Environment and activity affect skin temperature in breeding adult male elephant seals (*Mirounga angustirostris*)

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SUMMARY

The large body size and high rates of metabolic heat production associated with male mating success in polygynous systems creates potential thermoregulatory challenges for species breeding in warm climates. This is especially true for marine predators carrying large blubber reserves intended for thermoregulation in cold water and fuel provision during extended fasts. Thermographic images were used to measure changes in skin temperature (T_S) in adult male northern elephant seals (*Mirounga angustirostris*) over the breeding season. Environmental variables, primarily ambient temperature and solar radiation, were the principal determinants of mean and maximum T_S. When controlled for environmental variables, dominance rank significantly impacted mean T_S, being highest in alpha males. Behavioral activity significantly influenced T_S but in a counter-intuitive way, with inactive males exhibiting the highest T_S. This was likely due to strong impacts of environmental variables on the kinds of behavior exhibited, with males being less active on warm, humid days at peak solar radiation. We classified thermal windows as areas in which T_S was one standard deviation greater than mean T_S for the individual seal within a thermograph. Thermal features suggest active physiological thermoregulation during and after combat and significant circulatory adaptations for heat dumping, as evidenced by recurring locations of thermal windows representing widely varying T_S values. Frequent observations of localized T_S above 37°C, particularly after combat, suggest the production of thermoregulatory stress during breeding behavior. Our findings demonstrate the importance of environmental drivers in shaping activity patterns during breeding and provide evidence for thermoregulatory costs of successful breeding in large polygynous males.

Key words: thermoregulation, northern elephant seal, thermal window.

INTRODUCTION

Polygynous mating systems often select for large body size and high rates of energy expenditure in breeding males (Clutton-Brock, 1988). Increased thermal inertia and high rates of metabolic heat production might cause thermoregulatory stress, especially when environmental features limit the ability of breeding males to dump heat. Relative humidity and vapor pressure might inhibit the ability to use evaporative cooling, and high ambient temperatures can reduce gradients for heat-flow across the body surface. The necessity to stay within a territory or in close proximity to females might limit the ability of males to thermoregulate behaviorally. Thermoregulatory stress might also lead to water stress as elevated body temperatures increase cutaneous and respiratory water loss. Water stress can be crucial when breeding behavior necessitates fasting or limits the availability of food or water.

Thermoregulatory costs associated with breeding have been shown in a variety of ectotherms for which environmental temperatures directly influence body temperature and energy expenditure (e.g. Saeki et al., 2005; Anderson et al., 1994; Shine, 1980). In endotherms, environmental temperatures above the upper critical temperature or high rates of metabolic heat production can lead to thermal stress, especially in large animals, where body size limits the effectiveness of loss of surface heat. One group of large endotherms that might be particularly susceptible to thermal stress during breeding is the pinnipeds. Pinnipeds exhibit a variety of features to minimize heat loss while foraging in cold marine waters, including a thick, subcutaneous layer of blubber. In most species, males fast completely from food and water while breeding,

necessitating the possession of large blubber reserves at the onset of breeding along with reduced evaporatory and urinary water loss while on shore. Physiological or behavioral thermoregulation mechanisms often drive reproductive behavior in pinnipeds. Female New Zealand fur seals, southern sea lions, Juan Fernandez fur seals and grey seals are known to migrate to tide pools, the shoreline or directly into the ocean during periods of increased solar radiation and air temperature (Twiss et al., 2002; Francis and Boness, 1991; Campagna and Le Boeuf, 1988). Males defending territories with access to water, in which greater numbers of females aggregate, enjoy increased copulatory success compared with that of males guarding waterless areas (Francis and Boness, 1991; Campagna and Le Boeuf, 1988).

Adult male elephant seals arrive at the breeding colony with large blubber reserves and establish a dominance hierarchy through combat. Both metabolic heat production and reproductive success are directly influenced by dominance rank (Deutsch et al., 1990). Despite fasting completely from food and water for months, breeding males exhibit high rates of energy expenditure, averaging $195\pm49\,MJ\,day^{-1}$ over the entire breeding season, or 3.1 times the predicted basal metabolic rate based on body size (Kleiber, 1975), and lose ~36% of their original body mass (Deutsch et al., 1994). In addition, elephant seals exhibit one of the lowest mass-specific rates of water turnover of any animal, suggesting low rates of evaporatory and urinary water loss (Lester and Costa, 2006; Ortiz et al., 2006). With a large blubber layer and an absence of sweat glands, the major mechanism of a male elephant seal for heat loss is the convective system of dilating blood vessels directly under the

skin (Riedman 1990; Øritsland et al., 1978). However, White and Odell discovered that physiological mechanisms such as vasodilation and evaporatory cooling might be inadequate forms of heat dissipation in northern elephant seals (White and Odell, 1971). The presence of direct solar radiation might prevent the effectiveness of this avenue for heat loss (Twiss et al., 2002), particularly in high-ranking males, which secure central positions in harems and cannot retreat to the water as a thermoregulatory aid without ceding access to females.

