Weaning age and supersuckling in Galápagos Sea Lions (Zalophus wollebaeki): Maternal, offspring and environmental drivers of life-history strategies

Authors: Childs, Alexandra*†[1]; Feldmann, Carlina[2]; Dyck, Julia[2]; Stoehr, Svenja[1]; Twiss, Sean D.[3]; Krüger, Oliver[1,4].

Affiliations:
1 Department of Animal Behaviour, Faculty of Biology, Bielefeld University, Konsequenz 45, 33501, Germany.
2 Department of Business Administration and Economics, Bielefeld University, Universitätsstraße 25, 33615 Bielefeld, Germany.
3 Department of Biosciences, Durham University, Durham DH1 3LE, UK.
4 Joint Institute for Individualisation in a Changing Environment (JICE), Bielefeld University and University of Münster, Konsequenz 45, Bielefeld 33615, Germany.

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***Corresponding Author:** Alexandra Childs; alexandra.childs@uni-bielefeld.de
†**Current Address:** Department of Animal Behaviour, Faculty of Biology, Bielefeld University, Konsequenz 45, 33615 Bielefeld, Germany

Abstract

Weaning marks a critical life-history transition in mammals, shaped by maternal investment strategies, offspring condition, and environmental constraints. In Galápagos sea lions (*Zalophus wollebaeki*), weaning age is highly variable, with some individuals continuing to suckle into adulthood (supersucklers). Using 20 years of mark-recapture data from 1890 individuals, we applied multi-state capture-recapture models to investigate the probability of weaning age, and logistic regression models to explore the drivers of supersuckling. We examined maternal effects (age, birth interval, and pup condition at birth), offspring traits (sex, early growth), and environmental variability (Oceanic Niño Index [ONI]). Weaning probability peaked at four years of age, with 95% of individuals weaned by this time. Longer birth intervals were associated with later weaning. Offspring sex had no influence on weaning probability. However, ONI affected juvenile survival, indirectly shaping weaning outcomes. No intrinsic predictors of supersuckling were identified, although low resource availability during an individual's second or third year of life increased the likelihood of becoming a supersuckler. While weaning is typically driven by escalating mother-offspring conflict, the persistence of supersuckling challenges this paradigm. We propose that the regular occurrence of supersuckling in this species may therefore be socially driven, reflecting the maintenance of long-term mother-offspring relationships that contribute to a complex adult social structure. This study highlights the interplay between environmental unpredictability and social behaviours in shaping life-history strategies.

1. Introduction

Weaning in mammals marks the end of maternal nutritional investment and is a fundamental life-history transition for offspring. The timing of weaning is shaped by a complex interplay of maternal investment strategies, offspring condition, and environmental constraints (Lee 1996; Schulz & Bowen 2005; Avery & Zinn 2023). As an energetically costly form of parental care, lactation must be balanced against the mother's future reproductive success, leading to an inherent mother-offspring conflict over the duration of care (Trivers 1974). Offspring who benefit from protracted maternal investment in the form of nutrition may have increased chances of survival (Gerber et al. 2021; Dittus & Baker 2023; Vitikainen et al. 2023). However, gluttonous offspring, once weaned, may be unable to maintain the same nutritional input and subsequently perish (Reiter et al 1978). Mothers, on the other hand, may incur an immediate cost to body condition and reproductive fitness but be rewarded for their extended investment through delayed generational success (Péron et al. 2019; Zipple et al. 2020; Bleu et al. 2021; Chapman et al. 2021; Nielsen et al 2023).

Amongst pinnipeds the duration of lactation is particularly variable due to their terrestrial or floe ice breeding and aquatic foraging (Pomeroy 2011; Avery & Zinn 2023). Phocids generally exhibit abrupt weaning after an intensive lactation period, whereas otariids (eared seals) experience prolonged lactation and a gradual transition to nutritional independence that can last up to 36 months in some species (Sepúlveda & Harcourt 2021). This lengthily dependence increases the potential for variability in weaning age and may intensify mother-offspring conflict (Trillmich & Wolf 2008; Sepúlveda & Harcourt 2021; Dittus & Baker 2023). Maternal investment may be determined by pup traits such as sex, mass and demand (Goldsworthy 2006; McDonald et al. 2012; Kraus et al. 2013). However, lactation duration, and therefore weaning age, is frequently dictated by maternal factors such as parity, maternal resources and reproductive experience (Schulz & Bowen 2004; Trillmich & Wolf 2008; Costa & Maresh 2022). Environmental factors such as predation (Ferguson 2006) and climatic variability (Burkanov et al. 2011; Costa & Valenzuela-Toro 2021; Schwarz et al. 2022) further influence weaning by affecting maternal foraging success and offspring condition. During periods of resource scarcity, females may prioritize their own survival and future reproductive opportunities, leading to earlier weaning or decreased investment in current offspring (Soto et al. 2004). Conversely, in times of higher resource availability, prolonged lactation may be more feasible, allowing offspring to remain nutritionally dependent for extended periods.

Galápagos sea lions (GSL) *Zalophus wollebaeki* are an endangered otariid endemic to the Galápagos archipelago. As an equatorial species GSL are exposed to extreme stochastic environmental fluctuations in the form of El Niño events which directly impact resource availability for foraging mothers (Soto et al. 2004; Schwarz et al. 2022). The reproductive period is protracted starting in September and ending in January (Pörschmann et al. 2010) although females show high asynchronosity and low seasonality in their breeding cycle (Villegas-Amtmann et al. 2009). There are high amounts of individual variation in age at primiparity (4-9 years) and the time until the birth of the next sibling (birth interval). However, females produce on average, a single pup every two years from the age of six (Kalberer et al. 2018). The expected lifespan for

GSL is 21 years (Krüger et al. 2021) and the oldest recorded age at parturition is 18 years (*personal communication*). Adoption and alloparenting are extremely rare in this species (Childs et al. 2025). Reproductive overlap is not uncommon and, whilst some females have been observed supporting multiple dependent offspring, more often than not, the situation results in sibling competition and the rejection or death of one offspring (Trillmich & Wolf 2008). Recent research has shown that GSL exhibit a prolonged and flexible lactation period lasting between one and three years (Childs et al. 2025), with some individuals, 'supersucklers' continuing to suckle into adulthood. However, robust statistical analysis of age at weaning has yet to be conducted.

Accurately determining weaning age is crucial for understanding both the physiological and ecological determinants of maternal investment strategies in otariids (Costa & Valenzuela-Toro 2021; McHuron et al. 2023). However, direct observations of weaning are often logistically challenging, particularly in long-lived, wide-ranging marine species (Trillmich et al. 2016; Osiecka et al. 2020; Hastings et al. 2021). Multi-state hidden Markov models (HMMs) provide a powerful tool for inferring weaning transitions from mark-recapture data, allowing estimates of state probabilities and the role life-history traits and environmental fluctuation may play in variability (Hastings et al. 2021).

Using multi-state capture-recapture models (MSCRM) framed as HMMs, we investigate weaning age in GSL in relation to life-history traits and environmental conditions. We predicted that low resource availability, represented by the Oceanic Niño Index (ONI) anomaly, would delay weaning. Moreover, we hypothesised that male offspring would wean later due to male-dominant size dimorphism and that lower maternal investment and inexperience would prolong the lactation period. Based on the MSCRM results we further explored the possible drivers of supersuckling using logistic regression models (LRM). We theorise that supersucklers exhibit slower growth than their non-supersuckling conspecifics and that poor environmental conditions during the year of expected weaning may lead to delayed weaning. A better understanding of weaning patterns and the mother-offspring relationship in this species is particularly relevant in the context of increasing environmental variability, as shifts in resource availability may influence maternal investment strategies.

2. Methods

2.1. Data collection & Study Site

Caamaño islet (0°45’S, 90°16’W) is located off the southern coast of Santa Cruz, Galápagos, and is home to a breeding colony of GSL that has been intensively studied since 2003 (Wolf & Trillmich, 2007). Data for this study were collected between February 2003 and April 2024 during two annual field seasons (October–December and February–April) and grouped by reproductive season (August–July), referred to by the calendar year in which each season began. All individuals that are born on, or regularly use the islet are given a pit-tag, and marked using Allflex tags, resulting in a database of extensive individual life history (for details on capture methodology see Wolf & Trillmich 2007; Meise et al. 2013). Identification rounds were conducted daily (2-5 times), during which the ID, location, and suckling events of all individuals present on the islet were recorded (for details on identification rounds see Trillmich et al. 2016; and for suckling events Childs et al. 2025). Missing tags were recorded whenever tag-loss was observed and used as means of tracking an individual’s absence from the database. Considerable effort was made to mark unidentified mothers and replace missing tags to maintain life history records.

Mother-offspring pairs were identified through direct observation of birth, perinatal bonding, or repeat suckling events within a month (Childs et al. 2025). Each individuals’ date of birth (DoB) was categorised: where ‘exact’ is accurate to the day, ‘weak’ is ± 2 weeks, and ‘unknown’ is greater than 2 weeks uncertainty. Field-based age estimates for juveniles have proven to be highly accurate (Jeglinski et al. 2010). We therefore recategorised all individuals originally labelled as ‘unknown’ DOB and first marked at, or under, 6 months of age as ‘roughly known’ so that they could be reassigned to their appropriate reproductive year of birth. All individuals born before 2003, when data collection first began, were categorised as DOB ‘unknown’. Individuals with unknown DoB were not included in any statistical modelling or testing involving age.

