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**Maternal and offspring effects on the timing of parturition in western Steller sea lions
(*Eumetopias jubatus*)**

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Draft

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Abstract:

Identifying factors that affect the timing of parturition among annual breeders is important to aid our understanding of how variations may adversely affect population trends over both short and long temporal scales. We investigated the effect of several parameters on the timing of parturition among individual Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) over six years between 2005 and 2016 using an information theoretic approach. In addition to the random effect of year, birth and care of a pup in the previous year had the largest effect on parturition, causing a 2.4-day delay. Maternal age was negatively correlated with timing of parturition and male pups were born nearly a day earlier than female pups on average. There was limited support for effects of sex and mass with heavier pups born marginally earlier than lighter ones. This study illustrates some of the complexity of variables that can influence the timing of birth in this species and which should be considered in models that attempt to identify long-term trends in changing marine ecosystems.

Key words: birth timing, *Eumetopias jubatus*, mixed effects model, offspring influence, Steller sea lion

Introduction

Large mammals that breed annually tend to exhibit synchronized parturition that is often correlated with seasonally abundant food resources at temperate to polar latitudes (Ims 1990). Nevertheless, the timing of parturition does vary to some degree among individuals and between years based on maternal age and body condition among other things. Much contemporary research on birth timing has tested for effects of these factors with implications that climate conditions, food availability, status, disease or contaminant loads directly or indirectly affect maternal body condition (e.g., Gilmartin et al. 1976; Skogland 1984; Rachlow and Bowyer 1991; Lunn and Boyd 1993; Bowen et al. 2003). Additionally, climate conditions and food availability can influence the growth of a developing fetus and whether or not the mother skips a year of giving birth, which in turn, have been correlated with subsequent parturition date (Drickamer 1974; Rotella et al. 2016).

Some variation in birth timing is likely adaptive, allowing populations to self-regulate based on food availability, population density effects and individual fitness (Gaillard et al. 2000), but changes in the timing of parturition due to long-term environmental variation may be more difficult to overcome and can have lasting effects on a population (Post et al. 1997; Soto et al. 2004). Furthermore, birth timing and the variables that affect it are likely species specific among mammals (Racey 1981; Hogg et al. 2017). Therefore, it is of interest and importance to understand factors affecting natural variation in the timing of parturition within each species that is of special concern. Despite this importance, research studies are rarely able to test relative strength of evidence for many factors simultaneously on the timing of parturition because of the type of long-term dedicated research that is necessary.

The Steller sea lion (*Eumetopias jubatus* (Schreber, 1776); SSL) is a species that has received much research attention in recent decades due to a dramatic population decline since the 1970s that resulted in their 1997 listing as endangered in the western portion of their range (Loughlin 1998). Like most mature female pinnipeds, SSL typically give birth to one offspring annually and mate within a few weeks post-parturition. The embryo will enter a period of diapause for 3 to 4 months before active gestation is resumed for the ensuing 8 ½ months (Pitcher and Calkins 1981; Atkinson 1997; Pomeroy 2011). It is, however, difficult to assess variation in the onset of active gestation among wild pinnipeds (Pomeroy 2011), though not impossible (Testa et al. 2010). Variation in the timing of full-term parturition is easier to observe and in SSL, it is already known to be associated with maternal age, parity (Maniscalco et al. 2006; Hastings and Jemison 2016), and rookery location (Pitcher et al. 2001), with little data previously available to test for additional influencing parameters. Yet, several additional factors have been shown to be associated with variation in the timing of parturition in several other pinniped species (e.g., Lunn and Boyd 1993; Boltnev and York 2001; Rotella et al. 2016).

In this study, we broaden work on the timing of parturition in SSLs by examining several potential explanatory variables for their relative strength of evidence using an information theoretic framework. In so doing, we shed some additional light on interannual changes that likely result from environmental variation, and the effects of some inherent characteristics that can have an influence pinniped reproductive timing. This work also represents the only individual-based, longitudinal study of the timing of parturition within the endangered population segment of SSLs.

