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Effects of environmental variables on surface temperature of breeding adult female northern elephant seals, *Mirounga angustirostris*, and pups

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ABSTRACT

Pinnipeds spend extended periods of time on shore during breeding, and some temperate species retreat to the water if exposed to high ambient temperatures. However, female northern elephant seals (*Mirounga angustirostris)* with pups generally avoid the water, presumably to minimize risks to pups or male harassment. Little is known about how ambient temperature affects thermoregulation of well insulated females while on shore. We used a thermographic camera to measure surface temperature (T_s) of 100 adult female elephant seals and their pups during the breeding season at Point Reyes National Seashore, yielding 782 thermograms. Environmental variables were measured by an onsite weather station. Environmental variables, especially solar radiation and ambient temperature, were the main determinants of mean and maximum T_s of both females and pups. An average of 16% of the visible surface of both females and pups was used as thermal windows to facilitate heat loss and, for pups, this area increased with solar radiation. Thermal window area of females increased with mean T_s until approximately 26 °C and then declined. The T_s of both age classes were warmer than ambient temperature and had a large thermal gradient with the environment (female mean 11.2 ± 0.2 °C; pup mean 14.2 ± 0.2 °C). This large gradient suggests that circulatory adjustments to bypass blubber layers were sufficient to allow seals to dissipate heat under most environmental conditions. We observed the previously undescribed behavior of females and pups in the water and determined that solar radiation affected this behavior. This may have been possible due to the calm waters at the study site, which reduced the risk of neonates drowning. These results may predict important breeding habitat features for elephant seals as solar radiation and ambient temperatures change in response to changing climate.

1. Introduction

Most endothermic animals are strict homeotherms, regulating core body temperature within a narrow range during active periods. An animal that cannot dissipate heat effectively risks heat stress (i.e. hyperthermia). Hyperthermia can lead to negative effects on reproduction and long-term survival (Hansen, 2009; Speakman and Król, 2010) and, in extreme cases, can be lethal (Bartholomew and Wilke, 1956; Reiter et al., 1978). The primary mechanisms by which animals release excess heat are conduction, convection, evaporation and radiation (McNab, 2002). Heat loss through those mechanisms can be facilitated by increased blood flow to dilated vessels in peripheral areas, such as the head and extremities (Klir and Heath, 1992; Lynch et al., 2011; Mauck et al., 2003; Molyneux and Bryden, 1978). Thermoregulation is especially difficult for species that inhabit both aquatic and terrestrial habitats. The same morphological and physiological adaptations necessary for animals to retain heat in cold aquatic environments (e.g. enhanced insulation) pose potential problems for the animals while on land in tropical or temperate climates (Noren, 2002; Norris and Kunz, 2012).

Pinnipeds are an excellent example of animals that thermoregulate in diverse thermal habitats. Seals and sea lions spend the majority of their lives at sea, but can spend extended time in terrestrial habitats during reproduction or molting (Reidman, 1990). While at sea, these animals must be able to overcome the

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high rate of heat loss to water (Dejours, 1987). Adaptations for heat retention in water include a thick blubber layer or dense fur for insulation, low surface area to volume ratio, shunting of blood away from extremities, and counter-current heat exchangers in the peripheral vasculature (Bartholomew and Wilke, 1956; Reidman, 1990; Williams and Worthy, 2002). Some of these heat-conserving features can be problematic for pinnipeds while on land in temperate habitats (Bartholomew and Wilke, 1956; Beenjtes, 2006; Hansen et al., 1995; Twiss et al., 2002). Phocids can sometimes combat overheating and release excess heat by shunting blood to thermal windows on their body using dilated arteriovenous anastomoses, allowing for superficial cooling (Mauck et al., 2003; Molyneux and Bryden, 1978; Norris et al., 2010).

In addition to physiological and morphological adaptations for maintaining core body temperature, pinnipeds employ behavioral thermoregulation. These behaviors are necessary at high temperatures when physiological mechanisms are unable to effectively reduce heat gain, especially during breeding when individuals must remain on land for extended periods of time. In general these behavioral strategies improve the efficiency of anatomical and physiological mechanisms for dissipating heat. Otariids use behaviors that allow them to release excess heat through their large flippers. They will adjust body positions to expose their flippers to the wind, which increases convective heat loss, or immerse their flippers into tidepools (Beentjes, 2006; Campagna and Le Boeuf, 1988). Northern fur seals, *Callorhinus ursinus*, are known to exhibit a jughandling position where one foreflipper and both hind flippers are raised above the water in an arc formation, which facilitates heat dissipation because of air flow over the wet surface (Liwanag, 2010). Temperate phocids rely on behaviors that enhance heat release through the thermal windows on the trunk of their bodies through evaporation of wet pelage (Molyneux and Bryden, 1978; Norris et al., 2010; Twiss et al., 2002).