Sex verification and morphological measurements were taken every time an individual was captured. Individuals were weighed with an electric scale, and length was measured from the tip of the snout to the tip of the tail (see Mueller et al. 2011). All individuals were captured 1. for marking, 2. to observe pup growth during their first 2 months, 3. annually to measure juvenile morphological differences and cohort response to environmental variations (Wolf & Trillmich

2007). To avoid disturbance to the mother-offspring relationship, offspring are only captured when their mother is absent. Offspring body condition was calculated using scaled mass index (SMI) (Peig & Green 2009) for both birth (10-day-old or less) and early life (90-day-old mean) as indicators of offspring health and maternal investment (Mueller et al. 2011). Which we take as representative of maternal investment due to the offspring's nutritional dependence on milk at this life stage (Jeglinski et al. 2012; Schwarz et al. 2022). For investigating growth differences between supersucklers and non-supersucklers, SMI was calculated for each time point (age) where both length and weight measurements were available.

Birth interval, measured as the number of years until the birth of the next sibling, was used to gain insight into the effect the presence of a younger sibling may have on weaning age as sibling conflict is not uncommon in this species and females are known to reject older offspring upon the birth of a new pup (Trillmich & Wolf 2008). Due to the possibility that longer than average intervals (2 years, Kalberer et al. 2018) might be due to tag-loss, unrecorded miscarriages or stillbirths, females not observed on the islet for more than 2 years were excluded from the sample. We further cross-referenced all individuals with known multiple-year tag-loss to check for mothers who may have given birth, but no offspring was assigned due to an inability to positively identify the pair.

Throughout the study, we define pups as individuals younger than 6 months, after which all GSL are referred to as juveniles until they reach 5 years of age and are assumed to be adults (Trillmich et al. 2016). Due to high site fidelity and limited exploration, deaths of individuals under the age of 1 year were accurately recorded either by recovering the body, disappearance from the site of birth and entire islet for very young individuals (< 3 months), or repeated observations of the mother without her offspring over the course of a field season. Deaths of individuals older than 1 year are only recorded if a body is recovered and a positive ID obtained. We used correlated ONI anomaly (NOAA Climate Prediction Centre 2024) and sea surface temperature ([SST] Galápagos Climatology Database 2024), aggregated and averaged by reproductive year, to represent food availability (Soto et al. 2004; Mueller et al. 2011).

2.2. Multi-state capture-recapture model

For this study weaning is defined as the point in time when an offspring stops suckling. We employed MSCRM which we frame as an HMM (see *supplementary material*) and used the package `LaMa` (2025) in R (version 4.3.3) for building the HMM likelihood. We assumed three possible latent states for offspring: unweaned, weaned, and absent (Figure 1). All animals' trajectories begin in their reproductive year of birth when they are certainly unweaned. From there, they may transition to the weaned state after a certain number of seasons, followed by the absent state after additional season(s). Alternatively, they may transition from the unweaned state directly to the absent state. We assumed irreversible state transitions such that an offspring, once considered weaned, cannot return to unweaned, and once considered absent, will stay absent. A potential trajectory with one state per season could be U, U, U, U, W, W, A. As our primary interest lies in age at weaning, we included the animal's age in years as a covariate in the state process. Finding the appropriate functional form of this covariate was addressed during model selection (see sp. *Methods*).

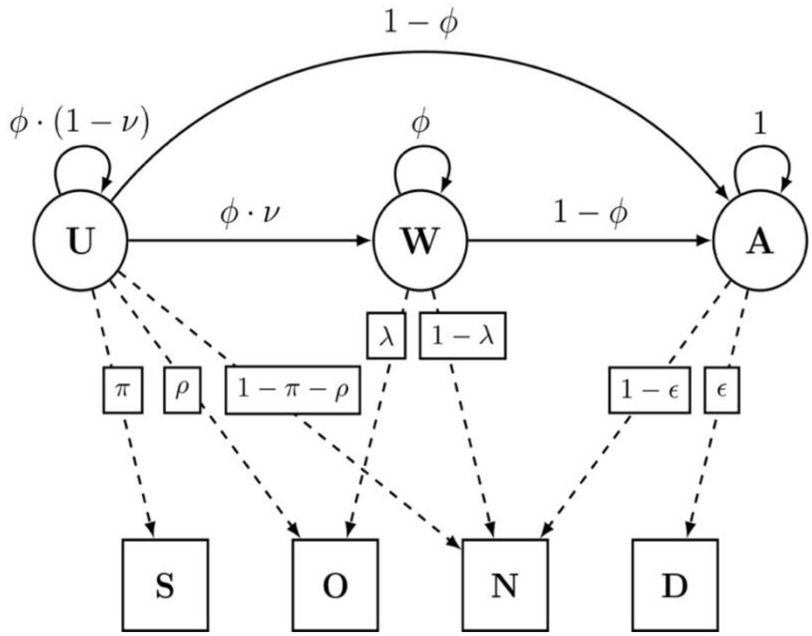

Figure 1. Both processes of the MSCRM for the observations suckling (S), observed (O), not observed (N), dead (D) generated given the states unweaned (U), weaned (W), and absent (A). Solid lines show possible state transitions. Dashed lines indicate possible observations given each state. Lines corresponding to probabilities of zero and index are omitted for visual clarity.

To describe the state dynamics over time, we modelled the survival rate ϕ_t for $t = 1, \dots, T$ and the weaning rate ν_t as functions of an animal's age. It should be noted that the survival rate refers only to apparent survival from the age of one year onwards, as the absent state is comprised of dead animals as well as those who were no longer seen on the islet. Given the latent state, different observations could have arisen: an unweaned animal can be observed suckling with probability π, observed but not suckling with probability ρ_t, or not observed $(1 - \pi_t - \rho_t)$. In the weaned state, an animal can either be observed (but not suckling) with probability λ_t, or not observed $(1 - \lambda_t)$. Absent animals can either be recovered dead with probability ε_t or not observed $(1 - \varepsilon_t)$. We accounted for observation effort by writing $\pi_t, \rho_t, \lambda_t, \varepsilon_t$ as functions of the number of observation rounds in each season t.

The variables offspring sex, ONI, offspring birth SMI (as a proxy for maternal fitness), birth interval and maternal age in years (at the time of the birth of her offspring) were investigated and their effect assessed by comparing models using the specific subset both with and without the variable included. SST was investigated during early exploration. GSL are known to be entirely nutritionally dependent on milk until 12 months (Jeglinski et al. 2012; Piedrahita 2015). Individuals who died before reaching 1 year of age were therefore unable to provide us with information to estimate the probability of any of the possible state transitions. Although the MSCRM may have been flexible enough that the inference on weaning would not change, we were concerned that the flexibility would become absorbed as the model attempted to explain early age survival. As this study's central focus was to investigate age-at-weaning in GSL, we decided to exclude all individuals registered as deceased before the age of 1 year (*n* = 156).

We used the Viterbi algorithm (Zucchini, MacDonald & Langrock 2016, Chapter 5) to obtain the most likely state sequence for each animal given the data and the model parameters. Model selection for the functional form of the age covariate and inclusion of other covariates in the state process was guided by the AIC whilst a visual inspection of results served as a final criterion for judging the relevance of added complexity.

2.3. Logistic regression model

LRMs were used to investigate the probability of an offspring becoming a supersuckler. We classed supersucklers as offspring deemed unweaned by the selected MSCRM i.e. after the 95% weaning threshold, which conforms with standard statistical practices (Wei et al. 2006; Waldmann 2018) and previous work on this behaviour (Childs et al. 2025). Supersucklers are therefore 4 years of age or older. In order to understand the drivers behind the likelihood of individuals becoming supersucklers we analysed both time-invariant and time-variant variables. The former consisted of offspring age, age at the birth of a sibling, sex, SMI, and maternal age at parturition. The latter were ONI anomaly average and observation effort for each reproductive year. Additionally, we incorporated the decoded state of the offspring in each season based on the MSCRM. For an unbiased comparison between supersucklers and non-supersucklers, we only included non-supersucklers who according to the MSCRM had not transitioned to the absent state at 4 years old. This resulted in a dataset of 766 individuals: 650 non-supersucklers and 116 supersucklers.

Based on this data an LRM was fitted including offspring sex and ONI anomaly. A series of LRMs were then built using subsets of data to investigate whether maternal fitness and experience affects the probability of their offspring becoming a supersuckler: 1. maternal age and birth, 2. birth SMI, 90-day average SMI, and both SMI measurements, 3. birth interval, and the data for this latter LRM. To control for any possible external ONI or cohort effects, we included year of birth as a random effect in all models. The effect of a variable was informed by significance results and BIC, which also guided model selection and parameter inclusion for all LRMs. Missings were checked for informativeness by comparing the proportion of supersucklers in the data group with missing values, with the data group with non-missing values for that variable.