Materials and methods

Study site and methods

We conducted this study at a SSL rookery on Chiswell Island in the eastern Gulf of Alaska (59° 36.126'N, 149° 34.105'W) and within the endangered, western distinct population segment. This location has long been used as a rookery but the population has declined dramatically from 1,459 adults and 564 pups in 1956 (Mathisen and Lopp 1963) to 90 adults and 50-80 pups in the early 2000s (Maniscalco et al. 2006), reflecting population declines throughout the western range of Steller sea lions. However, reproductive rates of adult females have been very good (ca. 70%) in recent years (Maniscalco et al. 2014). Beginning in 1999, up to six remotely operated video cameras were used to conduct observations at Chiswell Island. Cameras were viewable and controllable in real-time from the Alaska SeaLife Center 65 km away and provided complete spatial coverage of the Chiswell Island rookery. Additional details about the Chiswell Island rookery and remote video equipment can be found in Maniscalco et al. (2006).

Adult females ($n = 152$) with unique brands, tags, or natural markings were tracked throughout the breeding season and across multiple years in most cases. Hot-iron branding is widely accepted as the safest and most appropriate means to permanently mark pinniped species (Merrick et al. 1996; Daoust et al. 2006; McMahon et al. 2007). Branding and all related work was conducted in accordance with Alaska SeaLife Center's IACUC Animal Use Protocol No. R16-02-01 and earlier versions, and NMFS Permit Nos. 18438, 14324, and earlier versions.

Since 2001, scan sampling (Altmann 1974) for identifiable females and their pups was conducted four to ten times daily from at least 6:00 AM to 10:00 PM; earlier and later hours were added around the summer solstice when light levels were sufficient for viewing sea lions. Digital photos of those animals and their distinguishing marks were taken at least once per week. Offspring of these females were captured near the end of the pupping seasons, weighed,

measured, sexed, and given a unique mark during years 2005, 2007, 2008, 2010, 2011, and 2016. Only these six years were used in the analysis because it was of interest to test for the effects of pup sex and birth mass on the timing of parturition. Exact age of pups at time of sampling was determined by subsequent association with their mothers whose time of parturition was known to within ± 4 hrs (Maniscalco et al. 2010; Maniscalco 2014).

Data Analysis

Linear regressions of capture mass versus age were conducted for each sex and cohort of pups. The residuals were then added to the y-intercepts to obtain birth mass estimates for each individual pup. Birth mass estimates obtained in this manner are considered valid and of high quality due to our sample size and knowledge of the sex and exact age of the pups (Schulz and Bowen 2004).

Data were tested for multivariate normality using the Anderson-Darling test in R package mvnTest (Henze and Zirkler 1990). Data were then analyzed in R using the lmer function of package lme4 (Bates et al. 2015). This package allowed us to test mixed-effect models with female ID and year as random effects. Six additional predictor variables were tested for effect on the response variable of Julian date of birth. The fixed effects included, two pup-related variables (pup sex and pup birth mass), and four maternal variables, maternal experience, a quadratic effect of maternal experience, parity, and whether or not the female gave birth in the previous year. A few of these predictor variables warrant further explanation as follows.

Only 7% of the adult females were branded or tagged in this study and exact ages were known for only these individuals. Therefore, as a proxy for maternal age, we used experience which was defined as the observation year minus the year of first known birth by each female +1

(range = 1 – 14). Since most SSL give birth for their first time at 4 – 6 yrs of age (Pitcher and Calkins 1981), we assume this sample consisted of females aged 4 – 20 yrs. Estimating age in this way is not equivalent to the usual definition of maternal experience which is typically defined as overall number of births (Sydeman et al. 1991). Our intent was to obtain a better proxy for maternal age by including years in which females did not give birth.

Regarding birth in a previous year which was scored as 0 or 1, we had a very high sighting probability (99.9%) of mature females that give birth in our study sample each year due to excellent spatial and temporal coverage of the rookery throughout the pupping season (Maniscalco et al. 2014). However, some females lose their pups at a very early age due to a variety of reasons (Maniscalco et al. 2008), and if a female lost her pup within one month of its birth, she received a score of 0 for a previous year's birth because she would not have endured the year-long burden of lactation which is energetically the most costly aspect of reproduction among pinnipeds (Oftedal et al. 1987). Maternal parity was also scored as 0 or 1 indicating whether a female was primiparous or multiparous respectively.

