Thermoregulatory Physiology and Behavior of the Northern Elephant Seal, *Mirounga angustirostris*, amid Environmental Change

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ABSTRACT

Unfettered anthropogenic activities are changing the earth's climate, fueling more frequent anomalous temperature events that pose a unique thermal challenge to semi-aquatic species. Northern elephant seals spend most of their lives at sea and haul out on shore to reproduce and molt, a simultaneity that rests on adaptations for heat retention underwater and heat loss on land. When ambient temperatures exceed physiological limits, seals rely on behaviors that are facilitated by habitat heterogeneity. Little is known about how environmental variables and habitat quality influence thermoregulation of seals on shore. Here, we used infrared thermography to derive surface temperature and thermal window area of adult female and weanling elephant seals during the 2021 and 2022 breeding seasons at Point Reyes National Seashore, Farallon Islands National Wildlife Refuge, and Año Nuevo State Park. Mean surface temperature was 24 ± 6 ºC for cows and 28 ± 5.9 ºC for weanlings, with significant effects from environmental variables – particularly ambient temperature – and site. Thermal window area and surface temperature exhibited opposite relationships in cows and weanlings, suggesting that adults have greater control over thermoregulatory strategies. At Point Reyes and the Farallon Islands, where topography offers fewer opportunities to behaviorally thermoregulate than Año Nuevo, cows entered the water with pups to cool down, placing them at risk of drowning. Despite consistent temperatures across sites, cows at Año Nuevo did not enter the water. Thus, habitats provide critical refugia for behavioral thermoregulation that must be protected to help animals withstand additional stress amid climate change.

KEYWORDS

Infrared thermography, Climate change, Marine mammal, Thermal window, Thermoregulatory behavior

INTRODUCTION

For eons, species have adapted to abiotic and biotic changes in their local environment through evolved physiological and behavioral responses. In the age of climate change, such adaptations and innate capabilities are being tested as nature is pushed to the brink of irreversible change. Driven primarily by the burning of fossil fuels in the energy, industry, transportation, and agriculture sectors, greenhouse gas concentrations are at their highest levels in two million years, resulting in a planet that is approximately 1.1°C warmer than it was in the late 1800s (IPCC 2022). Anthropogenically induced climate change is exposing species to conditions that are unprecedented at a pace that may exceed animals' adaptive capacity (IPCC 2022, Simmonds and Isaac 2007, Moore 2008). Coastal ecosystems in particular face a precarious future as rising seas and intensifying storm events are eroding shorelines, inundating beaches that serve as critical habitat for animals (Funayama et al. 2013, García-Reyes and Largier 2010, Webster et al. 2005, Emanuel 2005, IPCC 2022). Against the backdrop of centuries of overharvesting and poor coastal disaster management that have caused the decline of over 65% of coastal and intertidal habitat, climate change is culminating in widespread extirpations and range contractions (Adger et al. 2005, Jackson et al. 2001, Lotze et al. 2006). Together, increasing temperatures and habitat degradation form a cataclysmic storm for coastal ecosystems, posing a unique challenge to amphibious species that have adapted to life at sea and on land.

Northern elephant seals (*Mirounga angustirostris*) spend the majority of their lives at sea and haul out on shore from December through March to breed and molt. When underwater, northern elephant seals forage offshore of the North Pacific, in the Gulf of Alaska, and near the Aleutian Islands, regularly diving to depths of 400 to 800 meters. As the rate of heat loss for aquatic homeotherms is 1.5-4.5 times greater in water than air, northern elephant seals have fur and thick blubber as an insulating layer to reduce thermal conductance (Hindle et al. 2015, Liwanag 2008). Northern elephant seals also modify their circulatory system by shunting blood away from extremities to prevent heat loss to the environment (Davis 2019, Mauck et al. 2003, Norris et al. 2010). Thermoregulation is essential for northern elephant seals to maintain their body temperature at an optimal level for biological functioning, though it is a challenge as the same morphological and physiological adaptations necessary to retain heat underwater may result in hypothermia on land if they cannot dissipate heat effectively (Noren 2002, Norris and Kunz 2012).

When moving from the deep ocean to sandy beaches, northern elephant seals must acclimatize to drastically different thermal demands, relying on physiological adjustments and behavioral strategies to dissipate excess heat (Norris and Kunz 2012). Through opposite circulatory adjustments that divert blood towards the surface of the skin, northern elephant seals create thermal windows, which are small areas of comparatively higher temperature than the rest of the body that enable evaporation of water trapped in the animal's pelage, facilitating heat transfer by convection (Davis 2019, Mauck et al. 2003, Norris et al. 2010, Norris and Kunz 2012). While thermal windows are a thermoregulatory strategy to rid excess heat, the mechanisms driving the presence of thermal windows are not fully understood and this phenomenon does not seem ubiquitous in all pinnipeds (Mauck et al. 2003, Guerrero et al. 2021). In both southern and northern elephant seals, thermal windows are more common in the flippers and head where insulation is comparatively low, suggesting that not all body sites have the same role in thermal balance (Guerrero et al. 2021, Codde et al. 2016). The appearance and growth of thermal windows varies with ambient temperature, solar radiation, and wind speed, suggesting an adaptive role in the midst of environmental change (Mauck et al. 2003, Guerrero et al. 2021, Codde et al. 2016). In addition to thermal windows, northern elephant seals engage in behavioral responses to avoid overheating while on land (Paterson et al. 2022). Behaviors include flipping sand over their bodies to block solar radiation, exposing their flippers to the wind to increase convective heat loss, and moving closer to the water's edge to lie on damp sand or be exposed to sea spray (Beentjes 2006, Norris et al. 2010, Twiss et al. 2002).

Thermoregulatory capacity plays a determinant adaptive role to northern elephant seal survival in environments where resources and temperature vary, though the effectiveness of physiological and behavioral strategies is reciprocally shaped by local environments (Terrien et al. 2011). Meteorological conditions and habitat features may constrain or promote tactics of heat loss for northern elephant seals while on land, for instance through access to ample sand to flip onto their bodies or shaded areas that act as a reprieve from solar radiation. For molting southern elephant seals, moving from beach to aggregate in wallows or vegetation allows animals to increase skin surface temperature while minimizing heat loss, which is advantageous as body condition decline is concomitant with a lowering of skin surface temperature (Paterson et al.

2022). Local topography thus shapes heat transfer between skin surface and the surrounding environment, with ramifications on behavior and fitness as the scale of interannual pupping site fidelity may depend on topographical variation (Twiss et al. 2002, Pomeroy et al. 2000). Access to heterogeneous coastal habitat is therefore critical for elephant seal breeding success and is becoming more salient in light of rising temperatures. However, coastal erosion of beaches is washing away access to thermal refuge and opportunities for behavioral thermoregulation (Funayama et al. 2013, Nur et al. 2022). In northern elephant seal rookeries located on beaches and islands offshore California and Baja California, Mexico, winter and spring temperatures have steadily climbed since the late 1950s and El Niño-Southern Oscillation events are likely to bring more rainfall to this region accompanied by floods, landslides, and coastal erosion (Cayan et al. 2008, Funayama et al. 2013).

