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Animal behaviour

The extra burden of motherhood: reduced dive duration associated with pregnancy status in a deep-diving mammal, the northern elephant seal

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The cost of pregnancy is hard to study in marine mammals, particularly in species that undergo pregnancy while diving continuously at sea such as elephant seals (genus *Mirounga*). We analysed the diving behaviour of confirmed pregnant and non-pregnant northern elephant seals (*M. angustirostris*, $n = 172$) and showed that after an initial continuous increase in dive duration, dives of pregnant females become shorter after week 17. The reasons for this reduction in dive duration remain unknown, but we hypothesize that increased fetal demand for oxygen could be the cause. Our findings reveal an opportunity to explore the use of biologging data to investigate pregnancy status of free-ranging marine mammals and factors that could affect pregnancy success.

1. Introduction

The cost of reproduction is central to understanding the trade-offs between current and future reproductive success [1,2]. Research on mammals has primarily examined the energetics of gestation and lactation [3,4], but females incur additional costs associated with morphological changes and an increased physiological burden [5]. In marine mammals, these costs are particularly hard to account for, because pregnancy occurs while at sea. One of the few studies on this subject links morphological changes in pregnant bottlenose dolphins (*Tursiops truncatus*) to an increase in energetic costs as they experience higher drag forces [6]. Whether pregnancy affects the aerobic capacity of diving mammals is still unknown, yet their foraging ability depends on their capacity to remain underwater, and is ultimately determined by their body oxygen storage [7]. Pregnancy could affect dive performance if the oxygen demand of a growing fetus constrains the time a mother can spend underwater foraging.

Gestation in mammals is typically associated with higher blood volume [8,9], which implies larger total body O_2 stores. Pregnancy is also linked with an increase in the basal metabolic rate (i.e. higher rate of O_2 consumption) [10,11]. Furthermore, although the presence of specialized fetal haemoglobin has not been confirmed in pinnipeds, their fetuses do have a haemoglobin molecule with higher O_2 affinity than adults [12], which may protect the fetus from hypoxia. Therefore, pregnancy likely impacts the O_2 available to the mother.

Adult female elephant seals (genus *Mirounga*) haul out twice a year: to breed (approx. four weeks) and moult (approx. six weeks); they spend the rest of their time diving continuously at sea [13,14] (figure 1). These dives can be close to 2 h in duration, and reach depths of over 2000 m [13,14]. Deep-diving species typically maximize their O_2 storage by having greater blood volume and higher concentrations of haemoglobin and myoglobin than shallow-diving species [7]. Blood

Table 1. Mass-at-departure, recovery, trip duration and diving metrics of adult female northern elephant seals, *Mirounga angustirostris*, according to pregnancy status.

	n	mass at departure (kg)	mass at recovery (kg)	trip duration (d)	dive depth (m)	dive duration (s)
pregnant	155	308.8 ± 36.0	478.2 ± 49.2	227.7 ± 35.7	475 ± 142	1427 ± 535
non-pregnant	17	299.5 ± 37.5	507.4 ± 46.7	204.5 ± 61.8	466 ± 150	1462 ± 714

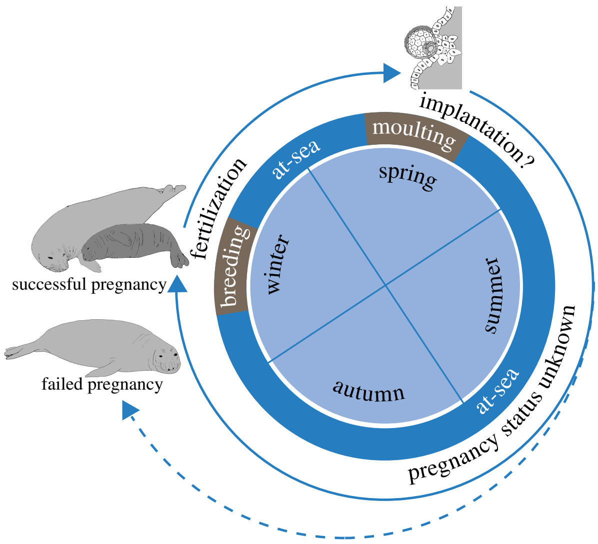

Figure 1. Annual cycle of adult female northern elephant seals. Breeding (approx. four weeks) and moulting haul-out (approx. six weeks) are indicated in brown. Individuals spend the rest of their annual cycle diving continuously at sea (blue). Timing of egg is uncertain. Pregnancy can only be confirmed when the female hauls out. (Online version in colour.)

volume also increases as animals spend more time at sea, representing a possible conditioning effect from repeated breath-holds and hypoxia [15,16].

