

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

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ABSTRACT

17 Pinnipeds spend extended periods of time on shore during breeding, and some temperate species
18 retreat to the water if exposed to high ambient temperatures. However, female northern elephant
19 seals (*Mirounga angustirostris*) with pups generally avoid the water, presumably to minimize
20 risks to pups or male harassment. Little is known about how ambient temperature affects
21 thermoregulation of well insulated females while on shore. We used a thermographic camera to
22 measure surface temperature (T_s) of 100 adult female elephant seals and their pups during the
23 breeding season at Point Reyes National Seashore, yielding 782 thermographs. Environmental
24 variables were measured by an onsite weather station. Environmental variables, especially solar
25 radiation and ambient temperature, were the main determinants of mean and maximum T_s of
26 both females and pups. An average of 16% of the visible surface of both females and pups was
27 used as thermal windows to facilitate heat loss and, for pups, this area increased with solar
28 radiation. Thermal window area of females increased with mean T_s until approximately 26°C and
29 then declined. The T_s of both age classes were warmer than ambient temperature and had a large
30 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
31 large gradient suggests that circulatory adjustments to bypass blubber layers were sufficient to
32 allow seals to dissipate heat under most environmental conditions. We observed the previously
33 undescribed behavior of females and pups in the water and determined that solar radiation
34 affected this behavior. This may have been possible due to the calm waters at the study site,
35 which reduced the risk of neonates drowning. These results may predict important breeding
36 habitat features for elephant seals as solar radiation and ambient temperatures change in response
37 to changing climate.

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

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43 **1. Introduction**

44 Most endothermic animals are strict homeotherms, regulating core body temperature
45 within a narrow range during active periods. An animal that cannot dissipate heat effectively
46 risks heat stress (i.e. hyperthermia). Hyperthermia can lead to negative effects on reproduction
47 and long-term survival (Hansen, 2009; Speakman and Król, 2010) and, in extreme cases, can be
48 lethal (Bartholomew and Wilke, 1956; Reiter et al., 1978). The primary mechanisms by which
49 animals release excess heat are conduction, convection, evaporation and radiation (McNab,
50 2002). Heat loss through those mechanisms can be facilitated by increased blood flow to dilated
51 vessels in peripheral areas, such as the head and extremities (Klir and Heath, 1992; Lynch et al.,
52 2011; Mauck et al., 2003; Molyneux and Bryden, 1978). Thermoregulation is especially difficult
53 for species that inhabit both aquatic and terrestrial habitats. The same morphological and
54 physiological adaptations necessary for animals to retain heat in cold aquatic environments (e.g.
55 enhanced insulation) pose potential problems for the animals while on land in tropical or
56 temperate climates (Noren, 2002; Norris and Kunz, 2012).

57 Pinnipeds are an excellent example of animals that thermoregulate in diverse thermal
58 habitats. Seals and sea lions spend the majority of their lives at sea, but can spend extended time
59 in terrestrial habitats during reproduction or molting (Reidman, 1990). While at sea, these
60 animals must be able to overcome the high rate of heat loss to water (Dejours, 1987).

61 Adaptations for heat retention in water include a thick blubber layer or dense fur for insulation,
62 low surface area to volume ratio, shunting of blood away from extremities, and counter-current
63 heat exchangers in the peripheral vasculature (Bartholomew and Wilke, 1956; Reidman, 1990;
64 Williams and Worthy, 2002). Some of these heat-conserving features can be problematic for
65 pinnipeds while on land in temperate habitats (Bartholomew and Wilke, 1956; Beenjtes, 2006;

66 Hansen et al., 1995; Twiss et al., 2002). Phocids can sometimes combat overheating and release
67 excess heat by shunting blood to thermal windows on their body using dilated arteriovenous
68 anastomoses, allowing for superficial cooling (Mauck et al., 2003; Molyneux and Bryden, 1978;
69 Norris et al., 2010).