Adult female northern elephant seals (cows) and their young are uniquely vulnerable to the effects of climate change. Cows and pups are constrained in their ability to compensate for physiological adaptations with behavioral strategies as pups are slow to develop swimming skills and will not normally enter the water until after weaning, precluding them from retreating into tide pools or nearshore water to cool down (Reiter et al. 1978). However, cows and pups have been observed in shallow water on days of high solar radiation, suggesting that behavioral thermoregulation is necessary as solar radiation increases and makes it more difficult to lose heat through convection to air and radiative heat loss (Codde et al. 2016). This rare behavior for northern elephant seals poses risks to pups from drowning and to cows from undesired mating attempts as a result of leaving the harem (Le Boeuf 1972). Cows and pups may also face physiological trade-offs and increased susceptibility to warming due to their respective life history stages (Crocker et al. 2001). Mammalian reproduction is energetically expensive, thus cows minimize the amount of energy expended on their own maintenance metabolism while on shore (Crocker et al. 2001). Simultaneously fasting and lactating on land further depletes cows' energy reserves, compromising their ability to withstand additional stress imposed by increasing temperatures. While cows' robust fat stores obstruct heat loss, this impediment dissipates across the breeding season as lactating females lose about 40% of their body mass, corresponding to a 50% loss in body fat (Crocker et al. 2001). Nursing pups gain a mass consisting of about 55% fat, thus the thermal challenge initially cumbersome to cows becomes a struggle for their weanlings (Crocker et al. 2001). Thermoregulatory challenges loom throughout development as large weaned pups with a high body lipid content show elevated resting metabolic rates and exhibit increased thermal conductance with rising ambient temperature (Noren 2002).

The aim of this study was to investigate the effects of warming and habitat quality on the thermoregulatory capacity of adult female northern elephant seals and weanlings by comparing animals across three rookeries along the California coast. We used infrared thermography, a non-invasive method that enables skin surface temperature to be measured across an animal's entire visible body, to evaluate thermal properties of northern elephant seals in their natural setting during the 2021 and 2022 breeding seasons. As thermoregulatory capacity is largely shaped by physiology, behavior, and habitat heterogeneity, we examined the effects of environmental variables and behavior on seal surface temperature and thermal window area across three unique haul-out habitats. While it is impossible to truly project the future of species in the midst of ongoing climate change, warming and habitat degradation will likely inhibit northern elephant seals' ability to effectively offload heat, requiring animals to supplement physiological strategies with thermoregulatory behaviors.

METHODS

Study sites and subjects

This study was conducted during the northern elephant seal breeding and pupping seasons (January-April) across two years (2021 and 2022) in three rookeries along the northern California coast (Figure 1). The sites – Año Nuevo State Park (ANSP), Point Reyes National Seashore (PRNS), and Farallon Islands National Wildlife Refuge (FINWR) – represent heterogeneous haul-out habitats with distinct topography and tidal influences. Rookeries in ANSP are found in sandy beaches with gradual slopes, ideal for breeding. However, northern elephant seals are highly exposed to storm surge and mixed semidiurnal tidal patterns force diel movement of the entire harem (Hooper et al. 2019). Drakes Beach, one of four dominant breeding sites in PRNS, is a seasonally wide stretch of beach backed by large sandstone cliffs, relatively protected from intense waves and receiving land deposition from landslides. While the Drakes Beach harem experiences minimal topographic and tidal challenges, the site's dark substrate and thermal environment drives females and pups to move towards the water in response to high solar radiation (Codde et al. 2016). FINWR comprises several rocky island rookeries off the coast of San Francisco. Southeast Farallon Island (SEFI) lacks easy access points between the ocean and the harem, requiring northern elephant seals to maneuver around large rocks to get to the breeding site. While SEFI is relatively protected from tidal movements, the island is made of granite and is nearly devoid of sand. Female northern elephant seals have been observed moving in response to solar position, suggesting that the dark substrate and lack of sand are exposing animals to thermal stress (Hooper et al. 2019).

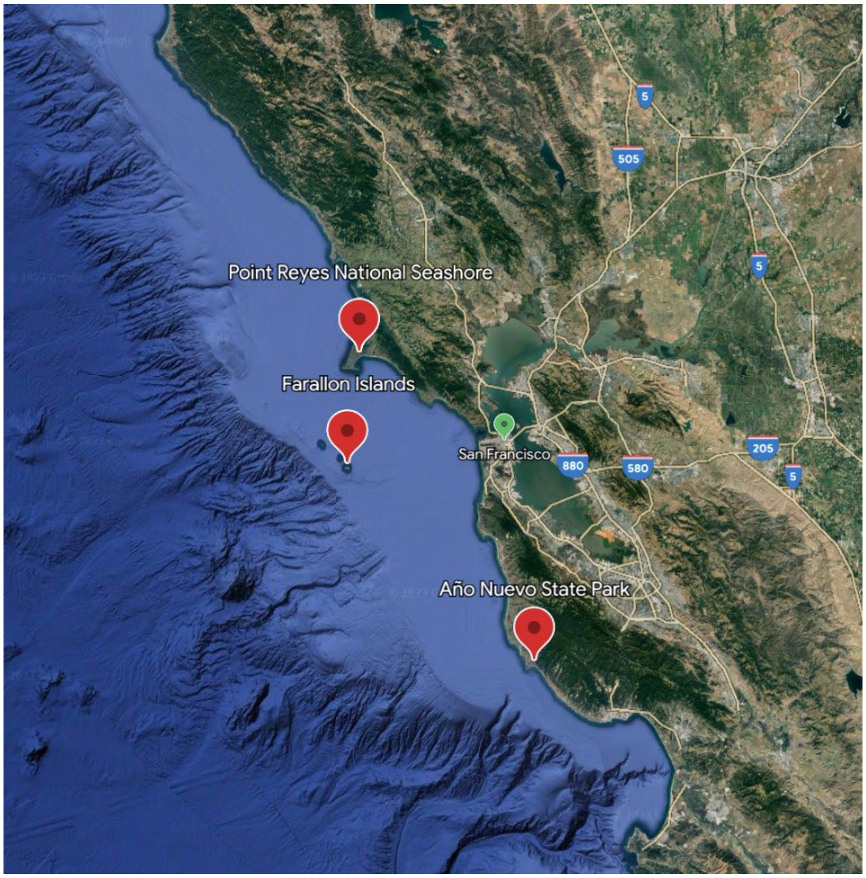

Figure 1. Map of study sites. Point Reyes National Seashore (38°00'36.2"N 122°58'55.0"W), Farallon Islands National Wildlife Refuge (37°41'52.9"N 123°00'21.7"W), and Año Nuevo State Park (37°07'01.8"N 122°19'50.4"W) in relation to San Francisco. Map created in Google Earth.

On weather permitting days throughout each breeding season, we observed and photographed seals in each site and classified their lifestage as cow or weanling. When possible, reserve staff and biologists at each site dye-marked seals with a unique identifier on one or two areas of their posterior body (cows) or on either flank (pups) using hair dye, or attached flipper tags to seals (Codde et al. 2016). We recorded seals' unique identifier numbers, however, not every seal had a number associated with it.

