Author for correspondence:
Caitlin Karniski
e-mail: cbk27@georgetown.edu

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Senescence impacts reproduction and maternal investment in bottlenose dolphins

Caitlin Karniski[1], Ewa Krzyszczyk[1] and Janet Mann[1,2]

[1]Department of Biology, and [2]Department of Psychology, Georgetown University, Washington, DC 20057, USA

CK, 0000-0002-1377-5118

Reproductive senescence is evident across many mammalian species. An emerging perspective considers components of reproductive senescence as evolutionarily distinct phenomena: fertility senescence and maternal-effect senescence. While fertility senescence is regarded as the ageing of reproductive physiology, maternal-effect senescence pertains to the declining capacity to provision and rear surviving offspring due to age. Both contribute to reproductive failure *in utero* making it difficult to differentiate between the two prenatally in the wild. We investigated both components in a long-lived mammal with prolonged maternal care through three parameters: calf survival, interbirth interval (IBI) and lactation period. We provide clear evidence for reproductive senescence in a wild population of bottlenose dolphins (*Tursiops aduncus*) using 34+ years of longitudinal data on 229 adult females and 562 calves. Calf survival decreased with maternal age, and calves with older mothers had lower survival than predicted by birth order, suggesting maternal-effect senescence. Both lactation period and IBIs increased with maternal age, and IBIs increased regardless of calf mortality, indicating interactions between fertility and maternal-effect senescence. Of calves that survived to weaning, last-born calves weaned later than earlier-born calves, evidence of terminal investment, a mitigating strategy given reduced reproductive value caused by either components of reproductive senescence.

1. Introduction

Reproductive senescence, the age-related decline of reproductive output and success, is intrinsically linked to life-history theory from an evolutionary perspective. Theories on reproductive senescence generally stem from non-adaptive arguments for the evolution of general somatic senescence, defined by the degenerative change in function of all organ systems [1,2]. These (non-mutually exclusive, non-exhaustive) theories for the evolution of senescence include (i) mutation accumulation, where the strength of selection decreases with age due to extrinsic mortality [3,4], allowing for the accumulation of deleterious late-acting mutations in a population, (ii) antagonistic pleiotropy, in which alleles that are beneficial to survival early in life are detrimental to later reproduction [5], and (iii) the disposable soma theory [6], in which early reproduction comes at an energetic cost of somatic maintenance, resulting in physiological senescence. These theories for both reproductive and somatic senescence are driven by life-history trade-offs including the trade-off between reproduction and somatic investment, and the trade-off between early- and late-life reproduction [7]. Given the high costs of reproduction [8,9], early reproductive investment may come at the expense of late-life fertility, as demonstrated in longitudinal field studies [10,11]. This trade-off in particular can impact the rate of senescence [10], so examining senescence in the context of these factors can shed light on these evolutionary theories.

Here we examined reproductive senescence in a novel way: through two of its interacting components, fertility senescence and maternal-effect senescence. Further, we applied this model in wild bottlenose dolphins, a long-lived species

with prolonged maternal care. We examined the effects of senescence on prenatal factors (through the interaction between fertility and maternal-effect senescence) and postnatal maternal care (maternal-effect senescence). Both prenatal and postnatal impacts of senescence have profound effects on individual reproductive value [12] and population dynamics [13], thus impacting evolutionary processes.

Reproductive senescence is common across mammalian species [12,14–16], and studies of reproductive senescence in wild and captive populations use physiological (e.g. histological examination of the reproductive tract to infer pregnancy and ovulation rates [17], and endocrine analyses to measure progesterone levels [18]) and demographic (e.g. increase in reproductive failure and decrease in fecundity [19,20]) metrics. Recently, Moorad & Nussey [21] proposed a novel perspective that divides reproductive senescence into discrete (yet interacting) components: fertility senescence and maternal-effect senescence. Fertility senescence is considered to be the ageing of reproductive physiology (e.g. through a decrease in primordial follicles [22]), while maternal-effect senescence pertains to the declining capacity to provision and rear surviving offspring due to age [12]. Considering each of these components is important, as evolutionary theories on reproductive senescence might miss the role somatic ageing plays in reproduction, particularly when it comes to maternal provisioning and care. However, differentiating between what qualifies as maternal-effect senescence is not straightforward. Here we discuss some of the main difficulties in identifying maternal-effect senescence and offer a modified operational definition.