Most thermal studies in marine mammals have focused on counter-current heat-exchange systems, behavioral thermoregulation and thermoregulatory use of appendages (e.g. Beentjes, 2006; Willis et al., 2005; Meagher et al., 2002; Boyd, 2000; Kvadsheim and Folkow, 1997; Pabst et al., 1995; Campagna and Le Boeuf, 1988; McGinnis et al., 1972; Hampton et al., 1971), whereas few reports have examined changes in body temperature in breeding male pinnipeds (Whittow et al., 1971). An alternative approach to measuring thermal stress is thermography. Thermography is a non-invasive method allowing the observation of radiant heat at the surface of an organism. Use of thermal cameras as an accurate temperature-measurement tool has been validated previously (McCafferty, 2007; Willis and Horning, 2005; Cena and Clark, 1973). Thermographic observations have been described on a variety of species, including foxes, reindeer, barn owls, rabbits, zebra and elephants (McCafferty, 2007; McCafferty et al., 1998; Klir and Heath, 1992; Mohler and Heath, 1988; Folkow and Mercer, 1986). Thermography in phocid seals is likely to be facilitated by their short fur, which reduces the potential for errors associated with fur length and camera viewing angle (McCafferty, 2007). Thermography has been used in captive phocid seals to observe transient areas of increased skin temperature (Mauck et al., 2003). These 'thermal windows' have been described as "body surfaces functioning as a temporary heat dissipater during heat stress" (Mauck et al., 2003) and might be important for mitigating thermal stresses resulting from environmental influences and reproductive behaviors. The definition of thermal window by Mauck and colleagues (Mauck et al., 2003) is more limited than the historical use of the term for an area through which heat can pass easily, even without the requirement of thermal stress (Molyneaux and Bryden, 1978). Nevertheless, it is a useful definition for understanding how animals transiently respond to conditions of heat stress to regulate body heat.

In this study, we used thermography to investigate the effects of environmental variables, dominance rank and behavior on the skin temperatures of male northern elephant seals. We examined the location and proportion of thermal windows in relation to these same variables and considered the effect of environmental factors on behavior. The results of this investigation provide insight into the thermal stress associated with successful male breeding behavior and into how alterations in skin temperature facilitate heat transfer with the environment to mitigate thermal stressors.

MATERIALS AND METHODS
Study site and subjects
We followed 82 breeding male northern elephant seals (*Mirounga angustirostris* Linnaeus) between January and March 2008 at Año Nuevo State Park, CA, USA. Early in the breeding season, male elephant seals were given unique marks on either flank with hair bleach (Clairol). Subjects were observed for 4–6 h each day throughout the breeding season, including four nocturnal observation sessions. Each male was thermally photographed at least once per day over a period of 40 days of observation. During combat between two males, a time-series of thermal photographs was taken as quickly as allowed by the camera (approximately 1 per min), over a minimum of 5 min and up to 15 min post combat, to observe changes in skin temperature. On average, each male contributed 31±22 thermographs for a total sample of 2553 images.

Infrared thermography
A FLIR ThermaCAM B2 (±0.1°C) was used to obtain thermographic photos. The camera was factory calibrated by FLIR just before 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). When possible, in order to obtain a lateral view of the entire body, thermal images were taken at a fixed distance of 6.7 m relative to an external reference. When this was not possible, distance to the male was estimated using an external reference. Image temperatures were derived after correction for reflected radiation based on ambient temperature, relative humidity and distance to the seal. A pelage emissivity of 0.98 was assumed based on results from previous studies of infrared emissivities of mammals in which the variation was between 0.98 and 1.00 (Hammel, 1956). Mean skin temperature (T_S) and identification of the magnitude, size and location of thermal features were obtained using Analyze 8.1 software (Mayo Clinic, Rochester, MN, USA) (Robb, 2001; Robb and Barillot, 1989; Robb et al., 1989). No attempt was made to correct for measurement error due to wind speed. Wind speeds were high on all days (see Results) and were greater than speeds where wind speed rapidly alters temperature measurement, and the measurement effect is small when compared with actual convective cooling (Mollman et al., 2007).

Environmental variables
Ambient temperature (T_a) and relative humidity were recorded by an ExTech Data Logger 42270 (temperature resolution 0.1°C, relative humidity accuracy ± 3.0%) located with the observer. Data were recorded automatically every 60 s and were matched with the time-stamp of corresponding thermograms. Solar radiation, vapor pressure and wind speed data were obtained through the website database of the California Irrigation Management Information System (http://www.cimis.water.ca.gov/cimis/welcome.jsp), using the weather station closest to Año Nuevo State Park (~3 km).

