Thermal windows on the trunk of hauled-out seals: hot spots for thermoregulatory evaporation?

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Summary

Seals have adapted to the high heat transfer coefficient in the aquatic environment by effective thermal insulation of the body core. While swimming and diving, excess metabolic heat is supposed to be dissipated mainly over the sparsely insulated body appendages, whereas the location of main heat sinks in hauled-out seals remains unclear. Here, we demonstrate thermal windows on the trunk of harbour seals, harp seals and a grey seal examined under various ambient temperatures using infrared thermography. Thermograms were analysed for location, size and development of thermal windows. Thermal windows were observed in all experimental sessions, shared some common characteristics in all seals and tended to reappear in similar body sites of individual seals. Nevertheless, the observed variations in order and location of appearance, number, size and shape of thermal windows would imply no special anatomical site for this avenue of heat loss. Based on our findings, we suggest that, in hauled-out seals, heat may be transported by blood flow to a small area of the wet body surface where the elevation of temperature facilitates evaporation of water trapped within the seals' pelages due to increased saturation vapour pressure. The comparatively large latent heat necessary for evaporation creates a temporary hot spot for heat dissipation.

Key words: thermoregulation, thermal window, heat dissipation, evaporation, seal, *Phoca groenlandica*, *Phoca vitulina*, *Halichoerus grypus*.

Introduction

Due to the high heat capacity and thermal conductivity of water, the heat transfer coefficient in the aquatic environment is significantly higher than that of air at similar temperatures (Dejours, 1987; Nadel, 1984). Possible strategies of marine mammals to compensate for the high cooling power of water could be an elevated basal metabolism and various heat-conservation mechanisms. Although still controversial, heat loss models, as well as available physiological data, predict, at least for the large whales and adult pinnipeds, no need for elevated metabolic rates relative to terrestrial mammals (e.g. Donohue et al., 2000; Folkow and Blix, 1987; Gallivan and Ronald, 1979; Hokkanen, 1990; Watts et al., 1993; but compare Ryg et al., 1993). Among heat-retaining strategies, an insulating layer of blubber reduces thermal conductance while vascular countercurrent heat exchangers in the appendages prevent excessive convective heat flux from the body core to the skin (Pabst et al., 1999; Williams and Worthy, 2002). Furthermore, surface-to-volume ratios of marine mammals are, on average, 23% smaller than in terrestrial mammals of similar size (Innes et al., 1990), thereby reducing the body surface available for heat loss. However, these heat-conserving

adaptations must be circumvented when excess heat needs to be dissipated during exercise or in warmer waters. The amphibious pinnipeds may also face the problem of hyperthermia while on land (Hansen et al., 1995; Watts, 1992), which seals are often thought to solve by entering the cooling water (Tarasoff and Fisher, 1970). The question remains whether there are special heat-dissipation mechanisms that would allow pinnipeds to get rid of excess heat when hauled out.

In principle, excess body heat can be transferred to the environment by conduction, convection, evaporation and radiation, or a combination of these physical mechanisms. The conductive heat flow through blubber down the temperature gradient between body core and environment is proportional to the respective temperature difference and has been described by a modified Fourier equation (Kvadsheim et al., 1997). This equation calculates heat loss from parameters such as temperature difference across the blubber, body length, body radius and body core radius, and the thermal conductivity of blubber, which has often been determined using tissue samples from dead animals (Kvadsheim and Folkow, 1997; Kvadsheim

et al., 1994; Worthy, 1991; Worthy and Edwards, 1990). Most heat loss models are based on the assumption that at low temperatures seals reduce heat loss through blubber to this inevitable conductive transfer while excess body heat produced at higher ambient temperatures or during exercise can be transported to the body surface, bypassing the blubber layer by convectional blood flow (e.g. Hokkanen, 1990; Kvadsheim and Folkow, 1997).

Having reached the body surface, heat is transferred by thermal conduction to the surrounding medium, i.e. to the substrate the seal is lying on, to the nearest layers of surrounding air or to the water next to the body. For the body region in contact with the ground, heat transfer is limited to this conductive process (Hind and Gurney, 1998; Ohata and Whittow, 1974). A proportion of the heat reaching body surfaces not in contact with the ground may be bound in the water or air trapped within the seal's pelage, which thus may provide an isolating layer at least when the seal is dry (Sokolov, 1962; Tregear, 1965). The heat transferred to the medium next to the body can be swept away in a forced convection process with water or air passing by the seal's body surface. The heat capacity of a given volume of water is higher than that of the same volume of air by a factor of almost 3500, and the heat conductivity of water exceeds that of air by a factor of approximately 25 (but compare Nadel, 1984). These differences lead to considerably higher heat-transfer rates from a seal's warm body surfaces in water as compared with in air. By contrast, probably the highest heat loss from a hauled-out wet seal results from cutaneous evaporation that continues until the seal's pelage has dried (Hind and Gurney, 1998). The resultant heat flux depends on the temperature and vapour pressure of the air next to the wet seal's surface and on the water content of the pelt. In the absence of detailed measurements on evaporation from a seal's wet body, Hind and Gurney (1998) used a simplified approach to estimate the total heat flux as the volume of water evaporated multiplied by the latent heat of evaporation and divided by the time to dry. Although variations occur over the drying period, as well as with changing weather conditions (e.g. passive heating by incoming radiation or high air temperatures, which force evaporation, *versus* rain and cold conditions, which slow down evaporation), the major determinant of the amount of evaporative heat loss can be assumed to be the pelt's water content. Some terrestrial mammals increase evaporative heat loss by sweating or panting. However, probably due to the adverse evaporative water loss of these mechanisms and the normally permanent access to cooling water, this kind of evaporative heat loss seems relatively unimportant in seals (Boily and Lavigne, 1996; Folkow and Blix, 1992; Matsuura and Whittow, 1974).

In physiological terms, the major transport mechanism for controlling heat loss in seals seems to be the convective process of varying cutaneous blood flow (Hammel et al., 1977). When seals are exposed to high temperatures, vasodilation in vessels leading to the periphery results in an increased blood flow to the skin. The skin of phocid seals has numerous arteriovenous anastomoses, which presumably facilitate heat dissipation *via* high cutaneous blood flow (Bryden and Molyneux, 1978; Molyneux and Bryden, 1975, 1978).

