ARTICLE

Marine Mammal Science

Birth timing after the long feeding migration in northern elephant seals

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Abstract

Northern elephant seals migrate long distances from feeding grounds to raise pups during a brief period on breeding beaches. Because gestation sets a parturition date months in advance, timing of the arrival must be precise; an early arrival would waste foraging time, but a late arrival would cause parturition failure. We used satellite-tracked animals to examine this timing, establishing arrival and birth dates in 106 migrating females and estimating how far they traveled in the days just before birth. Females arrived a mean of 5.5 days prior to birth (range 1–11, $SD = 1.5$), and females arriving later in the breeding season had 1.8-day shorter prebirth intervals relative to early arrivers. There was no correlation between female body condition, nor female age, and the prebirth interval. The last 15 days prior to birth, animals traveled as far as 1,465 km. Those farthest from the colony traveled >100 km per day, three times faster than animals near the colony at the same time. Despite migrations covering several thousand kilometers while pregnant, female elephant seals were able to time their arrival within days. This allows them to maintain a precise annual birth cycle for many years consecutively.

KEYWORDS
birth timing, elephant seal, marine mammal migration, *Mirounga angustirostris*, parturition, phenology

1 | INTRODUCTION

Reproductive phenology, or the timing of reproduction, is a core feature of life history in animals and plants. A prominent phase of the reproductive schedule in migratory animals is the transition between migration and reproduction. In birds, the phrase "arrival biology" is used to describe this transition, known variously as the prechick, postarrival, prebreeding, or prelaying period (Perrins, 1970; Rubolini et al., 2007; Saino et al., 2004; Vergara et al., 2007; Wingfield et al., 2004). The transition is a small part of the annual cycle, but its timing underlies reproductive success. From a distant location, animals must initiate a long migration so that they arrive at the breeding ground on a precise schedule (Ahola et al., 2004; Mayor et al., 2017).

Mammals are also migratory, and marine mammals often travel long distances between feeding and breeding grounds. Elephant seals (*Mirounga* spp.), for example, spend most of their lives hunting for fish and squid in remote oceans but then migrate thousands of kilometers to birth and raise pups on land (Bradshaw et al., 2004; Campagna et al., 2000; Costa et al., 2012; Robinson et al., 2012). Unlike birds, which develop eggs after migration, gestation in pinnipeds begins months in advance, setting a parturition date and requiring precise timing of arrival at the breeding colony: too early means lost foraging time, while too late would mean birth at sea, likely fatal to the newborn. Female elephant seals maintain this precision and give birth year after year on a consistent cycle (Le Boeuf et al., 2019). Our broad goal is understanding how accuracy of the annual cycle limits female reproductive success (Costa et al., 1986; Crocker et al., 2001; Hassrick et al., 2013; Le Boeuf & Reiter, 1988; Le Boeuf et al., 2000; Reiter & Le Boeuf, 1991).

Our focus here is one link in the cycle, the timing of arrival from a long migration, just before birth. We take advantage of a sample of female northern elephant seals (*M. angustirostris*) that were tracked by satellite during their migration prior to parturition. Satellite-derived locations document movements at the end of the migration and the exact arrival time at the colony, while direct observations of pups establish parturition dates. With those observations, we can estimate the time interval between arrival and birth, allowing tests of the following hypotheses: (1) more experienced mothers time arrival more precisely and thus reduce the preparturition interval; (2) mothers in poor body condition must forage longer and thus shorten the interval; and (3) late-arriving mothers have a shorter interval to maintain the birth cycle. We also calculated the distance traveled in the last two weeks of the migration to examine females' ability to control arrival time, hypothesizing that animals farther from the colony traveled back at a higher rate.

2 | MATERIALS AND METHODS

2.1 | Breeding and the annual cycle

Northern elephant seals (*Mirounga angustirostris*) breed on remote beaches from Baja California to Vancouver Island. The largest colonies are in central California between 32° and 38°N. latitude (Le Boeuf et al., 2011; Lowry et al., 2014). Females spend a mean of 31 days ($SD = 4$) on the colonies in winter where they birth and nurse single pups, then copulate and wean the pup to depart on long foraging migrations (Figure 1). The females are far from shore for 2–3 months, then return to the colony in April or May to molt. At about this time, the fertilized ovum implants in the uterine wall, so gestation takes place during the following 7-month foraging migration in the summer and autumn (Le Boeuf, 1972; Le Boeuf & Laws, 1994).