Behavior
An activity category was assigned to individuals at the time the thermal photograph was taken. Categories included 'active', 'inactive', 'combat', 'post-combat' and 'copulation'. Inactive males were observed lying prone and unmoving, whereas active males were involved in locomotion unrelated to copulation and combat. Copulation categorized males successfully paired with a female and were actively attempting and/or achieving copulation. Combat males were involved in aggressive behavior against other males, whereas post-combat males were considered for up to 15 min from the end of an observed combat period. Dominance rank was determined from the outcome of observed agonistic interactions between males. Dominance hierarchies were constructed, and male elephant seals assigned ranks as alpha, beta, gamma or peripheral males for each harem based on a dominant–subordinate matrix. All interactions in which one male retreated from another were recorded, although interactions among peripheral males >50 m away from the harems were excluded. Of the 82 males in the study, 47 were ranked and used in analyses considering dominance rank. The sample included seven alpha males, eight beta males, nine gamma males and 23 peripheral males.

Analysis

The temperature difference between the body of the seal and the ambient air/sand temperature was used to threshold automatically the image of the seal from the total image utilizing Analyze 8.1. The threshold was then manually adjusted to ensure that only the body of the seal was included in the analysis. The average pixel value of all pixels contained within the threshold image of the seal was determined to produce the average T_S. Thermal windows were defined as localized areas greater than one standard deviation above the mean for the individual seal within a thermograph. This approach defined the area of thermal discontinuities on the skin surface and was used to calculate the area of thermal windows relative to the total area of the image of the seal.

Linear mixed models (PROC MIXED in SAS v9.1; SAS Institute) were used to assess the impact of environmental variables and behavior on skin temperature and thermal features. All models contained a random effects subject variable for each individual seal. Initial models contained all environmental variables and secondary interactions. Nonsignificant effects and interactions ($P>0.05$) were removed to arrive at the final model. Least-square means differences were used for *post hoc* comparisons. A generalized linear mixed model (PROC GLIMMIX in SAS v9.1; SAS Institute) was used to model the effects of environmental variables on behavioral categories. Data are presented as means ± s.e.m.

RESULTS

Mean skin temperature

The mean T_S value for all 2553 thermographs was 21.8±0.1°C. T_a, solar radiation, vapor pressure, behavior and month significantly affected the mean T_S (Table 1). Solar radiation and T_a had the strongest positive effects on T_S (Table 1; Fig. 1). *Post hoc* means comparisons for activity categories and months are shown in Table 2. Inactive males had the highest mean T_S, being greater than that of copulation, combat or post-combat seals. Mean male T_S decreased over the early part of the study period, being lower in February than January. When controlled for the significant effects of T_a, solar radiation and vapor pressure, dominance rank significantly affected the mean T_S of male elephant seals ($F_{3,1335}=3.13$, $P=0.03$). Alpha males had significantly higher mean T_S than gamma and peripheral males ($P<0.05$) but were not different from beta males (Table 3).

The mean thermal gradient ($T_a–T_S$), which determines the rate of heat flux across a surface, was significantly impacted by solar radiation and vapor pressure (Table 1). Behavior also strongly influenced the mean thermal gradient (Table 1). Inactive males had higher gradients than other activity categories except active males (Table 2). The thermal gradients of active males were only significantly higher than those of copulating males (Table 2). When
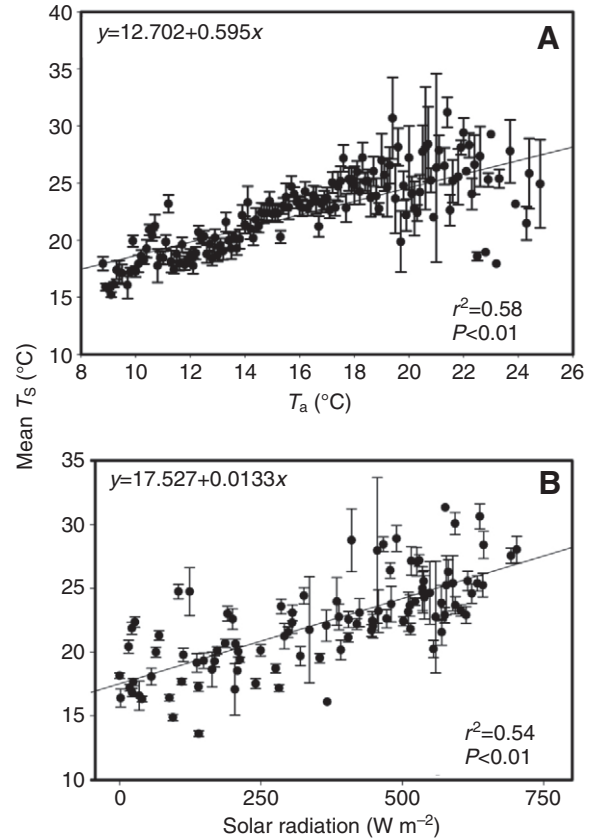

Fig. 1. Variation in mean T_S with T_a in all available thermographs. (A) Mean T_S was calculated from all pixels on a thermograph of the body surface. T_a was measured concurrently at the location of the camera. (B) Variation in mean T_S with solar radiation in all available thermographs. Data are means ± s.e.m.

controlled for significant effects of solar radiation and wind speed, surface thermal gradient varied significantly with dominance rank ($F_{3,1335}=5.61$, $P<0.01$). Peripheral males had lower thermal gradients than alpha males (Table 3).

