How dolphins use their blubber to avoid heat stress during encounters with warm water

M. E. Heath and S. H. Ridgway

Heath, M. E., and S. H. Ridgway. How dolphins use their blubber to avoid heat stress during encounters with warm water. Am. J. Physiol. 276 (Regulatory Integrative Comp. Physiol. 45): R1188–R1194, 1999.—Dolphins have been observed swimming in inshore tropical waters as warm as 36–38°C. A simple protocol that mimicked the thermal conditions encountered by a dolphin moving from cool pelagic to warm inshore water was used to determine how dolphins avoid hyperthermia in water temperatures (Tw) at and above their normal core temperature (Tc). Tw (2 sites), rectal temperature (T rect; 3 depths), and skin temperature (Tsk; 7 sites) and rate of heat flow (4–5 sites) between the skin and the environment were measured while the dolphin rested in a chamber during a 30-min baseline and 40–60 min while water was warmed at ~0.43°C/min until temperatures of 34–36°C were attained. Instead of the expected increase, Tc consistently showed declines during the warming ramp, sometimes by amounts that were remarkable both in their magnitude (1.35°C) and rapidity (8–15 min). The reduction in Tc occurred even while heat loss to the environment was prevented by continued controlled warming of the water that kept Tw slightly above Tsk and while metabolic heat production alone should have added 1.6–2°C/h to the Tc. This reduction in Tc could only be due to a massive redistribution of heat from the core to the blubber layer.

Tursiops truncatus; bottlenose dolphin; core temperature; heat flow; heat storage

SEVERAL ANATOMIC and physiological adaptations with probable thermoregulatory function have been described in dolphins. These include a streamlined body with a highly reduced total surface area for their total mass and a thick blubber layer that provides insulation (17, 23). In addition, bottlenose dolphins have a metabolic rate that is 1.6 to 2 times greater than that of terrestrial mammals of the same body mass (17, 24). Descriptions have been published of highly specialized vasculature in the appendages that likely functions in temperature regulation. Included are multiple veins surrounding arteries in all of the appendages (3, 14, 21, 23), suggested by Scholander and Schevill (21) to facilitate heat retention in the body, with countercurrent heat exchange from the warmer arterial blood to the cooler venous blood, because the latter flows back to the core. Also, the high degree of vascularization in the dorsal fin, pectoral flippers, and flukes (3, 14, 23) implies the importance of these appendages for heat loss. Another vascular countercurrent heat exchanger is suggested to cool selectively the dolphins’ internalized testes and thereby protect spermatozoa (18).

Although these many reports have focused on describing individual adaptations, there have been no studies demonstrating how dolphins manage to function in, and often move between, the wide range of water temperatures (Tw) they encounter on a daily or seasonal basis. Dolphins have been observed in a wide range of ambient T w from 1.1 to 31.1°C (7, 8) and even 36–38°C in shallow tropical waters (Ridgway, personal observation). The latter observation is remarkable because these temperatures are at or above core temperatures reported for dolphins, and, because they are submerged in water, dolphins cannot, as terrestrial mammals can, use evaporation to lose heat. This observation was the stimulus for the present investigation.

Our study used a simple protocol of steadily warming ambient water under highly controlled conditions to simulate the thermal conditions encountered by a dolphin moving from cool pelagic water to warm inshore or estuarine water. The dolphins responded to warmer water with a massive redistribution of heat within their bodies from the body core to peripheral tissues. This was demonstrated by significant reductions in core temperature instead of the pronounced increase that should have occurred due to metabolic heat production in conditions in which they could not lose heat to the environment. This unique thermoregulatory response acts to delay the onset of hyperthermia or heat stress for an hour or longer even during encounters with 36°C water. Clearly it is this mechanism that allows dolphins to explore and forage safely in the very warm summertime water that exists inshore in shallow tropical gulfs, bays, and estuaries.

