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 thermographs. 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 $11.2 \pm 0.2^\circ\text{C}$; pup mean $14.2 \pm 0.2^\circ\text{C}$). 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.

Keywords: infrared thermography; thermoregulatory behavior; northern elephant seal; thermal window.

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 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 (Beenjtes, 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 Messnick, 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 hours 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 thermally photographed, every effort was made to take an image of both the female and her pup, but sometimes that was not feasible because the pup was either obstructed or could not be positively associated with its mother. Therefore, not every female thermogram was paired with a pup thermogram. For each thermogram, it was also noted if the animal was in the water. Animals in water included those that moved into the water and those that allowed the incoming tide to

wash over them (i.e. did not retreat to an unoccupied area of beach). To determine the stage of lactation for each animal, the estimated age of the pup was recorded for each thermogram, when possible. The age categories included P1 (≤ 7 days old), P2 (8 – 14 days old), P3 (15 – 21 days old), and P4 (> 21 days old). Pup age categories were determined from known parturition dates or estimated from the physical characteristics of the pup as described in Adams et al. (2009).

2.2 Infrared thermography

A FLIR ThermaCAM B2 with 19° lens ($\pm 0.1^\circ\text{C}$; Wilsonville, OR, USA) was used to take 782 thermograms of adult females and pups (7 ± 6 thermographs per cow). The camera was factory calibrated by FLIR prior to the study, and calibration at distance was checked by referencing a temperature-controlled heat block and comparing the estimated temperature with that from a factory-calibrated PTC RHTemp1000 type J thermocouple (PTC Instruments, Los Angeles, CA, USA). Surface temperatures were derived after correction for reflected radiation based on ambient temperature, relative humidity (%), emissivity, and distance from camera to seal, using Flir software. Emissivity was set at 0.98 for dry animals and 0.96 for wet animals based on previous studies (Cuyler et al., 1992; Norris et al., 2010). Distance to the seal was measured with a laser rangefinder (Nikon Prostaff, Tokyo, Japan) for distances greater than 10 m and the distance was estimated for those less than 10 m. Distance from seals averaged 12.2 ± 5.0 m and ranged from 2.7 m to 32.5 m. Images were taken on the beach or from a bluff above the colony (height above colony ranges from approximately 3 to 8 m), depending on tide height and the location of the dye-marked seal. Observation angles varied between 0° and 14° , well below the range of angles where curvature effects create changes in apparent emissivity (Cheng et al., 2012).

2.3 Environmental variables

Ambient temperature (T_a) and relative humidity were measured by a temperature/relative humidity smart sensor (temperature accuracy $\pm 0.21^\circ\text{C}$, relative humidity accuracy $\pm 2.5\%$; Onset Computer Corporation, Bourne, MA, USA), solar radiation was measured by an Onset Silicon Pyranometer smart sensor (accuracy $\pm 10 \text{ W m}^{-2}$), and wind speed was measured by an Onset wind speed sensor (accuracy $\pm 1.1 \text{ m/s}$). All of the sensors were attached to an Onset HOBO Micro Station Data Logger located on the bluff above the colony. Measurements were taken automatically every 5 minutes, 24 hours per day. Time-stamped thermograms were then matched to the environmental data with the closest time within the 5 minute interval.

2.4 Analysis

For each thermogram, the temperature difference between the seal and the surrounding environment was used to manually select the seal's body from the total image using Analyze 12.0 software (Mayo Clinic, Rochester, MN, USA; Robb, 2001, 1999; Robb et al., 1989). The corresponding digital image was viewed to help ensure only the targeted seal's visible body was included in the analysis if there were other seals in close proximity or if sand was on parts of the body. Only images with seals that had at least 50% of their visible body unobstructed were included in the analysis. Analyze 12.0 was further used to analyze the thermograms for mean and maximum whole body surface temperatures (T_s), and to determine the total area of the surface used as thermal windows. Thermal windows were defined as localized areas greater than one standard deviation above the mean surface temperature of the individual in the thermogram (Norris et al., 2010). Each pixel in the thermogram had a temperature measurement, which allowed for precise measurement of the area of a thermal window relative to the total area of the visible body used in the analysis. The difference between mean surface temperature and ambient

temperature (thermal gradient) was calculated to determine potential heat flux across the visible body surface.