Maximum skin temperature

Maximum T_S for all 2553 thermographs averaged 33.1±0.1°C. T_a, solar radiation, month and behavior significantly affected the maximum T_S of male elephant seals (Table 1). Solar radiation and T_a were the strongest positive drivers of maximum T_S (Table 1; Fig. 2). *Post hoc* means comparisons for activity categories and months are shown in Table 2. Inactive males had the highest

Table 1. The effects of environmental variables on mean skin temperature (T_S), maximum T_S, thermal window area (TWA), thermal gradient and T_S variability as analyzed using a linear mixed-effect model with an individual seal as a random-effect subject

Environmental variable	Mean T_S		Max. T_S		TWA (%)		Thermal gradient		T_S variability	
	F	P	F	P	F	P	F	P	F	P
Ambient temperature	165.71	<0.01	115.96	<0.01	4.42	0.04	–	–	51.39	<0.01
Relative humidity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Solar radiation	243.21	<0.01	99.06	<0.01	42.34	<0.01	37.71	<0.01	22.13	<0.01
Vapor pressure	10.99	<0.01	n.s.	n.s.	14.5	<0.01	43.22	<0.01	17.48	<0.01
Wind speed	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Behavior	7.60	<0.01	87.47	<0.01	13.28	<0.01	4.79	<0.01	11.44	<0.01
Month	5.22	0.01	5.86	<0.01	15.81	<0.01	n.s.	n.s.	27.36	<0.01

n.s., not significant.

Table 2. *Post hoc* comparisons of least-square means of T_S between activity categories and months from linear mixed models

Activity category	Mean T_S	Max. T_S	TWA (%)	Thermal gradient	T_S variability
Inactive	22.1±0.1[b,c,d]	33.7±0.1[a,b]	16.3±0.2[c]	7.1±0.2[a,b,c]	3.63±0.05[a,c,d]
Active	21.9±0.4[a]	31.9±0.3[a,d]	16.2±0.4[a]	6.9±0.6[d]	3.24±0.12[a,b]
Combat	21.0±0.3[b]	30.1±0.3[b,d]	18.6±0.4[a,b,c]	6.2±0.5[a]	4.04±0.10[a,c]
Post-combat	21.3±0.3[d]	31.9±0.3[b,c]	17.0±0.0[c]	6.4±0.4[c]	3.44±0.10[c,d]
Copulation	20.5±0.5[a,c]	30.0±0.4[a,c]	16.8±0.6[b]	5.3±0.6[b,d]	3.99±0.16[b,d]
Month					
January	21.5±0.2[e]	31.9±0.2[e,f]	17.8±0.2[d]	6.0±0.3	4.18±0.06[e]
February	21.0±0.2[e,f]	31.4±0.2[e]	16.9±0.2[d]	5.9±0.2	3.82±0.07[e]
March	21.7±0.4[f]	31.2±0.3[f]	16.2±0.4[d]	5.4±0.5	3.18±0.12[e]

Data are means ± s.e.m.
TWA, thermal window area.
Same letters indicate significant differences.

maximum T_S, being significantly greater than all the other activity categories. Post-combat males followed, whereas copulating males had the lowest maximum T_S. Maximum T_S was greater in January than in February or March.

Variability of T_S

We used the standard error of the mean of the individual pixel temperatures in a thermograph multiplied by 100 as a measure of T_S variability. T_S variability increased with T_a, solar radiation and vapor pressure (Table 1). Behavior significantly affected T_S variability, which was greater in combat and copulation thermographs than all other categories (Table 2). T_S variability declined across the study, being significantly lower in each succeeding month (Table 2).

An average of 16.7% of the skin surface of males was classified as thermal windows. Thermal windows developed in consistent recurring body locations, appearing most commonly on the head, shoulders and foreflippers (Table 4). Most dynamic were windows on the lateral mid-trunk that developed as the proportion of the visible body surface classified as a thermal window area (TWA; %) increased. Environmental variables, month and behavior significantly affected TWA (Table 1). TWA increased linearly with solar radiation and vapor pressure and more weakly with T_a. Combat males had the greatest TWA, whereas inactive and active males had the lowest (Table 2). TWA declined with each succeeding month of the study (Table 2).

When controlled for significant effects of T_a, vapor pressure, solar radiation, month and activity, mean T_S significantly affected the TWA on male elephant seals ($F_{1,2460}$=6.28, P=0.01). TWA increased with mean T_S until mean T_S reached ~24°C, at which point TWA became more variable and declined (Fig. 3). There was a significant interaction between mean T_S and activity of male seals ($F_{4,2460}$=4.98,

P<0.01). This was likely due to differences among combat and post-combat males. When these data were considered separately, mean T_S was the sole driver of TWA ($F_{1,192}$=4.80, P=0.03) and none of the environmental variables impacted TWA.