METHODS

We studied six bottlenose dolphins (Tursiops truncatus, 139- to 238-kg body mass, see Table 1). The animals used in these studies were maintained under Federal Regulations promulgated under the Animal Welfare Act and in accordance with the National Research Council Guide. Protocols were approved by appropriate Institutional Animal Care and Use Committees. The dolphins were selected for their ability to rest quietly on a fleece-lined sling of a transport chamber (0.76 m deep x 0.8 m wide x 3.3 m long) while submerged in water to ~3-4 in. below the base of the dorsal fin (Fig. 1). A 1⁄2-horsepower pump (Hayward Pool Pump, Fairmont, CA) was used to continuously circulate the water in the chamber and through a J acuzzi heating system (One series; Teledyne Laars, Moorpark, CA) that was turned on and off as needed to carry out the protocol. The 1- to 2-h-long experiments included ~30 min of baseline when the dolphins were in San Diego Bay-temperature water (15–22°C) and a 30- to 60-min...
period when the $T_w$ was warmed at a rate of $\sim 0.43^\circ C/min$. The water was warmed to 34–36°C and maintained at this plateau level for another 20–60 min, specifically to observe the effects of exposure to warm water on core temperature, before return to baseline level.

$T_w$ was measured at both ends of the chamber in well-circulated water. Skin temperatures ($T_{sk}$) were measured, with thermocouples insulated from the water on the fluke, dorsal fin, pectoral flippers, and up to four locations along the trunk. Rectal temperatures ($T_r$) were measured with a probe that incorporated three thermocouples positioned at 8-cm intervals from the tip. This type of probe was used because of the report by Rommel et al. (18) of a vascular countercurrent heat exchanger 15–20 cm long adjacent to the colon in a region 15–35 cm past the anus, which could significantly affect measurements of $T_r$ at depths $\leq 40$ cm. Rectal probe depth was measured at the end of each experiment and ranged from 34 to 56 cm past the anus. It was $\leq 40$ cm deep in 8 of the 10 experiments. Heat flow through the skin was measured with heat flow disks (Concept Engineering, Old Saybrook, CT) applied to the fluke, dorsal fin, pectoral flippers, tail stock, and lateral trunk regions. The heat flow disks were held in place continuously at a standard constant pressure; a heat-conductive paste applied between the heat flow disk and the skin ensured complete thermal contact with the skin. The signal in millivolts collected from each heat flow disk was converted to Watts per square meter using the calibration coefficient unique to each disk and supplied by the manufacturer. Data were collected at 1-min intervals throughout the experiment using a Fluke data logger (model 2625A) and portable computer. Respiratory frequency was monitored by recording the number of breaths taken during 5-min periods. An electrocardiogram was monitored throughout the experiments for safety reasons.

### RESULTS

Figure 2 provides graphs of a representative experiment on one dolphin. Table 2 provides a summary of results from all 10 experiments, including air temperature, baseline $T_w$, the depth of the rectal probe, $T_r$ measures from all three thermocouples during the 5 min of baseline before initiation of the warming ramp, the minimum $T_r$ observed at each site that occurred during the warming ramp or plateau, and mean respiratory frequency during baseline and during the warming ramp and plateau. The mean difference in $T_r$ between the baseline values and the minimum values is also given. It was calculated as the mean of the three site means given for baseline minus the mean of the minima at the same three sites that occurred when the water was warmed. A summary of heat flow data is provided in Table 3. Included are the calculated mean heat flow during the baseline and the calculated mean of data collected from the onset of the warming ramp to the initiation of the plateau.

