

Thermal benefits of aggregation in a large marine endotherm: huddling in California sea lions

H. E. M. Liwanag^{1,2}, J. Orazé^{1,3}, D. P. Costa¹ & T. M. Williams¹

¹ Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, USA

² Department of Biology, Adelphi University, Garden City, NY, USA

³ The Royal Veterinary College, University of London, London, UK

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Correspondence

Heather E. M. Liwanag, Adelphi University,
1 South Avenue, Garden City, New York,
NY 11530, USA. Tel: (516) 877 4210,
Fax: (516) 877 4209
Email: hliwanag@adelphi.edu

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Abstract

Huddling is an important behavior for many endotherms, and it is associated with both social interactions and physiological regulation. Sea lions are highly communal pinnipeds that often congregate in large numbers on coastal rookeries. While this behavior serves a social role, it also has the potential to change the microhabitat and thus the local thermal conditions experienced by the animals. However, the thermal consequences of huddling in pinnipeds have yet to be quantified despite a propensity for close proximity in some species. To investigate this, we quantified the huddling behavior of California sea lions, *Zalophus californianus*, by measuring the proximity of individuals from digital photographs, and determined the thermal microhabitat of huddles using an infrared temperature monitor. All animals were measured on San Nicolas Island (California, USA) for 6 days in winter ($T_{\text{air}} = 13.2 \pm 2.1^\circ\text{C}$) and 7 days in summer ($T_{\text{air}} = 21.1 \pm 3.4^\circ\text{C}$). We found that sea lion huddling behavior increased in colder weather, as determined from three indices. First, a larger proportion (up to 97%) of the animals participated in huddles rather than resting alone during the winter season ($P = 0.010$). Second, the number of animals per huddle was larger (reaching 172 animals) during the colder season ($P = 0.019$). Lastly, sea lions participating in this behavior huddled more tightly in cold temperatures ($P = 0.023$). The temperature differential between the animals' skin surface and that of the surrounding substrate was significantly greater ($P < 0.001$) for huddling sea lions ($6.0 \pm 3.6^\circ\text{C}$) than for animals resting alone ($3.0 \pm 2.8^\circ\text{C}$). Furthermore, this differential was inversely proportional to ambient temperatures. These results are consistent with huddling behavior in California sea lions providing a significant thermal benefit that likely shapes their social behavior on land.

Introduction

There are both costs and benefits to aggregation in animals, and for grouping behavior to persist, the benefits must outweigh the costs. It has long been recognized that animals form aggregations for a variety of reasons, including social factors (e.g. kin influences, sociality, breeding), predator evasion, hibernation, aestivation, moisture control, sleep, and temperature regulation (Allee, 1927). While social factors often underlie the formation of animal aggregations, the size and nature of the groups are shaped by their physiological effects (Allee, 1927). These effects are particularly evident in endotherms, for which thermoregulation – maintenance of the core body temperature within a narrow range – is a matter of energetic significance and fundamental survival (Schmidt-Nielsen, 1997).

An animal's first response to changes in temperature is to alter its behavior. Behavioral control of heat exchange can

include daily torpor or seasonal hibernation, alteration of posture to adjust available surface area, and huddling (Stanier, Mount & Bligh, 1984). Huddling is ecologically significant to endotherms as a fundamental behavioral response to cold, and is important for survival (Hart, 1971). Huddling behavior can impart metabolic savings, thus reducing thermoregulatory costs (Hart, 1971; Stanier *et al.*, 1984; reviewed in Gilbert *et al.*, 2010). Huddling has been well studied in penguins as a crucial strategy for reducing thermoregulatory costs in extreme cold (Le Maho, Delclitte & Chatonnet, 1976; Pinshow *et al.*, 1976; Barre, 1984; Kirkwood & Robertson, 1999; Gilbert *et al.*, 2007). Advantages of huddling have also been demonstrated for a broad range of birds and mammals, further exemplifying the importance of this behavior for thermoregulatory energetic benefits and survival, across endotherms (reviewed in Gilbert *et al.*, 2010).