It is still unclear which body regions function as the main avenues for the dissipation of excess heat. Heat loss from the appendages can be controlled by blood flow to the flippers, where vascular countercurrent heat exchangers that prevent excessive heat loss under cold conditions can be occluded when heat dissipation is necessary (Tarasoff and Fisher, 1970). Gallivan and Ronald (1979) indicated that 84% of heat loss from harp seals (*Phoca groenlandica)* was lost from the flippers. Ryg et al. (1993) assumed that 15–25% of the total heat loss of a resting seal in water is lost by free convection from the appendages and that this value can increase to 66–77% during exercise. Referring to heat loss per unit skin surface area, Kvadsheim et al. (1997) assumed that heat loss from the flippers of harp seals in ice water was equal to heat loss from a respective trunk area. While these studies refer to heat transfer when the seal's body is at least partly submerged, there is especially little information about mechanisms and body regions important for cooling in air, with its dramatically different thermal characteristics. Hart and Irving (1959) demonstrated that the flipper temperatures of harbour seals (*Phoca vitulina vitulina*), both in air and in water, were more variable and less dependent on ambient temperature than temperatures of the back. They assumed a separate control of heat flow through the appendages and concluded that the flippers are the most responsive surfaces in varying heat dissipation (Hart and Irving, 1959; Irving and Hart, 1957). Contrary to the assumption that excess heat is mainly lost through the appendages, Molyneux and Bryden (1975) assumed that equally distributed arteriovenous anastomoses in the skin of Weddell seals (*Leptonychotes weddelli*) make the whole body surface of seals important for heat dissipation. Krumbiegel (1933) noted that the body trunk is an important avenue for heat loss when a seal is out of water. Using simple thermometers held on the animals' skin, he described circular shaped areas on the trunk of elephant seals (*Macrorhinus leoninus*) that reached temperatures high above ambient air temperature. Similarly, Øritsland (1968) recorded surface temperatures using a thermocamera and found that in exercising harp seals on land, not only the flippers but also the body trunk can function as an important heat dissipater. Body surface areas with elevated temperatures were observed to appear near the base of each flipper and to spread out towards the main part of the trunk. Warm spots were also observed in irregular patterns on the trunk surface.

In terrestrial animals, the term 'thermal window' has mainly been used for the bare or sparsely haired thermoregulatory surfaces mainly in the appendages, which promote heat loss by increased peripheral blood flow (e.g. Klir and Heath, 1992; Williams, 1990). Accordingly, in marine mammals, this term has often been used referring to the appendages as poorly insulated body regions protruding from the streamlined body (e.g. Meagher et al., 2002; Noren et al., 1999). However, the

early observations of Krumbiegel (1933) and Øritsland (1968) might characterise thermal windows in seals more broadly as body surfaces functioning as temporary heat dissipaters during heat stress.

Assuming that thermal windows on the trunk of seals play an important role for thermoregulation in air, we used infrared thermography to determine the appearance and development of thermal windows in three species of phocid seals in various ambient temperatures. With respect to these results, we speculate about the possible thermoregulatory mechanism of thermal windows on the trunk of seals.

Materials and methods

Animals

Thermograms of four harp seals (*Phoca groenlandica* Erxleben 1777), four harbour seals (*Phoca vitulina vitulina* L.) and one grey seal (*Halichoerus grypus* Fabricius 1791) were recorded. The harp seals (Babette, 18 years; Tyler, 11 years; Jamie, 7 years; and Lenny, 1 year of age) were kept at the Ocean Sciences Centre (OSC) at St John's, Newfoundland, Canada in flow-through tanks fed with water from the adjacent bay. Therefore, the water temperature in the tanks was subject to the temperature in the adjacent bay. The harbour seals (Henry and Schorsch, 4 years; Nick and Malte, 2 years of age) were kept at the Marine Mammal Research Lab at Zoo Cologne, Germany. The grey seal (Laslo, 12 years of age) was kept at Zoo Münster, Germany. The water temperature of the concrete holding pools at Cologne and Münster depended on the seasonal ambient temperature.

Infrared thermography

Thermograms were obtained using an AGEMA (www:flir.com) 870 Thermocamera (temperature resolution 0.1 K, internal calibration). For all recordings, an AGEMA 20° SW infrared lens was used. The thermocamera was equipped with an LCD screen and was connected *via* a CU 800 V control unit to a computer provided with a TIC-8000 interface card. The thermographic images were stored on hard disk using AGEMA Software 'Computer Aided Thermography System' (CATS E 100).

The holding pools of the animals at the OSC and Zoo Cologne were drained for each recording session. The drainage of the last 40–50 cm of water in the holding pools lasted about 5 min for the pool at the OSC and about 15 min for the pool at Zoo Cologne. During this time, the seals were allowed to move freely in the pool, where they often splashed and tried to swim in the last shallow water, thus, this time was not accounted for as time without water. After complete drainage of the tank, the harp seals at the OSC were allowed to rest at the bottom of the comparatively small pool. At Zoo Cologne, all four harbour seals were fenced into a small area (2 m×4 m) at the bottom of the pool, a procedure that normally took about 5 min. At Zoo Münster, the grey seal was trained to leave the pool and to enter a fenced dry area (2 m×4 m).

Thermograms were taken on 12 days for *Phoca vitulina vitulina* (in summer and winter), on 6 days for *Phoca groenlandica* (in winter) and on 1 day for *Halichoerus grypus* (in winter).

In each session, thermograms were recorded for a period of 1.5–2 h, with the first thermogram being recorded as soon as possible after the tank was completely drained or the animal left the water. However, recording of the first thermogram was sometimes delayed due to technical reasons or haul-out positions of the seals that were inappropriate for thermographic recording. The front and hind parts of a seal's body were recorded separately to obtain sufficient resolution of the thermographic images, while the time between these recordings was kept to a minimum. The distance between the body surface and the infrared camera ranged between 0.5 m and 2.5 m. For each thermogram, the recording time with respect to the moment when the tank was just drained or the animal left the water ($t=0$ min) was noted.

Analysis of thermograms

Thermograms were analysed offline using AGEMA IRwin5.1 software. For all thermograms, a rainbow colour scheme was chosen. In order to create overview thermographic images of each seal at various points of time, images of the respective front and hind part of a seal's body were joined together. In a series of successive overview thermograms created this way, individual thermal windows were identified and their development followed over time by numbering them from cranial to caudal and according to the order of their appearance. Body regions surrounding the eyes and vibrissae were excluded from the analysis, as they are supposed to be actively heated even under water to secure sufficient sensitivity of the vibrissal system (Mauck et al., 2000) and not for simple thermoregulatory reasons. Analysis tools from the IRwin5.1 software were used to examine maximum, minimum and mean temperatures in defined areas, at certain points or along profile lines.
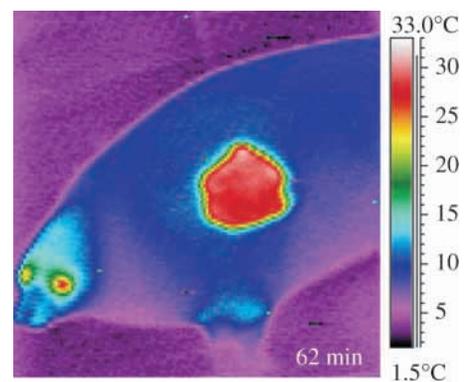

Fig. 1. Thermogram of the harp seal Tyler obtained 62 min after leaving the water. The thermal window on the left side of the seal is clearly visible and exhibits temperatures up to 24.2 K higher than those of the rest of the body surface.

Results

All seals showed thermal windows in every session, but thermal windows varied in size, number, shape and development. Individual thermal windows shared some common characteristics in all examined individuals, but the location and order of their appearance, as well as the pattern of their further development over time, showed variations between recording sessions even for a given individual. Thus, common characteristics of thermal windows are demonstrated here by showing some typical thermograms for the three species; further results are only described.