Infrared thermography

Using a FLIR One Pro infrared thermography camera attachment for iOS (accuracy ± 3ºC; Wilsonville, OR, USA), we took digital and thermographic photos of cows and weanlings, making every effort to maintain a perpendicular observation angle. For camera measurement parameters, we set emissivity to 0.98 and reflected temperature to 20 ºC, and we measured distance from seal using a Nikon laser rangefinder. In total, we captured 748 photos from ANSP, 981 photos from PRNS, and 922 photos from SEFI. Images were taken on the beach a few meters away from each seal depending on tide height and density of seal colonies.

Environmental variables

We used a Kestrel 3000 Weather Meter to measure temperature (°C), relative humidity (%), and wind speed (mph) every five minutes while in the field taking thermograms. We subsequently matched time-stamped thermograms to environmental data measured at the closest time within each five minute interval.

Behavior

For every seal that was photographed, we recorded the animal's coat condition (clean, sandy, or wet) as a proxy for behavior. As seals were not observed for multiple hours each day, recording instantaneous coat condition enabled inferences about previous attempts at behavioral thermoregulation that may have been missed in passing (i.e. sandy coat condition could imply previous sand flipping attempt and wet coat condition could indicate recent swim). We recorded accounts of sand flipping and rolling over sand, and noted if seals were present in shade, water, a puddle, or in the shoreline.

Thermogram analysis

To derive seal skin surface temperature metrics from each thermal image, we used the R package Thermimage, which enabled conversions of pixel data into temperature data (Tattersall 2017). We used ImageJ (or FIJI) to form a polygon around each seal's visible body and calculate mean, maximum, minimum, and the standard deviation of that animal's surface temperature and thermal window area. We defined thermal windows as localized areas greater than one standard deviation above the mean surface temperature of the seal in the thermogram and calculated the thermal window area percent (Norris et al. 2010).

Statistical analyses

Due to the hierarchical nature of the data, we used a linear mixed-effects model to evaluate the effects of environmental variables (temperature, wind speed, relative humidity), site (ANSP, PRNS, SEFI), lifestage (cow or weanling), and coat condition (clean, sandy, or wet) on mean surface temperature. Every model contained a random effects term for date to account for day-to-day variability. Individual seal could not be used as a random effects variable due to missing data on animal identification numbers, thus we could not account for within subject correlation. However, testing animal identification as a random effects term for seals in SEFI where this data was available for all individuals yielded no significant difference compared with the model using date as a random effects term, so animal identification was not included in the final linear model. To quantify the relationship between thermal window area and mean surface temperature, we performed a quadratic regression as the variables exhibited a quadratic relationship. We included mean surface temperature, environmental variables (temperature, wind speed, relative humidity), site (ANSP, PRNS, SEFI), lifestage (cow or weanling), and coat condition (clean, sandy, or wet) in the final quadratic model.

We visually assessed model residuals for approximate normality and homoscedasticity and subsequently performed ANOVA tests. To assess the effects of behavior on mean surface temperature and thermal window area, we used Tukey's Honestly-Significant Difference post-hoc tests to run pairwise comparisons of coat condition. All statistical analyses were carried out in R (version 4.2.3). Data are presented as means ± SD unless otherwise noted.

Ethical note

This research was conducted under the National Marine Fisheries Service permit numbers 21425 and 19108, and PRNS permit number PORE-2021-SCI-0004. Thermal imaging was approved by UC Berkeley IACUC under AUP: 20190612247. Participants in field work were trained to safely conduct their research around the seals and reduce the possibility of disturbance.

RESULTS

Environmental variables

Temperature across all sites varied from 4.2 ºC to 25 ºC, with a mean of 14 ± 2.7 ºC. Temperature was highest at PRNS, ranging from 5.6 ºC to 25 ºC, with a mean of 15 ± 3 ºC (Table A2). Temperature at ANSP ranged from 4.2 ºC to 19 ºC (mean 13 ± 2.3ºC), and at SEFI from 5.7 ºC to 24 ºC (mean 13 ± 2.2 ºC) (Tables A1, A3). Relative humidity across all sites varied from 26% to 100%, with a mean of 70 ± 11%. Relative humidity was highest at SEFI, ranging from 29% to 100%, with a mean of 77 ± 11% (Table A3). Relative humidity at ANSP ranged from 26% to 84% (mean 67 ± 7.9%), and at PRNS from 43% to 94% (mean 65 ± 8.7%) (Tables A1, A2). Wind speed varied from 0 mph to 25 mph, with a mean of 4.9 ± 4.1 mph. Wind speed was highest at SEFI, ranging from 1 mph to 25 mph, with a mean of 6.7 ± 4.6 mph (Table A3). Wind speed at ANSP ranged from 0 mph to 22 mph (mean 4 ± 3.5 mph), and at PRNS from 0 mph to 21 mph (mean 4 ± 3.6 mph) (Tables A1, A2).

Seal surface temperature

Mean surface temperature was 24 ± 6 ºC for all cows (n=707 thermograms) and 28 ± 5.9 ºC for all weanlings (n=1515 thermograms). Mean surface temperature was highest for cows at SEFI (25 ± 5.6 ºC) and highest for weanlings at PRNS (30 ± 4.7 ºC) (Figure 2). Both cows and weanlings at ANSP had the lowest mean surface temperature compared to other sites, at 19 ± 5.8

ºC and 25 ± 6.2 ºC, respectively (Figure 2). Temperature, site, lifestage, and coat condition had the strongest effects on mean surface temperature, along with significant effects from relative humidity and wind speed (Table 1). Mean surface temperature increased with temperature (Figure 3) and decreased with relative humidity (Figure B1) across all sites. Mean surface temperature decreased with wind speed at PRNS and SEFI, exhibiting the opposite trend at ANSP (Figure B2). For all environmental variables, the slopes of the regression lines for mean surface temperature at PRNS and SEFI were more similar than that at ANSP (Figures 3, B1, B2).