(a) Observing and defining maternal-effect senescence

While investigations of fertility senescence are more common in the literature due to the relative ease of histological observation in laboratory-reared or deceased wild specimens, identifying maternal-effect senescence in a natural population is arguably more challenging. Fertility senescence in wild animals can be determined with cross-sectional physiological data when age is discernable from deceased individuals [23], however maternal-effect senescence is more difficult to observe in natural populations because it involves longitudinal and behavioural monitoring of individuals and their offspring [24,25]. Longitudinal data are essential because individual variation may obscure population-level patterns of senescence due to differential survival or 'selective disappearance' [12,26,27]. Yet, the dearth of studies of maternal-effect senescence is particularly noticeable for long-lived mammals given that decades of research may be necessary to document somatic and reproductive senescence.

Furthermore, while a recent study examined the senescence of maternal effects in birds [28], observing maternal-effect senescence in viviparous species is more complex because fertility and maternal-effects are inextricably linked *in utero*. For example, prenatal androgen transmission is typically considered a maternal effect [29], yet the dysregulation of the hypothalamic–pituitary–ovarian axis that controls maternal androgen levels may be caused by oocyte depletion, a consequence of fertility senescence [30,31]. Because these two components interact heavily *in utero*, disentangling the two for the purpose of an operational definition is difficult. Maternal effects are defined as non-genetic vertical transmission that affects offspring phenotype [32]. Thus, for the purpose of this paper we propose refining the definition of maternal-effect senescence as *when somatic senescence impacts the mother's ability to care for and provision offspring (both pre- and postnatally), such that the offspring's phenotype (such as size, condition and viability) is altered*. This includes maternal care, a type of postnatal maternal effect encompassing lactation, infant carrying, provisioning, socio-ecological information transfer and protection from conspecifics and predators. Although maternal-effect senescence indicates a decrease in offspring fitness with maternal age, this does not preclude increased maternal investment as a compensatory strategy given a decreased ability to provide care.

Bottlenose dolphins are an excellent study species to explore this because they have among the longest, and most variable periods of direct maternal care of mammals [33,34] (see Results, this paper), allowing researchers to readily observe the extent to which maternal care may be affected by senescence. Furthermore, bottlenose dolphins belong to the family Delphinidae, and are closely related to the only non-human species with documented menopause [35–37]. Because there are relatively sparse data on basic reproductive life-history parameters in delphinids, a better understanding of reproductive senescence in bottlenose dolphins can provide context for how post-reproductive lifespans (PRLS) evolved in other delphinid species.

Though bottlenose dolphins (*Tursiops truncatus* and *T. aduncus*) are one of the best-studied cetaceans, research on somatic senescence is limited to a captive population of *T. truncatus* managed by the United States Navy Marine Mammal Program [38] and one free-living *T. truncatus* population in Sarasota Bay, Florida [39]. Reproductive senescence in *T. truncatus* has been suggested qualitatively from longitudinal [40] and capture–mark–recapture [41] data with small sample sizes, captive animals [42] and from drive fisheries data [17], yet little work has been done to empirically demonstrate reproductive senescence among free-ranging individuals. Previous work on age-specific foraging performance of *T. aduncus* in Shark Bay, Australia found a decreased likelihood of lactation past the age of 25 in a small subset of the population [43], yet an assessment of the reproductive trends with age of the population at-large is needed. Conversely, a few short-term studies suggest no relationship between maternal age and reproduction in *T. truncatus* [44,45]. While this would be the first study to empirically investigate reproductive senescence in wild bottlenose dolphins, few mammalian studies have examined maternal-effect senescence, specifically, age-related changes in maternal care. Several studies do address the effect of maternal age on maternally-mediated traits of offspring [12,25,46,47], but none have empirically modelled how fertility and maternal-effect senescence may independently or interactively affect offspring. To our knowledge this study is the first to examine the extent and interaction of two components of reproductive senescence on maternally mediated parameters with a wild, longitudinal dataset.

