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Research paper

Pairing ultrasonography with endocrinology to elucidate underlying mechanisms of successful pregnancy in the northern fur seal (*Callorhinus ursinus*)

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ABSTRACT

Reproductive success is one of the central tenets of conservation management programs, yet the inability to study underlying physiological processes in a minimally-invasive manner and the unpredictable nature of wild animal populations leaves large gaps in our knowledge of factors critical to successful reproduction in wild species. This study integrated ultrasonography of the reproductive tract and analysis of reproductive hormones in 172 northern fur seals (*Callorhinus ursinus*) to identify intrinsic factors associated with reinitiating embryonic growth at the end of diapause. Within the first 3–4 weeks of active gestation, pregnant fur seals ($n = 126$) had a larger corpus luteum and fewer antral follicles than non-pregnant fur seals, or those still in diapause ($n = 46$). This suggests that the conceptus drives changes in ovarian status to convey its presence to the female. Morphological changes in the reproductive tract associated with pregnancy were not reflected in differences in endocrine profiles (estradiol, estrone, progesterone, and relaxin) between pregnant and non-pregnant individuals. Hormone concentrations correlated more strongly with calendar date than with the presence or size of the conceptus, demonstrating that none of these reproductive hormones were reliable markers for early pregnancy diagnosis. Instead, the northern fur seal's long diestrus may serve to reduce the probability of a temporal mismatch between corpus luteum regression and embryo implantation. Indeed, conception rates were high and confirmed rates of pregnancy loss were relatively low (11%). In this study, minimally-invasive ultrasonography was used in wild pinnipeds to detect very early pregnancy (embryonic vesicles >2 mm) in combination with ovarian and endocrine dynamics at the time of embryo implantation, shedding light on mechanisms for maternal recognition of pregnancy. This study is also the first to track whether these same animals carried the embryo to term, by observing fur seals during the birthing season the following year. Data do not support the notion that decreased pregnancy rates or higher pregnancy loss rates are major contributing factors to the northern fur seal's population decline.

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1. Introduction

Maintenance of a stable population is contingent on the ability of animals to survive and reproduce. Mechanisms governing reproduction vary widely across and within taxa, but logistical, technical, and ethical challenges often prohibit the study of intrinsic physiologic factors that influence reproductive patterns in non-model or wild animal species (Comizzoli et al., 2009; Lopes et al., 2004; Wildt et al., 2010). In assessing reproductive rates, common practices once included sacrificing individuals and their pregnancies for dissection and collection of the reproductive tracts (Craig, 1964; Daniel, 1971). Endocrine profiles have also been used as markers for pregnancy (Boyd, 1991; Browne et al., 2006; Daniel, 1975; Gales et al., 1997; Reijnders, 1990); however, interpretation of hormone changes during the post-breeding period is confounded by the lack of knowledge about normal temporal changes in non-pregnant females (e.g., not bred), and those that are in early

Abbreviations: CA, corpus albicans; CL, corpus luteum; EV, embryonic vesicle.

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stages of gestation (Browne et al., 2006; Daniel, 1974, 1975). The development of reliable, minimally-invasive technologies for assessing reproductive phenology are particularly useful when sacrificing individuals is not a viable option, whether it be due to logistical constraints or to conservation measures set to protect species in declining populations (Testa et al., 2010).

Following conception, a pivotal step for reproductive success is maternal recognition of pregnancy (Roberts et al., 1996) where the embryo signals its presence in the uterus by either inhibiting luteolysis or by having a luteotrophic effect (Bazer, 2013; Bazer et al., 2010; Clemente et al., 2009; Geisert and Bazer, 2015). Without such a signal, the corpus luteum (CL) will begin to regress, marking the point at which pregnant and non-pregnant females become physiologically distinct (Roberts et al., 1996). Inadequate or mistimed maternal recognition of pregnancy results in the loss of the conceptus prior to placentation, and is a major contributor to female infertility in humans and other large mammals (Cross et al., 1994; Macklon et al., 2002; Teklenburg et al., 2010). While the mechanisms critical to maternal recognition of pregnancy are species-specific, well-studied laboratory mammals and agricultural livestock have revealed common endocrine changes associated with initiation of pregnancy. For example, during estrus there is a pronounced rise in estrogen production by preovulatory follicles, and this induces proliferative changes in the uterine endometrium via increased transcription of cell cycle genes, mitotic rates, and edema (Geisert and Bazer, 2015). Progesterone increases dramatically soon after ovulation and is responsible for differentiation of the endometrium to a secretory phase, and breaks down the transmembrane glycoproteins that act as a physical barrier to embryo attachment in the uterus (Geisert and Bazer, 2015). As gestation progresses and placentation occurs, relaxin concentrations increase and play a role in maintaining the differentiated endometrium, increasing angiogenesis and blood flow, and reducing rates of pregnancy loss (Anand-Ivell and Ivell, 2014).