Linear mixed models were used to evaluate the effect of environmental variables on the surface temperature, thermal windows, and thermal gradient of adult females and pups. All models contained a random effects term for each individual seal to account for within subject correlation. Initial models contained all environmental variables. Nonsignificant effects ($p > 0.05$) were removed concurrently to create the final model. Effect sizes for fixed effects were assessed using R^2 for mixed models (Edwards et al., 2008). Impacts of lactation stage on maternal and pup surface temperature and thermal features were examined using linear mixed models with individual mother or pup as a random effect. If significant differences were detected, least-square means for stages were compared using Student's t-tests. For linear mixed models, model residuals were visually assessed for approximate normality and homoscedascity. Multicollinearity was assessed for environmental variables using the variance inflation factor. A generalized linear mixed model (SAS v9.3; SAS Institute, Cary, NC, USA) with a binomial response and logit linking function was used to assess the effects of environmental variables on the behavior of adult female seals going into the water. All statistical analyses were conducted in JMP 12.0 (SAS Institute), except where stated otherwise. Data are presented as means $\pm$ s.e.m., unless otherwise noted.

3. Results

3.1 Environment

Environmental data encompassed the entire time period during which the study took place and, therefore, is a larger data set than that used for the surface temperature analyses. This data set includes measurements taken at night and at times during the day when thermograms of

seals were not being taken. Data are presented as a range and mean $\pm$ SD. Solar radiation varied from 0.6 W/m² to 829.4 W/m² (mean 105.7 ± 172.1 W/m²), with periods of greatest solar radiation in late February and early March. Ambient temperature ranged from a low of 5.3°C to a high of 24.7°C (mean 12.8 ± 3.0 °C), with the highest temperatures occurring in mid-January. Wind speeds varied from 0 m/s to 8.31 m/s (mean 1.0 ± 1.2 m/s); however, while seals were being photographed, the maximum wind speed never exceeded 3.0 m/s. Relative humidity ranged from 13% to 100% (mean 73.6 ± 25.6 %). Environmental conditions during acquisition of the thermographs are shown in Table 1 and reflect higher solar radiation and ambient temperatures during daytime.

3.2 Surface temperature

Mean T_s was 26.2 ± 0.2 °C for adult females ($n = 671$ thermograms) and 29.1 ± 0.2 °C for pups ($n = 658$ thermograms). The maximum T_s averaged 32.7 ± 0.2 °C for adult females and averaged 34.7 ± 0.2 °C for pups. Solar radiation had the strongest effect on both mean and maximum T_s for both age classes, along with significant effects from T_a and wind speed (Tables 2 & 3). Mean and maximum T_s increased with solar radiation (Fig. 1) and T_a and decreased with wind speed.

The mean thermal gradient ($T_s - T_a$) was 11.2 ± 0.2 °C for adult females and 14.2 ± 0.2 °C for pups, showing that for both age classes, surface temperatures were consistently warmer than ambient temperature. Solar radiation, T_a , and wind speed affected the thermal gradient of adult females (Table 2). The thermal gradient of pups was most strongly affected by ambient temperature, along with effects from solar radiation and wind speed (Table 3). For both adult females and pups, the thermal gradient became larger with increasing solar radiation and smaller with increasing ambient temperature and wind speed.

The area of visible surface used as thermal windows averaged 16.0% for both adult females and pups. None of the environmental variables significantly affected the proportion of the body classified as thermal windows for adult females (Table 2). However, thermal window area of pups increased with increasing solar radiation (Table 3). Thermal window area was affected by mean T_s for females ($F_{1,583.5} = 10.45$, $p = 0.001$), but not for pups when controlled for the effects of solar radiation ($F_{1,550.4} = 0.25$, $p = 0.62$). Thermal window area increased with mean T_s of adult females until approximately 26°C and then declined (Fig. 2). Location of thermal windows on the body was not recorded; however, many were seen in thermograms occurring throughout the trunk of the body (Fig. 3).