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

84 Northern elephant seals, *Mirounga angustirostris*, are an ideal system to examine thermal
85 stress of phocids on land. They are among the largest of phocids, develop thick blubber layers
86 and dive unusually deep in cold water (Robinson et al., 2012), but spend extended time on shore
87 in temperate and tropical habitats. While many examples of behavioral thermoregulation in
88 pinnipeds during the breeding season include individuals retreating into tide pools or the

89 nearshore water to cool off when they experience increased heat gain (Campagna and Le Boeuf,
90 1988; Francis and Boness, 1991; Gentry, 1973; Twiss et al., 2002; Whittow, 1978), there is a
91 lack of evidence showing adult female northern elephant seals and young pups exhibiting this
92 same behavior. Previous work on maternal behavior noted that adult females and pups moved
93 closer to the water's edge on hot days to lie on damp sand and be exposed to sea spray, but the
94 seals did not go into the water (Reiter et al., 1978). In contrast weaned pups were observed
95 entering the water when ambient temperature increased (Heath et al., 1977). The slow
96 development of swimming ability in elephant seal pups may preclude adult females and their
97 pups from going into the water. A pup is unable to swim during the first month of life and does
98 not usually enter the water until after weaning (Reiter et al., 1978). For the duration of the
99 lactation period, females remain onshore to keep their pup safe, but also stay with the harem for
100 protection against subordinates waiting to mate with the females. High ranking males will mate
101 with females in the harem near the end of the lactation period and some subordinate males mate
102 with females in the water as they depart the harem (Crocker et al., 2012). If adult females
103 approach the water's edge prior to departure, they can be exposed to unwanted mating attempts
104 from subordinate males (Le Boeuf, 1972; Reiter et al., 1978). These mating attempts may be
105 dangerous to females that are not receptive to mating and may affect the social structure of the
106 elephant seal breeding colony (Le Boeuf and Messnick, 1990; Le Boeuf et al., 1972). Therefore,
107 active cooling using the water's edge may not be a safe thermoregulatory strategy for adult
108 females with pups during the breeding season.

109 The northern elephant seal's thick blubber layer poses a thermoregulatory challenge
110 during times of increased air temperature. At the beginning of the breeding season, female
111 elephant seals have a large blubber layer that serves as an energy reserve while fasting and

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

123 Infrared thermography, which allows surface temperature to be measured across the
124 entire visible body, provides a non-invasive method to measure the infrared radiation emitted
125 from an object that can then be converted to temperature. This technique has been evaluated for
126 its effectiveness in measuring surface temperature of animals (Cena and Clark, 1973;
127 McCafferty, 2013, 2007; Nienaber et al., 2010) and various studies have used thermographic
128 cameras with captive animals (Cena and Clark, 1973; Klir and Heath, 1992; Paterson et al.,
129 2012; Willis et al., 2005). Few studies have used thermographic cameras to study thermal
130 properties of pinnipeds in their natural setting (Lynch et al., 2011; McCafferty et al., 2005;
131 Mellish et al., 2015; Norris et al., 2010). The objective of this study was to use infrared
132 thermography to measure the effects of environmental variables, including ambient temperature,
133 relative humidity, solar radiation, and wind speed, on the surface temperature of adult female
134 northern elephant seals and pups during the breeding season. We investigated changes in surface

135 temperatures of adult females and pups across the breeding season, examined the behavior of
136 females and pups going into the water during the breeding season, and explored how
137 environmental variables potentially affected that behavior.

138

139 **2. Methods**

140 *2.1 Study site and subjects*

141 This study was conducted at the Drakes Beach northern elephant seal colony in Point
142 Reyes National Seashore, California during the 2014 elephant seal breeding season (December
143 2013 – March 2014). The Drakes Beach colony is in a sheltered cove situated in Drakes Bay, and
144 is part of a larger colony that extends around Point Reyes Headland (Adams et al. 2009). Adult
145 female elephant seals were dye-marked with a unique identifier on one or two areas of their
146 posterior body using blue-black hair dye (Lady Clairol, Inc., Cincinnati, OH, USA) as they
147 arrived on shore or a few days after giving birth. Pups were dye-marked on either flank using
148 blonde hair dye a few days after birth. One hundred mother-pup pairs were included in this
149 study.

