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Reproductive Thermoregulation in Marine Mammals

How do male cetaceans and seals keep their testes cool without a scrotum? It turns out to be the same mechanism that keeps the fetus cool in a pregnant female

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Many cells and tissues of the body have an ideal temperature at which they perform best. Muscles are most efficient a few degrees above their resting temperature, hence the need for a warm-up before a rigorous workout. Neural tissue, on the other hand, is very sensitive to rising temperatures—an increase of only 4–6 degrees Celsius can disturb brain function, leading to convulsions and even death. To avoid such catastrophes mammals have evolved elaborate physiological mechanisms to regulate their core body temperatures (about 37 degrees in human beings). Unfortunately this core temperature is about three degrees above the ideal temperature for the production and storage of viable sperm cells. Many terrestrial mammals have solved this problem by evolving a scrotum, which holds the sperm-bearing testes away from the heat of the body.

Two groups of marine mammals, cetaceans and seals, do not have a scrotum; they maintain their testes inside the body where they are surrounded by blubber and muscle. The body temperatures of resting seals and dolphins are commonly between 36–38 degrees—high enough to inhibit the production of sperm in most other mammals. The core temperature of an active animal may be higher still. Active locomotory muscles can generate heat 10 to 100 times faster than resting muscles. Much of this heat flows into the abdominal cavity rather than away from it. Moreover, when these marine mammals dive, the flow of blood is redistributed away from the muscles and visceral organs, thus decreasing the amount of heat that can be transferred away from these tissues. Such conditions raise the question of how seals and cetaceans keep their reproductive tissues cool.

It's a question that applies equally well to female marine mammals. All mammalian females need to regulate the temperatures of their reproductive organs during pregnancy to produce viable offspring. Pregnancy may increase the female's metabolic rate as much as 40 percent, and the mass-specific metabolic rate of the fetus may be twice that of the mother's. The excess heat associated with the growth of the fetus must be transferred to the mother and out of her body. Studies on terrestrial mammals have demonstrated that an increase of just a few degrees in the fetal temperature can cause great distress to the fetus, leading to developmental abnormalities of the skeleton, the nervous system and other tissues. Spontaneous abortions and fetal death are real possibilities in such instances.

Pregnant terrestrial mammals, including human females, dissipate some of this excess heat through the abdominal surface, which acts as a large thermal window—somewhat analogous to the role of the male's scrotum. But the uterus of a marine mammal is surrounded by layers of muscle and blubber that effectively close this window. Here again there appears to be a thermal threat to the developing fetus.

Answering questions of reproductive thermoregulation in marine mammals poses a two-fold challenge. Beyond the technical difficulties of establishing anatomical and physiological evidence for a particular mechanism, these questions must be answered without bringing harm to these animals, which are already being threatened on several fronts by human activity. Our anatomical studies relied on carcasses that had been either washed ashore or accidentally caught in commercial fishing operations. Our physiological work on live animals employed noninvasive procedures similar to those used in routine veterinary care.

The research described here provides evidence of novel vascular structures that prevent thermal insults to reproductive tissues. Although the mechanisms employed by the dolphin differ from those of the seal, both appear to regulate the temperature of their reproductive systems by transporting cooled blood from the surface of the body to deep positions within the body. Moreover, the males and females of each species appear to rely on similar mechanisms. Although our anatomical descriptions are based on the common dolphin *(Delphinus delphis)* and the harbor seal *(Phoca vitulina)*, these structures are present in all the cetaceans and phocid (true) seals we have studied. (Sea lions and fur seals [otariids, or eared seals] possess

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Figure 1. Active dolphins and seals can generate enormous amounts of body heat that could potentially threaten the viability of sperm cells in the male and the life of a fetus in the pregnant female. Some of the thermoregulatory mechanisms used by terrestrial mammals cannot be employed by these marine mammals; instead they rely on novel vascular structures that help keep their reproductive organs cool.

scrotal testes, so they are more like terrestrial mammals.)

Cetacean Heat Exchange

In a mammal with a scrotum, the blood vessels associated with the testes have an elaborate architecture. The *testicular artery*, which provides oxygen and nutrients to the testis, is surrounded by a convoluted network of veins—the *pampiniform plexus*, which receives blood that has been cooled in the skin of the scrotum. The artery and the plexus are so closely juxtaposed that heat from the artery is transferred to the relatively cool venous blood returning from the scrotum. This is an example of a vascular countercurrent heat-exchange system: Blood flowing in one direction relays heat to blood flowing in the opposite direction *(Figure 3)*. Of course, such a system works only if there is a temperature gradient—one of the blood vessels must be cooler than the other.