Given their amphibious lifestyle, pinnipeds (seals, sea lions, and walrus) have sufficient insulation to overcome the high conductivity of water, which is 24 times higher than air, and one might expect them to be overinsulated on land (Dejours, 1987; Liwanag *et al.*, 2012a,b). However, many pinnipeds have been observed to huddle extensively while resting on land (Rowley, 1929; Peterson & Bartholomew, 1967; White & O'Dell, 1970; Sullivan, 1980; Heath, 1989). Because such a large number of homeothermic animals in close proximity should change the thermal microenvironment, it is likely that this behavior has thermoregulatory consequences for these animals. However, the thermoregulatory implications of huddling behavior in pinnipeds have yet to be quantified.

We tested the hypothesis that pinniped huddling behavior has a thermoregulatory role by examining the huddling behavior of the California sea lion, *Zalophus californianus*, on a Southern California colony. This species hauls out on shore year round, and has been observed to huddle extensively (Rowley, 1929; Peterson & Bartholomew, 1967; Heath, 1989). The objectives of this study were (1) to quantify the huddling behavior of California sea lions in defined thermal environments; (2) to determine whether sea lion huddling behavior imparts a thermal benefit to animals on haulouts.

Materials and methods

Study location and sites

California sea lions were observed on San Nicolas Island, Southern California, USA. Study sites were located on the western (Dos Coves Beach, DOS, 33.264N, 119.572W) and southern (Daytona Beach, DAY, 33.131N, 119.265W) parts of the island. Both sites had defined edges, so that the total number of animals at each site could be quantified absolutely. In the winter (non-breeding season), no sea lions hauled out at DAY; thus analyses were restricted to DOS, where sea lions of both sexes and all age classes hauled out and were observed to huddle. In the summer (breeding season), DOS was a breeding beach primarily occupied by dominant males, adult females, juveniles, and pups, whereas DAY was entirely occupied by non-breeding (subdominant) male California sea lions. Thus, the combination of DOS and DAY included both sexes and all age classes in the summer, and all were observed huddling at their respective beaches. In both seasons, northern elephant seals, *Mirounga angustirostris*, also hauled out at DOS (range: 0–28 seals), and were included in counts for accuracy but excluded from statistical analyses of sea lion huddling behavior. Experimental periods comprised 6 days in winter (January 2006) and 7 days in summer (July–August 2006).

Thermal environment

To characterize the thermal environment, a temporary weather station (Davis Instruments, Hayward, CA, USA) was erected on the cliff edge overlooking DOS during the experimental periods. The weather station recorded air temperature, wind speed, relative humidity, and barometric pressure every

Table 1 Summary of environmental variables measured on San Nicolas Island, California, during the winter and summer experimental periods

| | Winter | Summer |
|-----------------------------|--------------|--------------|
| Air temperature (°C) | 13.2 ± 2.1 | 21.1 ± 3.4 |
| Black bulb temperature (°C) | 21.6 ± 6.1 | 27.4 ± 5.8 |
| Wind chill temperature (°C) | 8.4 ± 3.9 | 19.5 ± 4.3 |
| Wind speed (m/s) | 5.2 ± 2.8 | 3.0 ± 1.8 |
| Relative humidity (%) | 66.5 ± 12.5 | 70.0 ± 13.1 |
| Barometric pressure (mbar) | 1026.1 ± 2.4 | 1017.0 ± 1.6 |

Values are presented as means ± 1 SD. Black bulb temperatures were measured by the observer during sampling. All other variables were measured continuously throughout each experimental period by a temporary weather station erected at the experimental site.

5 min for the entire experimental period (Table 1). An existing NOAA (National Oceanographic and Atmospheric Administration) weather station was located at one end of DAY; however, the weather station at DAY failed to collect data during the experimental period. Consequently, the data collected at DOS served as a proxy for both sites. During sampling periods, incident solar radiation was estimated at the location of the observer every 5–15 min using a black bulb thermometer (Bedford & Warner, 1934; Schmidt-Nielsen *et al.*, 1956; Table 1). In addition, the temperature of the substrate on which the animals were resting was measured using remote infrared thermometry, described below (Raynger PM4L5, Raytek Corporation, Santa Cruz, CA, USA).