150 Seals were observed 1 – 5 hours per day on 29 days throughout the breeding season.
151 Thermal and digital photographs were taken of each animal that could be identified by its
152 marking and was not fully obstructed by surrounding animals. Each time an animal was
153 thermally photographed, every effort was made to take an image of both the female and her pup,
154 but sometimes that was not feasible because the pup was either obstructed or could not be
155 positively associated with its mother. Therefore, not every female thermogram was paired with a
156 pup thermogram. For each thermogram, it was also noted if the animal was in the water. Animals
157 in water included those that moved into the water and those that allowed the incoming tide to

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

163 *2.2 Infrared themography*

164 A FLIR ThermaCAM B2 with 19° lens ($\pm 0.1^\circ\text{C}$; Wilsonville, OR, USA) was used to take
165 782 thermograms of adult females and pups (7 ± 6 thermographs per cow). The camera was
166 factory calibrated by FLIR prior to the study, and calibration at distance was checked by
167 referencing a temperature-controlled heat block and comparing the estimated temperature with
168 that from a factory-calibrated PTC RHTemp1000 type J thermocouple (PTC Instruments, Los
169 Angeles, CA, USA). Surface temperatures were derived after correction for reflected radiation
170 based on ambient temperature, relative humidity (%), emissivity, and distance from camera to
171 seal, using Flir software. Emissivity was set at 0.98 for dry animals and 0.96 for wet animals
172 based on previous studies (Cuyler et al., 1992; Norris et al., 2010). Distance to the seal was
173 measured with a laser rangefinder (Nikon Prostaff, Tokyo, Japan) for distances greater than 10 m
174 and the distance was estimated for those less than 10 m. Distance from seals averaged 12.2 ± 5.0
175 m and ranged from 2.7 m to 32.5 m. Images were taken on the beach or from a bluff above the
176 colony (height above colony ranges from approximately 3 to 8 m), depending on tide height and
177 the location of the dye-marked seal. Observation angles varied between 0° and 14° , well below
178 the range of angles where curvature effects create changes in apparent emissivity (Cheng et al.,
179 2012).

180 *2.3 Environmental variables*

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

189 *2.4 Analysis*

190 For each thermogram, the temperature difference between the seal and the surrounding
191 environment was used to manually select the seal's body from the total image using Analyze
192 12.0 software (Mayo Clinic, Rochester, MN, USA; Robb, 2001, 1999; Robb et al., 1989). The
193 corresponding digital image was viewed to help ensure only the targeted seal's visible body was
194 included in the analysis if there were other seals in close proximity or if sand was on parts of the
195 body. Only images with seals that had at least 50% of their visible body unobstructed were
196 included in the analysis. Analyze 12.0 was further used to analyze the thermograms for mean and
197 maximum whole body surface temperatures (T_s), and to determine the total area of the surface
198 used as thermal windows. Thermal windows were defined as localized areas greater than one
199 standard deviation above the mean surface temperature of the individual in the thermogram
200 (Norris et al., 2010). Each pixel in the thermogram had a temperature measurement, which
201 allowed for precise measurement of the area of a thermal window relative to the total area of the
202 visible body used in the analysis. The difference between mean surface temperature and ambient