2.2 | Study site and tagging methods

Researchers have studied the northern elephant seal colony at Año Nuevo (37.1086°N, 122.3378°W), 31 km north of Santa Cruz, California, since the late 1960s (Le Boeuf & Peterson, 1969; Reiter et al., 1981). Individuals are identified by numbered plastic tags attached to their hind flippers, allowing individuals to be followed throughout their
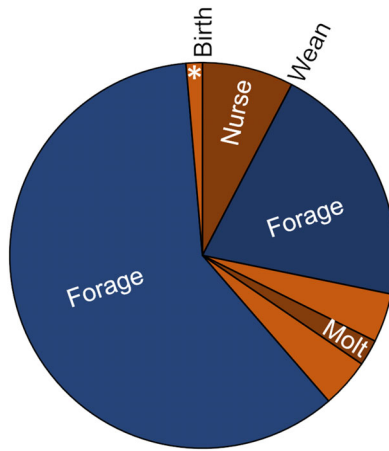
FIGURE 1 Annual cycle in adult female elephant seals. The year advances clockwise. Periods at sea are in blue, on land in brown (dark brown for molt and nursing, light brown for time before or after those life history events). The prebirth interval is marked with an asterisk.

21-year lifespans (Condit et al., 2014; Le Boeuf et al., 2019). To track locations at sea, ARGOS satellite transmitters, GPS tags, and time-depth recorders were deployed on individuals following chemical immobilization (see Costa et al., 2012; Crocker et al., 1997; Robinson et al., 2012 for details). Instruments were attached in the spring approximately 1 week after the end of hair replacement (molt) and recovered the next winter, 5 days after the birth of the pup (Costa et al., 2010). While the animals were sedated, detailed morphometric measurements were collected, allowing percent body fat to be calculated; percent fat was assumed to reflect female condition (Costa et al., 1986; Gales & Burton, 1987; Robinson et al., 2012; Simmons et al., 2010).

2.3 | Arrival and parturition

There were 266 females instrumented in May or June between 2002 and 2015, but only 164 were observed on the colony with a pup the following winter, and 30 of those had unreliable pup sightings. The remaining 134 records included consistent sightings of the female both before and after birth, but the most precise results came from 106 cases in which there was no gap between the last day seen without a pup and the first with a pup. In all 106 of these cases, the time of birth was observed with a precision of 24 hr, because observations of pups were confined to daylight hours during the short winter days. Though we occasionally see births at Año Nuevo, given 15 hr of winter darkness combined with the large number of females on the colony, we did not directly observe parturition in the 106 cases reported here. Of the 106 females with precise pup observations, 94 carried a time-depth recorder that measured depth below the ocean surface every 8 s, thus revealing arrival time on the beach with an accuracy <1 hr. The other 12 females did not have a depth record, only a position from the satellite tag. For these animals, we estimated arrival when a high-quality ARGOS location was within 1 km of Año Nuevo and remained there until the animal was observed (Costa et al., 2010), providing an arrival time with accuracy <12 hr.

2.4 | Data analysis

For these 106 breeding records, we defined the prebirth interval D as $P - A$, where P was the first date a pup was observed and A the arrival date. For purposes of future estimates for females with less complete observations, we

needed a probability distribution for D, so we tested several. Gamma, Gaussian, and Laplace distributions (Laplace, 1774) were fitted to the observations by likelihood methods, assuming a Poisson error. The two parameters of each distribution were estimated with a Metropolis sampler, generating posterior distributions and thus 95% credible intervals.

The 106 breeding records included 92 different individual females, with 14 individuals having two records. We found no variation in the prebirth interval, D, among females, since a model without a female effect was superior (lower Akaike information criterion) than a model with female identity included (lme4 package in R; Bates et al., 2015). We also checked for a year effect on D (13 different years, 2003–2016) and again found none using the same test. We thus present a single estimate of D, combining all females and years. Using standard, least-squares linear regression, we tested whether D correlated with the female's arrival date A ($N = 106$), age ($N = 85$ that had been tagged at birth, mean 8.2 years, range 5–18), and body fat upon arrival ($N = 104$ with morphometrics, mean body fat 34.5%, range 25.9%–40.3%).

The distance from the colony in kilometers was calculated 15, 10, and 5 days prior to parturition from the ARGOS satellite locations, using the 99 records for which the satellite tag was still working on those days. We calculated the net travel toward the colony between day 15 and day 10, which is the colony-distance on day 15 minus the colony-distance on day 10; it was divided by 5 to express net daily travel. The one female already on the colony on day 10 was excluded.

2.5 | Data availability

The 106 breeding records, including arrival and parturition dates plus distance traveled prior, are published as a Dryad Data Archive (Condit et al., 2021).