(b) Study objectives and predictions

The objective of this study was to examine how senescence impacts reproduction and maternal investment in bottlenose

dolphins using 34+ years of longitudinal data on 229 adult females and their 562 calves. We evaluated this through three parameters: calf survival, interbirth interval (IBI) and lactation period. Our hypothesis was that maternal-effect senescence impacts maternal ability to care for offspring from birth to weaning; as such, we predicted a decline in calf survival, defined as survival to age 3, with maternal age. Consistent with life-history theory and Trivers' parental investment theory [48], our second hypothesis was that both fertility and maternal-effect senescence interact to increase IBIs and lactation period with maternal age. We predicted that IBIs would increase with maternal age as a result of both pre- and post-conception factors. For example, IBIs may increase because of failure to ovulate, conceive and/or because of decreased attractivity (fertility senescence) as well as spontaneous abortions and stillbirths (interactions between fertility and maternal-effect senescence). We predicted that lactation period will increase with maternal age, particularly for the last offspring, as a mitigating strategy in light of a reduced reproductive value caused by either components of reproductive senescence [48]. Finally, we predicted later weaning for daughters than for sons because in our population, daughters maintain a stronger bond with their mothers more than sons [49], daughters are more likely to adopt maternal foraging tactics [50,51], and mothers adjust their diving behaviour to accommodate daughters more than sons [52]. In species with extensive maternal care, mothers confer reproductive value to the matriline (a maternal effect) through daughters [53].

2. Material and methods

(a) Subject details

Longitudinal demographic and reproductive data on 741 unique wild bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia were used in analyses for this paper. These 741 individuals included 229 adult females, for which their reproductive history of 562 calves were included in analyses. These counts reflect totals used across all analyses. Some individuals were used in analyses when they were both a mother and a calf. Each analysis used a subset of these totals based on data restrictions we applied, and most individuals were used in more than one analysis. These data are a part of a larger longitudinal database maintained by the Shark Bay Dolphin Research Project, initiated in 1984. Data were collected from boat-based behavioural surveys and focal follows [54]. Dolphins were individually identified through dorsal fin markings and calf ages were determined by (1) distinctive physical features of new calves upon first sighting [55], (2) body size and (3) sightings of the mother before and after calf birth [33]. Females who were already adults when first sighted were aged by the degree of speckling, which begins in the genital area around the onset of sexual maturity (8–12 years), spreads ventrally, and eventually to the dorsal side and fin by mid-20 s [56] (J Mann 2018, unpublished data). Birthdates for dolphins first sighted as juveniles were based on body size, refined with body speckling data, and are accurate within 1–3 years. Adult females with birthdate estimates that were greater than 3 years of precision were not used in analyses. Maternities were known by consistent observation of infant position and mother–calf association [33]. When genetic data were available, all maternity assignments were confirmed by DNA [57]. Weaning ages were determined as in Mann *et al.* [33], by taking a midpoint between the date of the last sighting of the calf in infant position (from

which all nursing occurs) and the date at which the calf last associated with its mother for 80% of sightings. IBIs are the time in between births, so this encompasses any failed conceptions and pregnancies between the first oestrous cycle after the first calf and the birth of the second.

(b) Statistical analyses

All analyses were performed in R v. 3.4.0 [58], and figures were generated using packages 'survival' [59], 'ggplot2' [60] and 'sjPlot' [61].

(i) Effects of maternal age on calf survival

We used generalized linear mixed models (GLMMs) to determine the effects of maternal age on calf survival for 423 calves of known survival born to 153 females. Analyses were performed with package lme4 [62]. Calf survival was binomial, and a calf was determined to have survived when sighted at or past 3 years of age. Calves of unknown survival to weaning were excluded from the dataset. This occurred if there was a gap in sightings around the average weaning age and neither mother nor calf was sighted again. Thus, we were unable to determine if this calf died before or after weaning. Maternal age was included as a fixed, continuous factor. In this population 22% of first births were at age 11 and 42% by age 12 [63]. Thus in order to ensure our data capture the beginning of reproductive years for females, we only used females in our analyses that were sighted often before their 11th birthday and during the years of early first reproduction (11–16). This is a conservative cut-off because females that had their first calf later would have to be sighted often every year to be sure we did not miss a consortship with males, pregnancy or birth. We also carefully documented sightings of females in consortships with adult males. For example, if a female was sighted with adult males at age 12, but no calf (or evidence of pregnancy) was seen the following year, she would be excluded from our first-born analyses. Thus, we are confident that our data capture the beginning of reproductive years for as many females as possible.