Combat, post-combat

As stated above, combat males had the highest TWA but some of the lowest mean and maximum T_S values. Thermal windows in combat and post-combat males, along with mean and maximum T_S, experienced rapid changes over time. Thermal photographic sequences of combat and post-combat males clearly illustrate thermal windows forming and expanding on the appendages and

Table 3. *Post hoc* comparisons of least-square means of T_S between ranks from linear mixed models

Rank	Mean T_S	Max. T_S	TWA (%)	Thermal gradient
Alpha	22.1±0.2[a,b]	33.9±0.3[a]	18.4±0.5[a]	7.3±0.2[a]
Beta	21.9±0.27	33.1±0.4	16.8±0.6	6.9±0.3
Gamma	21.2±0.26[a]	32.7±0.3	16.9±0.6	6.6±0.3
Peripheral	21.4±0.22[b]	32.3±0.3[a]	15.9±0.5[a]	5.9±0.2[a]

Data are means ± s.e.m.
TWA, thermal window area.
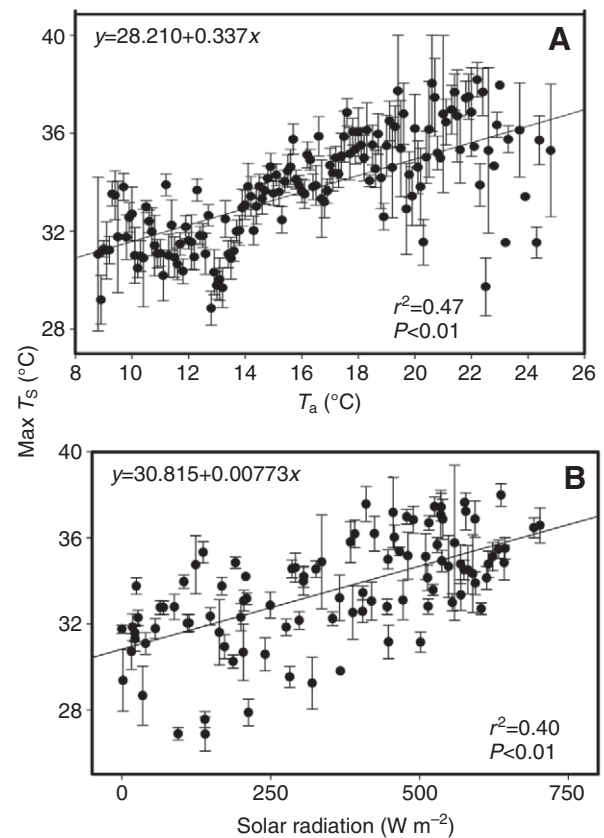Same letters indicate significant differences.

Fig. 2. (A) Variation in maximum T_S with T_a in all available thermographs. (B) Variation in maximum T_S with solar radiation in all available thermographs. Data are means ± s.e.m.

body trunk of male elephant seals (Fig. 4). The head and neck accounted for the majority of thermal window locations, with the shoulders, foreflippers and hindflippers all contributing similar amounts (Table 4). The hips and mid-trunk area of males were also frequent locations of thermal windows.

Combat and post-combat males varied in their strategy when balancing dumping heat with the TWA they used across their skin surface. The patterns suggested dynamic control of skin perfusion. One male in particular, the alpha male M3, exhibited a recurring pattern during multiple post-combat sequences taken over several months in which, as T_S increased, the TWA decreased, and both variables oscillated in a cyclical fashion (Fig. 5). Skin temperatures differed greatly with TWA among all categories of males. For animals with more than four post-combat thermal pictures, some males displayed a negative relationship ($N=5$) between T_S and TWA, whereas others showed a positive relationship ($N=5$). The remaining analyzed pictures exhibited no pattern ($N=7$).

Activity

We used our thermographs as a sample of the behavior of males and examined the effects of environmental variables on the types of behaviors exhibited. There were strong effects of environmental conditions on the types of activities displayed by males. T_a, relative humidity, vapor pressure and wind speed all affected behavior significantly (Table 5). Wind speed, which was not a significant variable in any of the previous models, had the largest influence on activity of males. Relative humidity, like wind speed, had a considerable effect on behavior while having no impact on the other response variables. Males were more likely to be inactive during hot, humid days with little or no wind.

Environmental data

Table 6 presents the monthly averages for daily means of T_a, relative humidity, solar radiation, vapor pressure and wind speed. Note the environmental data used in the statistical analysis are based on what were obtained during thermograph acquisition – that is, there are fewer samples at night, and thermographs were not obtained when it was raining. As a result, the monthly averages presented in Table 6 are from a larger data set and do not match that associated with the skin temperature data. These data are presented to give a context for the environmental changes experienced by the seals over the breeding season.

Table 4. Summary of the most common areas of thermal window occurrence on male elephant seals

Area	Number of thermal windows	Percentage of photos
Head	998	39.1
Neck	960	37.6
Shoulders	599	23.5
Foreflippers	580	22.7
Hindflippers	467	18.3
Hip	260	10.2
Mid-trunk	254	10.0
Penile opening	240	9.4

DISCUSSION

Skin temperature in breeding male northern elephant seals is highly responsive to environmental conditions, varying with T_a, solar radiation and vapor pressure. Solar radiation and T_a have strong impacts on mean and maximum T_S. We would expect solar radiation and T_a to influence the temperature of any exposed object. Active thermoregulation through altering skin perfusion in response to environmental variation was suggested by changes in T_S variability and thermal window proportions with T_a, solar radiation and vapor pressure. Males maintained a higher mean thermal gradient across the visible body surface as solar radiation increased, facilitating heat loss.