A vascular countercurrent heat-exchange mechanism is also known to exist in the dorsal fin and the flukes of cetaceans. These structures are usually thought of as hydrodynamic surfaces, allowing the animal to control its attitude as it swims through the water. But the dorsal fin and flukes also act as thermoregulatory devices. Because these structures are not insulated and because they have a large surface area relative to their volume, they may expose a considerable amount of blood to the cool ocean waters. A countercurrent heat-exchange mechanism in the dorsal fin and flukes appears to conserve heat that could be lost across these surfaces. It consists of venous plexuses—the *periarterial venous retia*—that surround central arteries *(Figure 5)*.

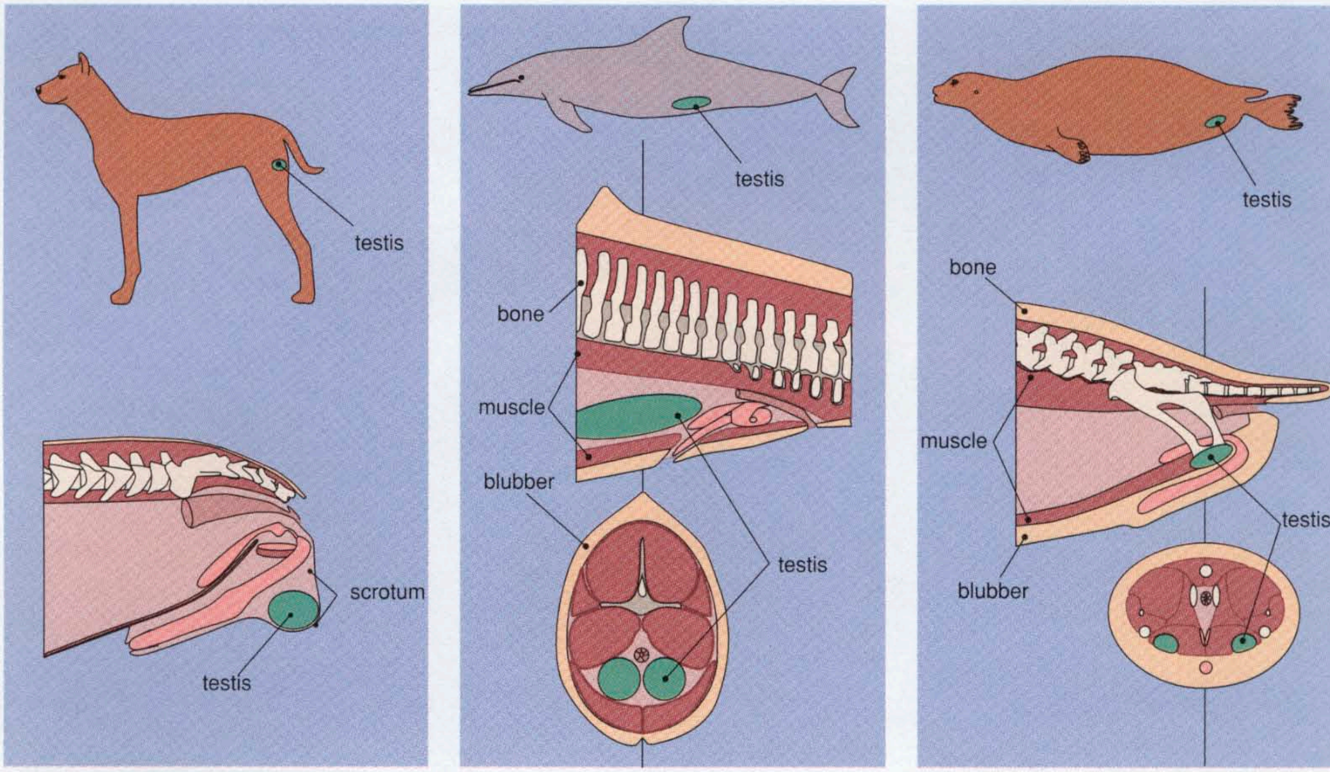

Figure 2. Male dolphins and seals have testes located within the body, unlike most terrestrial mammals *(left)*, which house their testes in an external sac (the scrotum). The scrotum is a highly vascularized pouch that allows heat to be exchanged between the testes and the environment through the surface of the skin, which acts as a "thermal window." Dolphins have cryptic testes *(middle)*, located entirely within the abdomen, beneath a layer of blubber and muscle. Seals have parabdominal testes *(right)*, which are located outside of the abdomen but wedged between muscle and a thick layer of blubber. Since the sperm cells of most mammals are not viable at high core body temperatures, the location of the testes in dolphins and seals suggests that some cooling mechanism must exist.

Thus these arteries can provide nutrients to the outlying tissues of the dorsal fin and flukes without losing much heat to the environment.