In order to control for early calf mortality due to residual complications that occurred *in utero* as a result of the mother's fertility senescence, we ran the model excluding neonatal mortalities (calves that died prior to their fourth month birthday, electronic supplementary material, table S1). Additionally, to control for calves that died as a result of maternal death (10 of 423 births, 2.36%), we ran the model excluding orphaned calf deaths (electronic supplementary material, table S2). Both of these results mirrored that of the model with all calves included, so the complete dataset is presented in the results this paper.

Individual variation in senescence may obscure population-level patterns of senescence if individuals with reduced reproductive performance also have lower longevity for example, and vice versa, rendering models vulnerable to a 'selective disappearance' bias [12,26,27]. Thus, maternal ID was included as a random factor in order to control for individual variation. Though a quadratic relationship with age was predicted [15,16,19], the model with a linear age term was found to be the best-fit model by Akaike information criterion and marginal R^2 values. All GLMM models were created with a binomial or Poisson error structure and logit or log link function respectively. Model fit was confirmed with likelihood ratio tests.

(ii) Residual analyses

Though both maternal age and birth order were found to affect calf survival in initial GLMM models as continuous and categorical factors, respectively, much of this is due to a predicted high collinearity between maternal age and number of calves. In order to explore the relative importance of these two factors, we extracted the residuals of models with either birth order or

maternal age only as fixed factors, then plotted these residuals against the other factor. Next we ran linear models of these residuals and the corresponding factors with package lme4 [62]. We found no relationship between birth order and the residuals of the model with only maternal age (electronic supplementary material, figure S1), suggesting that birth order alone does not explain the variation in calf survival when maternal age is accounted for. However, maternal age and the residuals of the model with only birth order were negatively correlated (electronic supplementary material, figure S2), suggesting that when birth order is accounted for, maternal age is a robust predictor of the variation in calf survival. Because of birth order as a confounding factor and the lack of the relationship between birth order and the residuals of the model with only maternal age, birth order was removed from all subsequent analyses that include maternal age.

(iii) Cox proportional hazards mixed effects models

For our IBI and lactation period analyses we used Cox proportional hazards mixed effects models with package coxme [64]. These models are typically used in survival analyses to examine how time to an event (death) is predicted by covariates, with the inclusion of a random effect to account for multilevel nested data [65]. We modified these models to determine how maternal age affects (1) the time between births ($n = 199$ females and a total of 469 calves) and (2) time to weaning ($n = 95$ calves born to 64 females). Because multiple calves are nested within one mother, we used maternal ID as a random factor, or 'shared frailty term' [65] to account for within-mother homogeneity that could result in increased or decreased hazards for a given matriline. For the IBI model, maternal age and calf mortality were included as fixed factors (continuous and binomial, respectively). IBIs were determined from females for which there was no greater than a 2-year sighting gap between the weaning or death of a calf and the birth of the following calf. This was to ensure no surviving calf could have been missed, although limited pre-natal or peri-natal mortality was still possible. Intervals were right-censored if the mother was still alive and had not yet had another calf at the time of the analysis, or the mother died (hereafter referred to as 'terminal intervals'). In order to account for declining health prior to death, terminal intervals were excluded from analyses (electronic supplementary material, figure S3). With these models maternal age was not a robust predictor of IBIs (electronic supplementary material, table S3), indicating that the effect seen with the complete dataset is primarily driven by a decline in maternal condition in the years before death.

For the weaning model, lactation period was measured by calf age at weaning. This model included only calves that survived to weaning, and also used maternal age as a fixed factor, and maternal ID as a random factor.

(iv) Effects of birth order on weaning age

Finally, to determine relative levels of reproductive investment throughout a female's life, we examined the effects of birth order on the weaning ages of her offspring. For 136 calves that survived to weaning, GLMMs were used to model the effects of birth order on weaning age with package lme4 [62]. Weaning ages were known with a precision of ± 6 months, but typically ± 3 months. Birth order was included as a fixed factor and was categorically defined as 'first,' 'middle' or 'last.' 'Middle' birth order encompassed any calves that were not the first or last calves of their mother. Calf sex was included as a fixed factor in the model to examine any sex effects on weaning in addition to a potential interaction between birth order and calf sex on weaning. Maternal ID was included as a random factor. Only calves with confirmed, known birth order, weaning age and sex were included in analyses. Calves that became independent as a result of their mother's death were excluded from analyses.