Quantification of huddling behavior

Huddling was defined as two or more animals resting with their bodies in physical contact. To quantify the behavior, three indices of huddling were measured using digital photogrammetry: (1) the proportion of animals at a site participating in huddles; (2) the average number of animals per huddle; (3) how tightly the animals were aggregated within each huddle. Once per day, digital photographs were taken of all the animals at each site (34 ± 10 photos per site; range = 21–61). Sampling periods occurred at various times of day on different days, in conditions with enough light to visualize the images. A minimum of 12 h separated the sampling periods on different days. Because California sea lions typically leave for their foraging trips at dusk (Antonelis, Stewart & Perryman, 1990), sampling periods occurring on separate days were considered independent samples.

In each photograph, every animal was marked digitally, using differently sized marks for huddled animals and individual (lone) animals. Using ImageJ software (NIH, Bethesda, MD, USA), the marks were isolated and counted. Data were combined for all photographs across a site for each sampling period, either manually or by merging the photographs in Adobe Photoshop (Adobe Systems Incorporated, San Jose, CA, USA), to determine the proportion of animals participating in huddles and the average number of animals per group at each site.

To quantify how tightly the animals were huddled, an ellipse was drawn around each huddle to best represent its

shape. Using ImageJ software, photographs were rotated up to 20° (but typically no more than 5°) to ensure the best fit ellipse for each huddle. Huddles that were obscured by rocks or other animals, or that could not be viewed properly with rotation, were excluded from this analysis. Once the best fit ellipse was obtained, the major and minor axes of the ellipse were determined. A huddling index was calculated by dividing the minor axis of the ellipse by the major axis. This index ranged from 0 to 1, with 1.0 representing a perfect circle. As a sphere exposes the least amount of surface area for a given length parameter (Heath, 2007), a more circular formation would generally represent a closer huddle, in which a greater amount of skin surface area would be in contact with other animals rather than the surroundings.

Thermal consequences of huddling

A remote infrared thermometer (Raynger PM4L5, Raytek Corporation, Santa Cruz, CA, USA), which measured surface temperature at a point location, was used to examine the thermal consequences of huddling. Temperature readings were rated to $\pm 0.1^\circ\text{C}$ within the measurement region, which was approximately 20 cm in diameter at 10 m distance from the target (spot:distance ratio = 1:50). The thermometer was used to record the surface temperatures of huddling sea lions (in the middle of the huddle) and sea lions resting alone. These animals comprised a representative subset of the animals at each site on a given day. For each huddle or animal measured, the temperature of the substrate on which the animals were resting was also recorded. The substrate temperature provided a proxy for the thermal microenvironment experienced by the animals, by generating an abiotic measurement influenced by all of the same thermal factors affecting the animals at that time (Gentry, 1973). Five repeated temperature measurements were taken at approximately the same location for each observation of animal surface (middle of a huddle, torso of a lone animal) or substrate temperature, and the average was used for analysis. From these temperatures, an index of the thermal conditions experienced by the animals was obtained, by calculating the temperature differential (ΔT) between the animal's surface (T_s) and the substrate (ambient or abiotic temperature, T_a):

$$\text{Temperature Differential } (\Delta T) = T_s - T_a \quad (1)$$

This differential provided a relative yet consistent measure with which to evaluate the thermal microenvironment for huddled animals compared with a lone animal.

Statistical analyses

Numerical values are presented as means ± 1 SD. Seasonal differences in environmental variables were compared between winter and summer with two-tailed Student's *t*-tests. The proportion of animals huddling and number of animals per group were also compared between the winter and summer seasons using two-tailed Student's *t*-tests. Huddling index was compared between seasons using a general linear model, with

group size as a covariate. For the analysis of thermal conditions, data from the winter and summer seasons were pooled, and substrate temperature was used as the predictor variable. Linear regressions were calculated using least-squares procedures and slopes were compared with ANCOVA (Systat 13, Systat Software, Chicago, IL, USA).

Results

Quantification of huddling behavior

All environmental variables measured were significantly different ($P < 0.001$) between the winter and summer seasons (Table 1). In the winter season, air temperatures were lower; incident solar radiation, measured as black bulb temperature, was lower; wind speeds were higher, resulting in lower wind chill temperatures; relative humidity was lower; and barometric pressures were higher. Because the two seasons represented distinct thermal environments, we used season as a categorical variable for the comparison of huddling behavior.