There is yet another venous return system in the dorsal fins and flukes of cetaceans that lies near the surface of each extremity. These superficial veins are collateral to the deep countercurrent heat-exchange system, providing an alternative flow of blood back to the body. Blood routed through these superficial veins is cooled by exposure to the environment. This cooled blood returns to the body and contributes to the general maintenance of the animal's body temperature.

Our anatomical investigations indicate that some of this cooled blood makes its way back to the heart by a route that passes very close to the testes. This route—the *lumbo-caudal venous plexus*—consists of a single layer of irregularly anastomosed, thin-walled vessels. The plexus is near the testes and is supplied by cool blood from the superficial veins of the dorsal fin and flukes *(Figure 6)*. The venous plexus distributes the cooled blood over a region deep within the abdomen that is roughly equivalent to the surface area of one side of the dorsal fin.

The lumbo-caudal venous plexus is, in turn, juxtaposed to an array of parallel, thin-walled arteries from the aorta—a *testicular arterial plexus*—that coalesce into the arteries supplying the testis. The direction of the blood flow in the arterial plexus is opposite to that of the venous plexus. This design provides strong anatomical evidence that cooled blood from the superficial veins of the dorsal fin and flukes could be used for indirect cooling of the testes by vascular countercurrent heat exchange.

Seals Have a Cooling Plexus

As one might expect, the pelvic anatomy of a phocid seal is very different from that of a cetacean or a terrestrial mammal. This difference in turn leads to an entirely different mechanism used to keep the testes cool in these animals. Two features in particular appear to account for the differences in seals. First, the knee joint lies within the contour of the body wall, bringing the ankle in close proximity to the anus. Second, seals have a very large, elaborate venous return system from the hind flipper in the pelvic region.

Because the position of the seal's hind limb is so unlike that of terrestrial mammals, the testes appear to be in an unusual location. Although the arterial supply to the seal's testes is similar to that of a terrestrial mammal such as a dog, the seal's testicular veins are not elaborated into a pampiniform plexus. There are, however, large venous plexuses near the seal's testes that are not part of its nutritional circulation. An *inguinal venous plexus* cups the deep aspect of each seal testis and separates the testis from the adjacent muscle mass. If supplied with relatively cool blood, this plexus could thermally isolate the testes.

The unusual structure and position of the seal's hind leg appears to provide just such an opportunity *(Figure 8, top)*. Since major blood vessels usually form branches at a joint, the relative positions of the joints in the seal's legs are associated with a unique branching pattern of veins. We have found three sites where veins carrying blood returning from the surface of the animal's hind flipper anastomose with the deep circulation. At least one of these, the *pudendo-epigas-*