3.3 Surface temperature changes across lactation

Pregnant females ($n = 1$) and the last stage of lactation (P4; adult female $n = 5$, pup $n = 11$) were removed from the models because of their small sample sizes. When environmental variables were included as covariates, together with seal ID, they accounted for >60% of the variation in mean and maximum T_s . When controlled for environmental variability, there was no effect of lactation stage on mean or maximum T_s in females or in pups ($p > 0.05$). In a model with environmental covariates, individual effects accounted for 45% of the variation in mean T_s of females, declining to 25% by the third week of lactation (Table 4). Individual effects accounted for similarly high proportions of the variance in maximum T_s across all lactation stages (24-37%). In pups, individual effects accounted for 27-37% of the variation in T_s or maximum T_s across lactation stages (Table 4).

The mean T_s of pups was significantly greater than the mean T_s of their mothers ($F_{1,1261} = 174.31$, $p < 0.0001$). This difference significantly increased across lactation ($F_{2,428} = 3.44$, $p = 0.03$) with pups being warmest relative to their mothers near the end of lactation ($\Delta 3.6^\circ\text{C}$) as

compared to the beginning of lactation ($\Delta 2.6^{\circ}\text{C}$; $p < 0.05$). On average, pup T_s was $3.1 \pm 0.2^{\circ}\text{C}$ warmer than their mothers.

When controlled for environmental covariates, the area of visible surface used as thermal window area (TWA) did not vary significantly across lactation for females ($p > 0.05$), whereas it did significantly vary for pups ($F_{2,449.7} = 2.55$, $p = 0.04$). When controlled for environmental covariates, thermal gradient did not change across lactation in either females or pups ($p > 0.05$).

3.4 Behavior

On eight days throughout the study period, mother-pup pairs were seen either entering the water or allowing the small waves to wash over their bodies. On many more occasions, the majority of the colony remained near the water's edge and had access to damp sand. Solar radiation was the only significant environmental variable that affected whether or not females were in the water ($F_{1,586} = 10.33$, $p = 0.001$), i.e. the likelihood that females would be in the water increased with solar radiation (Fig. 4).

4. Discussion

Surface radiative temperature was strongly influenced by environmental variables in lactating female elephant seals and their pups, with solar radiation being the strongest determinant of surface temperature. Seals gain a portion of their heat from conduction with their surroundings and radiation from the sun. Therefore, an increase in insolation will greatly affect the seals' heat load by increasing the direct absorption of radiation and by increasing the temperature of the substrate the seals are hauled out on. Cloud cover and wind can decrease the effects of solar radiation by reducing solar intensity and increasing convective heat loss, respectively (Campagna and Le Boeuf, 1988; Cena and Clark, 1973; Heath et al., 1977; White and Odell, 1971). However, during the current study there were little cloud cover and low wind

speeds, suggesting these factors did little to mitigate heat gain during periods of high solar radiation. These findings are consistent with previous studies that demonstrated impacts of solar radiation and ambient temperature on surface temperature in phocids (McCafferty et al. 2005; Norris et al. 2010).

Thermal gradients with the environment showed that seals were regularly warmer than T_a , indicating a flow of heat from the seal to the surrounding environment. Females ranged from 1.3°C below T_a to 25°C warmer than T_a and pups ranged from 0 to 26°C warmer than T_a . Phillips and Heath (1995) found in terrestrial animals that a thermal gradient of 1.5°C would lead to significant heat loss from the animal to the environment. In addition to the large thermal gradient, 95% of thermographs yielded mean T_s that were less than an expected core temperature of 37°C, suggesting an effective ability to transfer heat to the environment. In contrast, maximum T_s exceeded 37°C on >50% of thermographs, suggesting differential insolation of the body surface or circulatory adjustments to enhance heat loss. A wide thermal gradient range found in Weddell seals, *Leptonychotes weddellii*, in Antarctica was suggested to be due to differing thermoregulatory strategies of heat dissipation and conservation required during Antarctic summer conditions (Mellish et al., 2015). The consistently large positive thermal gradient in the current study suggests that females and pups were maintaining some level of skin perfusion throughout the breeding period to bypass insulation and facilitate heat dissipation.