3. Results

First, we examined the effects of maternal age on calf survival. Maternal ages at the time of birth ranged from 10.95 to 41.81 years. Of the 153 mothers used in analyses, 33 (21.57%) never had a surviving calf. However, this percentage does not include females who were never observed pregnant or with a calf, so this value underestimates the number of females with no calving success. We found that calves born to older mothers had higher mortality than calves born to younger mothers (figure 1, GLMM, estimate $= -0.06325$, s.e. $= 0.02015$, $z = -3.140$, $p < 0.005$). Additionally, there was a negative correlation between maternal age and the residuals of the model with birth order only included (LM: estimate $= -0.02049$, s.e. $= 0.00825$, $t = -2.484$, $p < 0.05$, electronic supplementary material, figure S2), indicating that maternal age likely explains the variation in the calf survival model for which birth order is accounted.

Mean $\pm$ SE for all completed IBIs is 4.25 ± 0.10 years, 2.85 ± 0.13 years after non-surviving calves only, and 4.97 ± 0.11 years after surviving calves only. IBIs increased with maternal age (figure 2a, Cox model, estimate $= -0.05107$, s.e. $= 0.01786$, $z = -2.86$, $p < 0.005$). While IBIs were predictably shorter when calves died (Cox model, estimate $= -1.71018$, s.e. $= 0.48299$, $z = -3.54$, $p < 0.0005$, see electronic supplemental material, figure S4 for IBIs of surviving calves only), the interaction between maternal age and calf mortality on IBIs was not significant ($p = 0.930$).

Weaning ages ranged from 2.56 to 8.59 years, with a mean of 3.98 years. Lactation period increased with maternal age (figure 2b, Cox model, estimate $= -0.05397$, s.e. $= 0.02726$, $z = -1.98$, $p < 0.05$) and last-born calves nursed for longer periods of time (figure 3, GLMM, estimate $= 0.15403$, s.e. $= 0.07329$, $z = 2.10$, $p < 0.05$) than earlier-born calves. However, we found no effect of calf sex on weaning age ($p = 0.37$), nor an interaction between birth order and calf sex on lactation time ($p = 0.44$).

4. Discussion

Results from our survival models demonstrated clear evidence for reproductive senescence, and that maternal age was a significant predictor of calf survival while birth order was not. Birth order explained little variation of the model when maternal age is accounted for (electronic supplementary material, figure S1), but maternal age was negatively correlated with the residuals from the model with only birth order included (electronic supplementary material, figure S2). This indicates that maternal age is a more robust predictor of calf survival than birth order. The negative relationship between maternal age and calf survival (figure 1) showed that calves born to older mothers had higher mortality than calves born to younger mothers. Further, the relationship between maternal age and the residuals of the model with only birth order included indicates that younger females had calves with higher than expected survival as predicted by birth order, and vice versa—that older females had calves with lower than expected survival as predicted by birth order alone. Similar to evidence of reproductive senescence in other mammals (e.g. olive baboons *Papio Anubis* [14], red deer *Cervus elaphus* [15], meerkats *Suricata suricatta* [16]), these results show reproductive senescence in this population. We attribute the decline
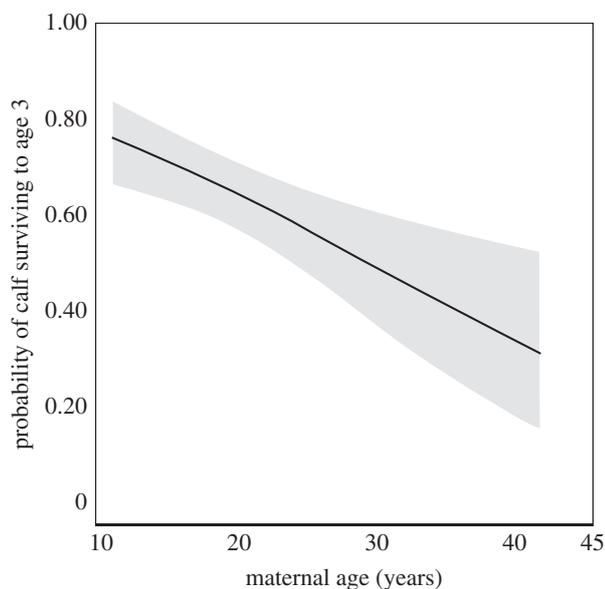
Figure 1. Partial effects of maternal age on calf survival. The probability of a calf surviving to age 3 decreased with maternal age (estimate = −0.06325, s.e. = 0.02015, z = −3.140, p < 0.005).