Appearance of thermal windows

Thermal windows on seals can be characterised as areas of the body surface clearly showing higher temperatures than the rest of the body (e.g. Fig. 1, red area). They are separated from the surrounding areas by narrow but regular transition zones to low temperatures (e.g. Fig. 1, yellow, green and blue areas at the edge of the thermal window).

In the first stage of development, thermal windows become visible in thermograms as small, often almost circular, areas with rather moderate temperature differences to surrounding areas (ΔT): for example, Fig. 2B, No. 6 [ΔT=12.7 K; maximum temperature of thermal window No. 6 ($T_{max}6$)=21.4°C]; Fig. 2C, No.11 (ΔT=8.5 K; $T_{max}11$=18.2°C); Fig. 3C, No. 3 (ΔT=8.3 K; $T_{max}3$=22.7°C); and Fig. 4B, No. 8 (ΔT=2.6 K; $T_{max}8$=17.7°C).

From their early stage to the fully developed stage, thermal windows enlarge with their centres remaining more or less in the same place and their maximum temperatures gradually rising to the temperature level of other already fully developed thermal windows in the same animal (e.g. Fig. 3A–B and Fig. 3C–D). Thus, the
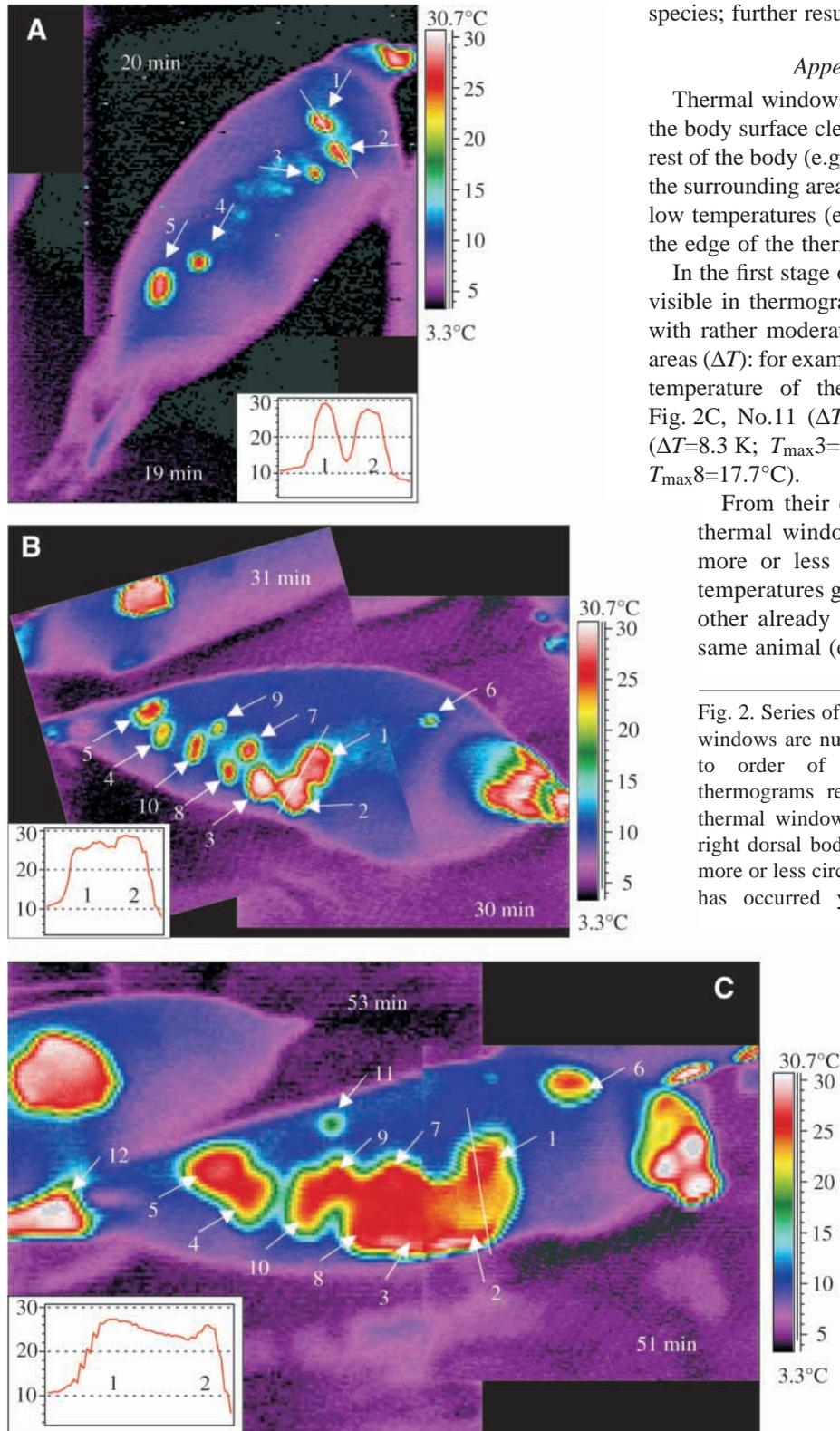

Fig. 2. Series of thermograms of the harp seal Jamie. Thermal windows are numbered from cranial to caudal and according to order of their appearance. (A) Arrangement of thermograms recorded after 19 min and 20 min. The first thermal windows on the seal's trunk have appeared on the right dorsal body side. Thermal windows are solitary and of more or less circular shape, and no fusion of thermal windows has occurred yet. The hind flippers show low surface temperatures. A temperature profile line (inset) reveals a sharp decrease in surface temperature between thermal windows 1 and 2. (B) Arrangement of thermograms recorded after 30 min and 31 min. Thermal windows on the right dorsal side of the seal's trunk have enlarged and partly fused (Nos. 1–3 and Nos. 4, 5; see also temperature profile line in inset), and new thermal windows have appeared (Nos. 6–10). (C) Arrangement of thermograms recorded after 51 min and 53 min. Thermal windows have further enlarged and fused to coherent areas (Nos. 1, 2, 3, 7, 8, 9, 10 and Nos. 4, 5, respectively; see also inset), and a new thermal window has just appeared (No. 11). Note that, at this time, hind flippers show high surface temperatures as well (No. 12).