The strong impacts of solar radiation on T_S are consistent with previous suggestions outlining the importance of this variable in affecting thermoregulatory behavior in pinnipeds (Beentjes, 2006; Twiss et al., 2002; Campagna and Le Boeuf, 1988; White and Odell, 1971). Direct exposure to solar radiation results in not only the animal absorbing heat but also the warming of the surrounding substrate, lowering any heat gradient and possibly adding to the heat gain of an animal through conduction (Campagna and Le Boeuf, 1988). Vapor pressure affected mean T_S to a lesser degree. In high vapor-pressure conditions, the environment is saturated with water vapor, making cutaneous and respiratory evaporation difficult. The strong influence of vapor pressure on T_S variability and thermal window proportions in our study suggests that males altered skin perfusion in response to reduced evaporatory capacity. In another study, Twiss and colleagues (Twiss et al., 2002) found significant impacts of vapor pressure on the spacing of female grey seals relative to tide pools.

Despite significant positive impacts of environmental variables on the response variables and increases in average solar radiation, vapor pressure and T_a over the study period, maximum male T_S, TWA and T_S variability all declined over the three months of the study (Table 2). Mean T_S declined over the first two months of the study and then rose in March. As the breeding season progresses, males deplete their blubber reserves in the competition to gain access to females. Similar to other pinnipeds such as harbor
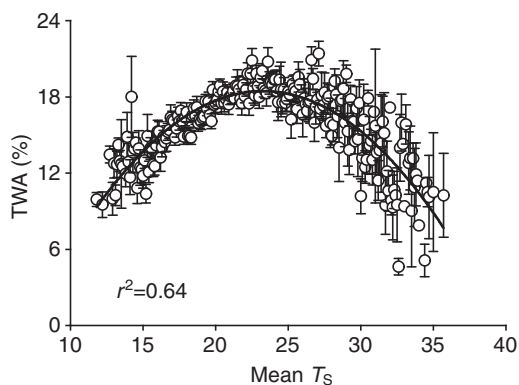

Fig. 3. Changes in the proportion of body surface defined as thermal windows (TWA; %) with mean T_S over the visible body surface. Thermal windows were defined as the areas in which T_S was one standard deviation above the mean T_S of the animal. Data are means ± s.e.m.

Table 5. The effects of environmental variables on behavior as analyzed using a generalized linear mixed model with an individual seal as a random-effect subject

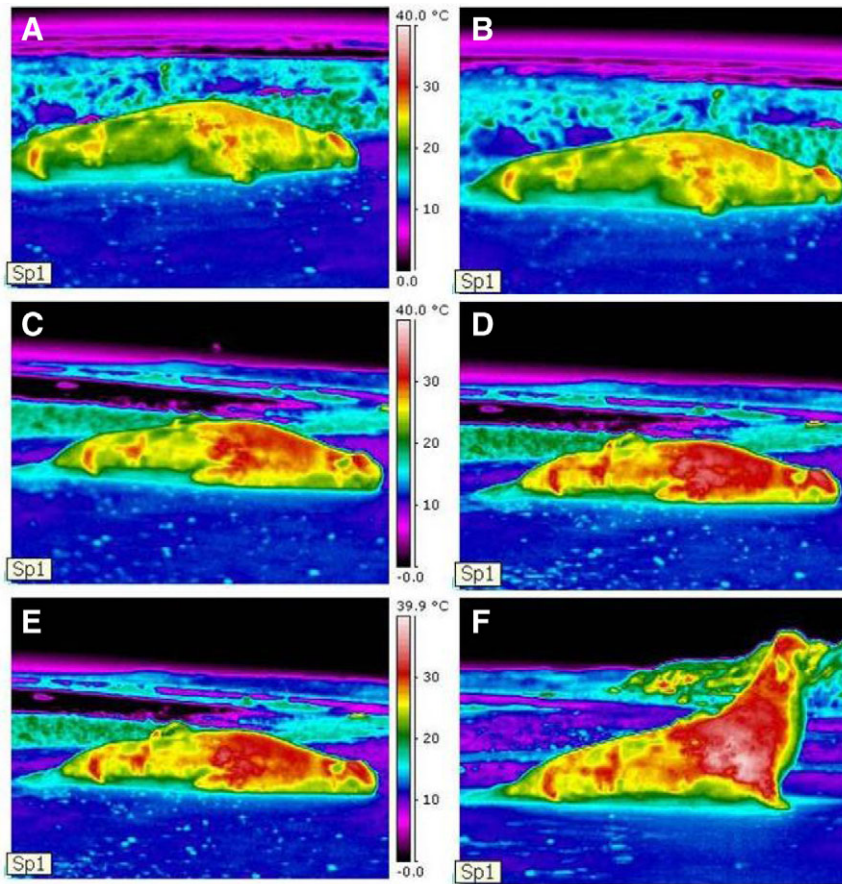|	Behavior	
Effect	F	P
Ambient temperature	9.11	<0.01
Relative humidity	13.74	<0.01
Solar radiation	n.s.	n.s.
Vapor pressure	6.88	0.01
Wind speed	20.96	<0.01