Many animal species, both terrestrial and marine, are known to use thermal windows to help dissipate heat (Erdsack et al., 2012; Mauck et al., 2003; Nienaber et al., 2010; Norris et al., 2010; Tattersall and Cadena, 2010; Weissenböck et al., 2010). The use of thermal windows requires fine-tuned control of skin perfusion, which allows for quicker heat loss and more spontaneous vasomotor control (Mauck et al., 2003; Weissenböck et al., 2010). Both female

elephant seals and pups used, on average, approximately 16% of the visible body surface as thermal windows. An identical proportion for adult male elephant seals was found in a previous study (Norris et al., 2010). The lack of a relationship between the average percentage of body surface used as thermal windows and body size or blubber thickness suggest the importance of conserved vascular anatomy in bypassing the blubber layer. However, in contrast to females, pup TWA was affected by solar radiation, perhaps due to the increased heat absorption by the black pup lanugo.

The mean T_s of pups was significantly warmer than maternal T_s , which is consistent with previous findings of young animals having a warmer temperature than adults of the same species (Bartholomew and Wilke, 1956; Noren et al. 2008; Tattersall and Cadena, 2010). Pups are most likely warmer than adults due to their elevated mass-specific metabolism. Additionally, the black pelage of elephant seal pups should absorb higher amounts of solar radiation than the lighter pelage of adults, which could lead to higher T_s (Cena and Clark, 1973). However, coat color also affects penetrance of solar radiation to the skin and it has been suggested that the dark natal coats of some pinnipeds may play a role in providing insulation against overheating from insolation (Erdsack et al., 2013). The increase in TWA with solar radiation in pups is consistent with this finding and suggests that interpretation of TWA in pups may be more complex than that for females. However, it has also been suggested that for coats with low insulation values, like that of elephant seal pups (Heath et al. 1977), increased thermal absorption in dark coats is more likely to penetrate to the skin and increase heat inflow associated with thermal radiation (Dawson et al., 2014).

Animals tend to become more heat tolerant and can usually endure ambient temperatures higher than they are normally exposed to as they age (Hansen and Lavigne, 1997; Noren et al.,

2008; Weissenböck et al., 2010). An increase in thermoregulatory capacity over time enables adults to be better at controlling changes in their skin temperature than juveniles of the same species (Tattersall and Cadena, 2010). In the current study, the thermal window area of adult female elephant seals was affected by mean T_s , whereas this was not the case for pups. This suggests females were better able to control the use of thermal windows to release excess heat or alternatively that some thermal windows defined in pups reflected surface heating by absorbed solar radiation. The thermal window area percentage increased in females until maternal mean T_s reached $\sim 26^\circ\text{C}$ and then started to decline. This inflection point was approximately the same as the mean thermal gradient ($\sim 11^\circ\text{C}$) above the mean T_a for the entire dataset ($\sim 15^\circ\text{C}$). The finding is consistent with that of a previous study for adult male elephant seals (Norris et al., 2010), in which the authors suggested that as mean T_s increases well above mean T_a , T_s becomes more homogenous across the body surface. In other words, thermal windows grow and merge such that most of the body surface assists with heat dissipation.

When controlled for environmental variation there was no effect of changing adipose insulation across lactation on T_s in females or in pups. In other words, when statistically held at mean environmental conditions, changes in insulation within individuals did not influence mean or maximum surface temperature, suggesting circulatory adjustments were sufficient to modify insulation and allow heat dissipation. As suckling pups increase adipose tissue mass and insulation, mass-specific heat production also declines by a factor of two (Crocker et al, 2001). Similar data are not available for lactating females. Given the availability of sequential thermographs across lactation for most females and pups, it is interesting that individual effects that were independent of lactation stage or environmental variables accounted for such a large portion of the variation in T_s in pups and females (24-45%). These effects may include individual

differences in resting metabolism, activity, blubber layers, coat coloration, skin perfusion and homeostatic control mechanisms.