Figure 2 illustrates the result of the experiment in which the most pronounced reduction in $T_r$ occurred (experiment 1 in Table 2), and the following describes the events in detail. During the baseline, $T_w$ was $\sim 15.5^\circ C$, $T_r$ (Fig. 2A) were between 36.6 and 36.7, $T_{sk}$ (Fig. 2B) of submerged regions were 15.5–17°C, and heat was flowing out of the dolphin (Fig. 2C) at a steady, low rate (10–80 W/m², depending on the site). Warming of the water began at 22 min. During the initial 15–19 min of the warming ramp (time = 22 to 37–41 min), $T_r$ (Fig. 2A) did not change noticeably. $T_{sk}$ (Fig. 2B) rose but lagged slightly behind the rise in $T_w$, and the direction of heat flow (Fig. 2C) was reversed, flowing from the water to the dolphin as shown for the pectoral flipper, flukes, and body wall. The dorsal fin was out of water, so its temperature and heat flow continued at near baseline levels. However, a change occurred beginning at $\sim 15$ min into the warming ramp (time = 37 min) and at a $T_w$ of $\sim 21^\circ C$, when $T_r$ began to decline. The decline was initially slow. As
$T_w$ reached 27–28°C (time = 48 min), $T_r$ began a more conspicuous decline that continued for 14 min. $T_r$ reached a minimum of 35–35.8°C (top), which was 0.9–1.3°C lower than their baseline levels. Within 4–8 min, $T_r$ began to rise again, at a rate of $\sim 0.03^\circ C/min$, while the warming ramp continued. Also occurring within the period when $T_r$ decline were plateaus and then declines in the rate of heat gain from the water for all submerged surfaces. Because this occurred while the warming ramp was continuing, the only possible explanation is a rise in temperature of peripheral tissues that was greater than the rise in $T_w$. The rate at which $T_r$ should increase during the experiment, based on previously measured resting metabolic rates in bottlenose dolphins (15, 23) is shown in Fig. 2. Given the metabolic heat production of dolphins, it would have been just as remarkable an observation if there had been no change in core temperature (rather than a reduction) during the exposure to warm water. However, it was the observed decline in core temperature that revealed the mechanism dolphins are using to tolerate very warm water.

The summary of $T_r$, respiratory frequency, and heat flow data provided in Tables 2 and 3 reveals the consistency among all the experiments. $T_r$ declined in all 10 of the experiments (mean $\pm$ SD, 0.5 $\pm$ 0.27; range of mean difference, 0.33–1.07°C) during either the warming ramp or beginning of the plateau. Because the timing of the decline in $T_r$ differed between experiments, averaging $T_r$ for all experiments would obscure rather than reveal the response. As is shown in Fig. 2B, the $T_s$ in all experiments followed, but some measures lagged slightly behind, $T_w$. Trends in heat flow (Table 3) were also similar in all experiments. Baseline respiratory frequency was between 1.4 and 4.1 breaths/min and either decreased or increased by <1 breath/min during warming.

**DISCUSSION**

Although observations of wild dolphins swimming in very warm water had shown us that these animals have some mechanism for short-term heat tolerance, the nature of the mechanism discovered in these experiments was completely unexpected. The dolphins consistently showed declines in $T_r$ during encounters with warm water in each of 10 experiments (Fig. 2A and Table 2). During warming ramps and plateaus of 70–140 min combined duration, $T_r$ increased by no more than 0.2°C above baseline levels and only after an initial decline in $T_r$. This is surprising because core temperature should have increased by 1.6 to $\sim 2.0^\circ C/h$ from resting metabolic heat production alone in such conditions in which the dolphins cannot lose their...
metabolic heat to the environment. Note that the metabolic rate of bottlenose dolphins is 1.6 to 2 times higher (15, 23) than in most mammals of similar mass (9).

Although the reduction in $T_{re}$ was unexpected in this situation, the $T_{re}$ recorded in this study (35.4–37.3°C) were always within the range of values reported previously for bottlenose dolphins (33.4–38.8°C) (4, 10, 11, 13, 15, 19). Also, even the largest decline in $T_{re}$ observed, 1.3°C, is less than one-half the 3°C decline in core temperature observed in a dolphin returned to its pool after it had been removed on a padded stretcher for 25 min (10). Heat flow levels recorded during baseline were within the range previously reported (4).