3 | RESULTS

3.1 | Arrival and the prebirth interval

Females arrived between December 28 and February 8, with a mean of January 15 ($SD = 8.3$ days). They gave birth $D = 1$–11 days later, between January 3 and February 9 (mean January 21, $SD = 7.9$ days). The 1-day and 11-day delays were outliers, however, since every other interval was 3–8 days (Figure 2). The sample mean of D was 5.49 days, with a standard deviation of 1.5 days. The Gaussian model fit the distribution of D better than gamma and Laplace distributions, though even the Gaussian failed to account for the narrow peak at 4 days (Figure 2). The Laplace distribution captured the steep peak but had a poorer fit in the tails.

3.2 | Variation in the prebirth interval

There was a significant negative relationship between arrival date and the prebirth interval (Figure 3). The mean interval for females arriving on January 1 was 6.3 days, decreasing to 4.5 days for females arriving on February 1. We found no relationship between female age and the prebirth period ($r^2 = 0.02$, $p = .18$), nor between a female's condition (body fat) and the interval ($r^2 < 0.01$, $p = .64$).

The shortest prebirth interval was a single female with a pup one day after arriving (Figures 2 and 3). She arrived just after midnight and was seen without a pup on the first day, then with a pup the following day, so the birth happened 15–30 hr after arrival. She was also the latest of all the females to arrive, on February 8, 24 days later than the average. All other females had at least a 3-day delay between arrival and parturition.
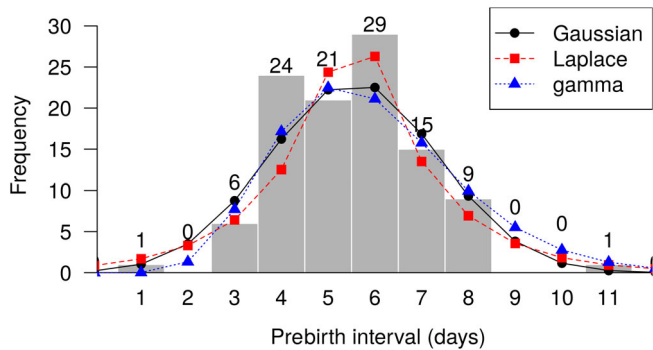
FIGURE 2 Observed prebirth interval. Histogram from 106 breeding records (gray bars with numbers above) and fitted distribution from three models. The Gaussian had the highest likelihood (by 1.4 log-likelihood units over the Laplace and 1.6 over the gamma). The best-fit Gaussian had $M = 5.53$ (95% credible interval 5.25–5.93) and $SD = 1.82$ (1.51–2.22).
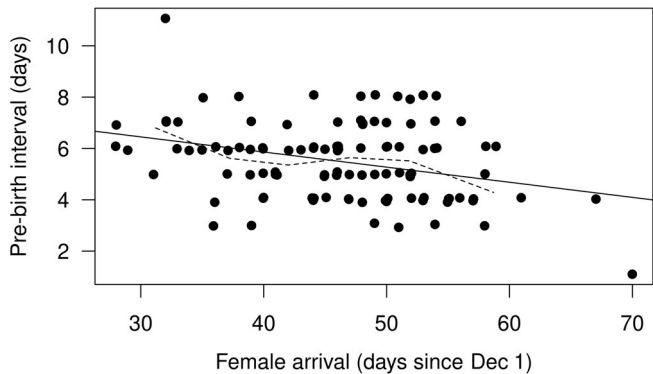

FIGURE 3 Prebirth interval versus arrival date. Regression from 106 breeding records. Arrival is given in days since December 1, so day 32 is January 1, day 63 is February 1. The regression coefficient is -0.059 ($p < .001$, $r^2 = 0.10$). The solid black line is the regression; the gray dashed curve connects the mean delay in 5-day intervals (<35, 35–39, 40–44 … ≥55). Points were offset slightly at random to reveal where multiple points coincide.

The single female who waited 11 days, 3 days longer than any other (Figure 2), was observed 16 times over those initial 11 days, by many different observers, never with a pup. She was then seen four times with a pup, and the pup was marked during the procedure to retrieve her satellite tag. She arrived on January 1, well before average, but not the earliest (Figure 3).