There were significant changes in all three indices of huddling behavior between the winter and summer seasons (Fig. 1). In the winter 82.5 \pm 16.2% of the sea lions at a site participated in huddles rather than resting alone, whereas 57.1 \pm 21.7% of the sea lions participated in huddles during the summer ($P = 0.010$). On average, there were three times as many sea lions per huddle in the winter (13.4 \pm 12.4, max = 172 animals) compared with the summer (4.6 \pm 1.8, max = 77; $P = 0.019$). Group size had a significant effect on the huddling index, such that larger groups tended to have lower huddling indices ($F_{1,307} = 18.984$, $P < 0.001$). When the effect of group size was taken into account, there was a significant difference in huddling index ($F_{1,307} = 5.224$, $P = 0.023$) indicating that sea lions huddled more tightly in the winter (0.364 \pm 0.161) than in the summer (0.340 \pm 0.134). Across

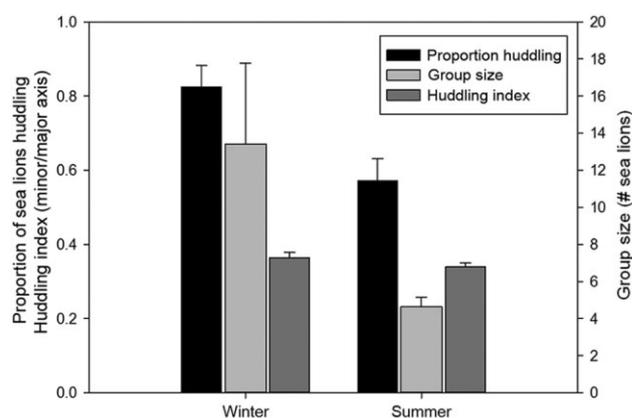


Figure 1 Comparison of California sea lion huddling behavior between winter and summer. Heights of the bars and lines represent means \pm SEM. Values for the proportion of sea lions participating in huddles (black bars) and huddling index (dark gray) are indicated on the left vertical axis. Values for group size (light gray) are indicated on the right vertical axis.

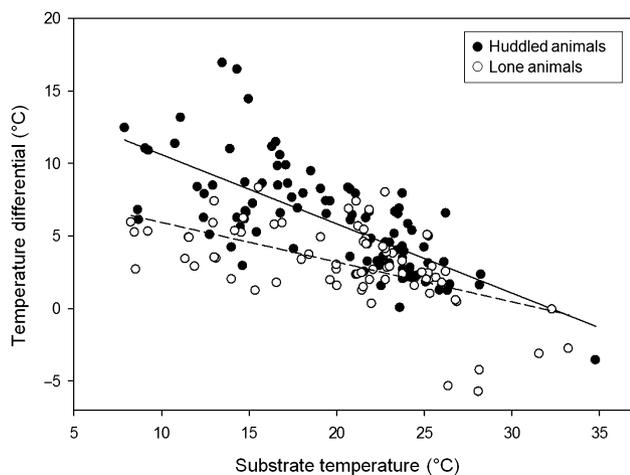


Figure 2 Thermal consequences of huddling behavior in California sea lions. The temperature differential (ΔT) between the animals' surface and the substrate was inversely related to substrate temperature. This relationship was more pronounced in huddled animals (black dots) compared with lone animals (white dots), such that huddled animals maintained higher ΔT . Solid line is the least squares regression for huddled animals; dashed line is the regression for lone animals.

seasons, the huddling index was inversely related to ambient air temperature ($F_{1,11} = 7.109$, $P = 0.022$). The total number of animals on the beach at DOS (349 ± 147.6 sea lions) did not differ between seasons ($P = 0.395$).

Thermal consequences of huddling

On average, huddled sea lions maintained a higher temperature differential (ΔT) between their surface and the substrate ($6.0 \pm 0.4^\circ\text{C}$) compared with sea lions resting alone ($3.1 \pm 0.3^\circ\text{C}$) (Fig. 2). Note that negative values of ΔT were associated with wet animals. Both lone animals and huddled animals demonstrated a significant increase in ΔT as substrate temperature decreased ($F_{1,167} = 115.462$, $P < 0.001$), but huddled animals maintained higher ΔT compared with lone animals on colder substrate ($F_{1,167} = 44.474$, $P < 0.001$). These differences in ΔT were not as pronounced at warmer substrate temperatures (Fig. 2).

