 |
| \( \Delta_4 \) | 5.1 ± 3.7 days | 213 |
in 2014 and January 14 ± 10 days in 2015) (Fig. 4, Table 1). These inter-annual differences in moult initiation date were supported by the raw survey data. In the first survey of 2013, 33% of observed seals had yet to begin moulting (moult code 0) and 12% had already completed the moult (moult code 4), whereas in a 2016 survey on that same date, 47% of seals had yet to begin moulting, and only 1% had completed the moult. The one exception was Attendant Parturients, in which moult initiation began significantly earlier in 2014 (January 15) than 2013 (January 19) and 2014 (January 18) (Fig. 4, Table 1, Tukey HSD on ANOVA, p < 0.05). While the 2016 moult surveys extended later than other years (Table 1), this would not have impacted moult initiation dates, as most seals seen after February 13–15 (final survey dates of 2013, 2014, and 2015) had started to moult (and thus moult start date would have already been detected prior to the end of surveys). Indeed, removing the 2016 sightings after February 15 still resulted in significantly later 2016 moult start dates as compared to other years for all reproductive categories. Sea ice break-out date varied by 33 days across the study years and both ice break-out and moult initiation dates were later in 2016 than other years (Table 1). The within-year moult phenology variance in our study may be artificially high because we do not control for some factors known to affect moult start (e.g., circulating hormone concentrations\(^47\), body condition\(^36\)).

Figure 4. Moult initiation dates across reproductive categories and years (panels; 2013 is the 2013 austral summer including the December 2013 – February 2014 moult) for Attendant individuals. Within each year, different letters denote significantly different moult initiation dates across reproductive categories (Tukey’s HSD, p < 0.05). During all study years, sexually mature females that did not produce a pup (Non-Parturients) moulted earlier than all other reproductive categories. On the contrary, sexually mature females that produced a pup (Parturients) tended to moult later than sexually immature females (Juvenile Females, significant difference in 2013, 2015, 2016), and Males (significant difference in 2013, 2016).
Links between pupping and moulting phenology in one season and pupping in the next. For sexually mature females, Year 2 pupping categories (Pupping, Skip-Pupping, or Non-Attendant) were significantly related to moulting initiation date in Year 1 (chi-square test, $\chi^2 = 18.923, p = 0.0153$): Early-Moulters contributed 4% less than expected to the Non-Attendant-Parous category whereas Late-Moulters showed the opposite trend, contributing 6% more than expected to Non-Attendant-Parous (Table S2). However, results also indicate that moulting phenology reflects previous reproduction dynamics rather than driving future reproduction dynamics, and that the Year 2 pupping categories were more strongly related to the Year 1 pupping categories, than by the dates of the intervening moult (chi-square test, $\chi^2 = 130.52, p < 0.0001$, Table S3). Further, Year 1 moulting timing did not help explain whether animals became Parturient, Non-Parturient, or Non-Attendant in Year 2 (multinomial logistic regression, AIC without moult = 1339, AIC with additive effect of moult = 1340). In general, individuals in a given pupping category in Year 1 were likely to remain in the same reproductive category in Year 2 (Table S3) and there was a strong relationship between Y1 and Y2 birthdates ($Y2PupDate = 0.63(±0.06) \times Y1PupDate-23.64, R^2 = 0.292$). When added into a multiple regression, moulting timing was not a significant explanatory factor in Y2 birthdates ($P = 0.173$). Thus, contrary to initial expectations, Year 2 pupping success and phenology are driven by Year 1 reproductive dynamics rather than the intervening moulting phenology.

Discussion

Reproductive history affects moulting phenology. Within sexually mature individuals, we found that post-parturient females and males moulted later than non-parturient females. Within parturient females, we found that later birth was associated with later moulting (see Table S1). Moulting initiation is likely delayed in these groups relative to sexually immature and non-parturient individuals by the elevated circulating cortisol and prolactin levels during lactation and elevated testosterone during breeding. Energetics may also contribute to carryover effects between reproduction and moulting; specifically, reduced body condition following offspring care may delay moulting onset until individuals regain enough energy stores for foraging. A similar phenomenon has been noted in several species of seals and birds, and terrestrial mammals.

The energetic implications of late moulting in parturient individuals is unclear. Because epidermal cells have a minimum temperature threshold for mitotic division, mismatches between moulting phenology and ambient conditions could lead to higher temperature differentials and consequently higher heat loss. In our study, the moulting initiation date of Attendant Non-Parturient (January 06 ± 12 days) aligned with the warmest air temperatures of the year (January 03–05); in contrast, Attendant Parturients initiated moulting on average 16 days later (in up to 5°C colder temperatures) than Attendant Non-Parturients (see Table 1). Thus, by moulting later, parturient individuals may experience increased moulting costs and require additional prey resources. These costs, in addition to the high energetic costs of lactation, may result in Parturients beginning the next reproductive cycle in poorer body condition, which could in turn lower pup weaning mass and diminish post-weaning survival and recruitment. However, higher quality individuals may be able to make up for these additional costs by foraging more over the intervening winter and spring.