Fig. 4. Post-combat thermal image sequence (A–F) of alpha male M3 taken at intervals of ~1 min immediately following a combat of duration 11 min. M3 was the alpha male at the largest harem in the study area and gave the largest sample of combat and post-combat sequences. The complete set of images was used to generate Fig. 5.

seals and Steller sea lions, northern elephant seal males appear to deplete blubber preferentially from certain areas when fasting (Mellish et al., 2007; Rosen and Renouf, 1997) (D.E.C., unpublished observations). Mean blubber thickness declines from 6.2 cm early in the breeding season to 3.6 cm by early March, but this proportion varies widely across the body surface (D.E.C., unpublished observations). As the insulation from the blubber decreases over time, the need for circulatory adjustments to bypass this insulation might also decline.

Using the thermographs as a random sample of male behavior revealed strong impacts of environmental variables on male activity. Males were least active on hot, humid days with low wind speeds, suggesting that thermoregulatory stress might be important in shaping breeding behavior. Indeed, many studies based on observing breeding behavior have concluded that there must be an environmentally induced thermoregulatory cost influencing pinniped behavior (Wolf and Kauermann, 2005; Francis and Boness, 1991; Campagna and Le Boeuf, 1988; Gentry, 1973). Our finding also helps explain the counterintuitive result that inactive males had the highest mean T_S values. Males might limit activities that produce the most metabolic heat to periods during which the environment is more conducive to heat loss. Interestingly, the two environmental variables most important in influencing male activity – wind speed and relative humidity – had no significant effect on mean or maximum T_S. Similarly, solar radiation, which has been the principal driver of all T_S response variables, had no impact on male activity. These results strongly suggest that males modify their behavior relative to the potential for convective or evaporative heat loss.

The insulation value of the fur of seals depends on the density of hairs, and any increase in convection, such as increased wind speeds, raises conductivity and decreases thermal resistance (Kvadsheim and Aarseth, 2002; Tregear, 1965). Elephant seals have sparse, short fur that might allow an increase in wind speed to disrupt the air layer surrounding the skin, effectively aiding heat dissipation (Scheffer, 1964). In arctic phocids, which are insulated by a denser fur layer than elephant seals, heat transfer to the air was found to occur primarily through natural convection (Hammel, 1955). With a wind-mediated increase in convective heat loss, elephant seal males

Table 6. Mean ± s.d. daily environmental data by month

Month	T_a (°C)	Relative humidity (%)	Solar radiation (W m^{-2})	Vapor pressure (kPa)	Wind speed (m s^{-1})
January	8.1±2.1	61.4±21.7	78.4±43.5	0.86±0.20	2.0±0.8
February	9.4±2.1	76.2±14.7	133.6±50.0	0.90±0.17	1.8±0.8
March	10.6±1.5	67.6±10.5	208.8±35.2	0.85±0.15	1.8±0.5
Mean	9.4±2.2	62.8±14.3	140.4±69.1	0.87±0.17	1.8±0.6

T_a, ambient temperature.
Note that these data include all available daily data from the weather station and do not match the environmental data concurrent with the thermographs.
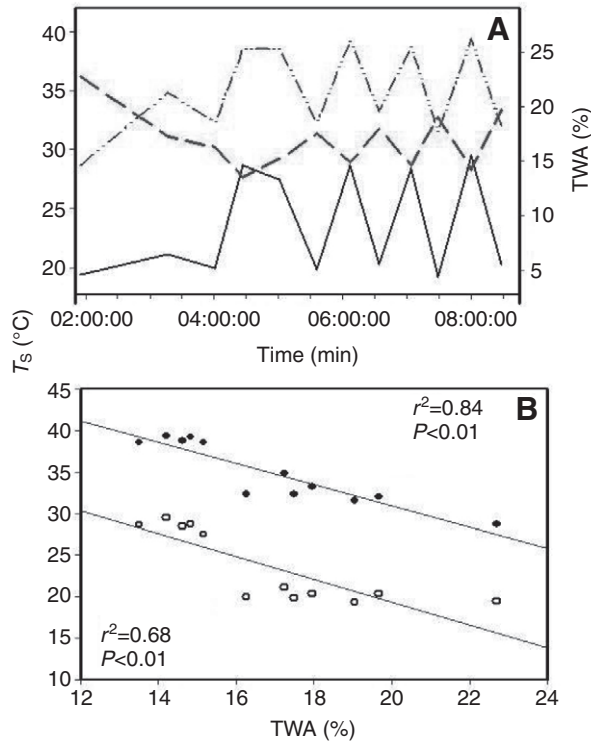
Fig. 5. Changes in mean T_S (solid line), maximum T_S (broken and dotted line) and proportional thermal window area (TWA; %, broken line) over a sequence of thermographs taken at intervals of 1 min after combat in male M3. (A) T_S and TWA varied in an inverse cyclical pattern. (B) Mean (open circles) and maximum (filled circles) T_S declined significantly with thermal window area. These patterns were repeated in all combat sequences taken involving M3. Other males showed less-consistent patterns.

are able to intensify their activity during periods of high solar radiation. Wind speeds were variable but relatively high on all days of the study, suggesting the existence of high rates of convective heat transfer.