Fig. 3. Series of thermograms of the harbour seal Nick showing the process of fusion of thermal windows in detail. (A) Thermogram recorded after 7 min. Two solitary thermal windows with surface temperatures 15 K higher than those in the surrounding areas have appeared on the left lateral neck region. A temperature profile line (inset) shows the first stage of fusion of these thermal windows. The surface temperature between thermal windows is elevated (approximately 21°C) but is clearly lower than temperatures within the thermal windows (approximately 29–31°C; see inset). (B) Thermogram recorded after 11 min. Fusion of thermal windows 1 and 2 is almost complete, but both thermal windows can still be identified. A temperature profile line shows only a slight decrease of temperatures between thermal windows (see inset). (C) Thermogram recorded after 50 min. Fusion is complete, the resulting thermal window has further enlarged and former thermal windows 1 and 2 can no longer be identified. A new thermal window (No. 3) with slightly elevated surface

temperatures (see also inset) has just appeared. (D) Thermogram recorded after 55 min. Thermal windows have further enlarged. The new thermal window, No. 3, almost reaches the peak temperature of the old thermal window, while the region in between the thermal windows is still cold (see inset).
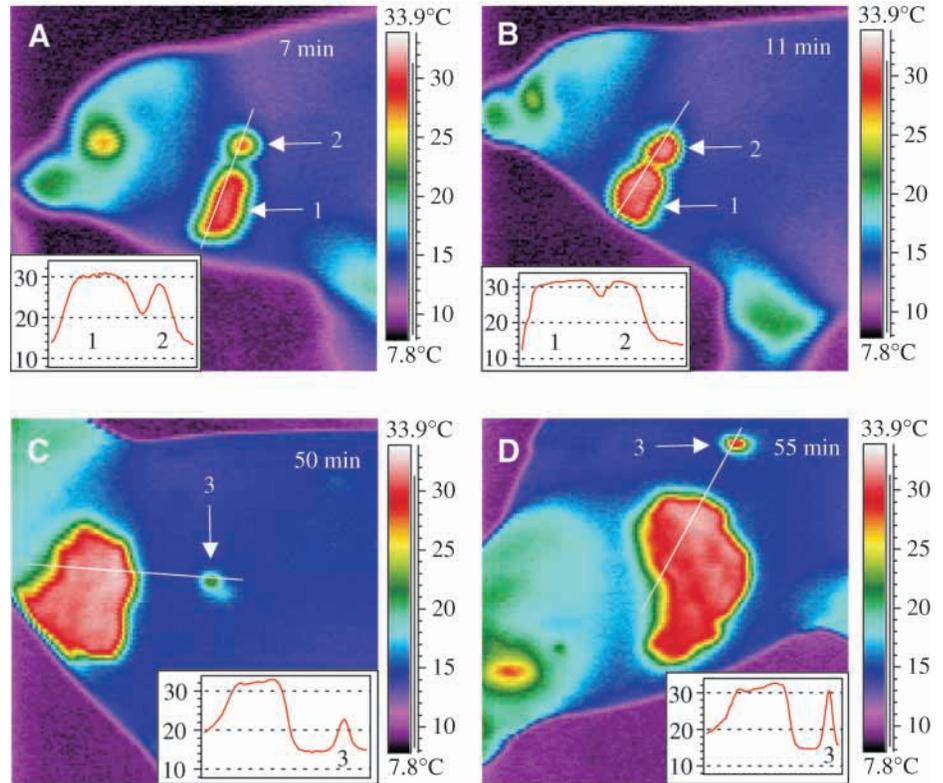
usage of the term 'fully developed thermal window' refers to temperatures of thermal windows rather than to size, such that at a given point of time various fully developed thermal windows of different sizes and ages reach similar maximum temperatures (Fig. 3A,D). The appearance of fully developed thermal windows can be described as sharply edged, often

still circular shaped, areas with clearly higher surface temperatures than in the surrounding areas: for example, Fig. 2C, No. 6 [ΔT=17.3 K; $T_{max}6$=25.5°C; maximum temperature of thermogram (T_{max}all)=29.8°C]; Fig. 3D, No. 3 (ΔT=16.2 K; $T_{max}3$=30.7°C; T_{max}all=32.7°C); and Fig. 4C, No. 8 (ΔT=10.4 K; $T_{max}8$=26.9°C; T_{max}all=29.1°C). The
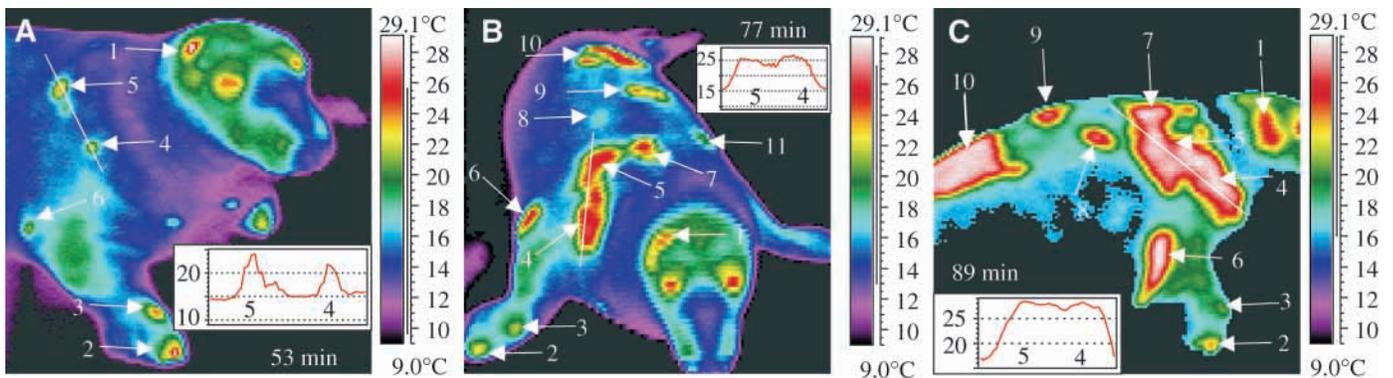
Fig. 4. Series of thermograms of the grey seal Laslo. (A) Thermogram recorded after 53 min. Thermal windows appear on the back of the head, the shoulder/neck region and the fore flipper. Thermal windows are clearly separated (see inset). (B) Thermogram recorded after 77 min. Thermal windows on the seal's body have enlarged and partly fused (Nos. 4, 5, 7; see also inset), while thermal windows on the right fore flipper remain comparatively cold. New thermal windows have just appeared on the seal's back (Nos. 8, 11). (C) Thermogram recorded after 89 min. Thermal windows on the seal's back have further enlarged and fused (Nos. 5, 7; see also inset), and thermal window 8 is fully developed.