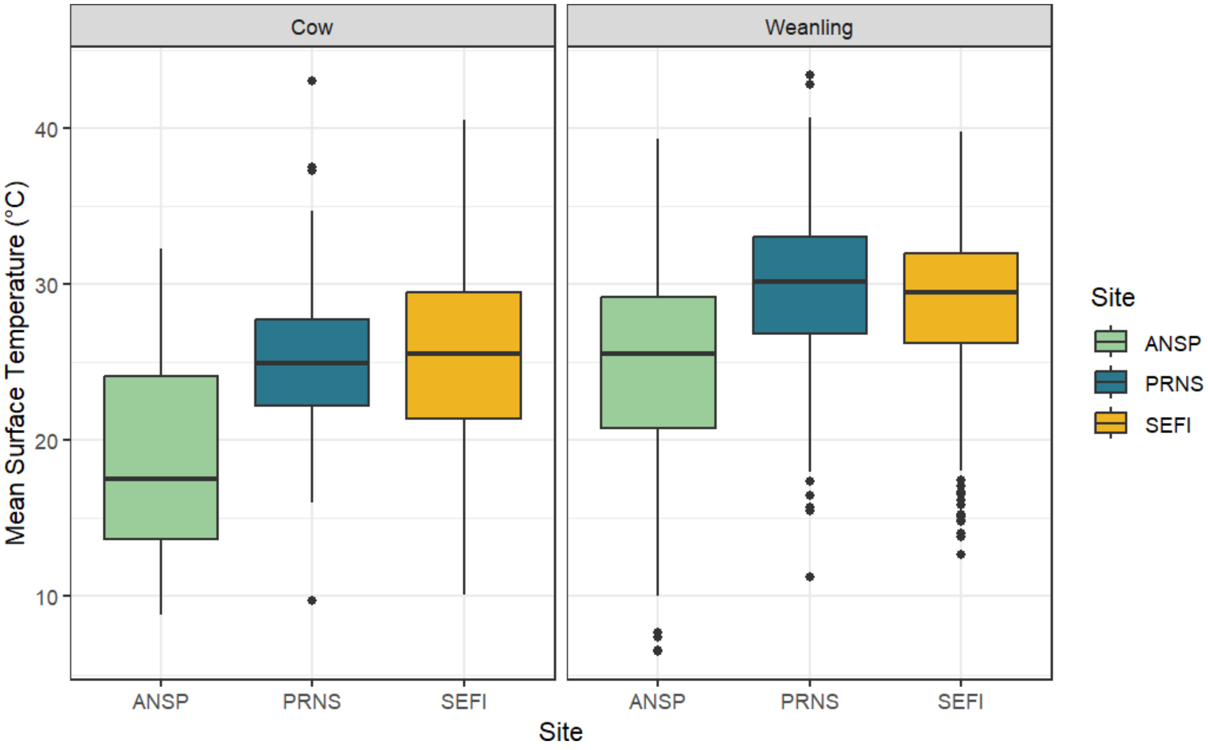

Figure 2. Variation in mean surface temperature across sites. Colors denote different sites and data presented by lifestage.

Table 1. Linear mixed-effects model results. F-statistics and p-values from ANOVA tests for the effects of environmental and animal variables on mean surface temperature.

Environmental and animal variables	**Mean surface temperature**	
	F	**Pr(>F)**
Temperature (ºC)	154.33	< 2.2e-16 ***
Relative humidity (%)	7.2	0.007339 **
Wind speed (mph)	6.62	0.010139 *
Site	86.797	< 2.2e-16 ***
Lifestage	96.63	< 2.2e-16 ***
Coat condition	67.17	< 2.2e-16 ***

*p-value<0.05
**p-value<0.01
***p-value<0.001

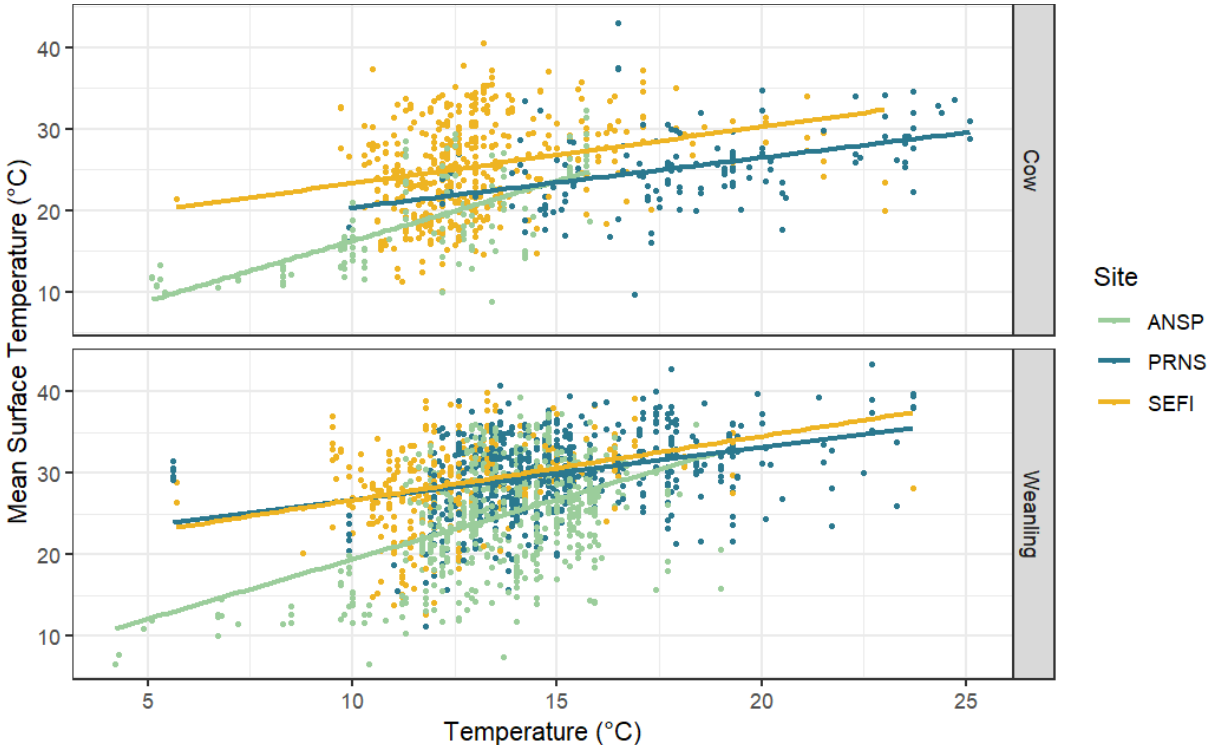

Figure 3. Variation in mean surface temperature with ambient temperature across sites. Colors denote different sites and data presented by lifestage.

Seal thermal window area

The area of visible surface used as thermal windows averaged 6.8 ± 4.2% for all cows (n=707 thermograms) and 6.5 ± 4.9% for all weanlings (n=1515 thermograms). Thermal window area percent was highest for cows at SEFI (6.9 ± 4.4%) and highest for weanlings at ANSP (7.4 ± 5.1%). Thermal window area percent was lowest for cows at PRNS (6.2 ± 3.9) and lowest for weanlings at SEFI (5.5 ± 4.8). Temperature, relative humidity, wind speed, coat condition, and seal mean surface temperature had the strongest effects on thermal window area percent, along with significant effects from lifestage (Table 2). Thermal window area percent and mean surface temperature showed the opposite relationship in cows and weanlings across all sites (Figure 4). Thermal window area percent of cows at ANSP and PRNS increased with mean surface temperature until approximately 27 ºC and then declined (Figure 4). For cows at SEFI, thermal window area percent started to decline at approximately 14 ºC (Figure 4). Thermal window area percent of weanlings decreased with mean surface temperature until approximately 40 ºC at PRNS and 33 ºC at SEFI (Figure 4). Weanlings at ANSP showed a steady decline in thermal window area percent with mean surface temperature starting at 6.5 ºC, the lowest recorded value of mean surface temperature at this site (Figure 4).

Table 2. Quadratic model results. F-statistics and p-values from ANOVA tests for the effects of environmental and animal variables on thermal window area.