3.3 | Migration rate prior to birth

At the farthest point on their migrations, females were 3,230 ± 1,026 km (mean ± SD) from the colony. At 15 days prior to parturition, they had returned most of the way, but were still 690 ± 261 km away (Figure 4); 11 animals were >1,000 km on day 15, and the farthest was 1,465 km. By 5 days prior, nearly half the females were on the colony (Figure 2), while the farthest was 448 km away. Between 15 and 10 days before parturition, females traveled an average of 316 km closer to the colony (63 km/day), and there was a strong positive correlation between distance at day 15 and their rate of approach (Figure 5).
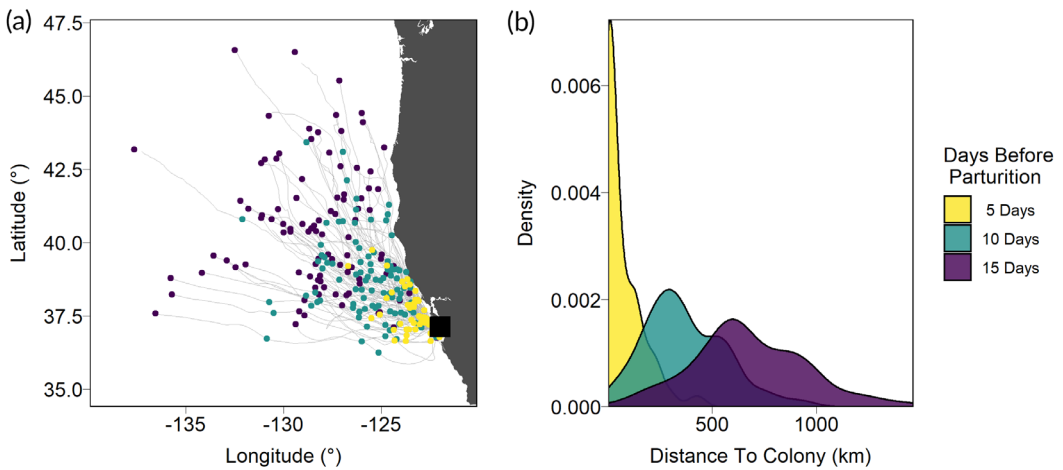
FIGURE 4 Movement at sea 15 days prior to parturition. A) Migration tracks over those 15 days, with position at day 15 in purple, day 10 in green, and day 5 in yellow. The colony is marked with a large black square (surrounded by yellow dots). B) Histograms of distance from colony at 15, 10, and 5 days prior to parturition for 99 females. At day 15, the mean ± *SD* was 690 ± 261 km, then 366 ± 187 at day 10 and 91 ± 65 at day (the two latter exclude animals already at the colony).
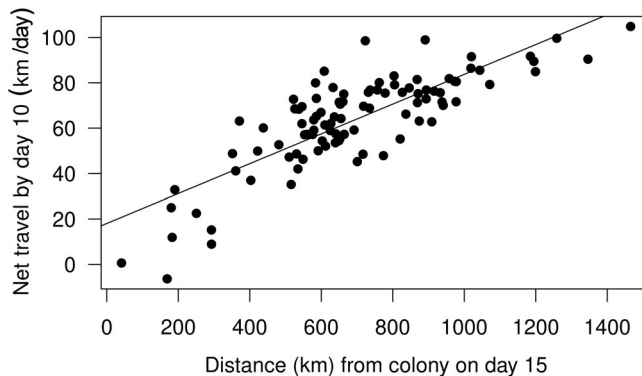

FIGURE 5 Prebirth distance traveled. Distance from the colony 15 days before birth (*x*-axis) versus net travel per day toward colony in the next 5 days (*y*-axis). The slope is +0.066 km faster daily travel for every kilometer further from the colony ($r^2 = 0.67$, $p < .001$, $N = 99$).

4 | DISCUSSION

Migrating female elephant seals arrived on the colony on average 5.5 days before giving birth, ranging from 1 to 11 days. Many traveled considerable distances in the last few days, including six that were still >1,200 km away 15 days prior to parturition. We found that females farther from the colony at 15 days traveled at a higher rate. Indeed, had those six farthest animals traveled at 63 km/day, as the average female did, they would not have arrived before parturition. Since elephant seal pups are unlikely to survive if born at sea (of the pinnipeds, only the walrus has been observed nursing aquatically; Boness & Bowen, 1996), the females' ability to adjust travel speed is essential. Females were evidently aware of their locations and adjusted their rate of travel to assure on-time arrival.

The narrow window between arrival and birth suggests strong selection pressures on both foraging duration and birth timing. In particular, our observation that late arriving females had a 2-day shorter preparturition interval, and

that a single very late female gave birth within 30 hr of arrival, further suggests that females are under pressure to forage as long as possible while giving birth within a short window. Foraging may have seasonal optima, limiting both ends of the foraging trip (Bowlin et al., 2010; Schindler, 2019). Pupping time may be limited to the cool winter, because warm air temperature is costly to elephant seals (Noren, 2002), or timed so that recently weaned pups begin foraging during spring upwelling or to avoid predators (Reiter et al., 1978). On the other hand, we found no evidence that females in poor condition shortened their prebirth interval, perhaps illustrating a lack of flexibility. In earlier work, we found that nonpregnant females arrive earlier in the season than pregnant females (Robinson et al., 2012), so the lack of flexibility in the preparturition delay was a surprise.