To understand the potential reproductive cost of mothers supporting a supersuckler we visually inspected the relationship between time until the birth of the next sibling and whether that sibling survived to yearling age for both supersucklers and non-supersucklers. We further investigated the number of female supersucklers who were reproductively active at the time of supersuckling. Here, reproductively active was defined as females who either gave birth within the same reproductive year as having been observed supersuckling - and were therefore pregnant at the time - or had already given birth to an offspring prior to their first observed supersuckling event. Male reproductive data were not available for this study. To assess whether supersucklers grow slower during early life than their non-supersuckling counterparts we plotted and visually inspected length, weight and SMI curves of supersucklers and non-supersucklers, separated by sex and fitted with a spline model.

3. Results

3.1. Multi-state capture-recapture model

All MSCRM model candidates and their fit can be found in Table 1. During early exploration no effect of SST was found nor was there any improvement to the fit of the MSCRMs, it was therefore excluded from all models. We found that accounting for observation effort (*n* = rounds per year) increased the model fit. Effort has a direct positive effect on the amount of suckling observed in the unweaned state: between 56.9% and 86.3% for min. and max. number of observation rounds, as well as the probability of observing an individual at all (33.1% - 48.2% in the weaned state). Dead individuals are also more likely to be recovered (0.2% - 2.7% in the absent state) with higher effort.

Table 1. All fitted MSCRM described by the covariates included in the observation process via Z and the state process via Y. Number of parameters (np) and number of individuals (nind) for which the corresponding variables were available are used as a basis for comparison via the AIC. Variable notation age_{dec} refers to the exponential decay function of age $age^2 * exp^{-age}$, SMI to the SMI of an individual's first 10 days, $sibl$ to time until sibling, m_{age} to the age of the mother. Index refers to the steps in model selection. The index in bold indicates the model that was preferred at each stage of model selection.

Index	**Covariates in Z**	**covariates in Y**	**np**	**nind**	**AIC**
0A	-	-	6	1890	38038.0
0B	$rounds$	-	10	1890	37586.4
1A	$rounds$	age	12	1890	37510.8
1B	$rounds$	age, age^2	14	1890	37091.2
1C	$rounds$	age, age^2, age^3	16	1890	37046.4
1D	$rounds$	age, age_{dec}	14	1890	37032.0
1E	$rounds$	$I(age\_t = 1), \ldots, I(age\_t = 14))$	38	1890	36821.0
2	$rounds$	$age, age_{dec}, sex, sex \cdot age, sex \cdot age_{dec}$	20	1890	37032.2
3	$rounds$	$age, age_{dec}, ONI, ONI \cdot age, ONI \cdot age_{dec}$	20	1890	36969.6
4A	$rounds$	$age, age_{dec}, ONI, ONI \cdot age, ONI \cdot age_{dec}, SMI, SMI \cdot age, SMI \cdot age_{dec}$	26	1266	24529.4
4B	$rounds$	$age, age_{dec}, ONI, ONI \cdot age, ONI \cdot age_{dec}$	20	1266	24526.2
5A	$rounds$	$age, age_{dec}, ONI, ONI \cdot age, ONI \cdot age_{dec}, sibl, sibl \cdot age, sibl \cdot age_{dec}$	26	317	5961.2
5B	$rounds$	$age, age^2, ONI, ONI \cdot age, ONI \cdot age^2$	20	317	5993.4
6A	$rounds$	$age, age_{dec}, ONI, ONI \cdot age, ONI \cdot age_{dec}, m_{age}, m_{age} \cdot age, m_{age} \cdot age_{dec}$	26	328	no convergence
6B	$rounds$	$age, age_{dec}, ONI, ONI \cdot age, ONI \cdot age_{dec}$	20	328	no convergence

Offspring effects

When including age as a functional form (MSCRM 1D), the preferred approach was $\text{age}^2 \cdot \exp(-\text{age})$. Although estimating an effect separately for each age category was supported by AIC, visual inspection showed no meaningful differences to model 1D. As less data was available for older ages additional complexity was deemed unnecessary. Exponential decay improved the overall fit compared to simple polynomials without increasing the number of parameters. We therefore favoured the model in its simplest form, using only exponential decay and the polynomial effect as parameters. This ensured the flexibility of the polynomial function is prioritised for younger ages whilst assuming the effect in older ages is captured sufficiently by the linear term. Viterbi decoding of model 1D provided age-at-weaning estimates of 50% by 1.5 years, 90% by 3 years, and 95% by 4 years (Figure 2). The highest number of state switches was observed between 1 - 2 years of age and rapidly decreased after this point (Figure S1). The highest number of switches to the weaned state was observed at 1.5 years of age. Switches to the absent state were extremely elevated throughout the first 2.5 years, peaking at the yearling stage and only levelling out towards the end of the 3rd year.

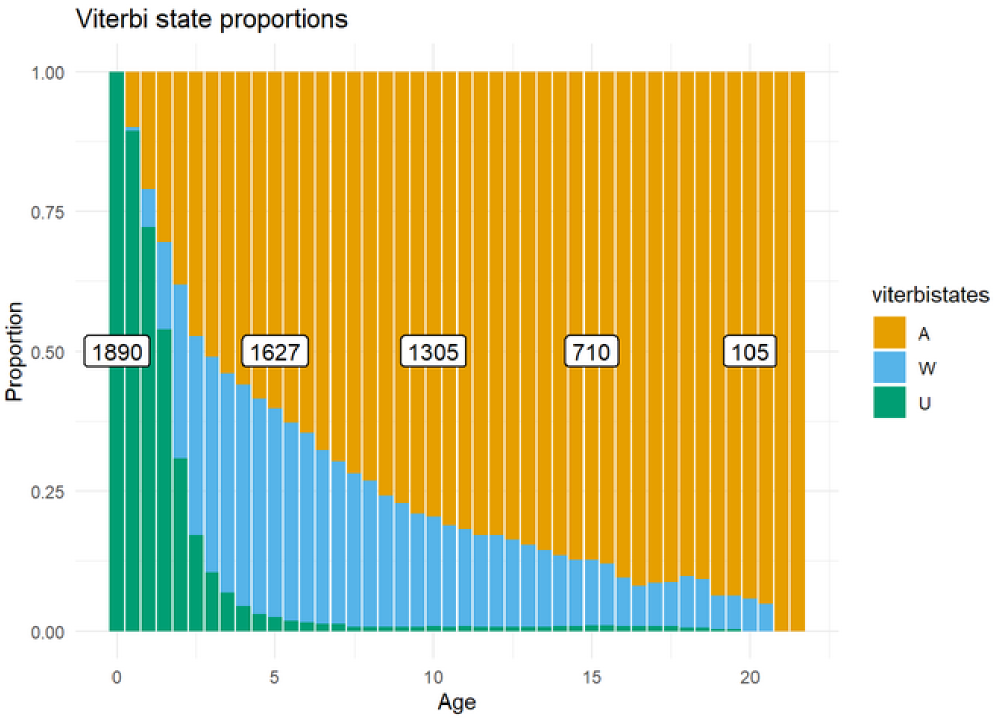

Figure 2. Viterbi state proportions from Model 1D showing the most likely state (unweaned [U], weaned [W], absent [A]) an individual is in at any given time point given their observational history and age. White-boxed numbers within the figure indicate the total number of possible observable animals at 5-year intervals.

Due to increasing exploration and time spent at sea, the likelihood of recovering a body and obtaining a positive ID for death registration dwindles dramatically with age. Over the entire data collection period 247 deaths have been recorded, of which 63% (*n* = 156) were individuals under 1 year of age. Only 40 adult deaths have been recorded. That these numbers are so low is likely due to most individuals within this population dying at sea or temporary haul-out locations. Without positive confirmation of these deaths' individuals remain in the dataset even after multiple years of absence. It should therefore be noted that the sample sizes (Figure 2 & 3) indicate the total number of possible observable individuals.

The selection of additional covariates was guided by a combination of AIC, BIC, and contextual considerations. Among animals that could be observed, both sexes were relatively evenly represented. We found no apparent effect of sex on weaning age in MSCRM 2, and both visual inspection and AIC indicated that including sex as a covariate was unnecessary. However, Viterbi decoding revealed a slight effect on the probability of females transitioning to the absent state later in life, with males more likely to transition at younger ages (Figure 3).