maximum temperatures differed from session to session, and the highest temperature difference observed between a fully developed thermal window and the other body regions was 24.2 K (Fig. 1). Within the central areas of thermal windows, only small temperature variations occurred, as becomes clear from the plateau-like peaks in temperature profile lines (e.g. insets in Figs 2B,C, 3A–D, 4C). The edges of enlarging fully developed thermal windows are not widened but remain
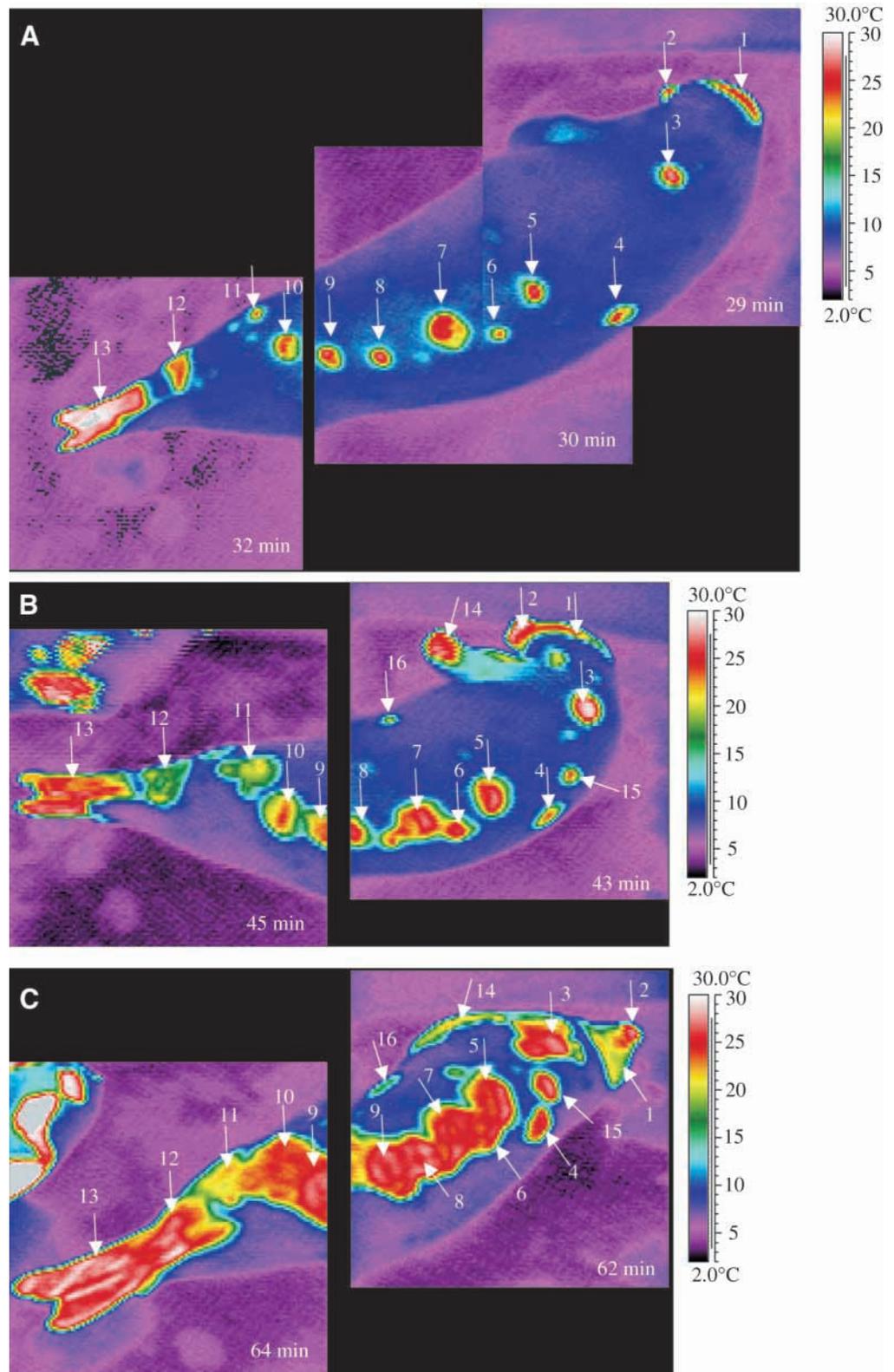

Fig. 5. Series of thermograms of the harp seal Jamie. Thermal windows are numbered from cranial to caudal and according to order of their appearance. (A) Arrangement of thermograms recorded after 29 min, 30 min and 32 min. Multiple thermal windows on the seal's trunk have appeared on the left dorso-lateral body side, contralateral to the side the seal is lying on. Thermal windows are solitary and of more or less circular shape; no fusion of thermal windows has occurred yet. The head (Nos. 1, 2) and the hind flippers (No. 13) show high surface temperatures as well, while the left fore flipper shows rather low temperatures. (B) Arrangement of thermograms recorded after 43 min and 45 min. Thermal windows on the seal's trunk have enlarged and partly fused (Nos. 6, 7 and Nos. 8, 9, 10), and new thermal windows have appeared (Nos. 14–16). (C) Arrangement of thermograms recorded after 62 min and 64 min. Thermal windows have further enlarged and fused to more or less coherent areas (Nos. 5–11 and Nos. 12, 13).

rather distinct, even when fusion occurs between neighbouring thermal windows (e.g. Fig. 2A,B, Nos. 1, 2; Fig. 3A,B, Nos. 1, 2; Fig. 5B,C, Nos. 4, 15). This is demonstrated, as profile lines through enlarging thermal windows show unchanging steep temperature declines at the transition zones to neighbouring colder areas. Over time, the enlargement and subsequent fusion of neighbouring thermal windows thus leads to irregular-shaped patterns of high-temperature areas stretching over the seal's body (e.g. Figs 2C, 4C, 5C, 6C,D), while the temperature of the remaining body surface stays largely unchanged or only increases slightly (Fig. 6).

At which sites of a seal's body surface do thermal windows occur?

Generally, thermal windows were observed to appear only in body regions that were in contact with air. By contrast, body regions that the seal was lying on (mainly the belly region or a body side) – although only observed as 'snapshots', e.g. when the seal rolled on its side – were never seen to show thermal windows but exhibited the same temperatures as the substrate. Thermal windows were often observed developing in body regions more or less contralateral to the body side that the seal was lying on (e.g. compare body sides that the seal is lying on and body sides of thermal windows in Figs 2, 5). Thus, the location of thermal windows seems to be, in part, dependent on the animal's haul-out posture.

The location of first appearance and the enlarging patterns of thermal windows were compared between recording sessions for each individual seal as well as among and within sessions for different individuals of the same species. Although thermal windows were not found to reappear in exactly congruent patterns on the seals' body surfaces, they tended to reappear in comparable patterns and similar body sites.

In the harbour seals, first thermal windows were mostly observed as comparatively small thermal windows clustered in the dorso-lateral region of the head, neck and cranial shoulder as well as the hind flippers (e.g. Fig. 3; compare Fig. 6A,E). In the harbour seal Henry, first thermal windows appeared in these body regions in all sessions (*N*=11 sessions). Similarly, the harbour seal Nick showed first thermal windows on the same body surfaces in all but one session (*N*=8 sessions); in this session, thermal windows appeared at first only on Nick's hind flippers and on his back. During five of eight sessions, the harbour seal Malte also showed first thermal windows as patterns of comparatively small thermal windows in the region of the head, neck and hind flippers, while in the remaining three sessions thermal windows in these regions were observed only after those appearing on the seal's back. During eight of 10 sessions, the harbour seal 'Schorsch' also showed first thermal windows on the neck, head and hind flippers, while in one session these regions showed thermal windows only in a later stage and in another session this seal already showed a coherent pattern of thermal windows covering the whole back to the hind flippers in the first thermogram.