Because elephant seals undergo pregnancy at-sea during their 8+ months post-moult trip (figure 1), our knowledge about this essential life-history phase is extremely limited. Fortunately, recent technological advances have enabled a wide range of physiological and behavioural measurements of free-ranging animals, including their diving behaviour [17]. We analysed diving data from confirmed pregnant and non-pregnant northern elephant seals (*Mirounga angustirostris*) to analyse whether dive duration, here understood as a measure of their diving/foraging performance, changes over the course of gestation.

2. Material and methods

Throughout this manuscript, we will use the term 'pregnant' to refer to animals that successfully returned to land and gave birth to a pup. 'Non-pregnant' refers to animals that returned to land but did not pup.

We collected diving data from 172 northern elephant seals captured at Año Nuevo State Park, California, USA, between 2004 and 2016 (table 1). Animals were sedated and handled following standard protocols [13], and instrumented with MK9 Time Depth Recorders (TDR, Wildlife Computers, WA, USA), programmed to collect diving data every 8 s. Animals were also outfitted with satellite tags to obtain location at sea and determine when animals came ashore [13].

Non-pregnant elephant seals ($n = 17$) returned either much earlier or later than pregnant females, and we confirmed whether individuals were nursing a pup upon instrument recovery. Diving data were corrected and analysed using the package *diveMove* [18], in R [19]. We used generalized additive mixed models (GAMMs) to explore the relationship between dive duration (DDur) and day of the trip (DoT), with pregnancy (fPreg) as categorical variable, individual identity as random effect and a gamma distribution (other diving metrics were also explored but are not included here; see the electronic supplementary material). GAMMs were fitted using the package *mgcv* [20], in R. Data are presented as mean ± s.d., unless stated otherwise.

3. Results and discussion

We found no difference in the mass at departure (ANOVA, $F = 0.78$, $p = 0.38$) or arrival ($F = 1.705$, $p = 0.19$) between pregnant and non-pregnant seals (table 1). Previous studies using linear mixed models have found no effects of pregnancy status on the dive duration of elephant seals in the weeks before or after their haul-outs [15]. Using the same approach, we found no differences in dive duration ($t = 0.64$, $p = 0.52$), or diving depths ($t = 0.45$, $p = 0.65$) between pregnant and non-pregnant seals. However, when we used GAMMs, we found that dive duration does change across the trip, and it does so in a nonlinear manner. Our model explained 67.8% of the deviance and revealed a significant relationship between DDur and DoT ($F = 631.4$, $p \ll 0.01$), and a significant interaction between DoT : fPreg, resulting in significantly different smoothers for pregnant and non-pregnant animals ($F = 67.2$, $p \ll 0.01$, figure 2).

Prior to day 120 (week 17), dive duration for both groups increased and pregnant animals dived for approximately 100 s longer than non-pregnant animals. After day 120, dive durations of pregnant seals decreased, while those of non-pregnant seals continued to increase; by day 204, non-pregnant females dived 400 s longer (figure 2). Previous research has shown that dive duration increases with trip duration, which has been related to a concurrent increase in mass and blood volume [15,21]. While this increase in dive duration had previously been linked to pregnancy [21], another study suggested that pregnancy status was not associated with the increased dive duration along a foraging trip [15]. Our results demonstrate that a nonlinear approach is required to fully characterize how dive duration changes across the period of gestation, and that pregnancy status does affect how this critical foraging parameter changes with time.