in calf survival with maternal age primarily to maternal-effect senescence because even after excluding neonatal mortality, which could be a consequence of fertility senescence, calves born to older mothers were more likely to die by age 3. This result suggests that older mothers have reduced ability to care for offspring due to senescence.

Surprisingly, in contrast to other mammalian species [66,67], first-born mortality was not higher in our population than later-born, and birth order was not a significant predictor of calf survival. At other *Tursiops* study sites, Sarasota, Florida [68], and Moray Firth, Scotland [40] first-born mortality is high, consistent with terrestrial mammals, yet the discrepancy between our results could be due to the extent in which anthropogenic contaminants play a role. Wells *et al.* [68] found that mothers offloaded toxins through lactation to their first-born calves, contributing to their significantly higher mortality than later-born calves. By contrast, Shark Bay is a relatively pristine environment, with few pollutants that may adversely affect first-born survival. Further, given that juvenile females frequently interact with calves and their mothers [69] for up to 10 years prior to producing their first calf, and that calves are physiologically precocial [70], adult maternal experience in a relatively undisturbed population may be less critical for calf survival than other factors (e.g. social and ecological [33,71]). This may partly explain why a linear model, rather than quadratic, was superior in explaining the decline in calf survival with maternal age. *Direct* maternal experience appears to be less important in this population, indicated by the highest rates of calf survival among young primiparous females, in contrast to the parabolic mid-life peak evident in other mammalian populations [15,16,19]. This result was also surprising given the higher levels of inbreeding [57] and aggression received from males [72] for young females compared to older.

The increase in IBIs with maternal age is indicative of a slowing reproductive rate with age, and serves as evidence for reproductive senescence in this and other species (e.g. chimpanzees, *Pan troglodytes* [73]; Barbary macaques *Macaca sylvanus* [74]; Hamadryas baboons *Papio hamadryas* [75]). The lack of an interaction between maternal age and calf
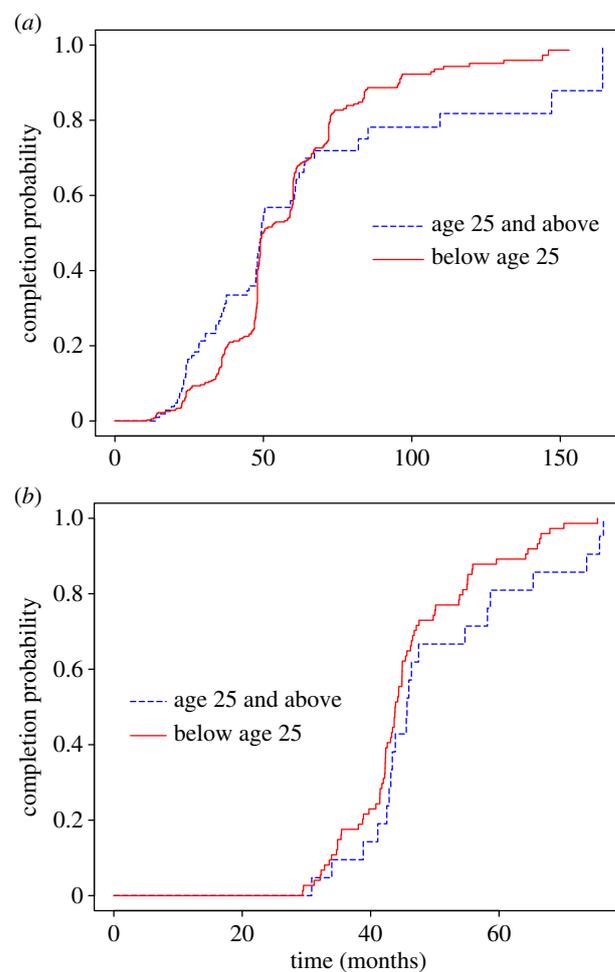