In the harp seals, at least in some individuals, thermal windows were also found to reappear in comparable patterns and similar body sites. The harp seal Jamie predominantly showed patterns of comparatively small but gradually enlarging thermal windows that fused to coherent areas covering the dorso-lateral back region, contralateral to the side on which the seal hauled out (Figs 2, 5; thermograms of the other four sessions showing similar patterns are not shown). Similar patterns of rather small thermal windows in comparable body regions were also found in three sessions for the harp seal Tyler, while in three other sessions comparatively large thermal windows were observed mainly in the dorso-lateral body region of this seal, either as a solitary thermal window (Fig. 1) or in combination with some smaller thermal windows.

In two other harp seals, Babette and Lenny, patterns of comparatively small thermal windows were only observed in the dorso-lateral body regions in one session each, while Babette also showed rather large thermal windows on the contra-lateral body side in the same session, but only in the abdominal region in two other sessions. Similarly, Lenny was observed in three sessions to develop a few large-sized thermal windows in the abdominal region, while in a further session this seal showed large thermal windows in the dorso-lateral region and patterns of continuously enlarging small thermal windows in the same region in a third session, respectively.

In the only session performed with the grey seal Laslo, first thermal windows were also found in the head/neck and shoulder region but appeared on the back and on the upper side of the front flippers as well (Fig. 4).

Development of thermal windows on the surfaces of hind flippers was regularly seen in harbour seals (e.g. Fig. 6A–D), although in some sessions individuals with only sparsely heated hind flippers were also observed as well (e.g. Fig. 6E,F). Harbour seal front flippers were only occasionally observed to show high surface temperatures (see Fig. 6B–D). In harp seals, thermal windows on the surfaces of the hind flippers were regularly observed as well, although they were not necessarily among the first thermal windows to appear in these seals (compare Figs 2, 5). There was no obvious interdependence between the appearance of thermal windows on the hind flippers and on other body sites. Likewise, thermal windows on the surface of at least one of the front flippers have often been observed in harp seals (e.g. Jamie showed thermal windows on at least one of the front flippers during all six sessions, Lenny showed them during four out of six sessions, and Babette during three out of four sessions, whereas for Tyler no thermal windows were observed on the front flippers), but they were normally not among the first thermal windows to appear.

Seasonal differences in the development of thermal windows over time

Thermal windows appeared in thermograms while the respective regions of seals' pelages were still wet (i.e. there were no visible signs of drying or otherwise less water content of that pelage region as compared with neighbouring regions).

The time of appearance of first thermal windows on the wet animal depended upon ambient temperature. In summer, first thermal windows in harbour seals often appeared immediately after the pool had been completely drained. During six 'summer sessions' with high air temperatures (32–36°C) and comparatively high water temperatures (15.6–21.5°C), all seals already showed first thermal windows in the first thermogram recorded (six thermograms showing first thermal windows were taken immediately after the pool was drained, eight were taken up to 10 min later and a further eight were taken up to 21 min later). In all summer sessions, all seals were observed to develop rapidly enlarging thermal windows that fused to coherent areas covering a large part of the seal's body (e.g. Fig. 6A–D). In one of the summer sessions, the first coherent
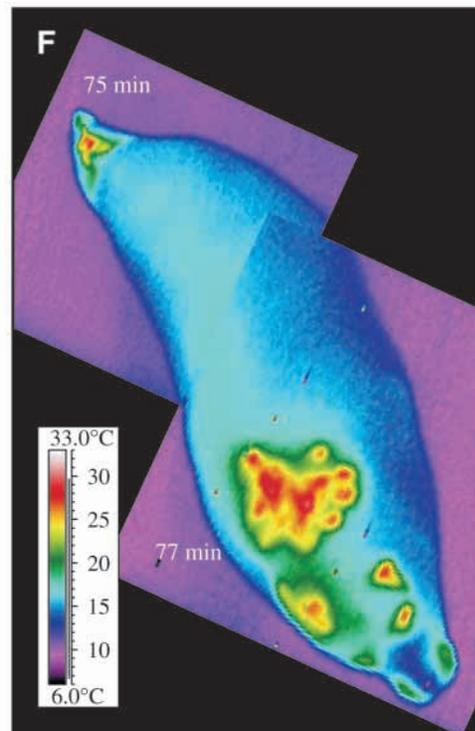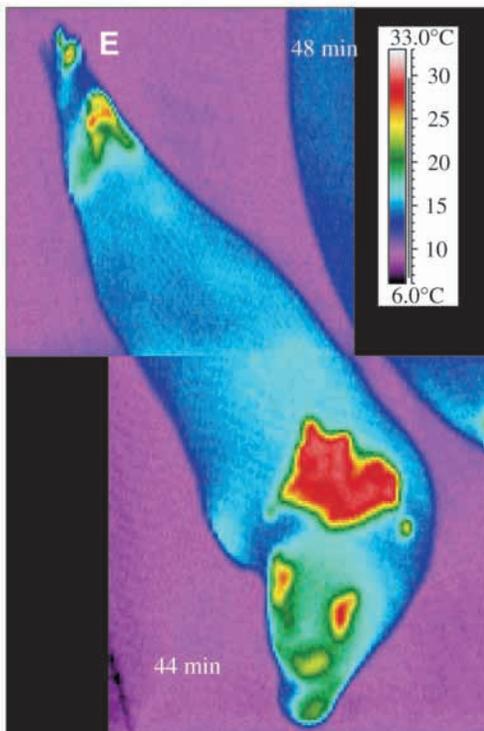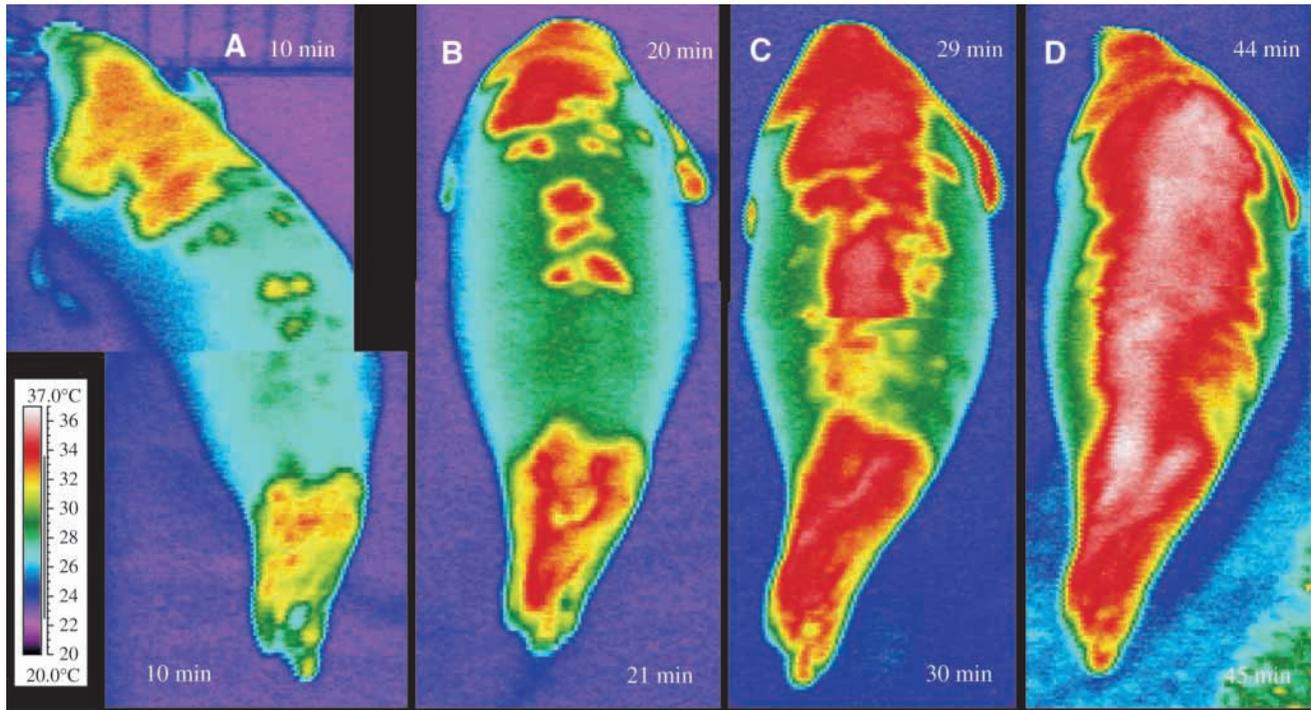
area resulting from fusing thermal windows could be recorded as early as 13 min after pool draining (for a comparable stage, see Fig. 6C); the latest time of fusion to a coherent area was after approximately 89 min.