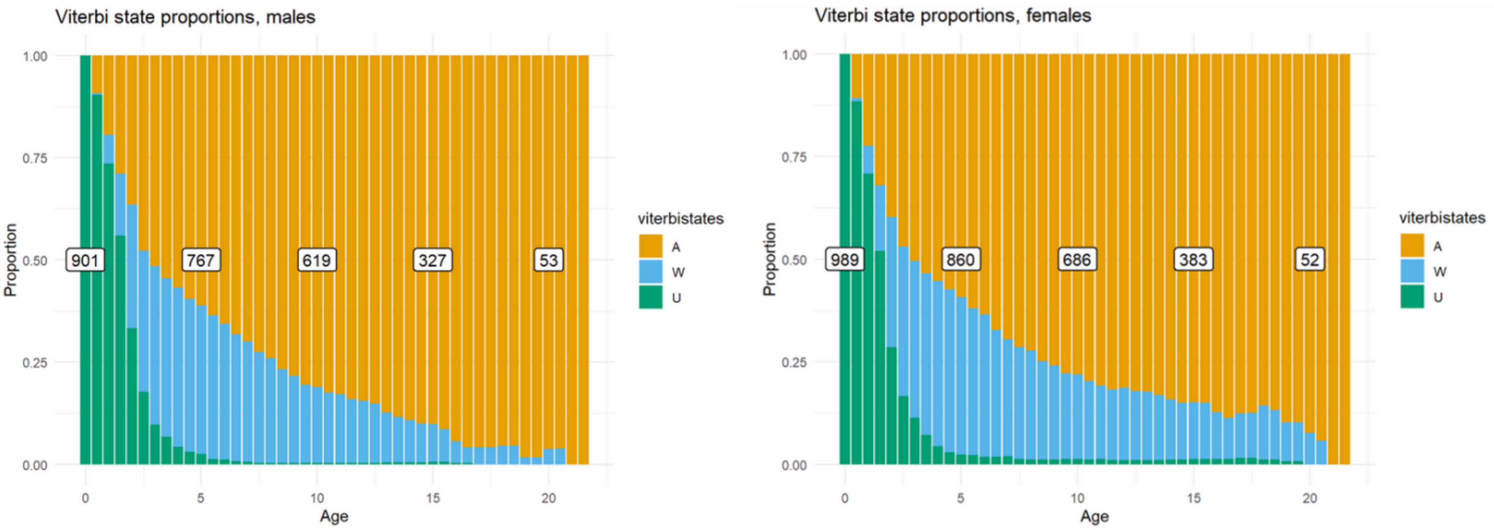

Figure 3. Viterbi state proportions from Model 2 showing the most likely state (unweaned [U], weaned [W], absent [A]) of an individual at any given time point is in according to sex. White-boxed numbers within the figure indicate the total number of possible observable animals at 5-year intervals.

Environmental effects

Visual inspection and AIC results of MSCRM 3 indicated that ONI should be retained as a covariate and a visualisation of the relationship (Figure 4) showed that there is a strong effect on juvenile survival between the ages of 1 - 4 years. This can be seen in the high variation in the number of individuals in both the unweaned (U) and absent (A) states between El Niño and La Niña conditions. During poor El Niño conditions individuals are much less likely to be in the unweaned state and more likely to transition to the absent state, indicating a reduced survival rate during these events compared to more favourable La Niña periods. No probability on survival prior to yearling age can be inferred due to the exclusion of these deaths from the model. The probability of individuals being observed in the weaned (W) state is also affected by ONI between the ages of 2 - 4, where during El Niño individuals between these ages are more likely to be observed in this state than during La Niña conditions. The effect of ONI on all states reduces with age showing only a slight influence on weaned and absent between the ages of 7-16.

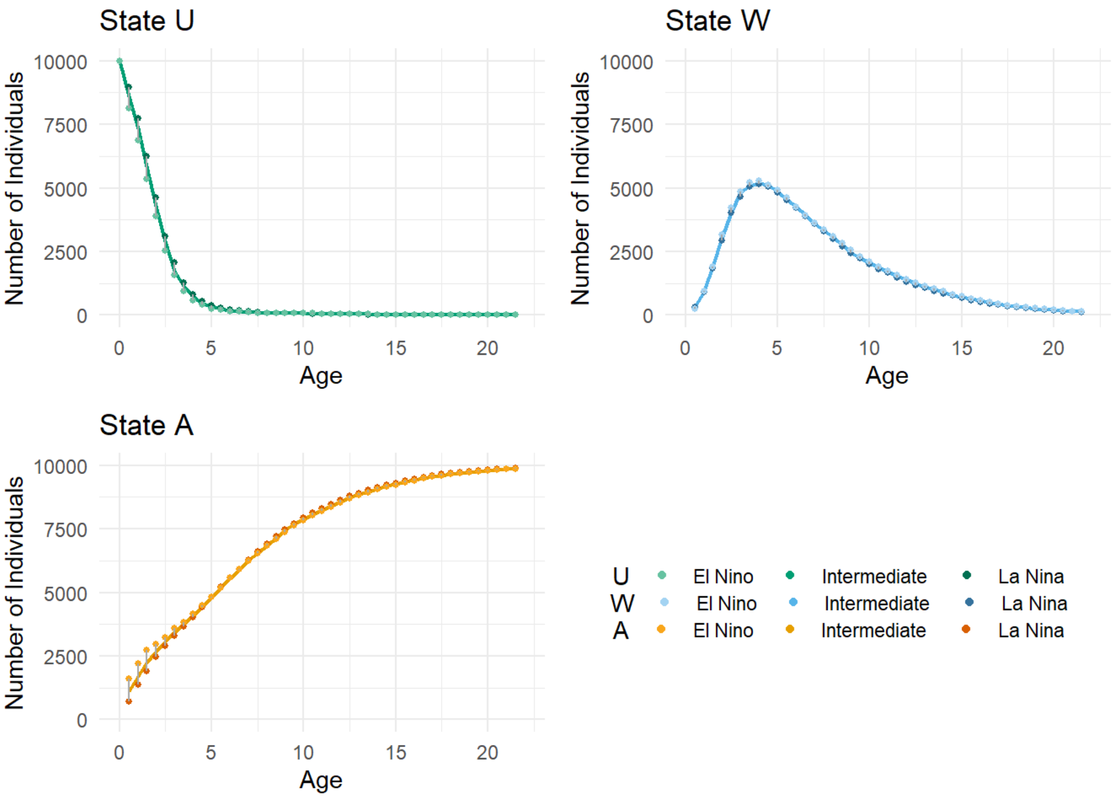

Figure 4. ONI category effect on state behaviours unweaned (U), weaned (W) and absent (A). Where the interaction during an Intermediate ONI event is represented by a solid line and El Niño (pale) and La Niña (dark) as points along this line.

Maternal effects

When investigating maternal life-history effects, information on mothers was unavailable or incomplete for most offspring, resulting in different subsets when incorporating variables related to an individual's mother. This provided the base for model fitting.

Including birth SMI as a covariate is neither supported by AIC nor did the weaning rate in the first few years of an individual differ given different SMI values. However, SMI did appear to have an effect on offspring survival (Figure S2) with survival rates estimated between 78% and 96% for offspring with minimum and maximum SMI values in the data, respectively. When birth interval was included as a covariate (MSCRM 5A & 5B) AIC results indicated a slight preference for its inclusion. The MSCRM suggests that a longer interval before the birth of the next sibling is associated with later weaning (Figure S3) with about 98% of offspring with an early sibling (born in the same year) weaned by age, but only 61% of offspring with a late sibling (born 7 years later) based on a simulated state distribution given the model.

The inclusion of maternal age in MSCRM 6A and 6B produced unstable results, preventing the identification of a global maximum. This was likely due to the small sample size (*n* = 328) and specificity of the subset. Due to the colony’s decline a large proportion of the females who recruited and successfully reproduced on Caamaño were first identified as juveniles or adults during the early years of data collection and therefore have unknown DOB (*personal communication*). Simplification of the models failed to yield more stable results; we were therefore unable to draw any meaningful conclusions of the effect this life-history trait may have on weaning age.

3.2. Logistic regression model

All LRM model candidates and their fit can be found in Table 2. Supersucklers and non-supersucklers were classified according to the offspring decoded states of MSCRM 3. Due to the lack of effect of SST in the MSCRM at an annual scale, SST was not included in any LRM. LRM 0B confirmed that sex has no significant effect on the probability of becoming a supersuckler. Averaged ONI anomalies were included for the year of birth and the first four years of their life as a covariate, in order to understand whether ONI during offspring's early life or the year they become a supersuckler are more important. We found that an increase in ONI anomaly during an individual's 2nd and 3rd year of life has a negative impact on their probability of becoming a supersuckler. Yet the inclusion of ONI anomalies did not greatly improve the model, with BIC indicating that no covariate inclusion was a better fit. In all other LRMs we therefore included the year of birth as a random effect to control for any cohort effect, and only ONI anomalies of the 2nd and 3rd year as covariates.

Table 2. All fitted LRMs predicting the probability for an individual to become a supersuckler described by the predictors and random effect included. The number of parameters (np) and number of individuals (nind) for which the corresponding variables were available are used as a basis for comparison via the BIC. Variable notation $ONI_0 - ONI_4$ refers to the oscillation index at the given age of an individual in, SMI_{10}, SMI_{90} to the SMI of an individual's first 10 or 90 days, $sibl$ to time until sibling, m_{age} to the age of the mother. Index refers to the steps in model selection. The index in bold indicates the model that was preferred at each stage of model selection.