Figure 2. Cox proportional hazards for IBIs (*a*) and time to weaning (*b*) according to maternal age. (*a*) Curves reflect the probability of completing an interval by giving birth to another calf. Females are binned according to their ages at the start of the interval (≥25 years or less than 25 years) for visualization purposes though maternal age was analysed as a continuous factor in the model. IBIs increased with maternal age (estimate = −0.05107, s.e. = 0.01786, z = −2.86, p < 0.005), thus older females had a lower likelihood of closing the interval by birthing another calf. (*b*) Curves reflect the probability of completing an interval by weaning off a calf. Females are binned according to their ages at the start of the interval (≥25 years or less than 25 years) for visualization purposes though maternal age was analysed as a continuous factor in the model. Lactation period increased with maternal age (estimate = −0.05397, s.e. = 0.02726, z = −1.98, p < 0.05), thus older females had a lower likelihood of closing the interval by weaning their calf.

mortality on IBI indicates that time between births increased with age regardless of offspring survival. Nevertheless, some of the increase in IBIs could be due to an increase in spontaneous abortions or unobserved stillbirths as a result of fertility senescence, thereby contributing to the longer time periods between births. Additionally, the fact that maternal age does not predict IBIs when excluding terminal intervals, but predicts IBIs with the full dataset, indicates that prolonged interbirth intervals are largely driven by the decline in maternal condition, which also diminishes her ability to conceive or complete another pregnancy before her death.

Further, lactation length increased with maternal age, exceeding eight years in some cases for last-born offspring. Because female bottlenose dolphins often become pregnant in the final year of lactation and tend to wean about six months into the next pregnancy [33], *in-utero* death due to
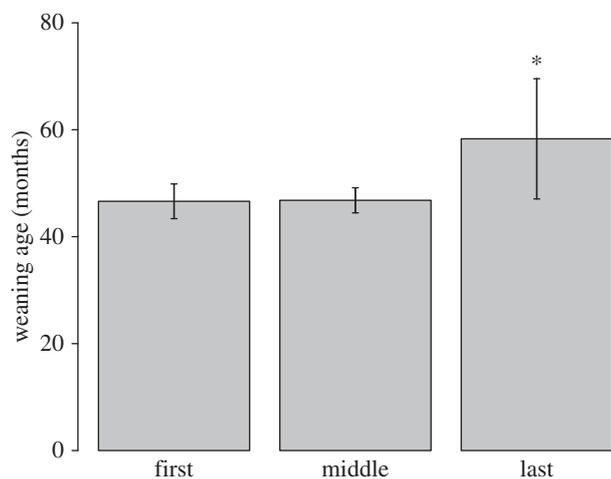
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Figure 3. Average weaning age of calves by birth order. Results of a GLMM indicate that last-born calves wean later than earlier-born calves (estimate = 0.15403, s.e. = 0.07329, $z = 2.10$, $p < 0.05$).

fertility senescence might result in sustained nursing of the existing calf. Changes in attractivity may also cause an increase in lactation period with age if successful matings do not occur. While males of some species prefer older females over younger females [76] potentially due to maternal experience, this may not be the case for bottlenose dolphins because parity is not a significant predictor of calf survival (see Results, this paper). While age-specific mate choice has not been explicitly examined in bottlenose dolphins, Watson-Capps' [72] finding that younger females received more aggression from males than older females did is an indication of male preference for females with higher calving success. Further, male–female association patterns during oestrous suggest males can detect female receptivity [77] indicating that older females may be less receptive and in turn, less attractive to males. Fetal loss and lower attractivity due to fertility senescence might help explain why older females nurse offspring for longer than younger females, and highlight the interaction in fertility and maternal-effect senescence in affecting IBIs and lactation period. In addition to being indicative of maternal-effect senescence, the tendency for mothers to nurse calves longer as they age may also represent a shift in the cost–benefit ratio of parent–offspring conflict [48]. An ability to conceive or carry another offspring would lessen the cost of prolonged nursing of the current offspring.