We used an information theoretic approach (Burnham et al. 2011) to assess the relative strength of evidence of the predictor variables on the timing of birth for Steller sea lions at the Chiswell Island rookery. The random effect of maternal ID was retained in all models to account for repeated measures on individual mothers. Study year was also considered as a random effect and compared against the maternal ID random intercept model before choosing fixed effects models to test. Sixteen additional models were then chosen based on professional biological reasoning and compared with the random intercept model. To avoid complications associated with multicollinearity (Cade 2015), we did not test the predictor of parity in any of the same models with maternal experience or previous year's birth. Likewise, pup sex and pup mass were

not modeled together without an interactive effect because of their known correlation at birth (Brandon et al. 2005). We compared the deviance ($-2 \log(L)$) of each of the models using Akaike's Information Criteria (AIC; Akaike 1973) with an additional correction for small sample bias (AICc; Hurvich and Tsai 1989). AICc weights are presented to express the probability that any tested model is the best model given the data. In many cases, multiple models can carry non-negligible amounts of weight and models with ΔAICc values of less than 7 should rarely be ignored (Burnham et al. 2011). In these cases, as in this study, parameter estimates and unconditional estimates of their standard error should be averaged based on AICc model weighted means following principles of multimodal inference (Burnham et al. 2011).

Results

Most mature females in this study only had one birth recorded with sufficient data over the six study years. There were 252 birth observations and related pup data for 152 females considered in the analysis. Overall average date of birth was 12 June and range of birth dates for the animals in this study was 24 May to 28 June. This represented >95% of pups born during the sample years. We failed to capture a few of the earliest born pups that were highly mobile and pups that were born late, after the day of sampling between 29 June and 05 July during the study years. Between 2001 and 2016, we observed live born pups as early as 05 May and as late as 31 July on the Chiswell Island rookery.

Regressions of pup mass on age for each sex and cohort were all highly significant ($P < 0.001$) and were previously published in part (Maniscalco 2014). Data for the analysis presented here were multivariate normal ($P = 0.305$).

Inclusion of the random effect of year was strongly favored, being 17.1 AICc points lower than the random intercept model and carrying virtually 100% of the AICc weight. Therefore, year was retained along with maternal ID as random effects for further model comparisons of the fixed effects.

The four best ranked models carried 87% of the AICc weight and expressed a linear effect of maternal age, a previous year's pup, sex of pup, and pup mass on the timing of parturition (Table 1). There was also limited support for a quadratic effect of maternal age among the models ranked fifth and sixth (Table 1). Parity was not favored among these best models but, by itself and with pup sex, it did fare slightly better than the random intercept model; whereas effects of mass and pup sex did not improve model fit without inclusion of the effect of a previous birth (Table 1).

Model averaged parameter estimates of fixed effects provide some insight into how both mother and developing offspring may affect the timing of parturition. A previous year's birth had the largest effect of the parameters tested with a greater than two-day delay in the timing of a subsequent birth (Table 2). Male pups were born more than half a day earlier than female pups and heavier pups marginally earlier than lighter ones. Additionally, older females gave birth earlier than younger females as noted by the negative parameter estimates (Table 2) and this remained true when taking into account the effect of a previous birth (Figure 1).

Considering the random effect of year, pups were born earliest in 2010 and latest in 2011 with an eight-day difference between these years (Figure 2). Variation across years was also evident for pup sex and mass. That is, male pups were not always born earlier than female pups and similarly, heavier pups were not always earlier than lighter ones (*ad rem* 2016, Figure 2). The effect of pup mass on date of parturition was somewhat weak but taking into account pup

sex, maternal age, and previous birth, the relationship was negative (Table 2) meaning larger pups were born earlier than lighter ones. However, although confidence intervals for the effects of pup sex and mass included zero (Table 2), we could not entirely discount their effects on parturition because these parameters were included in models with $<4 \Delta AICc$ and as such, should not be dismissed as irrelevant (Burnham et al. 2011).