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

205 Linear mixed models were used to evaluate the effect of environmental variables on the
206 surface temperature, thermal windows, and thermal gradient of adult females and pups. All
207 models contained a random effects term for each individual seal to account for within subject
208 correlation. Initial models contained all environmental variables. Nonsignificant effects ($p >$
209 0.05) were removed concurrently to create the final model. Effect sizes for fixed effects were
210 assessed using R^2 for mixed models (Edwards et al., 2008). Impacts of lactation stage on
211 maternal and pup surface temperature and thermal features were examined using linear mixed
212 models with individual mother or pup as a random effect. If significant differences were
213 detected, least-square means for stages were compared using Student's t-tests. For linear mixed
214 models, model residuals were visually assessed for approximate normality and homoscedascity.
215 Multicollinearity was assessed for environmental variables using the variance inflation factor. A
216 generalized linear mixed model (SAS v9.3; SAS Institute, Cary, NC, USA) with a binomial
217 response and logit linking function was used to assess the effects of environmental variables on
218 the behavior of adult female seals going into the water. All statistical analyses were conducted in
219 JMP 12.0 (SAS Institute), except where stated otherwise. Data are presented as means \pm s.e.m.,
220 unless otherwise noted.

221 **3. Results**

222 *3.1 Environment*

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

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

235 *3.2 Surface temperature*

236 Mean T_s was 26.2 ± 0.2 °C for adult females ($n = 671$ thermograms) and 29.1 ± 0.2 °C for
237 pups ($n = 658$ thermograms). The maximum T_s averaged 32.7 ± 0.2 °C for adult females and
238 averaged 34.7 ± 0.2 °C for pups. Solar radiation had the strongest effect on both mean and
239 maximum T_s for both age classes, along with significant effects from T_a and wind speed (Tables
240 2 & 3). Mean and maximum T_s increased with solar radiation (Fig. 1) and T_a and decreased with
241 wind speed.

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

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

258 *3.3 Surface temperature changes across lactation*

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

269 The mean T_s of pups was significantly greater than the mean T_s of their mothers ($F_{1,1261} =$
270 174.31, $p < 0.0001$). This difference significantly increased across lactation ($F_{2,428} = 3.44$, $p =$
271 0.03) with pups being warmest relative to their mothers near the end of lactation ($\Delta 3.6^\circ\text{C}$) as

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

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

278 *3.4 Behavior*

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

285 **4. Discussion**

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

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

299 Thermal gradients with the environment showed that seals were regularly warmer than
300 T_a , indicating a flow of heat from the seal to the surrounding environment. Females ranged from
301 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 .
302 Phillips and Heath (1995) found in terrestrial animals that a thermal gradient of 1.5°C would lead
303 to significant heat loss from the animal to the environment. In addition to the large thermal
304 gradient, 95% of thermographs yielded mean T_s that were less than an expected core temperature
305 of 37°C , suggesting an effective ability to transfer heat to the environment. In contrast,
306 maximum T_s exceeded 37°C on >50% of thermographs, suggesting differential insolation of the
307 body surface or circulatory adjustments to enhance heat loss. A wide thermal gradient range
308 found in Weddell seals, *Leptonychotes weddellii*, in Antarctica was suggested to be due to
309 differing thermoregulatory strategies of heat dissipation and conservation required during
310 Antarctic summer conditions (Mellish et al., 2015). The consistently large positive thermal
311 gradient in the current study suggests that females and pups were maintaining some level of skin
312 perfusion throughout the breeding period to bypass insulation and facilitate heat dissipation.

313 Many animal species, both terrestrial and marine, are known to use thermal windows to
314 help dissipate heat (Erdsack et al., 2012; Mauck et al., 2003; Nienaber et al., 2010; Norris et al.,
315 2010; Tattersall and Cadena, 2010; Weissenböck et al., 2010). The use of thermal windows
316 requires fine-tuned control of skin perfusion, which allows for quicker heat loss and more
317 spontaneous vasomotor control (Mauck et al., 2003; Weissenböck et al., 2010). Both female

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

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

339 Animals tend to become more heat tolerant and can usually endure ambient temperatures
340 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