The number of animals in the huddle also influenced ΔT , such that larger huddles were able to maintain a significantly higher temperature differential ($F_{1,94} = 35.385$, $P < 0.001$; Fig. 3). Due to colder substrate temperatures on average, ΔT was higher for winter huddling animals ($7.9 \pm 0.5^\circ\text{C}$) compared with animals huddling in the summer ($3.4 \pm 0.2^\circ\text{C}$, $P < 0.001$). However, the slope of the relationship between ΔT and group size was not significantly different between seasons (ANCOVA, $P = 0.24$; Fig. 3).

Discussion

Seasonal changes in huddling behavior

Sea lions are gregarious animals and form year round aggregations at haulout sites (Scheffer, 1958; Heath, 1989). Because

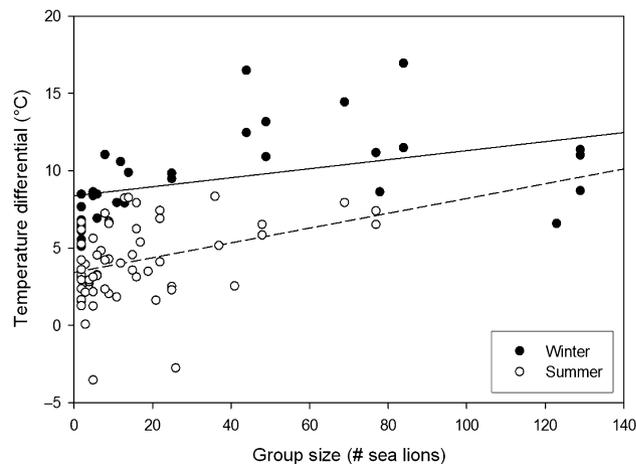


Figure 3 Effects of group size on the thermal consequences of huddling behavior in California sea lions. Data are for huddled animals only. Solid line is the least squares regression for winter huddles (black dots); dashed line is the regression for summer huddles (white dots). There is no significant difference in the slope of the two lines.

of their propensity to maintain body contact over a large surface area, sea lions have been described as thigmotactic (Kirkwood & Goldworthy, 2013). During the breeding season, which occurs in the summer, breeding males guard harems of females; in these situations, females often aggregate within the area guarded by their dominant male (Peterson & Bartholomew, 1967). However, the mating system alone does not drive this behavior, as we observed subdominant males huddling on a non-breeding beach (DAY) during the breeding season.

Our results demonstrate that California sea lions huddle more in the winter than in the summer. We found a consistent increase in huddling behavior across all three indices of huddling: proportion in huddles, average group size, and circularity of a huddle (Fig. 1). Because the study beaches were longer than they were wide, very large groups of sea lions could not form a circle in the limited space and would instead form oblong huddles following the shape of the beach. As a result, the circularity of a huddle was inversely related to group size. This obscured differences in the huddling index between seasons, as animals huddled more tightly in winter but also formed larger groups. Once we accounted for group size, we observed a significant difference in the huddling index between seasons. Additionally, the uncorrected huddling index was inversely related to ambient temperature. Thus, while our huddling index was not a perfect proxy for the closeness of aggregating animals, it allowed us to quantify differences in behavior. The seasonal changes observed for all behavioral indices were not a result of crowding, as the total number of animals on the breeding beach (DOS) did not differ between seasons. Therefore, we observed a clear increase in huddling behavior associated with the winter season, independent of mating system or crowding effects.