Environmental and animal variables	**Thermal window area**	
	F	**Pr(>F)**
Seal mean surface temperature (ºC)	260.01	< 2.2e-16 ***
Temperature (ºC)	31.85	1.883e-08 ***
Relative humidity (%)	16.94	3.999e-05 ***
Wind speed (mph)	18.11	2.176e-05 ***
Site	2.61	0.07
Lifestage	6.36	0.01*
Coat condition	9.31	9.395e-05 ***

*p-value<0.05
**p-value<0.01
***p-value<0.001

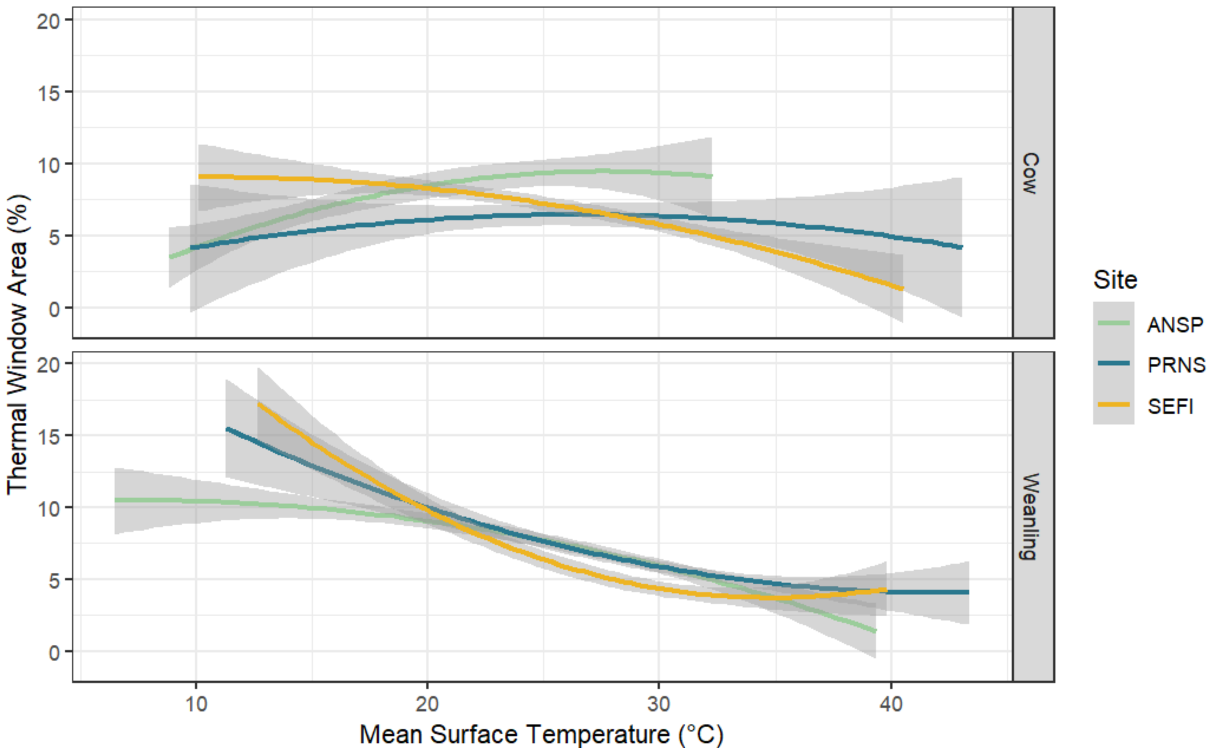

Figure 4. Variation in thermal window area with mean surface temperature across sites. Colors denote different sites and data presented by lifestage.

Behavior

Coat condition, a proxy for behavior, significantly influenced both mean surface temperature and thermal window area (Tables 1, 2). Post hoc mean comparisons for the effects of coat condition on mean surface temperature revealed that all pairwise differences were significant. For thermal window area, the differences in means between clean seals and seals that were sandy or wet were significant, but not between sandy and wet seals. Seals at SEFI were never sandy due to the lack of abundant sand in this habitat and cows at ANSP were never wet despite access to the shore (Figure 5). Across all sites, weanlings that were wet exhibited lower mean surface temperatures than clean or sandy seals in each respective location (Figure 5). The highest frequency of wet weanlings was recorded between 12 ºC to 16 ºC. The greatest proportion of clean seals occurred at SEFI for both cows (0.84) and weanlings (0.94) (Figure 6). Cows were most sandy at ANSP (0.54) and weanlings at PRNS (0.22) (Figure 6). Cows were most wet at SEFI (0.17) and weanlings at ANSP (0.11) (Figure 6).

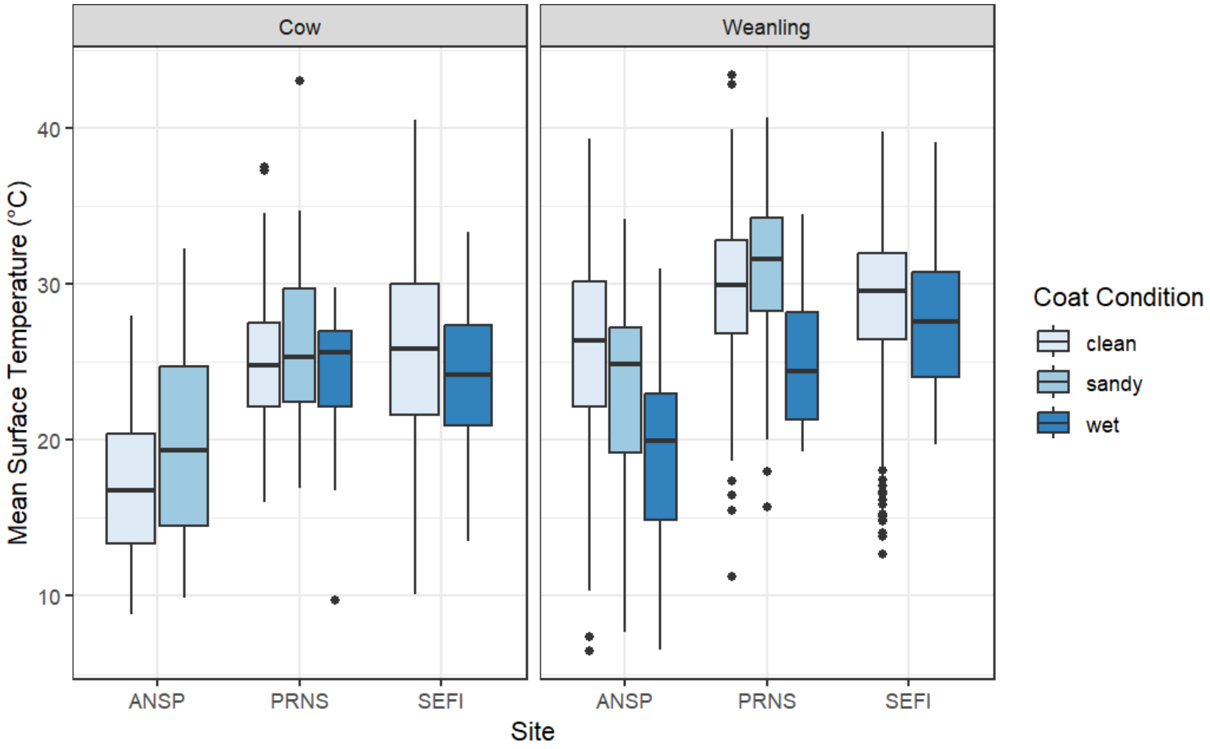

Figure 5. Variation in mean surface temperature across sites and coat condition. Colors denote different coat conditions and data presented by lifestage.