While maternal-effect senescence reduces a female's ability to care for offspring, it might also favour increased investment for the last-born offspring. Because very old females likely would not survive caring for a future calf, it would benefit these individuals to 'hedge their bets' and nurse their current and final offspring for as long as possible. At an average of 4.87 years, final-born calves in Shark Bay have among the longest lactation periods for any mammal (see [34]). The duration of lactation is predicted to increase with maternal age, particularly for the last offspring prior to maternal death, indicative of terminal investment [78]. As milk fat content is very high at peak yield and declines closer to weaning [79], the trade-off between producing another calf with costly high-fat milk, and nursing the existing calf at a relatively lower energetic cost to ensure survival results in enhanced investment in the last calf. Because lactation is so energetically costly, the lactation period is also closely linked with maternal condition

[80]. While the relationship between parity and milk composition has been studied in primates [81,82], the effect of maternal age on milk composition has received comparably less attention, and conclusions vary [83–85]. As such, the effect of maternal age on milk composition, a maternal effect, needs further study.

While reduced reproductive performance due to senescence and longer lactation periods present a paradox, given that energetic investment in lactation is linked to future reproductive value [86], terminal investment can be considered a mitigating strategy to increase maternal investment when reproductive potential is low. Additionally, Shark Bay dolphins are bisexually philopatric, where mothers continue to associate with juvenile sons and daughters after weaning [49,77], so nursing the final offspring longer may be a strategy to invest more in offspring that will not have the advantage of their mother's presence after weaning.

As such, it is important to note the proportion of late-weaning calves that served as their mother's final surviving offspring: of calves that nursed for longer than 4.87 years (average weaning age for last-born offspring), 31.82% (7/22) of their mothers had a subsequent calf survive to weaning compared to 90.63% (87/96) of mothers that nursed calves for less than 4.87 years. While seemingly counterintuitive, previous studies in Barbary macaques (*M. sylvanus*) [74], rhesus macaques (*Macaca mulatta*) [87], and wandering albatrosses (*Diomedea exulans*) [88] show that terminal investment and reproductive senescence may not be mutually exclusive [89].

Collectively, these results are clear indicators of reproductive senescence in this population. The reduction in calf survival with maternal age is consistent with maternal-effect senescence, yet the lengthening of lactation periods and IBIs with maternal age are likely evidence of both fertility and maternal-effect senescence. These components of reproductive senescence likely interact, although teasing apart the contribution of maternal-effect and fertility senescence to these reproductive parameters remains a challenge. As Moorad & Nussey [21] demonstrate that selection may act on these components separately, we hope that discussing ways that they may interact biologically and the consideration of these interactions will benefit the ability of future studies to observe these components and consider them in an evolutionary context.

Cetaceans are valuable taxa for comparative ageing research given their extreme life-history traits. For example, despite having a maximum lifespan of well over a century [90,91], bowhead whales do not appear to exhibit menopause. Furthermore, the fact that delphinids include the only other species outside of humans to definitively undergo menopause makes this group especially significant. Close examination of reproductive life-history characteristics of cetaceans may help unravel why some species of this group have evolved a PRLS while others have not. Specifically, as some evolutionary theories for the evolution of a PRLS centre on extended maternal care [5,92], examining how senescence impacts maternal care in a non-menopausal species may contribute to the understanding of a threshold of care required in order for menopause to evolve. For example, both the stop-early hypothesis [5] and the grandmother hypothesis [92] focus on how mothers continue investment in existing offspring after weaning, including toward reproductive daughters. In bisexually philopatric species such as Shark Bay dolphins, but also species

that show PRLS, mothers continue to invest directly and indirectly in offspring well after weaning [93,94]. In essence, following fertility senescence and maternal-effect senescence, menopausal females extend pronounced maternal care to existing offspring, similar to increased investment in the final offspring in this species.

Bottlenose dolphins in particular may be a valuable comparative model for understanding human ageing given similarities in age-related changes of haematological and serum chemistry [38], extensive maternal care, and phylogenetic relatedness to species with PRLS. Given this species' place in the family Delphinidae, the results of this study are especially relevant in the broader context of mammalian reproductive life histories. As the first empirical study of fertility and maternal-effect senescence and their interactions in a long-lived mammal with extensive maternal care, these results will help lend a greater understanding to the relative contributions of these components to reproductive senescence and the evolution of these reproductive life histories.

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