Thermal consequences of a social behavior

The consistent occurrence of huddling in the summer season and in warm ambient conditions indicates that there is likely an underlying social component to this behavior in sea lions. However, there are clear thermal consequences as well, which can serve as an advantage in colder conditions. Individual Steller sea lions, *Eumetopias jubatus*, and New Zealand sea lions, *Phocarcos hookeri*, make postural changes to reduce exposure of the poorly insulated flippers in colder ambient temperatures (Gentry, 1973; Beentjes, 2006); huddling sea lions similarly reduce flipper exposure by aggregating with other animals. Because sea lions can dissipate heat across the trunk (Schmidt-Nielsen, 1997; Willis *et al.*, 2005), huddling behavior can provide an even greater advantage in cold conditions both by reducing surface exposure and by enabling the sharing of heat with proximate individuals (Gentry, 1973).

The thermal consequences of huddling behavior manifested in a greater temperature differential (ΔT) between a sea lion's body surface (T_b) and the substrate (T_a) when huddling. The inverse relationship between ΔT and T_a is not surprising, given that sea lions are homeotherms and maintain a relatively constant core body temperature (Irving, 1969). However, changes in perfusion across the blubber can modulate heat loss across the body surface, reducing heat loss in colder environments (Kvadsheim & Folkow, 1997; Schmidt-Nielsen, 1997). The significantly greater slope of ΔT versus T_a in huddled animals suggests a reduced need for heat conservation when huddling. Additionally, the benefits of huddling are reduced at warmer ambient temperatures, as illustrated by the intersection of the regressions as substrate temperatures approach body temperature (Fig. 2).

The thermal advantages of large huddles have been demonstrated for penguins, such that animals rotate positions to the center of large aggregations in order to survive harsh winters (Gilbert *et al.*, 2006, 2007, 2008). The energetic advantages of larger group sizes have also been shown for huddling rodents (Gilbert *et al.*, 2010). Accordingly, we observed a greater ΔT in larger sea lion huddles, in both seasons. It is interesting that the slope of the relationship did not differ between seasons, although the ΔT itself was higher in the winter because of colder substrate temperatures (Fig. 3). Large huddles can help animals reduce heat loss to the surroundings, but sea lions may also dump heat across the trunk when huddling in warm environments (Schmidt-Nielsen, 1997; Willis *et al.*, 2005). In both cases, participating in larger huddles can result in higher body surface temperatures. Huddling behavior can thus provide a thermal benefit in cold conditions, but is not necessarily detrimental in warm conditions. Therefore, the social behavior can be maintained year round without hindering the animals, and the behavior is increased when it provides a thermal advantage, as seen with much larger maximum group sizes in the winter.

The interaction between the social basis of huddling and its thermal consequences is illustrated by pairs of nursing females with their pups. By our definition of huddling, nursing mothers and pups were considered huddles because they comprised two animals with their bodies in physical contact.

However, there is a clear social cause for this physical interaction, as such contact is necessary for nursing to occur. As a result, mother-pup pairs comprised a compulsory huddle during times of nursing. Some pairs joined larger huddles, while others were observed to nurse and huddle on their own. In either situation, the thermal consequences of huddling can be modulated by both postural and physiological (e.g. blood flow) adjustments on the part of the sea lions (Hafez, 1965; Gentry, 1973; Schmidt-Nielsen, 1997), allowing nursing pairs to gain an advantage from physical contact in cold environments without experiencing detrimental effects in warmer environments.

Implications

Pinnipeds lead an amphibious lifestyle, and must maintain homeostasis in both aquatic and terrestrial environments. Given the thermal challenges of the marine environment and the evolution of effective insulation (fur and blubber) to offset heat loss (Liwanag *et al.*, 2012a,b), much research has focused on how pinnipeds stay warm in the water (Ohata, Miller & Kajimura, 1977; Gallivan & Ronald, 1979; Donohue *et al.*, 2000; Liwanag *et al.*, 2009; Liwanag, 2010) or when hauled out in polar environments (Grav, Blix & Päsche, 1974; Ørtisland & Ronald, 1978; Blix & Steen, 1979; Taugbøl, 1982). For temperate species, research on terrestrial thermoregulation has largely focused on strategies for preventing overheating (Irving *et al.*, 1962; Ohata & Miller, 1977; Campagna & LeBoeuf, 1988). However, cold air temperatures, lack of solar radiation, and wind chill can create terrestrial conditions requiring heat conservation, even for pinnipeds in temperate climates.