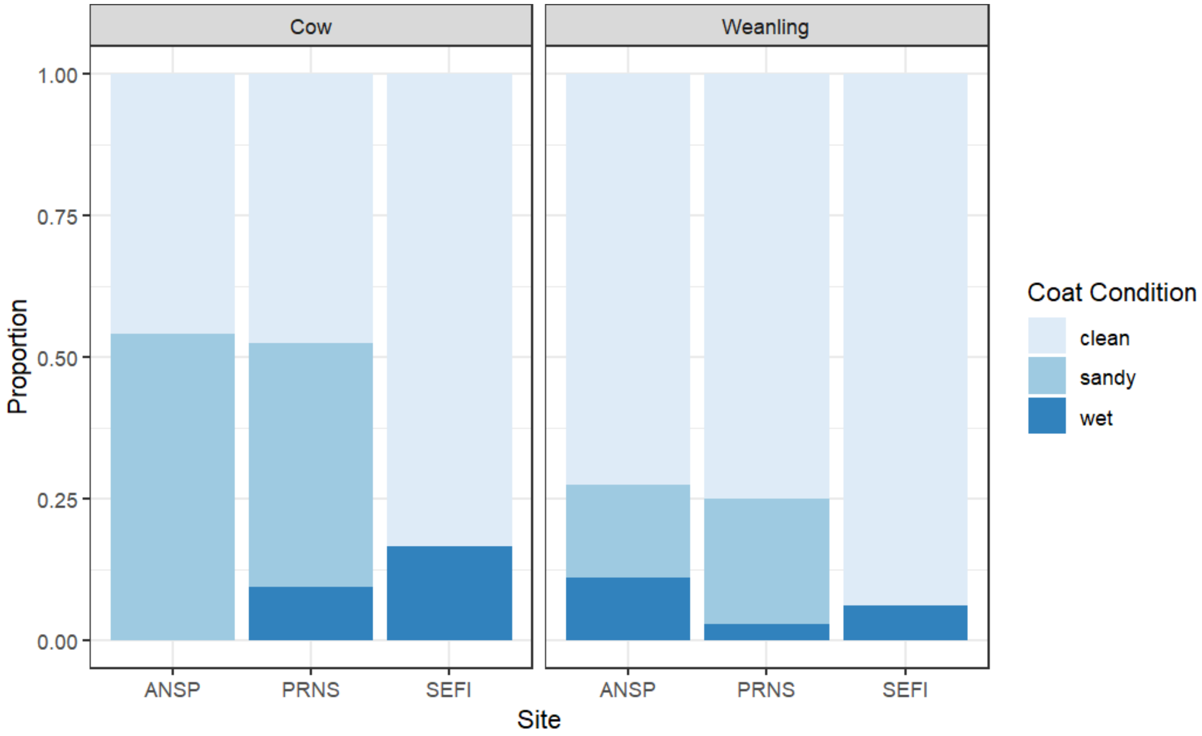

Figure 6. Proportion of seals with each coat condition across sites. Colors denote different coat conditions and data presented by lifestage.

DISCUSSION

Thermoregulation is essential to maintaining homeostasis while limiting the energetic costs of normothermia. When faced with thermal challenges, animals expend energy by enhancing physiological mechanisms, though behavioral strategies allow species to reduce the autonomic work associated with thermoregulatory responses (Terrien et al. 2011). Habitat heterogeneity is indispensable for thermoregulatory behaviors and it is necessary to maintain as rising temperatures and coastal degradation may shift energy budgets, increasing the need for behavioral thermoregulation. Studying northern elephant seal thermoregulation across different habitats, we show that ambient temperature affects mean seal surface temperature, imposing the greatest risks to weanlings that may not yet be skilled at dissipating excess heat through thermal windows. At ANSP – the least perturbed study site – cows were never wet whereas weanlings were wet across all sites, suggesting that habitat quality shapes thermoregulation as cows were able to behaviorally thermoregulate without entering the water and placing their pups at risk of drowning.

Seal surface temperature

Surface temperature of cows and weanlings was strongly influenced by ambient temperature, relative humidity, and wind speed. At PRNS, where mean ambient temperature was 2 ºC higher than at ANSP and SEFI, weanlings showed the highest mean surface temperature at 30 ± 4.7 ºC. At ANSP, where mean ambient temperature was lowest of all sites, both cows and weanlings had substantially lower mean surface temperatures. The strong impacts of ambient temperature on surface temperature are consistent with previous studies demonstrating a positive relationship between these variables in phocids (Codde et al. 2016, McCafferty et al. 2005, Norris et al. 2010). Similar studies found that solar radiation was the strongest determinant of surface temperature in northern elephant seals as direct exposure results in absorption of heat by seals and warming of surrounding substrate (Codde et al. 2016, Norris et al. 2010). This lowers any heat gradient and adds to the heat gain of an animal through conduction (Campagna and Le Boeuf 1988).

Cloud cover and wind speed can provide seals a reprieve from solar radiation by lowering solar intensity and increasing convective heat loss (Campagna and Le Boeuf 1988, Cena and Clark 1973, Heath et al. 1977, White and Odell 1971). Relative humidity, which is directly proportional to cloud cover, exhibited a negative relationship with mean surface temperature, yielding the greatest decreases in mean surface temperature at ANSP and PRNS where ambient temperatures were highest. Cloud cover and humidity may buffer seals from increasing temperatures, although their impacts could be affected by climate change as analyses of summer fog along the California coast reveal a 33% reduction in fog frequency since the early 20th century attributed to anthropogenic emissions (Johnstone and Dawson 2010). Wind speed reduced mean surface temperature at PRNS and SEFI, however, seals at ANSP showed an increase in mean surface temperature with wind speed despite speeds being consistent across ANSP and PRNS (4 ± 3.5 mph and 4 ± 3.6 mph, respectively). With more access to shade and abundant sand at ANPS, behavioral thermoregulation may act more strongly than wind speed to mitigate heat gain and reduce mean surface temperature at this habitat.

Seal thermal window area

Many marine and terrestrial species use thermal windows to dissipate heat, requiring control of skin perfusion to promote heat loss by increasing peripheral blood flow (Mauck et al. 2003, Erdsack et al. 2012, Weissenböck et al. 2010). While thermal windows are thought to play a critical role in thermoregulation for hauled-out pinnipeds, few studies have compared thermal windows in adults and pups to understand whether this strategy is innate or learned. On average, cows devoted 6.8 ± 4.2% of their visible body surface to thermal windows and weanlings used 6.5 ± 4.9%. Previous studies on northern elephant seals found that adult females, adult males, and pups used approximately 16% of their visible body surface as thermal windows, exhibiting a positive relationship with solar radiation (Codde et al. 2016, Norris et al. 2010). Although thermal window areas were found to be smaller compared with intraspecific studies, the consistency across cows and weanlings despite their different thickness in the adipose tissue layer suggests vascular anatomy is sufficient to bypass the blubber layer (Codde et al. 2016). Environmental variables significantly affected thermal window area, though there was no positive relationship between a site's mean ambient temperature and seal thermal window area, thus solar radiation may play a more determinant role in thermal window development.