By contrast, during four 'winter sessions' with low ambient temperatures (air, 5–12°C; water, 5.7–11.4°C), the first appearance of small, mostly solitary, thermal windows was observed only after 7-51 min (i.e. five thermograms with first thermal windows were recorded 7–20 min after pool drainage, seven thermograms with first thermal windows were recorded only 20–45 min after the pool was drained, while one seal was observed to show first thermal windows only after 51 min). In none of the winter sessions (duration, 66–93 min) did harbour seals show thermal windows that had enlarged and fused to coherent areas covering a larger part of a body side. In one seal, even a slight reduction of size and mean temperature in a fully developed thermal window could be observed (Fig. 6E,F).

A comparison between summer and winter was not possible for the harp seals and the grey seal, as all thermographic examinations of these seals were performed during the winter. In the harp seals, first thermal windows appeared after a rather broad range of time (5–51 min), while in the grey seal first thermal windows appeared only after 53 min (Fig. 4A).

Occasional observation of 'steaming'

During some of the thermographic sessions performed with the harbour seals and harp seals in winter, condensed water vapour could be observed rising from the seals' body surfaces. This 'steaming' only occurred after a thermal window became visible in the thermographic recordings. The source of water vapour condensing in the cold air was obviously the region of the seals' pelages where the thermal window appeared. However, due to changes in the seals' postures or due to weather conditions such as slight breezes, it was often difficult to determine the exact sources of the rising water vapour. Circumstantial evidence that the water vapour was rising from the thermal windows was nevertheless provided by the fact that these body surfaces dried much faster than the rest of the seals' bodies. During the summer sessions, steaming was never observed.

Discussion

Thermal windows have been described by infrared thermography both in humans and in various terrestrial animals (e.g. Cena and Clark, 1973; Øritsland et al., 1974; Phillips and Heath, 1992; Ring, 1990; Williams, 1990). However, high body surface temperatures may not always occur in the most favourable position for heat dissipation. The location of thermal windows is often determined by special physiological functions that require metabolites, oxygen or heat, all of which are easily transported by blood flow. For example, although foot pads of polar bears are thought to act as circulatory-controlled heat-dissipating areas, this might mainly serve to avoid tissue freezing when walking on ice (Øritsland et al., 1974). An interesting compromise between the needs of thermoregulation and sensory physiology has been found in seals and dolphins (Dehnhardt et al., 1998; Mauck et al., 2000), which provide their eyes and vibrissal follicles with warm blood to secure their function in the cold aquatic environment. In barn owls (*Tyto alba*), McCafferty et al. (1998) demonstrated highest surface temperatures in the facial disc, which is likewise thought to result from heating of the cranially located sensory organs. Thermoregulation for reproductive purposes has been described for dolphins and seals: cool venous blood returns from the body surface to the deep cavities to protect reproductive organs within the body core from high temperatures (Pabst et al., 1995; Rommel et al., 1992, 1994, 1995).

However, thermal windows serving as heat sinks tend to be located at the most appropriate body sites for heat dissipation. Easy to regulate by blood flow to the periphery, heat is best transferred from body surfaces of terrestrial animals *via* radiation, convection due to wind ('wind chill') or evaporation of sweat. Consistent with this view, thermal windows are documented on appendages offering high surface-to-volume ratios, such as the ears of elephants functioning as radiator-convectors (Phillips and Heath, 1992; but compare Williams,

Fig. 6. Series of thermograms of the harbour seal Henry obtained in summer (A–D) and winter (E–F). Note that the temperature range represented by the colour scale has been altered (16.8–37.0°C in A–D *versus* 6.0–33.0°C in E–F) in order to guarantee the best temperature resolution. (A) Arrangement of thermograms recorded after 10 min. Thermal windows have appeared on the hind flippers and in the dorsal neck/shoulder region (temperature range, 29.9–33.7°C), some comparatively small thermal windows have just appeared on the seal's back (31.1–32.6°C), while the other body regions are clearly colder (25.1–29.0°C). (B) Arrangement of thermograms recorded after 20 min and 21 min. Thermal windows have enlarged with slightly increased temperatures (30.2–35.1°C), and thermal windows are also visible on the right fore flipper (31.3–33.8°C). Although the area between thermal windows on the seal's back is already comparatively warm (approximately 29.3°C), the remaining body surfaces are still rather cold (25.6–28.1°C). (C) Arrangement of thermograms recorded after 29 min and 30 min. Thermal windows fuse to a rather coherent area (temperature range, 30.9–35.6°C), while the remaining body surfaces are still clearly colder (26.3–28.3°C). (D) Arrangement of thermograms recorded after 44 min and 45 min. Thermal windows have completely fused to a coherent area covering the seal's back and flippers (30.4–37.1°C). The lateral body regions clearly remain colder (26.2–28.1°C). (E) Arrangement of thermograms recorded after 44 min and 48 min. Some rather small thermal windows are visible on the seal's head and hind flipper region, while a fully developed thermal window covers the dorsal neck region (22.4–30.3°C). (F) Arrangement of thermograms recorded after 75 min and 77 min. While thermal windows seem not to have changed size, the thermal window covering the dorsal neck region shows a similar range of temperatures (22.3–30.1°C) but, on average, has become clearly cooler because high temperature areas within the thermal window have decreased in size. It can be speculated that this thermal window has already been closed and the respective body surface is now being cooled by the rather cold ambient air.

1990), the pinnae of rabbits (Mohler and Heath, 1988), the pinnae and legs of foxes (Klir and Heath, 1992) and the legs of reindeer (Folkow and Mercer, 1986; Johnsen et al., 1985).