Northern elephant seals, *Mirounga angustirostris*, are an ideal system to examine thermal stress of phocids on land. They are among the largest of phocids, develop thick blubber layers and dive unusually deep in cold water (Robinson et al., 2012), but spend extended time on shore in temperate and tropical habitats. While many examples of behavioral thermoregulation in pinnipeds during the breeding season include individuals retreating into tide pools or the nearshore water to cool off when they experience increased heat gain (Campagna and Le Boeuf, 1988; Francis and Boness, 1991; Gentry, 1973; Twiss et al., 2002; Whittow, 1978), there is a lack of evidence showing adult female northern elephant seals and young pups exhibiting this same behavior. Previous work on maternal behavior noted that adult females and pups moved closer to the water's edge on hot days to lie on damp sand and be exposed to sea spray, but the seals did not go into the water (Reiter et al., 1978). In contrast weaned pups were observed entering the water when ambient temperature increased (Heath et al., 1977). The slow development of swimming ability in elephant seal pups may preclude adult females and their pups from going into the water. A pup is unable to swim during the first month of life and does not usually enter the water until after weaning (Reiter et al., 1978). For the duration of the lactation period, females remain onshore to keep their pup safe, but also stay with the harem for protection against subordinates waiting to mate with the females. High ranking males will mate with females in the harem near the end of the lactation period and some subordinate males mate with females in the water as they depart the harem (Crocker et al., 2012). If adult females approach the water's edge prior to departure, they can be exposed to unwanted mating attempts from subordinate males (Le Boeuf, 1972; Reiter et al., 1978). These mating attempts may be dangerous to females that are not receptive to mating and may affect the social structure of the elephant seal breeding colony (Le Boeuf and Mesnick, 1990; Le Boeuf et al., 1972). Therefore, active cooling using the water's edge may not be a safe thermoregulatory strategy for adult females with pups during the breeding season.

The northern elephant seal's thick blubber layer poses a thermoregulatory challenge during times of increased air temperature. At the beginning of the breeding season, female elephant seals have a large blubber layer that serves as an energy reserve while fasting and lactating for approximately one month. The robust fat reserves impede heat loss, but the blubber layer thickness is reduced across lactation, lessening the difficulty of offloading heat. At the end of the breeding season, lactating females have lost about 40% of their body mass, which consists of about a 50% loss in body fat (Crocker et al., 2001). At birth, elephant seal pups have a thin blubber layer and rely on a dense, black pelage to conserve heat. As they nurse, pups gain mass and the blubber layer thickens. By the end of the nursing period, the mass gained by pups is approximately 55% fat (Crocker et al., 2001) and the thermal challenges initially faced by the female during times of high air temperatures become a potential challenge for the pups. Additionally, weaned elephant seal pups with large body size and high body lipid content have elevated resting metabolic rates and exhibit increased thermal conductance as ambient temperature increases (Noren, 2002).

Infrared thermography, which allows surface temperature to be measured across the entire visible body, provides a non-invasive method to measure the infrared radiation emitted from an object that can then be converted to temperature. This technique has been evaluated for its effectiveness in measuring surface temperature of animals (Cena and Clark, 1973; McCafferty, 2013, 2007; Nienaber et al., 2010) and various studies have used thermographic cameras with captive animals (Cena and Clark, 1973; Klir and Heath, 1992; Paterson et al., 2012; Willis et al., 2005). Few studies have used thermographic cameras to study thermal properties of pinnipeds in their natural setting (Lynch et al., 2011; McCafferty et al., 2005; Mellish et al., 2015; Norris et al., 2010). The objective of this study was to use infrared thermography to measure the effects of environmental variables, including ambient temperature, relative humidity, solar radiation, and wind speed, on the surface temperature of adult female northern elephant seals and pups during the breeding season. We investigated changes in surface temperatures of adult females and pups across the breeding season, examined the behavior of females and pups going into the water during the breeding season, and explored how environmental variables potentially affected that behavior.

2. Methods

2.1. Study site and subjects

This study was conducted at the Drakes Beach northern elephant seal colony in Point Reyes National Seashore, California during the 2014 elephant seal breeding season (December 2013–March 2014). The Drakes Beach colony is in a sheltered cove situated in Drakes Bay, and is part of a larger colony that extends around Point Reyes Headland (Adams et al., 2009). Adult female elephant seals were dye-marked with a unique identifier on one or two areas of their posterior body using blue-black hair dye (Lady Clairol, Inc., Cincinnati, OH, USA) as they arrived on shore or a few days after giving birth. Pups were dye-marked on either flank using blonde hair dye a few days after birth. One hundred mother-pup pairs were included in this study.

Seals were observed 1–5 h per day on 29 days throughout the breeding season. Thermal and digital photographs were taken of each animal that could be identified by its marking and was not fully obstructed by surrounding animals. Each time an animal was