We reject, for the following several reasons, the possibility that the observed reductions in $T_{re}$ represent only a transient shift in local tissue temperature in that region of the colon where a countercurrent heat exchanger occurs (18). 1) In 8 of the 10 experiments, the deepest measure of $T_{re}$ was made at depths of 40–56 cm, well beyond the location (15–35 cm past the anus) of the heat exchanger (18) and, therefore, representative of true core temperature. 2) $T_{re}$ did not rebound sharply after reaching its lowest level, as would be expected if it were due only to local shifts in tissue temperature that are not representative of core temperature. 3) $T_{re}$ increases slowly during the remainder of the warming ramp and plateau in $T_w$ and at a rate (0.026–0.033°C/min) to be expected from metabolic heat production in bottlenose dolphins (16, 24). 4) The heat exchanger depends on the heat loss from the flukes and dorsal fin region (18). In preliminary experiments, declines in $T_{re}$ of 0.8–0.9°C were recorded in dolphins submerged in warm water and gaining heat from both of these regions. 5) In the experiment shown in Fig. 2, the flukes are gaining heat and only the dorsal fin region is losing heat. If this area is, generously, estimated as ~0.50 m² at the mean rate of heat flow of 33.64 W/m², no more than 16.82 W were lost from this skin-air interface. This amount of heat loss can cool, by the requisite 2°C (sum of metabolic heat and reduced $T_{re}$), only 2.1 kg of tissue in this 238-kg dolphin. 6) It is impossible for the blood from the dorsal fin region to mix with blood from the flukes (which are gaining heat) and traverse >40 cm of warmer tissues before reaching the rectal region and not gain any heat en route. 7) Even if a 2.1-kg region of tissue could have been cooled by 2°C, it is impossible for it to cause, by tissue conduction, a similar reduction in tissue temperature at the 49-cm depth of the deepest thermocouple, located 9–14 cm beyond the described heat exchanger. 8) Heat is lost from the dorsal fin region throughout the experiment at a constant rate. Thus its effect on $T_{re}$ should be constant, and not confined to only 15 min in the middle of the experiment. It is concluded, therefore, that the decline in $T_{re}$ in response to warm water represents a true reduction in the temperature of the body core.

It is also clear that these reductions in core temperature were not due to heat loss to either the water or the air. During the warming ramp in particular, the changes in $T_{sk}$, lagged slightly behind the changes in $T_w$ (Fig. 2B). This is as expected because the water was being warmed externally and circulated through the tank. Because of this, heat flowed from the water to the
dolphins as documented by the heat flow measurements (Fig. 2C) and in accordance with the laws of heat flow and thermodynamics. The only exception occurred in Fig. 2, for the pectoral flipper over a 14-min period during the warming ramp (time = 46–60 min) when this dolphin raised the flipper T\[sub\]sk slightly (>0.5°C) above T\[w\] and heat flow was temporarily from the flipper to the water at <30 W/m\[sup\]2. Because the surface area of the flippers is ∼0.15 m\[sup\]2, this amounts to ∼4.5 W (or 4.5 J/s) leaving the dolphin. This was the only experiment in which this was observed, and it cannot account for the large decrease in T\[re\]. Likewise, the 16.82 W of heat loss from the region of the dorsal fin exposed to air cannot account for the amount of heat lost from the dolphin’s core. In contrast, during this same 15-min period when T\[re\] declines, an estimated 150.4 W was being gained from the environment via the flukes and body surface.

Finally, there is no indication that dolphins increase evaporative heat loss from their respiratory tract by panting during exposure to warm water. Baseline respiratory frequency ranged from 1.4 to 4.1 breaths/min for all experiments (Table 2). During the warming ramp and plateau, respiratory frequency sometimes increased and sometimes decreased, but by <1 breath/min. The breaths taken did not seem to increase in volume when the water was warmed, although tidal volume was not measured directly. Also, dolphins are breathing moist air from the layer immediately above the water surface, such that the inhaled air is already largely saturated with water. Thus the amount of evaporation that can occur from respiratory surfaces is limited to the difference in the amount of water in inhaled air of 17–22°C (15 mg/l to 19.8 mg/l in saturated air) for the different experiments, and the amount of water in saturated air being exhaled. Although it seems that exhaled air would be near core temperature (saturated 36°C contains 41.9 mg/l of water), measurements in experiments on six bottlenose dolphins by Coulombe et al. (2) revealed otherwise. They found the mean temperature and water content of inhaled air was 19.4°C and 14 mg/l, respectively, and for exhaled air, 22.9°C and 16.7 mg/l, respectively, with both being 75% saturated. This provides for only 2.7 mg/l water loss rather than the 26.9 mg/l if exhaled air was 36°C and 100% saturated. Irving et al. (6) measured tidal volumes from bottlenose dolphins of 5.5–10 liters. For the experiment shown in Fig. 2, the heat loss by evaporation from the respiratory tract during the time when core temperature declined is estimated as 0.1856 W. This is calculated from the change in respiratory frequency (0.17 breaths/min), assuming the greatest tidal volume of 10 liters, a 2.7 mg/l rate of water loss, and there being 580 cal/s (or 2426.7 W) heat loss per gram of water loss. Even if tidal volume had increased from the lower 5.5 liters during baseline to a full 10 liters during the warming ramp, only 0.835 W could have been lost from the respiratory tract via evaporation. The highest estimate of respiratory evaporative heat loss in all ten experiments was 0.83 W if tidal volume was unchanged at 10 liters or 3.73 W if tidal volume increased from 5.5 to 10 liters. It is clear from these calculations that the decline in body core temperature cannot be due to heat loss via evaporation from the respiratory tract.