Discussion

The results of this study illustrate the complexity of factors that may affect the timing of parturition among pinnipeds. These predictor variables have not previously been investigated in western SSL and there are others still that we were unable to examine in this study. Eastern SSL are genetically distinct from western SSL (O’Corry-Crowe et al. 2006) and appear to have differing levels of maternal care (Milette and Trites 2003; Maniscalco et al. 2006; Maniscalco 2014). Therefore, we may not necessarily expect the same influences on the timing of parturition between the two populations. Nevertheless, our findings are broadly comparable to results from similar studies with eastern SSLs (Hastings and Jemison 2016), other pinnipeds (Lunn and Boyd 1993; Rotella et al. 2016) and terrestrial mammals (e.g., Solberg et al. 2007; Wolcott et al. 2015), with maternal age and year commonly found to have meaningful effects on the timing of parturition. General scientific consensus suggests that these and other factors affect parturition through physiological constraints such that energetic deficiencies can cause reproductive delays (Boyd 1991; Gaillard et al. 2000).

The energy required for lactation and to nurse an offspring to independence is believed to be the most energetically expensive component in mammalian reproduction (Oftedal et al. 1987; Gittleman and Thompson 1988). Mature SSL will typically nurse an offspring for up to a year or

longer even while pregnant with a new pup (Pitcher and Calkins 1981). Therefore, it is not surprising that models tested with an effect of a previous birth and lactation were more highly favored compared to those without this effect. Indeed, the largest fixed effect in terms of variation in days for SSL in this study was the presence of a previous year's pup, correlating with a 2.4-day delay in subsequent parturition. In at least one capital breeder, the Weddell seal (*Leptonychotes weddelli* (Lesson, 1826)) that fasts while nursing an offspring for less than two months, the effect of a previous year's birth and lactation correlated with a half-day delay in subsequent parturition (Rotella et al. 2016). On the other hand, a previous birth did not have an effect on the length of gestation in an income breeder that feeds during lactation, the Antarctic fur seal (*Arctocephalus gazella* (Peters, 1875)) (Boyd 1996), perhaps because of the ability to replenish stores as do SSL during their four-months of lactation along with an eight-month recovery period. The effect of a previous birth and lactation, however, has not been tested among income breeders that have nearly year-long periods of dependence like the SSL but because of the large effect found here, its importance should not be overlooked where possible.

The effect of maternal age on the timing of parturition exhibits a typical negative correlation among mammals in that parturition trends earlier as females age (e.g., Lunn and Boyd 1993; Boltnev and York 2001; Wolcott et al. 2015). Older SSL can be more familiar with a rookery landscape, finding suitable locations for birthing quicker than younger animals (Parker et al. 2008). Furthermore, older animals are assumed to be more experienced at finding food and therefore less likely to be energetically compromised compared to younger, less experienced females. Body mass is often positively correlated with age in many animals. A study of growth based primarily on western SSL showed that females continue to gain mass as they age throughout life, although they attain 90% of their asymptotic mass by age 13 (Winship et al.

2001). A comparable study of growth has not been conducted on eastern SSL but they are generally smaller in size than western SSLs (Sweeney et al. 2014). The smaller size of eastern SSL may inhibit older females from pupping earlier as a quadratic effect (decreasing then increasing date of parturition) with maternal age was found in eastern SSLs (Hastings and Jemison 2016) in addition to Weddell seals (Rotella et al. 2016). Only a weak quadratic relationship of age was found in this study with a linear effect being more favored by the data. It is possible that our lack of a strong quadratic effect could be due to few observations of older females in our work but it could also be related to size and growth variations among the pinnipeds. In addition to age, size does matter in the timing of parturition in many mammals (Anderson and Fedak 1987; Boltnev and York 2001; Solberg et al. 2007); although maternal age rather than mass can be a sufficient explanatory variable for the timing of parturition in some species (Boltnev and York 2001). Experience, as in the number of offspring previously given birth to, can also have a quadratic effect on parturition date among pinnipeds (Sydeman et al. 1991).

The present analysis did not provide much support for our previous finding that primiparous females gave birth later than multiparous females (Maniscalco et al. 2006). The previous analysis was based on one year (2004), much smaller sample size (39 females), and did not take into account additional covariates. The data available for the present study more strongly support the effects of other factors over parity. Few other researchers have tested for an effect of parity on the timing of parturition in pinnipeds but those that have, also found little or no evidence for it (Lunn and Boyd 1993; Rotella et al. 2016). Age, mass, and condition are more typically tested and found to effect parturition as discussed above.