Inter-annual variation in ice dynamics affects moulting phenology. We found a significant effect of year on moulting initiation dates, with moulting beginning earliest in 2013 and latest in 2016 (see Table 1, Fig. 4) in most reproductive categories. The marked inter-annual differences in moulting phenology across 2013 and 2016 was reflective of sea ice break-out phenology: in 2016, the McMurdo Sound ice break-out occurred 21 days later and the moulting occurred 10–15 days later than in 2013. Limited pack ice retreat has been found to stunt and delay the annual phytoplankton bloom which would impact the food resources of Weddell seals. Low resource availability and consequently poor body condition may delay moulting via increased cortisol levels and suppressed thyroid hormones as has been found in birds.
Cross-year carryover effects between moulting and pupping. While there were links between Year 1 moult and Year 2 pupping, our data suggest Year 2 reproductive success is driven primarily by Year 1 pupping success and phenology rather than Year 1 moulting phenology (Tables S2, S3). In general, parous seals were likely to remain in the same pupping categories across Years 1 and 2 (Table S3); however, we found that Attendant Late-Parturients were more likely than expected to become Non-Attendant the following year. It is common for sexually mature birds and mammals to intermittently skip reproduction because it takes individuals more than one calendar year to acquire the capital needed for future reproduction. In support of this mechanism, non-breeding individuals are often in poorer quality due to stress, starvation, diseases, or parasites. We suggest that energetic constraints may be responsible for the increased probability of Attendant Late-Parturients becoming Non-Attendant: individuals with lower energy reserves are commensurately less likely to attend breeding colonies. Similar effects have been seen in other species. In red voles, for example, females that successfully reproduce and consequently moult later have lower overwinter survival due to delayed winter preparation.

We found no effect of sex, reproductive category, or year on moult duration, which we estimated to be 29.2 ± 7.7 (mean ± SD) days in Weddell seals. This moult duration is similar to non-catastrophic moult durations in other phocid seals and notably shorter than those of fur seals and sea lions (Family Otariidae; Table S5). Recent evidence suggests that Weddell seal life history events fill nearly an entire year, with embryonic diapause being very short or non-existent, gestation lasting 10 months, visible moult lasting 29 days (this study), and lactation lasting 45 days; however, some Weddell seals produce pups in many sequential years so a >365 day life history cycle is unlikely, at least for the best performing individuals.

In our study, Non-Attendant individuals were 10% more likely than expected to remain Non-Attendant (Table S3), although 76% of individuals returned to breeding colonies the subsequent year. Temporary emigration can reduce conspecific conflict and food competition but may increase predation risk because there is more open water access for predators. We found that the probability of colony attendance fluctuated across years, with more Non-Attendants and less Attendant Parturients following years of early (2015) or late (2016) ice break-out relative to years with more typical ice break-out phenology (Table 1). In juvenile Weddell seals, increased sea ice extent has been found to result in more frequent emigration, probably because higher sea ice extent corresponds to lower primary production and presumed lower foraging success, which in turn lowers the number of individuals able to reach the body condition threshold necessary for attending colonies. Another explanation is a shift in age structure following highly productive years to a higher frequency of older females, which are more likely to become Non-Parturient and Non-Attendant. In our study, inter-annual variation in colony attendance is likely an interaction between shifts in population age structure and fluctuating environmental conditions.

Implications of phenology disruptions. Phenological disruptions are increasingly likely under predicted global change scenarios and have already been documented in several species. For instance, breeding phenology advancement has been associated with spring temperature increase. Phenology disruptions may carry-over to other life history events or other years, and have larger impacts on population health than predicted if treated in isolation. These carry-over effects are particularly concerning in high-latitude environments that have stronger selection pressures. Furthermore, species may differ in their phenological plasticity, which can lead to mismatches between interacting species such as predators and prey.

To fully understand the ecological impacts of changing environments, researchers must first characterize the full annual cycle of life history events and how they interact with each other physiologically. Unlike Weddell seal birth phenology that is consistent across years and individuals (range = 37 days, SD = 7 days; 72), we found that moult timing is much more flexible (range = 75 days, SD = 14 days) without compromising reproductive success or altering future reproductive phenology in subsequent years. Thus, our data provide encouraging evidence that Weddell seals have some inherent phenological flexibility within the annual cycle with which to respond to fluctuating environmental conditions.

Data Availability
Data are available at: http://www.usap-dc.org/view/dataset/601131.

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Author Contributions
R.S.B., J.W.T., and J.M.B. conceived the ideas and designed methodology; R.S.B., A.L.K., and J.M.B. collected the data; R.S.B., J.W.T., A.L.K., G.A.B., and J.M.B. analysed the data; R.S.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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