In comparison, a 1°C reduction in core temperature over a 15-min period represents >67 W. This estimate assumes a specific heat of the tissues of 3.47 J/g (12) and that the core represents 75% (e.g., 178.5 kg) of the total body mass. The latter assumption is based on the report that total fat content in bottlenose dolphins is 18.5% total body mass (15), that all fat is located in the insulative subcutaneous layer (15), and that core extends to near the blubber layer (5). It is concluded that the marked reduction in T\[re\], which represents a true decline in core temperature, cannot be attributed to heat loss from the body and must be due to a massive redistribution of heat within the body from the core to the periphery. The redistribution of heat likely occurs both by conduction and by large increases in blood flow to the periphery, which rapidly transports heat to those tissues.

How reasonable is the suggestion that the reduction in core temperature is due to the redistribution of heat? Because the blubber layer acts as insulation in the cool pelagic water, when the dolphin moves into warm water, the blubber is cooler than both the ambient water and the body core. It is therefore a heat sink to both. Because almost all the temperature gradient between the initial 15.5°C water and the 36.6°C core temperature occurs in the blubber layer (5), we can assume an initial mean blubber temperature of ∼26°C. If the blubber and appendages represent 25% of total body mass (59.5 kg), then a 2°C reduction in core temperature would require a 6°C rise in mean blubber and appendage temperature to 32°C. The net heat gain from the water via the appendages and body surfaces at the measured rates would add another 2.2°C to the peripheral tissues over the entire span of the experiment, bringing their temperature to ∼34°C. This correlates well with the observation that, whereas the flippers and flukes reach equilibrium with the water at 70–80 min (as demonstrated by reaching zero heat flow), heat continues to be gained via the body wall until the very end, when T\[w\] is lowered to between 34 and 35°C. Finally, if a redistribution of heat within the body did not occur, then the reduction in heat gain from the environment by the submerged surfaces cannot be explained. This is because a 2.2°C increase in peripheral tissue temperature gained from the warm water is inadequate to bring the appendages and blubber to equilibrium with the water.

Importance of this thermoregulatory mechanism. These observations suggest that a common response of dolphins to encountering warm water is a redistribution of heat such that core temperature is reduced and blubber and appendage temperatures are increased. This is advantageous in two ways. First, it reduces the amount and rate of heat gained by the dolphin from the warm ambient water through a “preemptive strike” of actively warming its blubber layer and appendages rather than allowing these cool tissues, which normally
act as insulation, to act as an enormous heat sink to the warm ambient water. Second, it provides a safety margin in core temperature for the dolphin that has entered an environment that may pose a “heat stress.” In the experiment illustrated in Figure 2, instead of the dolphin becoming hyperthermic within a few minutes (as would occur if $T_{re}$ increased at onset of warming ramp due to addition of metabolic heat that cannot be lost to environment in these conditions), the decline in $T_{re}$ provides a remarkable hour-long delay to any increase in core temperature. This mechanism probably allows the animal to safely enter a very warm, shallow bay to forage briefly before returning to deeper and cooler waters offshore. For example, dolphins have been observed foraging in shallow, high-salinity bays of the Arabian Gulf in summer in $T_{aw}$ as high as 36–38°C (Ridgway, personal observation). The results of the present study suggest that these dolphins would probably be active in deeper, cooler water offshore. For example, dolphins have been observed foraging in shallow, high-salinity bays of the Arabian Gulf in summer in $T_{aw}$ as high as 36–38°C (Ridgway, personal observation). The results of the present study suggest that these dolphins would probably be active in deeper, cooler water of the gulf before and after such foraging excursions.