Both females and pups were seen in shallow water on multiple days of high solar radiation, which is not a typical behavior in this species. This behavior, although common with many other pinniped species (Campagna and Le Boeuf, 1988; Francis and Boness, 1991; Gentry, 1973; Limberger et al., 1986; Twiss et al., 2002), has not been documented for adult female elephant seals and pups prior to this study. Solar radiation was the significant environmental factor driving this behavior. A similar result was observed when female Juan Fernández fur seals, *Arctocephalus philippii*, moved from land to water in the early afternoon when there was a sudden increase in solar radiation (Francis and Boness, 1991). Female southern sea lions, *Otaria byronia*, have been observed immersing their hind flippers in tidepools as solar radiation increased (Campagna and Le Boeuf, 1988). This study suggested that as solar radiation increases and it becomes difficult to lose heat through convection to air and radiative heat loss, behaviors are undertaken to capitalize on heat loss through evaporative cooling and conduction to the water.

Elephant seals in breeding colonies that are experiencing increases in ambient temperature and solar radiation may also adopt this thermoregulatory behavior in order to aid in heat loss. However, the behavior may be constrained by associated energetic costs (Carrascal et al., 2001). Investigation in breeding adult males suggested that terrestrial locomotion was one of the most important determinants of energy expenditure while on shore (Crocker et al., 2012). Frequent movements associated with tidal height and thermoregulatory behavior could influence lactation efficiency and reduce investment in offspring (McDonald and Crocker, 2006). Alternatively, the risks and costs of fighting off males that approach in an attempt to mate may

be too high. Females that approach the water garner the attention of peripheral males (Cox and Le Boeuf, 1977; Le Boeuf, 1972). Subsequent interactions can become violent if the female resists mating or if she is injured during competition between multiple males (Le Boeuf and Mesnick, 1990). In the present study, females that entered the water on high solar radiation days prior to being in estrus did not elicit reactions from surrounding males. A possible explanation for this lack of sexual attention by the males could be impacts of the same thermal conditions on their behavior. Male elephant seals have been found to be the least active on hot, humid days with low wind speeds. During those times, the inactive males had the highest surface temperatures recorded in the study (Norris et al., 2010). Therefore, when females enter the water to increase conductive and evaporative heat loss, the environmental conditions may also inhibit the motivation of males to move and attempt copulation.

Thermoregulatory behaviors are strongly influenced by habitat (Beentjes, 2006; Campagna and Le Boeuf, 1988; Trites, 1990). Trees that provided cool tree trunks or shade were determined to be an important component of habitat quality for koalas and resting against the trees became a new thermoregulatory strategy used to increase heat loss during times of extreme heat (Briscoe et al., 2014). In the current study, periods of high insolation increased the probability that adult females and pups would move to the water. This behavior is possible due to the study site at Drakes Beach being in a protected bay with a lack of strong waves, which reduces the risk of pups being dragged out to sea or drowning. Female Juan Fernández fur seals have been observed rafting offshore during periods of increased solar radiation only at sites that had protected offshore waters (Francis and Boness, 1991). At other elephant seal breeding colonies where females and pups have not been seen entering the water, there might be strong enough winds to increase convective heat loss and reduce the effects of solar radiation thereby

negating the need for this novel behavior. These colony sites may also not allow for females and pups to enter the water if the surf is too strong. If these colonies experience increasing ambient temperature and increasing periods of high solar radiation, thermoregulatory requirements may alter what constitute important habitat components and breeding habitat preference might change to sites that have a protected and calm shoreline.

5. Conclusions

Endotherms that live in both aquatic and terrestrial environments must have the ability to reduce heat loss in the water, but also increase heat loss while on land in a temperate climate. Different life history stages have different thermoregulatory challenges and require alternative strategies for effective thermoregulation. Female northern elephant seals and their pups are particularly affected by environmental factors, especially solar radiation, as demonstrated by changes in surface temperature and thermal features that influence the release of excess heat. Solar radiation is also an important factor in determining thermoregulatory behaviors of adult females. This is the first study to report observations of female elephant seals and their pups immersing themselves in water during periods of increased solar radiation. Thermoregulatory requirements may interact with breeding habitat topography to shape social behavior of the colony and mating strategies, thus modifying desired qualities in breeding sites as environmental factors change in response to changing climate and as new colonies form with continued population expansion.