Although the impacts of gestation on O_2 stores in freely diving animals are still unknown, we expect that pregnancy will affect the diving ability. We suggest that the initial increase in blood volume and mass of the mother during the early stages of the pregnancy increases body O_2 stores. However, this trend reverses in the second half of the gestation, probably

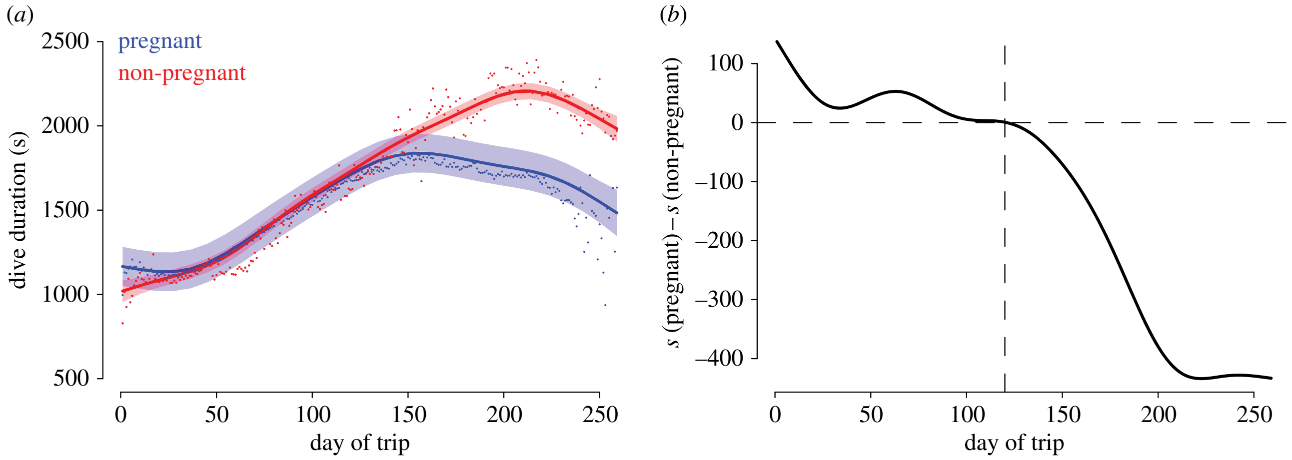

Figure 2. Predicted variation in dive duration along the gestational foraging trip of northern elephant seals. The shaded areas represent the 95% confidence intervals and dots represent daily geometric means. (*a*) Predicted dive duration for pregnant females (blue, $n = 155$, $n_{\mathrm{dives}} = 1\,909\,136$) and non-pregnant females (red, $n = 17$, $n_{\mathrm{dives}} = 207\,716$). (*b*) Differences in trends between pregnant and non-pregnant females (pregnant − non-pregnant).

owing to increased fetal O_2 demand. Humans have a gestation length similar to elephant seals and experience a period of significant development of connections in their brain [22] (estimated to consume 46–80% of the total fetal oxygen supply in developing humans [23]) and exponential increase in overall growth around weeks 23–27 of gestation [22,24], coinciding with the rapid decline in dive duration that we see in our data after day 150 (figure 2).

Although it is well documented that pinnipeds undergo embryonic diapause [25], it is still undetermined when the fertilized egg implants. As elephant seals gestate during their post-moult trip, pregnancy can only be confirmed when animals return to land, and it is uncertain whether females that did not have a pup were pregnant and aborted, or were never pregnant. Current biologging technology, however, allows us to obtain daily dive duration from wild-ranging marine animals via satellite [26], information that has the potential to be useful to discriminate pregnancy status of adult females.

We demonstrated that pregnancy potentially poses a cost for adult female elephant seals as it affects their diving capacity (duration), limiting the time that they can spend foraging underwater during the last weeks of their pregnancy. The reasons for this reduction in dive duration remain unknown, but we hypothesize that an increased fetal O_2 demand could be the cause, as oxygen-demanding tissues (i.e. brain) develop and the fetus experiences exponential growth during the second half of pregnancy. If this pattern holds for other marine mammals, it could be possible to assess reproductive state in free-ranging individuals from other populations and species, as well as explore the behavioural and environmental factors that contribute to the success of a pregnancy.

Ethics. Animal procedures were authorized under the National Marine Fisheries Services permits nos 786-1463, 87-143, 14636 and 19108. All protocols were approved by the IACUC, University of California Santa Cruz.

Data accessibility. Data available from Dryad (http://dx.doi.org/10.5061/dryad.k58fr) [27].

Authors' contributions. L.A.H. conceived the study. L.A.H., R.R.H. and M.S.T. analysed the data and wrote the manuscript. D.P.C. obtained funding and led data collection. All authors read and approved the final manuscript and agree to be held accountable for the content therein.

Competing interests. The authors declare no competing interests.

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