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

366 Both females and pups were seen in shallow water on multiple days of high solar
367 radiation, which is not a typical behavior in this species. This behavior, although common with
368 many other pinniped species (Campagna and Le Boeuf, 1988; Francis and Boness, 1991; Gentry,
369 1973; Limberger et al., 1986; Twiss et al., 2002), has not been documented for adult female
370 elephant seals and pups prior to this study. Solar radiation was the significant environmental
371 factor driving this behavior. A similar result was observed when female Juan Fernández fur
372 seals, *Arctocephalus philippii*, moved from land to water in the early afternoon when there was a
373 sudden increase in solar radiation (Francis and Boness, 1991). Female southern sea lions, *Otaria*
374 *byronia*, have been observed immersing their hind flippers in tidepools as solar radiation
375 increased (Campagna and Le Boeuf, 1988). This study suggested that as solar radiation increases
376 and it becomes difficult to lose heat through convection to air and radiative heat loss, behaviors
377 are undertaken to capitalize on heat loss through evaporative cooling and conduction to the
378 water.

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

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

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

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

415 **5. Conclusions**

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

429

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438

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- 588

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

Environmental variable	Minimum value	Maximum value	Mean \pm SD
Solar radiation ($W m^{-2}$)	20	670	390 ± 150
Ambient temperature ($^{\circ}C$)	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

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593 **Table 2.** Linear mixed model results (F-statistics and R^2 values) for effects of environmental
 594 variables on adult female mean surface temperature (T_s), maximum T_s , thermal window area
 595 (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

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601 **Table 3.** Linear mixed model results (F-statistics and R^2 values) for effects of environmental
 602 variables on pup mean surface temperature (T_s), maximum T_s , thermal window area (TWA), and
 603 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

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605 **Table 4.** The percent variation in surface temperature (T_s) or thermal window area proportions
 606 (TWA%) accounted for by individual female or pup during the first 3 weeks of lactation.
 607 Individual effects were assessed as a random effect in a linear mixed model containing
 608 environmental covariates. Stages of lactation are based on estimate of pup age: P1 (≤ 7 days old),
 609 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

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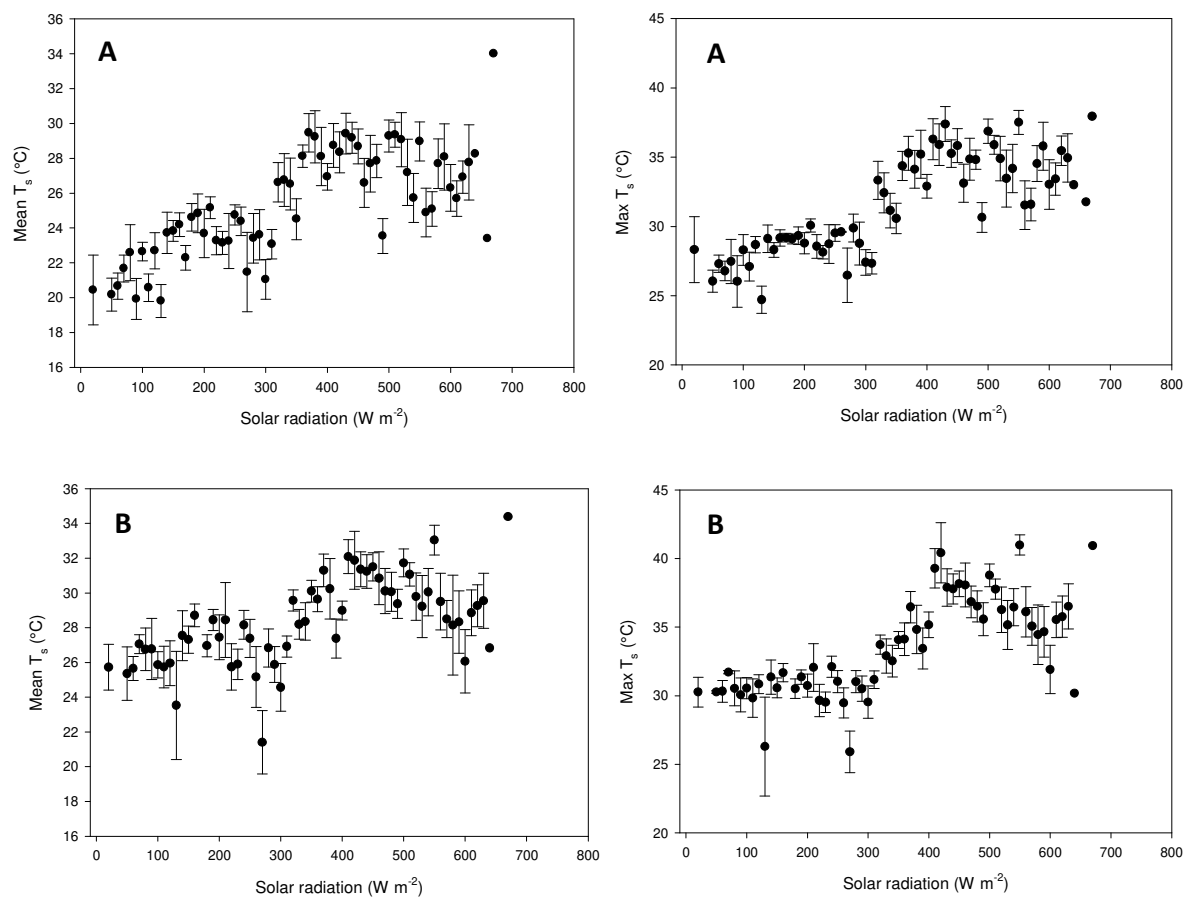