Inactive males can also use 'sand flipping' to insulate themselves against direct solar radiation on their dorsal surface. Weaned elephant seal pups, as well as other species of pinnipeds, have been observed sand flipping when exposed to direct solar radiation and increasing temperatures (Beentjes, 2006; Noren, 2002; Campagna and Le Boeuf, 1988). White and Odell reported skin temperatures of the backs of elephant seals under the sand to be an average of 5°C cooler than exposed skin (White and Odell, 1971). When controlled for environmental variables, there were still significant impacts of behavior on T_S response variables. In general, TWA% increased with mean T_S up to ~24°C then began to decline and became more variable (Fig. 3). This is consistent with increasing skin perfusion as the body warms until mean T_S becomes highly elevated above ambient. This inflection point is just greater than the mean thermal gradient (~7°C) above the mean T_a (~15°C) for the dataset, suggesting that, as mean T_S increases well above T_a, T_S becomes more homogeneous. We must acknowledge, however, that the inflection point and the dynamics of the relationship between the TWA and T_S are somewhat dependent on our definition of a thermal window (i.e. a region bounded by a temperature one standard deviation above the mean). Where the inflection occurs will vary with the quantitative definition of thermal window, within reason, but the pattern should generally be the same.

Perhaps most important in interpreting these data are the differences between the way activity influences mean T_S and T_S variability. Both T_S variability and TWA were highest during combat behavior, suggesting that this activity requires adjustments in skin perfusion to facilitate loss of metabolic heat. This is also implied by the dynamic nature of T_S after combat. Thermal images taken successively throughout combat and post-combat periods demonstrate prompt modifications in T_S, TWA and T_S variability. Variations in thermal window locations, patterns and characteristics are seen between individuals of all activity categories. Scars or wounds created by combat or predator injury, removed of any fur, are natural heat dissipation areas because of their increased conductive and convective properties and were sometimes the original sites of spreading thermal windows. Although rapid changes tended to reduce the significance of *post hoc* comparisons of response variables for post-combat thermographs, they suggest alterations in skin perfusion based on inputs from both core and peripheral temperature sensors. The dynamic nature of skin perfusion suggested by the current study implies simple mathematical models of heat flux across the body surface [e.g. eqns 1–4 in Kvadsheim et al. (Kvadsheim et al., 1997)] that consider blubber at a fixed depth or model the ratio of body and core based on the temperature differential at the blubber–core interface might not adequately reflect the dynamic nature of insulation and its plasticity in the context of thermal stress.

Thermal windows functioned as temporary heat dissipaters following combat and could be the most efficient means of heat loss available to combative males (Fig. 4). A significant area of the body surface of a seal was immediately committed to heat loss during combat, allowing a male to compete as long as possible in varying environmental conditions. Over the course of this study, males involved in more lengthy combat were often observed retreating/pushing towards the water. If both combatants entered the surf, the loser swam away and hauled out at another location along the beach, whereas the winner made his way back to the harem, resting at intervals until reaching his destination. Water has a conductivity that is 25 times that of air, making evaporatory cooling a quick and efficient method of heat loss. Victorious males of combat that ended either near or in the water probably used evaporation and conduction to wet sand as heat loss mechanisms, mitigating the thermal stress resulting from combat.

Dominance rank accounted for significant variation in surface thermal characteristics when controlled for environmental variables. Alpha males had the greatest mean T_S, maximum T_S, TWA and thermal gradient across the visible body surface compared with peripheral males. Peripheral males might benefit from the ability to enter the water frequently – in contrast to ranking males. Some of these effects might also stem from the different body characteristics of males, for which alpha males have a larger body size and blubber thickness compared with those of peripheral males. These data provide evidence of a thermal cost to being a competitive breeding male. Such attributes might influence the higher water efflux rate reported for alpha males (Ortiz et al., 2006).

CONCLUSIONS

Polygynous breeding systems often select for strong sexual dimorphism, with successful males having large body size and high rates of energy expenditure. In marine endotherms adapted for thermoregulation in cold water, these features might result in significant thermal stress, even in temperate climates. Solar radiation, along with other environmental variables, plays an important role in determining skin temperature, skin temperature variability, thermal

gradient and body surface area used for heat dissipation in breeding adult male elephant seals. Environmental variables, especially wind speed, might influence breeding behavior and thermal stress associated with activity. High wind speeds might help enable activity during periods of high solar radiation. Altered thermal features on the skin surface of ranking males suggest that traits and behaviors associated with breeding success might result in increased thermal stress.

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