As animals are exposed to new thermal environments over time, adults develop a greater thermoregulatory capacity than juveniles, enabling greater control and better regulation of skin surface temperature (Tattersall and Cadena 2010). This may extend to thermal windows, with previous research showing that thermal window area is affected by mean surface temperature in adult female northern elephant seals but not pups, suggesting that adults exert greater control over thermal windows. In the present study, lifestage and mean surface temperature significantly influenced thermal window area, such that cows and weanlings showed opposite uses of thermal windows. Thermal window area of cows increased with mean surface temperature until approximately 27 ºC and then declined, consistent with other studies that have found an inflection point at approximately 24 ºC in adult male northern elephant seals and 26 ºC in adult females (Codde et al. 2016, Norris et al. 2010). As mean surface temperature rises above mean ambient temperature, thermal windows grow and merge so that most of the body surface can dissipate heat, thus surface temperature becomes more homogenous across the body (Codde et al. 2016).

While the relationship between thermal window area and mean surface temperature has been described in adult northern elephant seals, few, if any, studies have illustrated the relationship in weanlings. We found that weanlings showed a near opposite inflection point, suggesting that younger animals do not know how to properly use thermal windows to dissipate excess heat. A study on harbor seals comparing animals that were voluntarily hauled out on shore or induced to stay on shore by a trainer found that hauling out seals developed thermal windows in minutes irrespective of environmental conditions, whereas seals in the training situation did not develop thermal windows (Erdsack et al. 2012). As a significant energy loss can ensue when pinnipeds enter the water with open thermal windows, the researchers postulated that the disparity in thermal windows between the two groups resulted from hauled out seals being prepared to stay ashore and induced hauled out seals being prepared to enter the water (Erdsack et al. 2012). Entering the water may prime pinnipeds to better control their thermal windows after learning of the energetic costs associated with this phenomenon, which may explain why weanlings are not adept at controlling their thermal windows to regulate heat loss.

Behavior

The manner in which climate change and associated habitat variability affect animals depends not only on their physiology, but also on their behavior. Weaned northern elephant seals experience an acute thermal challenge in air compared to water, associated with elevated metabolic rates and thermal conductance that increases more steeply with rising air temperature compared with water temperature (Noren 2002). We found that weanlings entered the water at all study sites, presumably to begin learning how to swim. However, the largest number of wet weanlings was recorded at higher ambient temperatures, suggesting that northern elephant seals enter the water from a young age as a form of behavioral thermoregulation. A previous study documented the novel behavior of pups entering the water with increased solar radiation at Drakes Beach, noting that it has not been reported at other elephant seal breeding colonies (Codde et al. 2016). We observed cows with pups going into the water at PRNS and SEFI but not ANSP, suggesting that in habitats with fewer opportunities to behaviorally thermoregulate, seals must triage in times of thermal stress by approaching the water to cool off and potentially leading their pups astray. Other factors beyond the scope of this study may influence cow and weanling behavior, including maternal age, diel patterns, and harem size (Hooper et al. 2019).

Compared to weanlings, cows engaged in more sand flipping and roll over attempts to create a more favorable gradient for heat dissipation, which may reflect both their learned behavior over time and lower mean surface temperature, the latter of which likely decreases the need to enter the water. At ANSP, cows were most sandy and never seen as wet, yet this site had the greatest proportion of wet and lowest proportion of sandy weanlings. Unlike SEFI and PRNS, pups at ANSP are influenced by a semidiurnal tidal pattern, resulting in high harem density at high tide followed by female and pup redistribution at low tide (Hooper et al. 2019). Mother-pup separation may therefore be strongest at ANSP, and more pronounced for younger mothers. This may hinder pup learning and diminish younglings' behavioral repertoires, resulting in fewer sand flipping attempts by weanlings in this site. With the most favorable environmental conditions for breeding and the least observed climate change impacts of the three sites, ANSP may offer seals the most opportunities for behavioral thermoregulation, lowering the need for cows to expend energy by locomoting towards the ocean and risking undesired mating attempts.

Limitations and Future Directions

Pinnipeds experience thermoregulatory costs associated with molting, which may be exacerbated by environmental changes (Walcott et al. 2020). Although this study did not coincide with the adult female molt period, we studied molting weanlings. Molt status was not included in our analyses, although metabolic heat loss in pinnipeds may differ with stage of molt, with possible effects on surface temperature and behavior (Paterson et al. 2022). To optimize the proliferation of hair follicles and skin cells during the molt, elephant seals increase skin surface temperature closer to their core body temperature by increasing blood perfusion at the skin surface (Paterson et al. 2022, Khamas et al. 2012). Seals also spend more time on land during this energetically demanding period of shedding and renewing their coat, which may preclude weanlings from entering the water. The variation in surface temperatures and behavior we observed could therefore be driven by a combination of intrinsic and extrinsic factors (Guerrero et al. 2021).

Nonetheless, we believe our results remain robust to this confounding variable as prior studies echo that environmental variables, not molt status, are the main driver of surface temperature and thermal window appearance (Guerrero et al. 2021, Walcott et al. 2020). Solar radiation should be considered as an environmental variable, especially in infrared thermography studies because much of the long wave solar radiation that hits a seal's fur can be reradiated off the animal as infrared, affecting surface temperature (Dawson et al. 2014, Dawson and Maloney 2017, Walcott et al. 2020). As ambient conditions can provide selective pressure on molt phenology, future studies should consider how additional confounding variables may arise from the altered timing of seasonal events (Walcott et al. 2020). While our results suggest that thermoregulatory strategies, particularly thermal window area, differ across lifestage and between sites, the explanation underlying this difference is still unknown, impetus for research on additional intrinsic and extrinsic factors that may be driving this mechanism. As climate change imposes additional stress to marine mammals, research assessing the potential synergistic effects between thermal anomalies and other environmental variables is necessary to protect northern elephant seals and inform salient conservation practices.

Conclusions

Environmental variables – primarily ambient temperature – and habitat quality have strong effects on northern elephant seal surface temperature, which animals control by offloading excess heat through thermal windows and engaging in behaviors to reduce the risk of heat stress. Pups and weanlings represent critical life history stages for this species as they exhibit ineffective use of thermal windows and pups' inability to swim precludes them from certain thermoregulatory behaviors, nonetheless, we observed pups entering the water with cows on days with high ambient temperature. As rising temperatures exceed physiological capacities, pups may succumb to dangerous behaviors to avoid hyperthermia, but preserving habitat quality could expand access to topographical resources that enable safer behaviors. Our finding that cows at ANSP were never wet provides evidence that animals can withstand hot temperatures by seeking out cool microclimates and engaging in heat dissipating behaviors that do not entail submerging in water, but only if their habitat provides such refugia and resources. Environmental change studies must become a blueprint for conservation ecologists to safeguard the elements of habitats required for the full expression of thermoregulatory behaviors. Using marine mammals as sentinels of ecosystem change, swift action is needed to protect northern elephant seals from rising temperatures and coastal erosion, two of a myriad of environmental stressors induced by climate change.