The effects of pup sex and mass on timing of parturition are somewhat complicated. Some researchers have observed an effect of these variables among large phocids such as Weddell seals (Rotella et al. 2016) and gray seals (*Halichoerus grypus* (Fabricus, 1791)) (Anderson and Fedak 1987), while no effect of pup birth mass or sex has previously been observed among relatively small otariids such as the northern fur seal (*Callorhinus ursinus* (L., 1758)) (Boltnev and York 2001), Antarctic fur seal (Lunn and Boyd 1993), or a smaller phocid, the harbor seal (*Phoca vitulina* (L., 1758)) (Bowen et al. 1994). Thus, maternal mass may play a role in the interspecific differences of pup sex and size effects on birth timing as SSL are the largest of the otariid pinnipeds with maternal masses >200 kg; whereas these other mature female otariids and harbor seals are <150 kg at maturity (Boness and Bowen 1996). However, pup sex and pup mass were not supported by the data without inclusion of the effect of having a previous year's birth or maternal age in the present study. Therefore, it may be important to control for these variables to best understand the effects of pup-related factors on the timing of birth.

There are at least two additional points to consider for effects of pup sex and size on the timing of parturition. First, the greater size at birth for male SSL compared to female SSL may indicate a mechanical stimulation of the uterine wall by a growing fetus which has been shown to contribute to the onset of labor in some mammalian species (Shynlova et al. 2009). Male pups are born larger than female pups in SSL (Brandon et al. 2005) and many other species of pinniped that are sexually dimorphic as adults (Kovacs and Lavigne 1992; Trillmich 1996). Yet, this argument would not explain the temporal differences in birth between the sexes in Weddell seals (Rotella et al. 2016) in which male and female pups are similar in size at birth (Bryden et al. 1984). Second, it has been suggested that earlier born males provide some evidence for the

Trivers-Williard hypothesis (Rotella et al. 2016) which argues for greater investment in male offspring for mothers in good condition (Trivers and Willard 1973). There has been some evidence to support this hypothesis in at least one pinniped (Bradshaw et al. 2003). However, to provide appropriate support for this hypothesis as an influence on the timing of parturition, we need to account for maternal body condition and interannual variations in food availability and quality which we were unable to do in this study. It would also be necessary to show a meaningful fitness benefit conferred upon male offspring with earlier seasonal births. We do not expect that the current variation in the timing of parturition in western SSL has much bearing on neonatal survival because in SSL neonatal survival is strongly dependent on the irregular timing and intensity of storm surges that can wash young pups out to sea (Kaplan et al. 2008; Maniscalco et al. 2008).

It is commonly assumed that interannual influences on the timing of births are related to food availability or some other environmental variable. Stress related to disease prevalence or increased predatory activity (e.g., killer whales, *Orcinus orca* (L., 1758)) (Mashburn and Atkinson 2007) may also influence pupping rates or fetal development but evidence for these effects is more difficult to prove. For western SSL, ocean primary productivity and variations in prey availability have been correlated with population trends (Trites and Donnelly 2003; Lander et al. 2013) but there have been no studies of these effects on the timing of births in SSL. Nevertheless, effects of interannual variations in environmental conditions on the timing of parturition have been found in some pinnipeds (Boyd 1996; Soto et al. 2004), terrestrial mammals (Adams and Dale 1998; Wolcott et al. 2015), and non-mammalian species (e.g., Votier et al. 2009). Environmental conditions are typically associated with prey availability in these studies but not always (Wolcott et al. 2015). Therefore, a much broader ecosystem study would

be necessary to determine how the interannual variations in the timing of births found in this work are related to environmental or feeding conditions.

Some degree of environmental variation can always be expected from year to year and these variations are expected to influence the timing of birth whether through food availability and maternal condition or other factors not yet understood. It is the long term trends in birth timing related to environmental variation that are of the greatest concern as a consequence of continuing climate change. With consistent and detailed monitoring, long-term trends in the timing of birth may signal signs of trouble that need to be addressed. These studies should, however, take into account variation in predictor variables as described here.