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589

Table 1. Summary environmental data recorded during the periods when thermograms were being taken.

Environmental variable	Minimum value	Maximum value	Mean $\pm$ SD
Solar radiation (W m^{-2})	20	670	390 ± 150
Ambient temperature ($^{\circ}\text{C}$)	9.3	22.8	15.0 ± 2.9
Wind speed (m/s)	0.0	3.0	0.8 ± 0.7
Relative humidity (%)	25.1	100	69.3 ± 23.0

Table 2. Linear mixed model results (F-statistics and R^2 values) for effects of environmental variables on adult female mean surface temperature (T_s), maximum T_s , thermal window area (TWA), and thermal gradient ($T_s - T_a$).

Environmental variables	Mean T_s		Max. T_s		TWA		Thermal gradient	
	F	R^2	F	R^2	F	R^2	F	R^2
Solar radiation	86.75*	0.28	136.34*	0.38	n.s.	n.s.	86.75*	0.28
Ambient temperature	26.06*	0.13	40.52*	0.20	n.s.	n.s.	73.98*	0.31
Wind speed	24.10*	0.10	26.16*	0.11	n.s.	n.s.	24.10*	0.10
Relative humidity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

* $p < 0.0001$
n.s., no significance

Table 3. Linear mixed model results (F-statistics and R^2 values) for effects of environmental variables on pup mean surface temperature (T_s), maximum T_s , thermal window area (TWA), and thermal gradient ($T_s - T_a$).

Environmental variables	Mean T_s		Max. T_s		TWA		Thermal gradient	
	F	R^2	F	R^2	F	R^2	F	R^2
Solar radiation	43.62**	0.17	114.93**	0.35	48.40**	0.08	43.62**	0.17
Ambient temperature	6.81*	0.05	28.76*	0.16	n.s.	n.s.	140.25**	0.52
Wind speed	9.93*	0.04	15.93*	0.07	n.s.	n.s.	9.93*	0.04
Relative humidity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

* $p < 0.01$; ** $p < 0.0001$
n.s., no significance

Table 4. The percent variation in surface temperature (T_s) or thermal window area proportions (TWA%) accounted for by individual female or pup during the first 3 weeks of lactation. Individual effects were assessed as a random effect in a linear mixed model containing environmental covariates. Stages of lactation are based on estimate of pup age: P1 (≤ 7 days old), P2 (8 - 14 days old), P3 (15 – 21 days old).

Stage of lactation	Mean T_s		Max. T_s		TWA		Thermal gradient	
	Adult female	Pup	Adult female	Pup	Adult female	Pup	Adult female	Pup
P1	45	36	25	34	2	4	25	36
P2	29	27	37	37	0	0	22	27
P3	25	32	24	33	0	8	23	32

Figure 1. Variation in mean surface temperature (T_s) and maximum T_s with solar radiation for (A) adult females and (B) pups. Data are means $\pm$ s.e.m. within binned values of solar radiation to the nearest ten $W m^{-2}$.

Figure 2. Variation in thermal window area (TWA) of the visible body surface with mean surface temperature (T_s) of adult females. Data are means $\pm$ s.e.m. within binned values of mean T_s to the nearest tenth $^{\circ}\text{C}$. A quadratic curve was fitted to the graph to show the inflection point among the data points ($F_{2,203} = 5.76$, $p = 0.004$).

Figure 3. Two thermograms of elephant seals with thermal windows. The associated digital picture is included for aid in identifying the seals. (A) The adult female in the center of the thermogram has thermal windows with maximum surface temperature (T_s) of 29.5°C and the mean T_s is 21.6°C. The pup, which is directly behind the adult female, has thermal windows with maximum T_s of 31.1°C and the mean T_s is 24.7°C. (B) The adult female in the center of the thermogram has thermal windows with maximum T_s of 29.8°C and the mean T_s is 18.3°C. The pup at the ventral side of the adult female has thermal windows with maximum T_s of 32.0°C and the mean T_s is 22.5°C.

Figure 4. Logistic regression for the probability of adult females going into the water as solar radiation changes. Curve fitted is the monotonic change in probability derived from the logistic regression parameters. Dotted lines represent 95% confidence limits.