Index	random effect	predictors	BIC	nind	np
0A		-	***658.04***	766	1
0B		$sex, ONI_0, ONI_1, ONI_2, ONI_3, ONI_4$	*677.24*	766	7
1A	*cohort*	m_{age}	*102.91*	98	3
1B	*cohort*	-	***98.41***	98	2
2A	*cohort*	SMI_{90}	*425.74*	492	3
2B	*cohort*	SMI_{10}, SMI_{90}	*430.38*	492	4
2C	*cohort*	SMI_{10}	*426.44*	492	3
2D	*cohort*	-	***422.27***	492	2
3A	*cohort*	*sibl*	*99.87*	140	3
3B	*cohort*	-	***95.97***	140	2

The results of LRM 1A indicate that maternal age at birth does not play an important role in the probability of offspring becoming a supersuckler. The proportion of offspring without a known-age mother was similar for supersucklers and non-supersucklers, however, we still assume some structure in the missingness that might not have been addressed in this model setup. Within this LRM only a few offspring with older mothers (+12 years) were included; since the data collection period did not span more than a single lifetime, the younger the mother, the more likely her age was to be in the data set. We therefore concluded that if there was an effect, we might not be able to find it, and that this variable should be excluded from further analysis.

We found no relationship between becoming a supersuckler and SMI at birth or early life SMI and so excluded this variable from further analysis. It should be noted that the proportion of missing values for SMI was slightly higher for supersucklers than non-supersucklers, likely a reflection of colony proportional differences. There was also no indication of a relationship between birth interval to the next sibling and the probability of an offspring becoming a supersuckler. Due to the exclusion of mothers with recorded absence (2+ years) from the database and the previously stated data imbalance, the proportion of missings for supersucklers was again much higher than for non-supersucklers. Additional visualisation of birth interval and survival of the next sibling to yearling age (Figure S4), suggested that there may be some relationship between sibling first-year survival and older offspring becoming a supersuckler but further highlighted the high number of missing values. We concluded that, due to the small and imbalanced sample size, it was unlikely that we might be able to find the effect if there was one and that this variable could be excluded from further analysis.

Visual inspection of weight, length and SMI curves (Figure S5) showed high overlap between the predicted means for pups who would become supersucklers and those who would not, indicating no difference in growth between supersucklers and non-supersucklers. The widening of the confidence intervals (95%) from 700 days (1.9 years) onwards indicates that the curve becomes implausible at this point due to the reduced sample size.

Conflict of Interest

None declared.

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Supplementary material

1. Methods: Model formulation of the MSCRM

The multi-state capture-recapture model (MSCRM) belongs to the class of hidden Markov models (HMMs) comprising two stochastic processes: the state process and the observation process. HMMs assume that (partially) hidden states determine the distribution of the observations at each point in time.

State Process:

The state process $\{S_t\}_{t=1,\dots,T}$ is defined as a Markov chain with s_t the state at season t. It aims to describe the weaning process by distinguishing the unweaned state "U" and the weaned state "W". Additionally, the absent state "A" accounts for events of death and emigration. This absorbing state ensures that dead or absent animals which cannot be observed anymore are not considered weaned and the weaning process is therefore only informed by animals that can be observed. The upper half of the directed graph in Figure 1 shows the possible state transitions. Notably, once the unweaned state is left, an animal cannot transition back to it. The same applies for the weaned state. Therefore, the following transition probability matrix$\Gamma = (\gamma_{UU}\ \gamma_{UW}\ \gamma_{UA}\ 0\ \ \gamma_{WW}\ \gamma_{WA}\ 0\ 0\ 1\ ) = (\phi \cdot (1-\nu)\ \phi \cdot \nu\ 1-\phi\ 0\ \ \phi\ 1-\phi\ 0\ 0\ 1\ )$ is assumed with γ_{kl} denoting the probability of switching from state k to l for all $k, l\ \in \{U, W, A\}$.

In defining a survival rate that reflects the probability that an animal continues to be observable, and the assumption that survival rate is independent of the current state, we could then rewrite the entries in Γ in terms of this survival rate ϕ and a weaning rate ν. In practical terms, by estimating only γ_{UU} and γ_{UW} and considering that $\gamma_{UU} + \gamma_{UW} + \gamma_{UA} = 1$, we can derive $\phi = \gamma_{UU} + \gamma_{UW}$ and $\nu = \frac{\gamma_{UU}}{\gamma_{UU}+\gamma_{UW}}$.

Covariates that were assumed to affect the weaning and survival rate (ν, ϕ) could be included in the state process leading to an inhomogeneous Markov chain $\{S_t\}$ with Γ_t and therefore (ν_t, ϕ_t) varying over time. In order to do so, the transition probabilities to be estimated are linked to linear predictors $\tau_{j,t} = Y_t \beta_j\ for\ j = 1,2\ and\ t = 1, \dots, T\#(1)$ given the covariate matrix Y_t and the regression coefficients β_j such that $\gamma_{UU,t} = \frac{expexp\,(\tau_{1,t})}{1+expexp\,(\tau_{1,t})\,+expexp\,(\tau_{2,t})}$ and $\gamma_{UW,t} = \frac{expexp\,(\tau_{2,t})}{1+expexp\,(\tau_{1,t})\,+expexp\,(\tau_{2,t})}$.

Observation process:

The observation process $\{X_t\}_{t=1,\dots,T}$ depends on the underlying state process $\{S_t\}$ as depicted in the bottom half of Figure 1. The observations $x_{t,q}$ correspond to being observed suckling (S), being observed but not suckling (O), not being observed (N), or recovered dead (D) for each field season t and each animal q.

We constructed three state-dependent probability distributions as follows:

$X|j \sim Categorical(q_{\cdot|j})$, for $j = U, W, A$

$$q_{\cdot|U} = (\pi, \rho, 1-\pi-\rho)$$

$$q_{\cdot|W} = (0, \lambda, 1-\lambda, 0)$$

$$q_{\cdot|A} = (0,0,1-\epsilon, \epsilon)$$

Given the unweaned state U, we obtained a categorical distribution where individuals who were observed suckling had probability π, observed doing something else had probability ρ and unobserved with probability $1-\pi-\rho$. Given the weaned state W and the absent state A, the distributions are essentially Bernoulli with λ the probability of being observed given the weaned state and ϵ the probability of being recovered dead.

We collect variables that are assumed to affect the resighting probability and thereby the distribution of observations in a covariate matrix Z_t and build a linear $\eta_{i,t} = Z_t\alpha_i$ for $i = 1,2,3,4$ and $t = 1, \dots, T$ with $\alpha_{i,t}$ the regression coefficients.

The four parameters $\rho_t, \pi_t, \lambda_t, \epsilon_t$ are then time varying by being linked to the linear predictors as follows:

$$\rho_t = \frac{exp\,exp\,(\eta_{1,t})}{1+exp\,exp\,(\eta_{1,t})\,+exp\,exp\,(\eta_{2,t})}$$

$$\pi_t = \frac{exp\ exp\ \left(\eta_{2,t}\right)}{1 + exp\ exp\ \left(\eta_{1,t}\right)\ + exp\ exp\ \left(\eta_{2,t}\right)}$$

$$\lambda_t = \frac{1}{1 + exp\ exp\ \left(\eta_{3,t}\right)}$$

$$\epsilon_t\ = \frac{1}{1\ +\ \ exp\ exp\ \left(\eta_{4,t}\right)}$$

Parameter estimation and state decoding:

By framing the model as a hidden Markov model, we leveraged inferential tools like the forward algorithm to estimate the latent weaning process and the Viterbi algorithm to decode the most likely state sequence. Note that we constructed a partially hidden Markov model in the sense that a suckling observation "S" and a death recovery "D" inform directly about the state having generated this observation. We used the package LaMa in R for conveniently building the HMM likelihood and maximized the likelihoods directly by using the numerical optimizer nlm.

2. Results

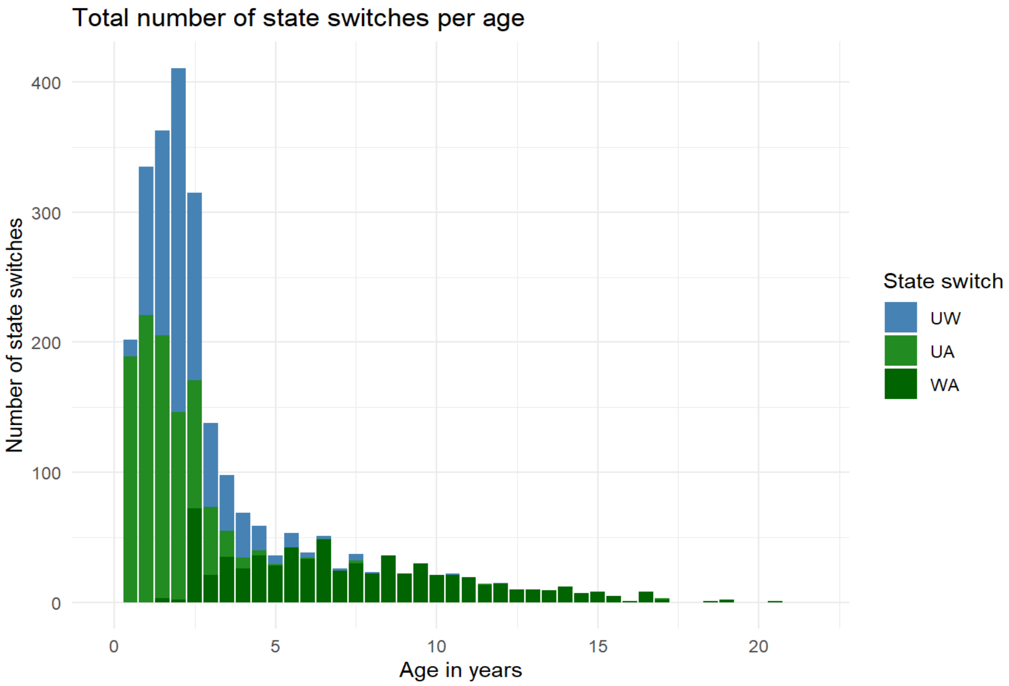

Figure S1. Total number of switches between each state according to offspring age: unweaned-weaned (UW, blue), unweaned-absent (UA, light green), weaned-absent (WA, dark green).