Figure 1. Variation in mean surface temperature (T_s) and maximum T_s with solar radiation for (A) adult females and (B) pups. Data are means \pm s.e.m within binned values of solar radiation to the nearest ten $W m^{-2}$.

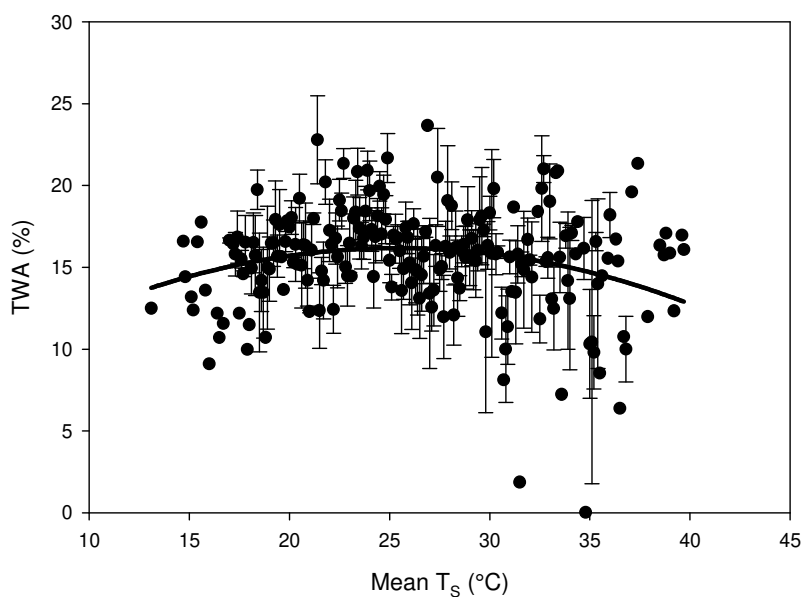
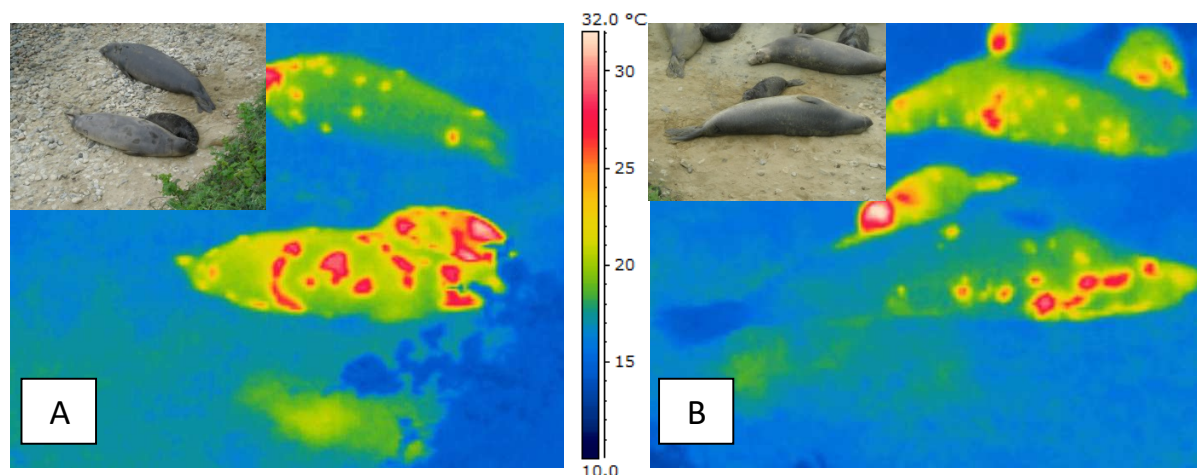
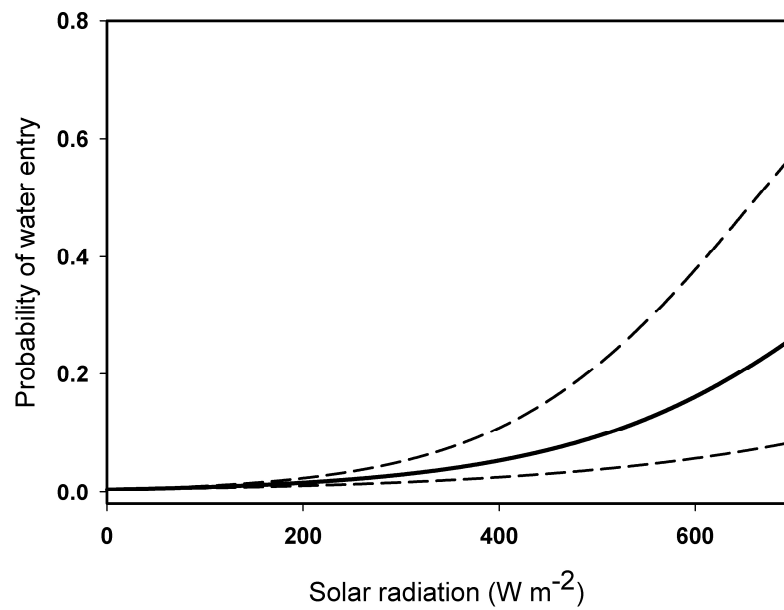


Figure 2. Variation in thermal window area (TWA) of the visible body surface with mean surface temperature (T_s) of adult females. Data are means \pm s.e.m. within binned values of mean T_s to the nearest tenth $^{\circ}\text{C}$. A quadratic curve was fitted to the graph to show the inflection point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



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 701 **Figure 3.** Two thermograms of elephant seals with thermal windows. The associated digital
 702 picture is included for aid in identifying the seals. (A) The adult female in the center of the
 703 thermogram has thermal windows with maximum surface temperature (T_s) of 29.5°C and the
 704 mean T_s is 21.6°C. The pup, which is directly behind the adult female, has thermal windows with
 705 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
 706 thermogram has thermal windows with maximum T_s of 29.8°C and the mean T_s is 18.3°C. The
 707 pup at the ventral side of the adult female has thermal windows with maximum T_s of 32.0°C and
 708 the mean T_s is 22.5°C.

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