The occurrence of embryonic diapause adds complexity to the otherwise well-characterized sequence of endometrial proliferation/secretion, embryo attachment (i.e., implantation), and maternal recognition of pregnancy in other species (Renfree and Shaw, 2000, 2014). In species with diapause, the fertilized zygote develops only until reaching the blastocyst stage, before entering a period of metabolic quiescence and dramatically slowed mitotic growth (Daniel, 1971; Fenelon et al., 2014). In pinnipeds, the CL becomes vacuolated and progesterone secretion wanes during embryonic diapause (Atkinson, 1997; Boshier, 1981; Craig, 1964; Daniel, 1975; Harrison, 1948; Reijnders, 1990), but this process is reversible and luteinization occurs around the time of embryo attachment and the start of active gestation (Boshier, 1981; Craig, 1964). The mechanisms signaling the end of the blastocyst's period of suspended animation remain largely unknown. Pinnipeds offer a unique opportunity to study the physiologic shifts that occur at the time of embryo attachment in wild animals due to the predictability with which animals congregate at on-shore rookeries. Because of commercial harvests for pelts prior to the Fur Seal Act (years: 1911, 1944, 1966, 1983) and the North Pacific Fur Seal Convention (1957), northern fur seals (*Callorhinus ursinus*) have been studied extensively to monitor their behavior, movements, and reproductive record.

Northern fur seals give birth in July–August each year (mean date: July 9; York and Scheffer, 1997; Trites and York, 1993), with ~70% of the world's population residing on the Pribilof Islands off the coast of Alaska. In a highly polygynous breeding system, the males develop a hierarchical breeding territory to build harems as females return to terrestrial rookeries for birthing (Bartholomew and Hoel, 1953). Within one week of parturition, increased ovarian follicular development leads to ovulation, and females are bred (Bartholomew and Hoel, 1953; Craig, 1964). After fertilization, the embryo enters an obligate (seasonal) period of diapause thought to be controlled by photoperiodic cues (Fenelon et al., 2014; York and Scheffer, 1997). Simultaneously, female fur seals nurse their pups for the next four months, utilizing an income-breeding strategy by alternating between foraging for self-maintenance and returning to the rookery to provision the pup (Bartholomew and Hoel, 1953; Boltnev and York, 2001). Embryonic diapause in this species is thought to keep the demands of lactation separate from the demands of active gestation; that is, re-initiation of embryonic growth and attachment does not occur until mid-November, after the pup is weaned (Gentry, 1998; York and Scheffer, 1997). In humans and domestic species in which it has been critically examined, the incidence of pregnancy loss is greatest during the embryonic phase, declining to a small fraction after the start of the fetal stage (i.e., after implantation and organogenesis). Further, age and nutritional plane may exert control over the probability of conception (Boyd, 1984; Testa and Adams, 1998). Therefore, the end of diapause in northern fur seals coincides with the time of the year that females are in relatively poor condition, and may serve as a critical period that distinguishes which females will continue with gestation and which will undergo embryonic loss.

Northern fur seals are currently listed as a vulnerable species under the International Union for Conservation of Nature (IUCN; Gelatt et al., 2015) and non-lethal methods are needed to assess reproductive status in an effort to determine the cause of population stasis. In this regard, the use of minimally-invasive ultrasonography has been developed as a means of early pregnancy detection in pinnipeds (Adams et al., 2007; Shero et al., 2015; Testa et al., 2010). To date, the temporal dynamics between hormone concentrations and early embryo development in marine mammals have not been critically investigated, nor have events during the peri-implantation period been paired with direct observations of pregnancy status or gestational outcomes (i.e., embryo loss vs. pup birth). Direct and immediate knowledge of pregnancy status by ultrasonography provides the opportunity to relate endocrine dynamics with morphologic characteristics of the ovaries and uterus, and establish physiologic linkages with reproductive events such as non-pregnancy, embryonic growth and viability, implantation, and gestational loss in the same individuals.

The goals of this study were to characterize early pregnancy in northern fur seals, and assess rates of reproductive success (i.e., giving birth) and gestational loss. In an effort to elucidate the mechanisms involved at the end of diapause in northern fur seals, we examined the morphologic and hormonal dynamics of the reproductive system near the expected time of embryo attachment. Results are expected to provide a basis for the establishment of indices that may be used to identify pregnancy during the earliest stages of active gestation for use in captive breeding programs and wildlife conservation management.

2. Methods

2.1. Animal handling

Female northern fur seals were captured and physically restrained (Gentry and Holt, 1982) on St. Paul Island, Alaska on 13–14 November 2005 ($n = 10$), 11–16 November 2007 ($n = 96$), and 18–24 November 2008 ($n = 66$) between 10:00 and 18:00 h. All were captured and weighed at the Polovina Cliffs rookery (57°10′46″ N, 170°9′42″ W) except for 26 captured at Tolstoi rookery (57°08′11″ N, 170°20′50″ W) in 2008. Twenty-six seals in 2008 were anesthetized with isoflurane for tooth extraction. All others were examined without sedation while restrained in sternal

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