All long-distance migrants must balance travel against reproductive timing to reduce the interval between arrival at a breeding site and birth or oviposition. In cases where the interval has been quantified, caribou gave birth 4 days after arrival (Gurarie et al., 2019) and humpback whales 17 days (Craig et al., 2003), while pied flycatchers laid eggs 10 days after arrival, black-throated blue warblers 20 days (Ahola et al., 2004), and salmon 2 days (Dickerson et al., 2002). White storks, though, waited a much longer 59 days (Fulin et al., 2009). There are important contrasts among these species, however, since gestation occurs throughout the migration in the large mammals, but birds develop eggs after arrival. Shorebirds in Greenland offer a well-studied example of the latter, because the eggs and young are provisioned entirely by local feeding (Morrison & Hobson, 2004; Ramenofsky & Wingfield, 2006; Wingfield et al., 2004), whereas in elephant seals and many whales, all provisioning—gestation through nursing—is supported by foraging at distant feeding grounds. The birds are thus under selection to adjust the prebreeding delay in response to food availability on the breeding ground (Both & Visser, 2001; Mayor et al., 2017; Rubolini et al., 2007), a factor irrelevant in elephant seals and capital-breeding whales. Overall, the short interval in elephant seals and caribou, 4–5 days, can be traced to gestation while migrating. It is also possible that the timing of parturition in mammals may be under female control, perhaps triggered by arrival at the birthing grounds—in pinnipeds, the sudden onset of gravity on land is a plausible but untested mechanism for triggering parturition.

The flexibility needed to time arrival at breeding grounds must be set against the need to make navigation decisions weeks earlier. In this respect, elephant seals resemble other long-distant migrants and can serve as a model for inference about general theories (Hays et al., 2016; Schwenk et al., 2009). Spatio-temporal analysis of satellite tracks can test hypotheses about how animals decide when and where to travel (Horton et al., 2020). An important theme is how flexibility is incorporated into migration cycles, since flexibility is critical in the face of environmental variation, anthropogenic or not. Pinnipeds and their semiaquatic life may be especially interesting in this regard because they must cope with both terrestrial and marine environments. Finding the cues animals use to time migrations, and how route fidelity incorporates flexibility, is a key question (Horton et al., 2017).

Advances in remote tracking that include physiology as well as position offer the means to examine navigation cues and the timing of migration decisions. Is an elephant seal's decision to return toward the colony based solely on internal physiology related to pregnancy, or are environmental features integrated? How do immediate cues, internal or not, affect the full cycle from one breeding event to the next (Bowlin et al., 2010)? Our long-term goal is to elucidate the timing of the full cycle in female elephant seals, including reproduction, foraging, as well as the annual molt, and to understand how phenological stability and flexibility affect annual and lifetime reproductive success (Beltran et al., 2019; Le Boeuf et al., 2019).

4.1 | Conclusions

Female elephant seals migrate long distances from foraging grounds to the breeding colony while pregnant, arriving on the beach in a narrow window just 5.5 ± 1.5 days before birth. They travel an average of 690 km toward the colony in the last 15 days—over 1,200 km in some cases—and can increase their progress as needed to ensure arrival before the pup is born. Females are under selection to maintain a tight birth schedule year after year to optimize

both nursing and foraging, and the precise timing between arrival and birth at the breeding colony appears to play an important role.

AUTHOR CONTRIBUTIONS

Richard Condit: Conceptualization; data curation; formal analysis; methodology; software; validation; visualization; writing – original draft; writing – review and editing. **Roxanne Beltran:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – review and editing. **Patrick W Robinson:** Conceptualization; investigation; methodology; project administration; supervision; writing – review and editing. **Dan Crocker:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing – review and editing. **Daniel P Costa:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – review and editing.

ETHICS STATEMENT

Access to Año Nuevo State Park was granted by the California Department of Parks and Recreation. Tagging and observation of seals were authorized by National Marine Fisheries Service permits 14535, 14636, 21425. The animal use protocol was approved by the University of California at Santa Cruz Institutional Animal Care and Use Committee and followed the guidelines established by the Canadian Council on Animal Care and the Ethics Committee of the Society of Marine Mammalogy.

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