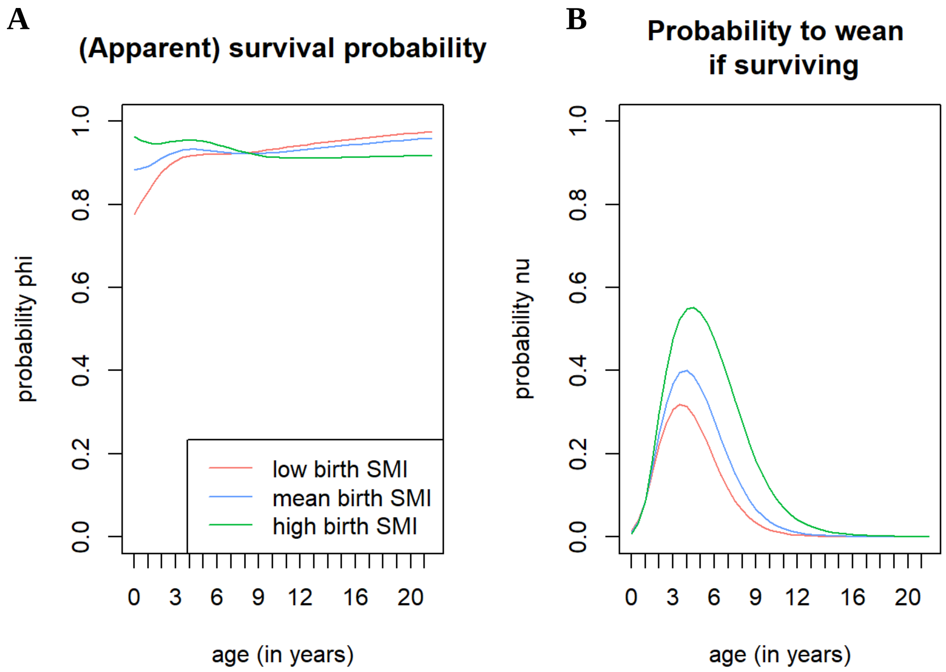

Figure S2. Apparent survival probability (A) of offspring according to their birth SMI, indicated by red (low birth SMI), blue (mean birth SMI) and green (high birth SMI) lines, and their age. As well as their probable age at weaning if they survive (B).

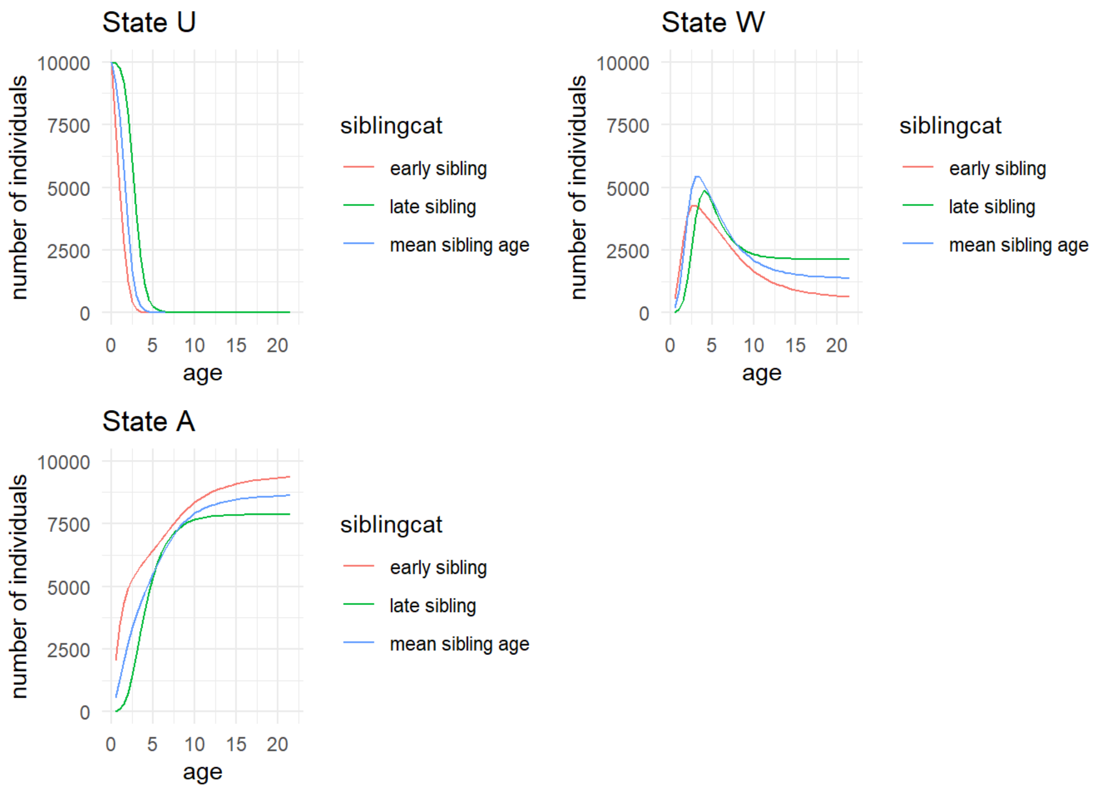

Figure S3. Birth interval effect - calculated as time until the birth of the next sibling - on state behaviours unweaned (U), weaned (W) and absent (A) according to offspring age. Indicated by solid lines where red is a short interval (early sibling = 1 year), blue is a mean interval and green a long interval (late sibling = 7 years) they survive (B).

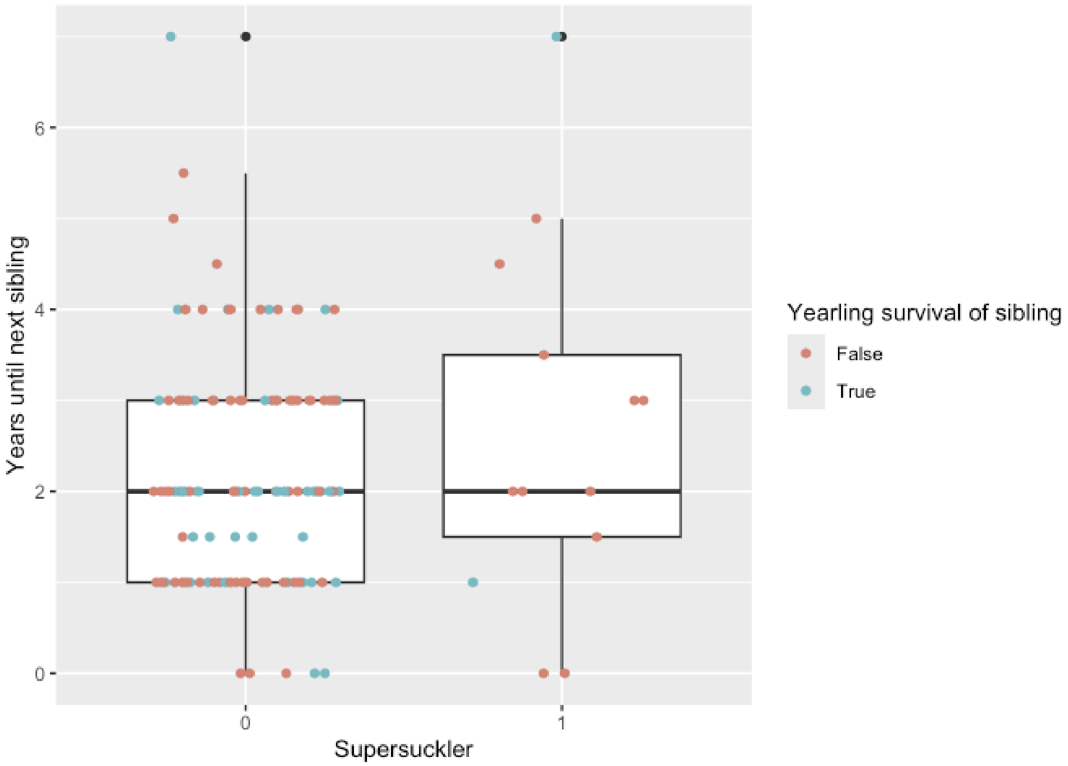

Figure S4. A visualisation of the possible relationship between supersuckling and younger sibling survival to yearling age, where all younger siblings are plotted as jitter points according to the birth interval between them and the elder offspring and grouped according to the elder offsprings classification as a supersuckler or non-supersuckler. Younger sibling survival to yearling age is denoted by the colour of their point where blue is ‘survived’ and red is ‘did not survive’.