Thermal windows in permanently submerged marine mammals are found in peripheral body sites such as flukes and dorsal fins of cetaceans (Kanwisher and Ridgway, 1983; McGinnis et al., 1972; Meagher et al., 2002; Noren et al., 1999). These body sites protrude from the streamlined body so that thermal conduction and convection become the most effective heat-transfer mechanisms while diving and swimming. For example, heat flow from the tip of the pectoral flippers of the Atlantic bottlenose dolphin (*Tursiops truncatus*) increased 3–4-fold after swimming at a speed of $1\ \mathrm{m\ s^{-1}}$ for 6–7 min (Hampton et al., 1971). There is an obvious conflict between the thermoregulatory response to excess heat requiring increased superficial blood flow and the diving response demanding decreased blood flow for oxygen conservation. The solution is a hierarchy of these responses in dolphins, which are able to delay heat dissipation through thermal windows at the dorsal fin and the fluke blade until the post-dive recovery period (Noren et al., 1999; Williams et al., 1999). Similarly, thoracic body surface temperature depends on the diving cycle in the Antarctic fur seal (*Arctocephalus gazella*; Boyd, 2000), although the temperatures measured on the dorsal thorax are thought to differ markedly from those on the appendages that function as the main thermal windows.

Heat dissipation in hauled-out seals represents a kind of dilemma. The mechanisms working on the basis of the high heat transfer coefficient to water are ineffective while on land, and heat-transfer mechanisms working effectively in terrestrial animals seem insufficient or unavailable in the mainly water-adapted pinnipeds. It is thus tempting to speculate by which mechanism thermal windows on the trunk of seals could offer a solution to this dilemma.

In our study, thermal windows were observed in all seals during all sessions. Our results generally confirm the earlier findings of Krumbiegel (1933) on an elephant seal and Øritsland (1968) on a harp seal. Comparing thermograms obtained at an ambient temperature of –13°C, –5°C and 0°C, Øritsland (1968) concluded from the increasing areas with high surface temperature that these warm body sites function to increase heat dissipation. Our result that initial size and growth of thermal windows in seals depended on season and ambient temperatures is consistent with that conclusion and strongly suggests a thermoregulatory role. However, the obvious variations in size, number, shape, order and location of appearance and in the pattern of development would not suggest a special anatomical site for heat transfer by thermal windows on the trunk of seals. This is consistent with a study on Weddell seals by Molyneux and Bryden (1975), who described arteriovenous anastomoses (AVAs) that are probably important for heat dissipation but could not find any difference in structure, distribution and density of AVAs in body and flipper skin.

The observation of Krumbiegel (1933) of a 'steaming' hauled-out elephant seal, as well as our own observations on colder days, made the mechanism of heat transfer obvious: after a thermal window became visible in the thermographic images, condensed water vapour could be observed rising from the respective pelage region. Thermal windows appeared in thermograms while the respective regions of the seal's pelage were still wet (i.e. no visible signs of drying or otherwise less water content as compared with neighbouring regions could be observed). Furthermore, it was obvious that these regions subsequently dried much faster than did the rest of the seal's body. Thus, a thermal window was not the result of a progressive drying process that started in that region of a seal's pelage and thereby reduced the amount of water to be heated there, but, rather, was the reason for the drying process in that region. Thus, 'forced evaporation' of water contained in the seal's pelage seems to be the mechanism responsible for heat loss from thermal windows (for a simplified estimation of evaporative heat flux, see Hind and Gurney, 1998).

It might be a thermoregulatory advantage for a seal to restrict thermal windows to comparatively small areas. A seal's pelage can store a limited volume of water per unit body surface, and the amount of heat to be dissipated from the seal's body surface by heating and finally evaporating this coolant should be maximised but controlled over time. The saturation vapour pressure giving the partial pressure of vapour directly over a water surface when no net transfer of water molecules occurs depends only upon temperature. The higher the temperature, the more water molecules can escape from the liquid water to the vapour space. According to the Clausius–Clapeyron relationship, saturation vapour pressure grows by a factor of approximately two with every 10 K of temperature elevation (e.g. Rogers and Yau, 1989). Raising the temperature of water contained in a comparatively small area of pelage to a higher level (i.e. opening a thermal window), could thus be more favourable in terms of heat dissipation than spending the same energy to heat the water at the whole body surface only by a few degrees. The increasing rate of evaporation made possible by the high saturation vapour pressure over a thermal window could be used to dissipate excess heat by the conversion of liquid water into the gaseous phase. After the water has completely evaporated from a thermal window, the air within the pelage of the now dry region could be passively heated by the surrounding atmosphere or could be heated to even higher temperatures by solar irradiance. Blood flow should now be directed to another surface area to force evaporation (i.e. another thermal window could be opened) or blood flow to the periphery could be completely restricted if no more heat has to be dissipated, for example on cold days. How this kind of thermoregulation is physiologically controlled remains to be examined.

This strategy for dissipation of heat might be advantageous for reasons concerned with thermoregulation, circulation physiology and ecology. From a thermoregulatory point of view, dissipating heat by evaporating water from comparatively small thermal windows might work earlier at an efficient level, might be more regular over time and, furthermore, might be more accessible to spontaneous

physiological control than heating the whole body surface at once. Heating the water volume trapped within the whole pelage slowly but at once would result in comparatively low heat dissipation per unit body area during a first stage after leaving the water, because available excess heat is then distributed and heats the water only according to its heat capacity (approximately 4.2 kJ K^{-1} kg^{-1}). Having eventually reached a temperature, and thus a saturation vapour pressure, necessary for evaporation during a second stage, the evaporating water within the pelage could withdraw heat from the seal's body according to the comparatively huge latent heat of vaporisation (approximately 2.5×10^3 kJ kg^{-1}). While heat dissipation to the water within the whole pelage might be sufficient for the seal's thermoregulatory needs during the first stage, however, during the second stage, there might not be enough excess body heat to satisfy the huge needs of latent heat of vaporisation for the whole water volume trapped within the pelage to evaporate more or less at once. Thus, in the second stage, the seal might lose too much heat if it would allow excessive blood flow to the periphery.

From a physiological point of view, it might be advantageous for circulatory reasons to restrict an enhanced cutaneous blood flow to thermal windows. Although many pinniped species have comparatively large volumes of blood at their disposal (Kooyman, 1989), increased blood flow to the periphery could be disadvantageous with respect to the increased cardiovascular requirements such as higher heart rate and overall cardiac output securing the maintenance of a blood pressure level necessary for a sufficient perfusion of all other important organs. With respect to the requirement of a restricted blood flow as part of the diving response, it could also be advantageous for a seal to stay physiologically prepared for a flight into the water that might become suddenly necessary (compare Noren et al., 1999; Williams et al., 1999). According to our own experience, dry seals have a characteristic smell as compared with wet seals. Thus, it could be adaptive at least for some arctic seals not to heat a large body surface in order to avoid being detected by polar bears.

In conclusion, thermal windows on the trunk of hauled-out seals might be used to effectively and continuously dissipate excess body heat by controllable evaporation. The seal's pelage might serve as a kind of storage site for water used as an evaporating coolant.

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