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APPENDIX A: Environmental Variables

Table A1. Summary of environmental variables at ANSP.

Environmental variable	Minimum	Maximum	Mean ± SD
Temperature (ºC)	4.2	19	13 ± 2.3
Relative humidity (%)	26	84	67 ± 7.9
Wind speed (mph)	0	22	4 ± 3.5

Table A2. Summary of environmental variables at PRNS.

Environmental variable	Minimum	Maximum	Mean ± SD
Temperature (ºC)	5.6	25	15 ± 3
Relative humidity (%)	43	94	65 ± 8.7
Wind speed (mph)	0	21	4 ± 3.6

Table A3. Summary of environmental variables at SEFI.

Environmental variable	Minimum	Maximum	Mean ± SD
Temperature (ºC)	5.7	24	13 ± 2.2
Relative humidity (%)	29	100	77 ± 11
Wind speed (mph)	1	25	6.7 ± 4.6

APPENDIX B: Seal Surface Temperature

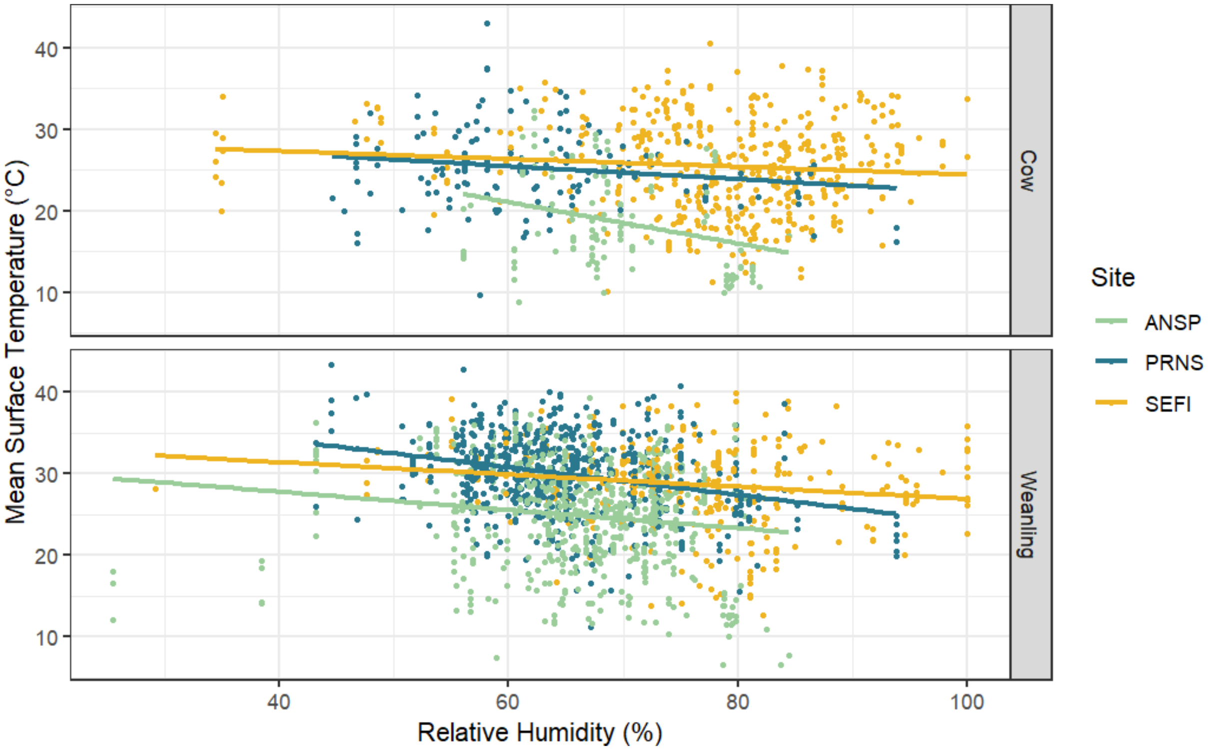

Figure B1. Variation in mean surface temperature with relative humidity across sites. Colors denote different sites and data presented by lifestage.

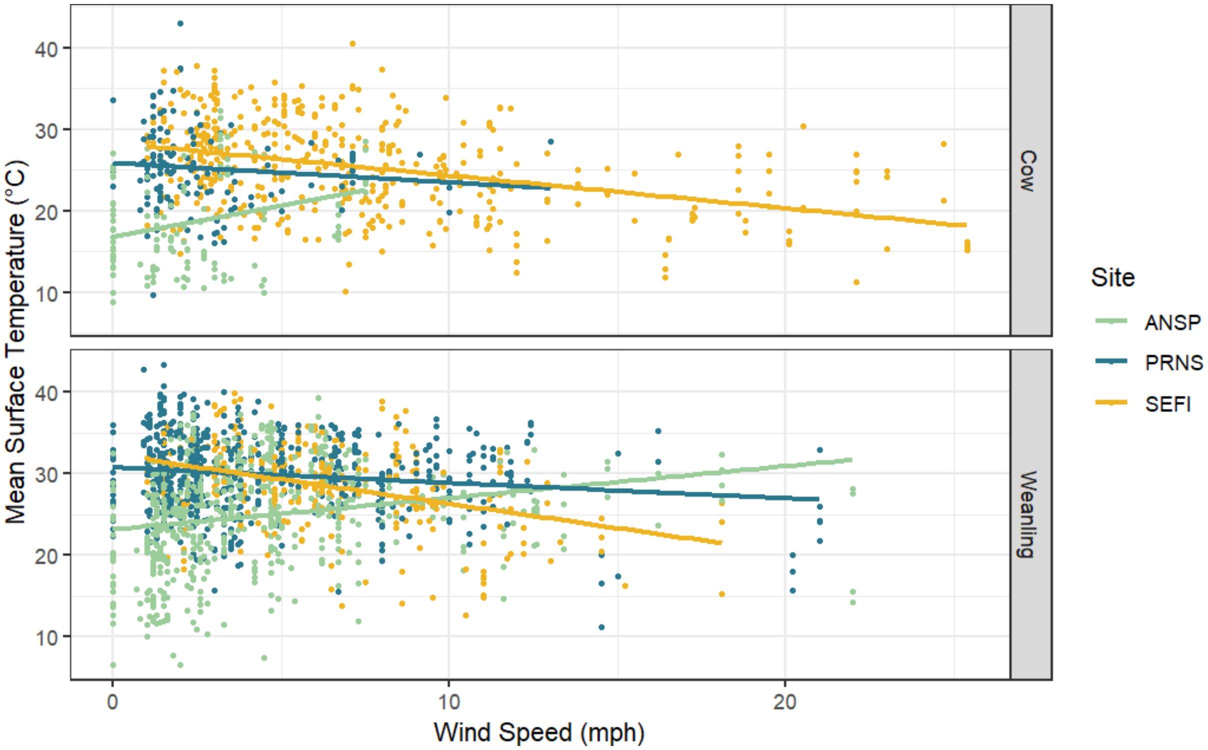

Figure B2. Variation in mean surface temperature with wind speed across sites. Colors denote different sites and data presented by lifestage.