It is important to note that the reduction in $T_{re}$ did not begin immediately as the warming ramp was initiated but rather occurred several minutes (15–20 min) into the warming ramp. This suggests that this thermoregulatory response is neither a passive nor an immediate response to all encounters with warmer water, but rather that it is a controlled response that is probably orchestrated by the nervous system and likely stimulated and driven by $T_{sk}$ and/or rate of change in $T_{sk}$.

There are several factors that can influence the effectiveness of this thermoregulatory mechanism, including 1) the temperature of the blubber and skin layers before the dolphin encounters warmer water, 2) the magnitude of the difference in temperature of the core and peripheral tissues, and 3) the mass of the core and peripheral tissues. These variables contribute to the variations in the magnitude of the drop in core temperature observed in experiments. Also note that this mechanism can be used only once time during each encounter with warmer water because the peripheral tissues can be warmed only once. Finally, it is important that this mechanism be used only when there is a real threat of heat stress, because once the heat from the core moves to peripheral tissues, it cannot be gathered back to the core.

There are characteristics of this response in dolphins that identify it as a true thermoregulatory adaptation and distinguish it from responses observed in other mammals. Humans and other homeotherms increase blood flow to the skin significantly to enhance heat loss to the environment. A small reduction in core temperature of short duration sometimes occurs as a by-product of this response in humans moving quickly from a cold to a hot environment (1). This temporary reduction in core temperature provides no advantage to human survival. In sharp contrast, the described thermoregulatory response by dolphins unequivocally provides an advantage to their survival during encounters with very warm water. Furthermore, blood flow to peripheral tissues is increased, not to increase heat loss to the environment as in terrestrial mammals, but rather to delay hyperthermia by both reducing core temperature and limiting heat gain from the water.

Remarkable thermoregulatory responses have been reported in some terrestrial mammals, including the camel (20) and oryx (22) that inhabit hot, arid environments. Their response to heat stress involves a combination of evaporative heat loss and heat storage; the latter increases in camels when they are dehydrated (20). A large increase in core temperature during the day earmarks heat storage. The heat is lost back to the environment at night. Schmidt-Nielsen et al. (20) point out that heat storage is valuable to terrestrial mammals both in limiting the amount of heat that is gained from the hot environment and in conserving body water. This is true because the increase in body temperature diminishes the temperature gradient between the environment and the animal. As heat gain is reduced, the need for evaporative heat loss is also diminished. In dolphins, the redistribution of heat from the core to the peripheral tissues is another adaptation that provides this same advantage of reducing total heat gain from the environment. Because core temperature never increased $>0.2°C$ above baseline levels during these highly controlled short-term studies with dolphins, the degree to which dolphins use heat storage as a thermoregulatory strategy remains unclear.

There are other reasons why it is difficult, and perhaps inappropriate, to compare the thermoregulatory ability of marine mammals with that of terrestrial mammals. The terrestrial and marine environments are different and mandate different responses. For example, evaporation is an essential mechanism in mammals for heat loss in hot terrestrial environments. However, this powerful heat loss mechanism, which requires an air-water interface, is essentially unavailable in dolphins, which spend their lives submerged in water, do not pant, and are inhaling air that is already saturated with water. Also, dolphins must contend with a higher rate of metabolic heat production than terrestrial mammals (17, 24). Finally, most terrestrial mammals lack the subcutaneous blubber needed for the redistribution of heat that occurs in dolphins. The exceptions, pigs and hippopotamuses, are unlikely to encounter in their habitat the rapid transition from cool to warm temperatures that make this response useful.

Despite the limitations imposed by their aquatic environment, dolphins have evolved a unique thermoregulatory response to safely extend their range into the warmest marine water environments. The key- stone of their response is an impressive redistribution of heat in the body from the core to the peripheral tissues. The sudden shift from using the blubber layer and appendages as insulation in cool water to exploiting them as a heat sink in response to heat stress was unexpected and is the most remarkable aspect of the dolphins’ thermoregulatory response.

We thank Dr. W. G. Miller and the marine mammal trainers at Bioscience Division, Naval Command Control and Oceans Surveillance Center for their technical assistance.
This research was funded by the Office of Naval Research. Address for reprint requests: M. E. Heath, Biodiversity Research and Application Association, PO Box 22683, San Diego, CA 92192-2683 (E-mail: MEHeath@compuserve.com).

Received 18 August 1998; accepted in final form 24 November 1998.

REFERENCES