Whether changes in the timing of parturition result from variation in timing of conception, embryonic implantation, or length of gestation, the primary unifying factor is likely energetics. If a female cannot find sufficient food, is compromised by fighting disease or infection, is burdened by prolonged lactation, or has not reached full potential growth, parturition may be delayed (Boyd 1991; Boyd 1998; Pitcher et al. 1998; Soto et al. 2004). The latest SSL birth observed at the Chiswell Island rookery was on 31 July to a six year old female who nursed her first born pup over the previous year while injured from an ingested fish hook. Anecdotal observations during the previous autumn showed her growing extremely thin with purulent discharge from her mouth over at least a two week period. There was little doubt that she was energetically compromised and struggling with infection. Under some conditions when a female is in poor condition, a fetus may also be aborted (Pitcher et al. 1998; Gibbens et al. 2010). Disease, malnutrition, and other factors may also cause premature births that may confound analyses such as this. Nevertheless, studies such as presented here are necessary to better understand the factors that can affect the timing of birth. Thereby, if long-term shifts do occur,

we can understand some of the internal and external factors that played a role in the change and potentially implement strategies to mitigate adverse population level effects.

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Table 1. Modeling results of fixed effects on the timing of birth ranked by AICc scores. Fixed effects include if a mother gave birth in the previous year (PrevBth), maternal age (Age), quadratic effect of maternal age (Age²), maternal parity (Parity), sex of the pup (PupSex), and estimated birth mass of the pup (Mass).

Model Rank	Model Structure	K	AICc	ΔAICc	AICc Wt.	Log. Lik.
1	~Age+PrevBth	6	1682.87	0.00	0.39	835.26
2	~Age+PrevBth+PupSex	7	1683.62	0.76	0.27	834.58
3	~Age+PrevBth+PupMass	7	1684.76	1.89	0.15	835.15
4	~Age+PrevBth+PupSex*Mass	9	1686.48	3.61	0.06	833.87
5	~Age ² +PrevBth	6	1687.79	4.93	0.03	837.73
6	~Age ² +PrevBth+PupSex	7	1688.32	5.45	0.03	836.93
7	~PrevBth	5	1689.71	6.85	0.01	839.74
8	~Age	5	1690.08	7.22	0.01	839.92
9	~PrevBth+PupSex	6	1690.35	7.48	0.01	839.00
10	~Parity	5	1691.05	8.19	0.01	840.41
11	~PrevBth+PupMass	6	1691.40	8.53	0.01	839.53
12	~Parity+PupSex	6	1691.72	8.85	0.00	839.69
13	~Age+PupMass	6	1691.88	9.02	0.00	839.77
14	~ Age ²	5	1692.50	9.63	0.00	841.13
15	~1 (Random Intercept)	4	1693.00	10.14	0.00	842.42
16	~PupSex	5	1693.04	10.17	0.00	841.40
17	~PupMass	5	1694.63	11.76	0.00	842.19

Table 2. Model averaged parameter estimates, standard errors, and 95% confidence intervals of important fixed effects.

	Estimate	Std. Error	95% CI
Maternal Age	-0.459	0.153	-0.758, -0.160
Previous Birth	2.371	0.722	0.835, 3.906
Pup Sex (Male)	-0.653	0.557	-1.842, 0.371
Pup Mass	-0.020	0.031	-0.081, 0.042

Draft

Figure captions

Figure 1. Timing of parturition at age for females that gave birth in a previous year (solid line) and those that did not (dashed line) $\pm$ 95% confidence intervals. Data adjusted for interannual variation.

Figure 2. Timing of birth relative ($\pm$ SE) to the interannual mean (12 June) and estimated birth mass ($\pm$ SE) for male (solid squares) and female (open diamonds) SSL pups across the six study years at Chiswell Island.

Draft

Figure 1. Timing of parturition at age for females that gave birth in a previous year (solid line) and those that did not (dashed line). Data adjusted for interannual variation.

239x236mm (300 x 300 DPI)

Figure 2. Timing of birth relative ($\pm$ SE) to the interannual mean (12 June) and estimated birth mass ($\pm$ SE) for male (solid squares) and female (open diamonds) SSL pups across the six study years at Chiswell Island.

238x158mm (300 x 300 DPI)