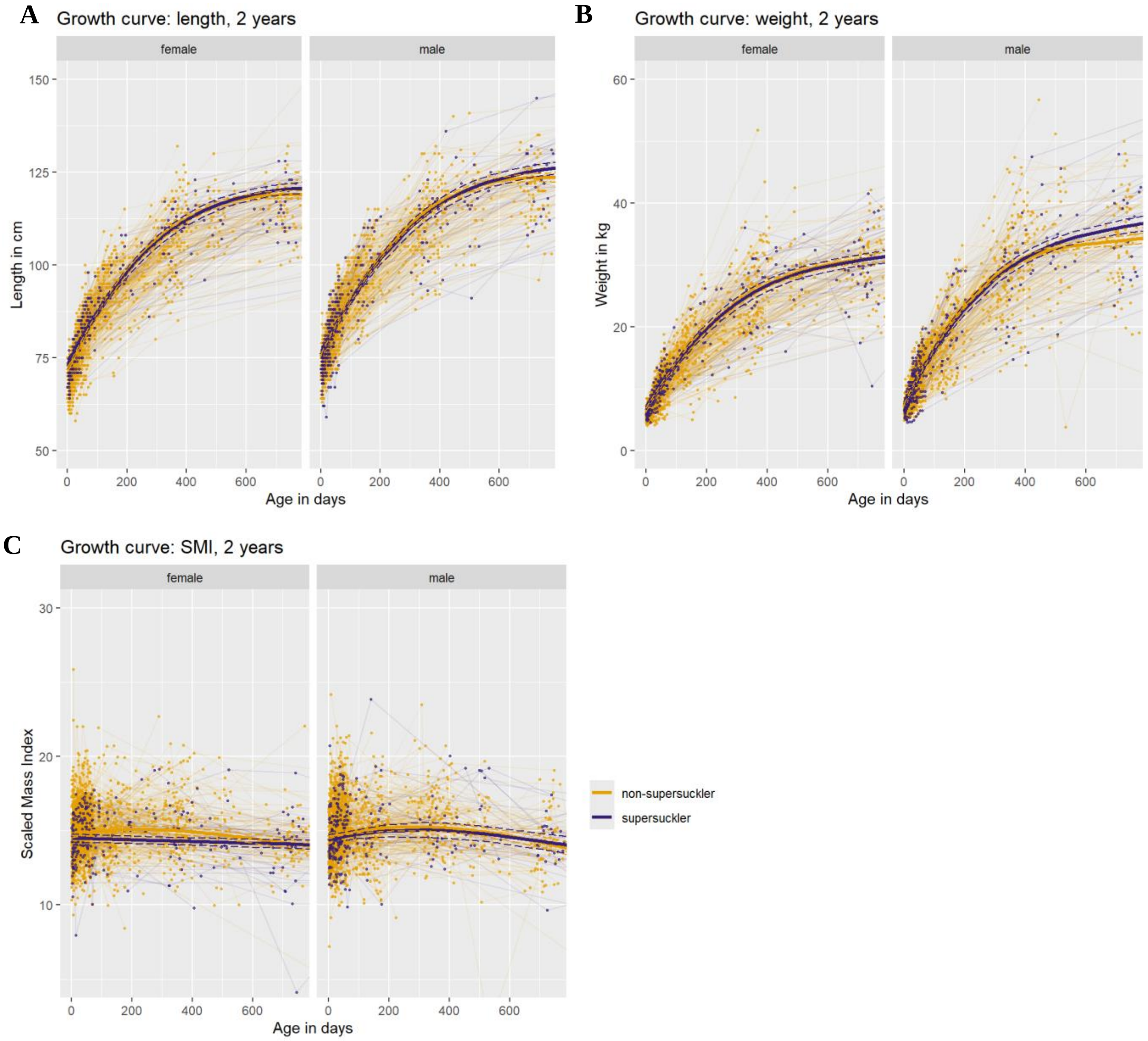

Figure S5. The thick lines show the predicted average **a)** body weight, **b)** length and **c)** SMI given the age and sex for individuals later becoming supersucklers (orange) and non-supersucklers (purple). The dashed lines indicate the 95% confidence intervals of the predicted mean.

Bibliography

Avery, J. P., & Zinn, S. A. (2023). Extraordinary diversity of the pinniped lactation triad: lactation and growth strategies of seals, sea lions, fur seals, and walruses. *Animal Frontiers*, *13*(3), 86–95. https://doi.org/10.1093/af/vfad037

Bleu, J., Meylan, S., Clobert, J., & Massot, M. (2021). Grandmaternal age at reproduction affects grandoffspring body condition, reproduction and survival in a wild population of lizards. *Functional Ecology*, *36*(4), 826–836. https://doi.org/10.1111/1365-2435.13996

Burkanov, V., Gurarie, E., Altukhov, A., Mamaev, E., Permyakov, P., Trukhin, A., Waite, J., & Gelatt, T. (2011). Environmental and biological factors influencing maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) in Russia. *Journal of Mammalogy*, *92*(2), 352–366. https://doi.org/10.1644/10-MAMM-A-194.1

Chapman, S. N., Lahdenperä, M., Pettay, J. E., Lynch, R. F., & Lummaa, V. (2021). Offspring fertility and grandchild survival enhanced by maternal grandmothers in a pre-industrial human society. *Scientific Reports 2021 11:1*, *11*(1), 1–10. https://doi.org/10.1038/s41598-021-83353-3

Childs, A., Feldmann, C., Stoehr, S., Demarthon, R., Piedrahita, P., Twiss, S. D., & Krüger, O. (2025). Milking it: repeated post-weaning suckling events in Galápagos Sea Lions *Zalophus Wollebaeki*. *BioRxiv*, 2025.03.26.645415. https://doi.org/10.1101/2025.03.26.645415

Chilvers, B. L., Robertson, B. C., Wilkinson, I. S., & Duignan, P. J. (2007). Growth and survival of New Zealand sea lions, *Phocarctos hookeri*: birth to 3 months. *Polar Biol*, *30*, 459–469. https://doi.org/10.1007/s00300-006-0203-9

Costa, D. P., & Valenzuela-Toro, A. M. (2021). When Physiology and Ecology Meet: The Interdependency Between Foraging Ecology and Reproduction in Otariids. In C. Campagna & R. Harcourt (Eds.), *Ethology and Behavioural Ecology of Otariids and the Odobenid* (1st ed., pp. 21–50). Springer Nature. https://doi.org/10.1007/978-3-030-59184-7_2

Costa, D. P., & Maresh, J. L. (2022). Reproductive Energetics of Phocids. In D. P. Costa & E. McHuron (Eds.), *Ethology and Behavioral Ecology of Phocids* (pp. 281–309). Springer Nature Switzerland. https://doi.org/10.1007/978-3-030-88923-4_8

Dittus, W., & Baker, A. (2024). Maternal care in wild toque macaques (Macaca sinica) involves prolonged lactation and interbirth intervals as adaptations to reduce maternal depletion and infant mortality in harsh environments. *American Journal of Primatology*, *86*(2), e23584. https://doi.org/10.1002/AJP.23584

Ferguson, S. H. (2006). The Influences of Environment, Mating Habitat, and Predation on Evolution of Pinniped Lactation Strategies. *Journal of Mammalian Evolution*, *13*(1), 63–82. https://doi.org/10.1007/s10914-005-9003-1

Galapagos Climatology Database", dataZone, Charles Darwin Foundation, https://datazone.darwinfoundation.org/en/climate/puerto-ayora. Accessed 12 August 2024.

Gerber, N., Auclair, Y., König, B., & Lindholm, A. K. (2021). Population Density and Temperature Influence the Return on Maternal Investment in Wild House Mice. *Frontiers in Ecology and Evolution*, *8*, 602359. https://doi.org/10.3389/FEVO.2020.602359/TEXT

Goldsworthy, S. D. (2006). Maternal strategies of the New Zealand fur seal: Evidence for interannual variability in provisioning and pup growth strategies. *Australian Journal of Zoology*, *54*(1), 31–44. https://doi.org/10.1071/ZO05041

Hastings, K. K., Johnson, D. S., Pendleton, G. W., Fadely, B. S., & Gelatt, T. S. (2021). Investigating life-history traits of Steller sea lions with multistate hidden Markov mark–recapture models: Age at weaning and body size effects. *Ecology and Evolution*, *11*(2), 714–734. https://doi.org/10.1002/ece3.6878

Jeglinski, J. W. E., Mueller, B., Pörschmann, U., & Trillmich, F. (2010). Field-Based Age Estimation of Juvenile Galapagos Sea Lions (*Zalophus wollebaeki*) Using Morphometric Measurements. *Aquatic Mammals*, *36*(3), 262–269. https://doi.org/10.1578/AM.36.3.2010.262

Jeglinski, J., Werner, C., Robinson, P., Costa, D., & Trillmich, F. (2012). Age, body mass and environmental variation shape the foraging ontogeny of Galapagos sea lions. *Marine Ecology Progress Series*, *453*, 279–296. https://doi.org/10.3354/meps09649