Here, we have shown that huddling constitutes a social behavior with thermoregulatory consequences for sea lions. Animals of all age classes can benefit from the behavior, but it may be especially important for sea lion pups. Smaller body size results in a larger surface area to volume ratio, such that pups have proportionately more surface area through which heat can be transferred; in addition, thermoregulatory capabilities are slow to develop in otariid seals (Donohue *et al.*, 2000; Liwanag *et al.*, 2009). Consequently, huddling may help pups to reduce their thermoregulatory costs while waiting on land for their mothers to return from foraging. Indeed, pups often huddle together in groups when their mothers are away (Ono, Boness & Oftedal, 1987; H. E. M. Liwanag, pers. obs.). Additionally, pups benefit from physical contact with their mother during nursing (Schusterman, Hanggi & Gisiner, 1992).

Huddling may also facilitate the drying of the fur when wet animals emerge from the water. During this study, we often observed wet animals actively seeking and joining existing huddles. As sea lions are capable of moving heat across the trunk (Schmidt-Nielsen, 1997; Willis *et al.*, 2005), wet animals can utilize the heat generated by other animals in the huddle to accelerate the rate at which their fur dries. Once again, this advantage could be especially important for young pups, as the natal pelt, or lanugo, tends to hold water and becomes thermally ineffective when wet (Irving *et al.*, 1962; Blix &

Steen, 1979; Blix *et al.*, 1979; Kvadsheim & Aarseth, 2002; Erdsack, Dehnhardt & Hanke, 2013).

The nature of huddling behavior in sea lions may be related to the type of insulation utilized. Within the otariid family, sea lions have a moderate blubber layer and sparse, wettable fur, whereas fur seals have thinner blubber and a dense, non-wettable pelage (Liwanag *et al.*, 2012*a,b*). The dense fur exhibited by fur seals forms an effective thermal barrier that cannot be bypassed by perfusion of the skin (Irving *et al.*, 1962; Schmidt-Nielsen, 1997), but the comparatively sparse fur of sea lions allows heat to dissipate across the pelage (Willis *et al.*, 2005). Several sea lion species (Australian sea lion, *Neophoca cinerea*; California sea lion, *Zalophus californianus*; Steller sea lion, *Eumetopias jubatus*; South American sea lion, *Otaria flavescens*) have been observed to huddle, and sea lions have been described as thigmotactic or positively thigmotropic, meaning the animals actively seek physical contact with conspecifics (Vaz-Ferreira & Palerm, 1961; Peterson & Bartholomew, 1967; Stirling, 1972; Gentry, 1973; Kirkwood & Goldsworthy, 2013). In contrast, huddling behavior has only been described for the adults of one fur seal species (Australian fur seal, *Arctocephalus pusillus*; Stirling & Warneke, 1971), and most adult fur seal species are observed to rest apart on haulouts rather than in huddles (Gentry, 1973; Kirkwood & Goldsworthy, 2013; D. P. Costa, pers. obs.). This difference in behavior may well be related to the ability to share heat with proximate individuals in huddles, which is dictated by the insulation of each group. As sea lions rely on blubber for insulation against the cold, the epidermis, a living tissue, remains at or near ambient temperature in most circumstances. Huddling would allow individuals to increase blood flow to the peripheral tissues and enhance tissue repair and maintenance.

Interestingly, only a few phocid seal species (harbor seal, *Phoca vitulina*; northern elephant seal, *Mirounga angustirostris*; southern elephant seal, *Mirounga leonina*) have been observed to huddle (Gentry, 1973; Riedman, 1990). Phocids have a sparse, wettable fur like sea lions, across which heat can be dissipated (Mauck *et al.*, 2003; Erdsack *et al.*, 2012); but they also have a much thicker blubber layer (Liwanag *et al.*, 2012*a,b*). It may be that the high thermal resistance of the overall insulation in phocids (Liwanag *et al.*, 2012*b*) and larger body sizes in many species reduce the need for huddling. The large-bodied walrus, *Odobenus rosmarus*, however, is considered positively thigmotactic, possibly because of its polar distribution and extremely sparse pelage (Scheffer, 1964; Riedman, 1990). Ultimately, more research on huddling in pinnipeds is needed to better understand interspecific differences in this behavior.

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