Kalberer, S., Meise, K., Trillmich, F., & Krüger, O. (2018). Reproductive performance of a tropical apex predator in an unpredictable habitat. *Behavioral Ecology and Sociobiology*, *72*(7), 108. https://doi.org/10.1007/s00265-018-2521-7

Kraus, C., Mueller, B., Meise, K., Piedrahita, P., Pörschmann, U., & Trillmich, F. (2013). Mama's boy: sex differences in juvenile survival in a highly dimorphic large mammal, the Galapagos sea lion. *Oecologia*, *171*(4), 893–903. https://doi.org/10.1007/s00442-012-2469-7

Krüger, O., Kalberer, S., Meise, K., Schwarz, J., Derango, E., Piedrahita, P., Páez-rosas, D., & Trillmich, F. (2021). Galápagos Sea Lion (Zalophus wollebaeki, Silvertsen 1953). In G. Heckel & Y. Schramm (Eds.), *Ecology and Conservation of Pinnipeds in Latin* (1st ed., pp. 145–163). Springer Nature. https://doi.org/,https://doi.org/10.1007/978-3-030-63177-2_8

Koslik J (2025). _LaMa: Fast Numerical Maximum Likelihood Estimation for Latent Markov Models_.R package version 2.0.3, <https://janoleko.github.io/LaMa/>

Lee, P. C. (1996). The meanings of weaning: Growth, lactation, and life history. *Evolutionary Anthropology: Issues, News, and Reviews*, *5*(3), 87–98. https://doi.org/10.1002/(SICI)1520-6505(1996)5:3<87::AID-EVAN4>3.0.CO;2-T

McDonald, B. I., Goebel, M. E., Crocker, D. E., & Costa, D. P. (2012). Dynamic influence of maternal and pup traits on maternal care during lactation in an income breeder, the antarctic fur seal. *Physiological and Biochemical Zoology*, *85*(3), 243–254. https://doi.org/10.1086/665407

McHuron, E. A., Adamczak, S., Costa, D. P., & Booth, C. (2023). Estimating reproductive costs in marine mammal bioenergetic models: a review of current knowledge and data availability. *Conservation Physiology*, *11*(1). https://doi.org/10.1093/conphys/coac080

Meise, K., Piedrahita, P., Krüger, O., & Trillmich, F. (2014). Being on time: size-dependent attendance patterns affect male reproductive success. *Animal Behaviour*, *93*, 77–86. https://doi.org/10.1016/j.anbehav.2014.04.019

Mueller, B., Pörschmann, U., Wolf, J. B. W., & Trillmich, F. (2011). Growth under uncertainty: The influence of marine variability on early development of Galapagos sea lions. *Marine Mammal Science*, *27*(2), 350–365. https://doi.org/10.1111/j.1748-7692.2010.00404.x

Nielsen, M. L. K., Ellis, S., Weiss, M. N., Towers, J. R., Doniol-Valcroze, T., Franks, D. W., Cant, M. A., Ellis, G. M., Ford, J. K. B., Malleson, M., Sutton, G. J., Shaw, T. J. H., Balcomb, K. C., Ellifrit, D. K., & Croft, D. P. (2023). Temporal dynamics of mother-offspring relationships in Bigg's killer whales: opportunities for kin-directed help by post-reproductive females. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2000). https://doi.org/10.1098/rspb.2023.0139

NOAA Climate Prediction Center (2024) *Oceanic Niño Index (ONI) data*. Available at: https://www.cpc.ncep.noaa.gov/data/indices/oni.ascii.txt [Accessed 20 August 2024].

Osiecka, A. N., Fearey, J., Elwen, S., & Gridley, T. (2020). Prolonged Nursing in Cape fur Seals (Arctocephalus pusillus pusillus) at Cape Cross Colony, Namibia. In *African Zoology* (Vol. 55, Issue 3). African Zoology Circulation Office. https://doi.org/10.1080/15627020.2020.1768144

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos*, *118*(12), 1883–1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x

Piedrahita, P. (2015). *Mother-offspring relations and transition to independence in the Galapagos sea lion (Zalophus wollebaeki)*. PhD thesis. Bielefeld: Bielefeld University.

Pomeroy, P. (2011). Reproductive cycles of marine mammals. *Animal Reproduction Science*, *124*(3–4), 184–193. https://doi.org/10.1016/j.anireprosci.2010.08.021

Pörschmann, U., Trillmich, F., Mueller, B., & Wolf, J. B. W. (2010). Male reproductive success and its behavioural correlates in a polygynous mammal, the Galápagos sea lion (*Zalophus wollebaeki*). *Molecular Ecology*, *19*(12), 2574–2586. https://doi.org/10.1111/j.1365-294X.2010.04665.x

R Core Team (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reiter, J., Stinson, N. L., & le Boeuf, B. J. (1978). Northern elephant seal development: The transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology*, *3*(4), 337–367. https://doi.org/10.1007/BF00303199

Schulz, T. M., & Bowen, W. D. (2004). Pinniped Lactation Strategies: Evaluation of Data on Maternal and Offspring Life History Traits. *Marine Mammal Science*, *20*(1), 86–114. https://doi.org/10.1111/j.1748-7692.2004.tb01142.x

Schulz, T. M., & Bowen, W. D. (2005). The evolution of lactation strategies in pinnipeds: A phylogenetic analysis. *Ecological Monographs*, *75*(2), 159–177. https://doi.org/10.1890/04-0319

Schwarz, J. F. L., DeRango, E. J., Zenth, F., Kalberer, S., Hoffman, J. I., Mews, S., Piedrahita, P., Trillmich, F., Páez-Rosas, D., Thiboult, A., & Krüger, O. (2022). A stable foraging polymorphism buffers Galápagos sea lions against environmental change. *Current Biology*, *32*(7), 1623-1628.e3. https://doi.org/10.1016/j.cub.2022.02.007

Sepúlveda, M., & Harcourt, R. G. (2021). Maternal Behavior in Otariids and the Walrus. In C. Campagna & R. Harcourt (Eds.), *Ethology and BehavioralEcology of Otariids and theOdobenid* (pp. 51–61). Springer. https://doi.org/10.1007/978-3-030-59184-7_3

Sikes, R. S., & Gannon, W. L. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, *92*(1), 235–253. https://doi.org/10.1644/10-MAMM-F-355.1

Soto, K. H., Trites, A. W., & Arias-Schreiber, M. (2004). The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *Journal of Zoology*, *264*(4), 419–428. https://doi.org/10.1017/S0952836904005965

Trillmich, F., & Wolf, J. B. W. (2008). Parent–offspring and sibling conflict in Galápagos fur seals and sea lions. *Behavioral Ecology and Sociobiology*, *62*(3), 363–375. https://doi.org/10.1007/s00265-007-0423-1

Trillmich, F., Meise, K., Kalberer, S., Mueller, B., Piedrahita, P., Pörschmann, U., Wolf, J. B. W., & Krüger, O. (2016). On the Challenge of Interpreting Census Data: Insights from a Study of an Endangered Pinniped. *PLOS ONE*, *11*(5), e0154588. https://doi.org/10.1371/journal.pone.0154588

Trivers, R. L. (1974). Parent-Offspring Conflict. *American Zoologist*, *14*(1), 249–264. https://doi.org/10.1093/icb/14.1.249

Villegas-Amtmann, S., Atkinson, S., & Costa, D. P. (2009). Low Synchrony in the Breeding Cycle of Galapagos Sea Lions Revealed by Seasonal Progesterone Concentrations. *Journal of Mammalogy*, *90*(5), 1232–1237. https://doi.org/10.1644/08-MAMM-A-319.1

Vitikainen, E. I. K., Meniri, M., Marshall, H. H., Thompson, F. J., Businge, R., Mwanguhya, F., Kyabulima, S., Mwesige, K., Ahabonya, S., Sanderson, J. L., Kalema-Zikusoka, G., Hoffman, J. I., Wells, D., Lewis, G., Walker, S. L., Nichols, H. J., Blount, J. D., & Cant, M. A. (2023). The social formation of fitness: lifetime consequences of prenatal nutrition and postnatal care in a wild mammal population. *Philosophical Transactions of the Royal Society B*, *378*(1883). https://doi.org/10.1098/RSTB.2022.0309

Waldmann, E. (2018). Quantile regression: A short story on how and why. *Statistical Modelling*, *18*(3–4), 203–218. https://doi.org/10.1177/1471082X18759142

Wei, Y., Pere, A., Koenker, R., & He, X. (2006). Quantile regression methods for reference growth charts. *Statistics in Medicine*, *25*(8), 1369–1382. https://doi.org/10.1002/sim.2271

Wolf, J. B. W., & Trillmich, F. (2007). Beyond habitat requirements: individual fine-scale site fidelity in a colony of the Galapagos sea lion (*Zalophus wollebaeki*) creates conditions for social structuring. *Oecologia*, *152*(3), 553. https://doi.org/10.1007/s00442-007-0665-7

Zucchini, W., Macdonald, I. L., & Langrock, R. (2017). Forecasting, decoding and state prediction. In *Hidden Markov Models for Time Series: An Introduction Using R, Second Edition* (2nd Edition). Chapman and Hall/CRC. https://doi.org/10.1201/B20790