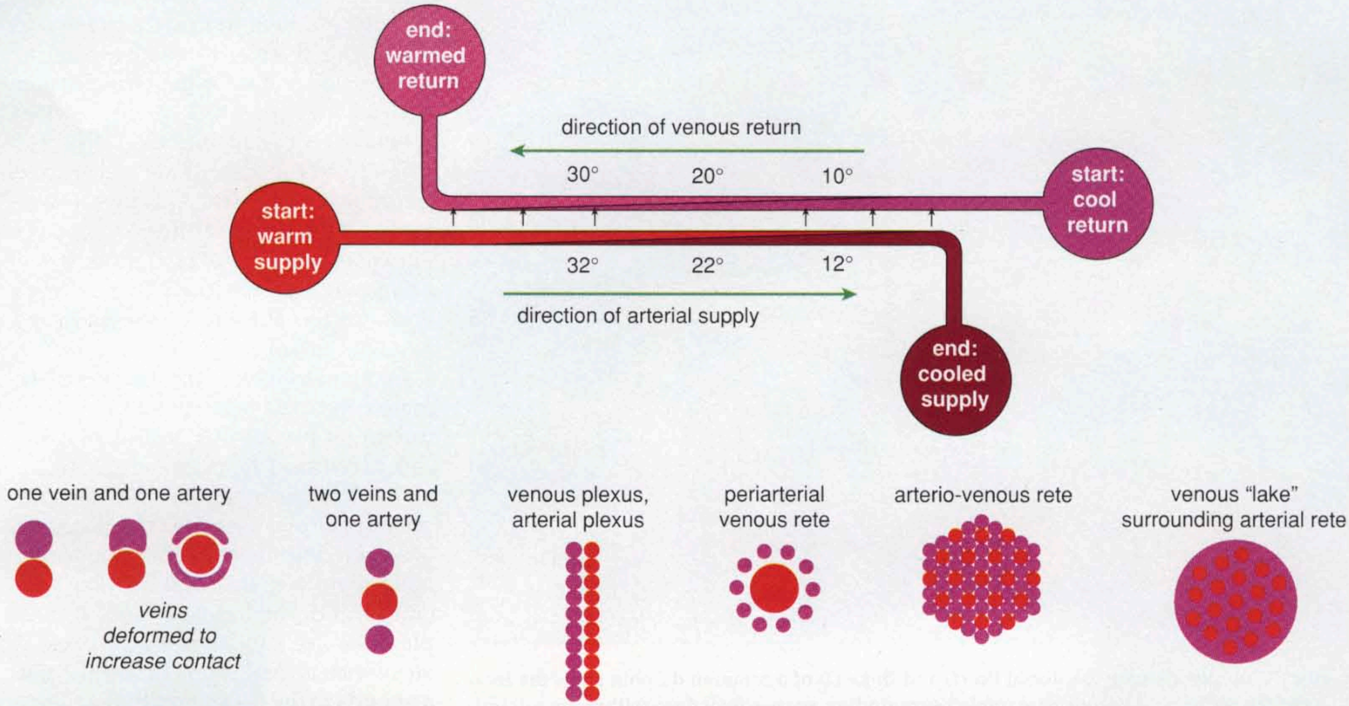

Figure 3. Countercurrent heat-exchange mechanisms can maximize the flow of heat from a warm artery *(red)* to a relatively cool vein *(violet)* if the two blood vessels are adjacent to each other. The flow of the warm and cold blood in opposite directions along their points of contact increases the amount of heat *(black arrows)* that is transferred. Increasing the surface area of contact between the two vessels further increases the efficiency of heat exchange; this can be accomplished in several ways *(bottom)*, each of which has been found in various mammals.

tric anastomosis, provides venous blood from the flipper to the *inguinal venous plexus* that cups each testis.

The exposed surfaces of the seal's hind flippers have been shown to be important sites where heat is dumped from the body. Major heat-dumping sites are, by definition, also major sources of cooled venous return. Thus blood from the hind flipper flowing through the inguinal plexus could establish a thermal gradient allowing direct heat transfer away from the testes and the adjacent muscles *(Figure 8, bottom)*.

Keeping the Fetus Cool

In some terrestrial mammals a fetal temperature only half a degree above the mother's provides a thermal gradient that drives heat away from the fetus to the mother. This tight thermal coupling is critical for adequate temperature regulation of the fetus, but it also prevents the fetus from thermoregulating independently from the mother. Any physiological or anatomical condition that interferes with the ability of the fetus to transfer metabolic heat to the mother will cause the fetal temperature to increase until a new thermal gradient is established.

The amount of heat that can be transferred from the fetus to the mother across the placenta depends primarily on blood flow through the uterus. Experimental studies in sheep and baboons show that fetal temperature rises if the flow of blood decreases through the uterus. In terrestrial mammals, most of the fetal heat is passed to the mother via the umbilical circulation, so that about 85 percent of the fetal metabolic heat is transferred by convection at the fetal-maternal interface at the placenta. The remaining 15 percent is transferred by conduction across the uterine wall to the mother's abdominal wall and out to the environment. In terrestrial mammals this thermal window is a relatively thin layer of stretched muscle and skin in the abdominal wall. Passage of heat through this thermal window can be experienced firsthand simply by feeling the relatively warm abdomen of a pregnant terrestrial mammal.

In an active pregnant dolphin or seal, heat is unlikely to be transferred from the fetus across the uterus to the mother's abdominal wall because the blubber and locomotory muscles do not permit a proper thermal gradient. Pregnant dolphins and seals not only appear to lack an abdominal thermal window, but the generation of heat by the locomotory muscles that surround

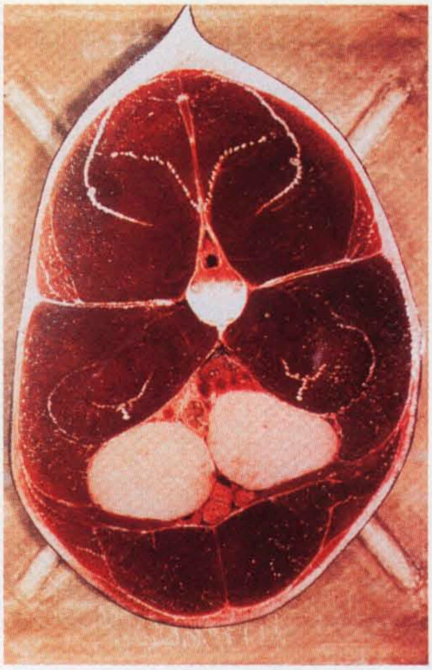

Figure 4. Dolphin testes *(white)* are entirely surrounded by massive, heat-producing locomotory muscles *(red)*. Reduction in the flow of blood to the muscles during a dive—which reduces the amount of heat that can be removed from the muscles—suggests that the testes may experience thermal loading beyond core body temperatures during certain behavioral activities. (Photograph originally appeared in Boice, Swift and Roberts 1964.)

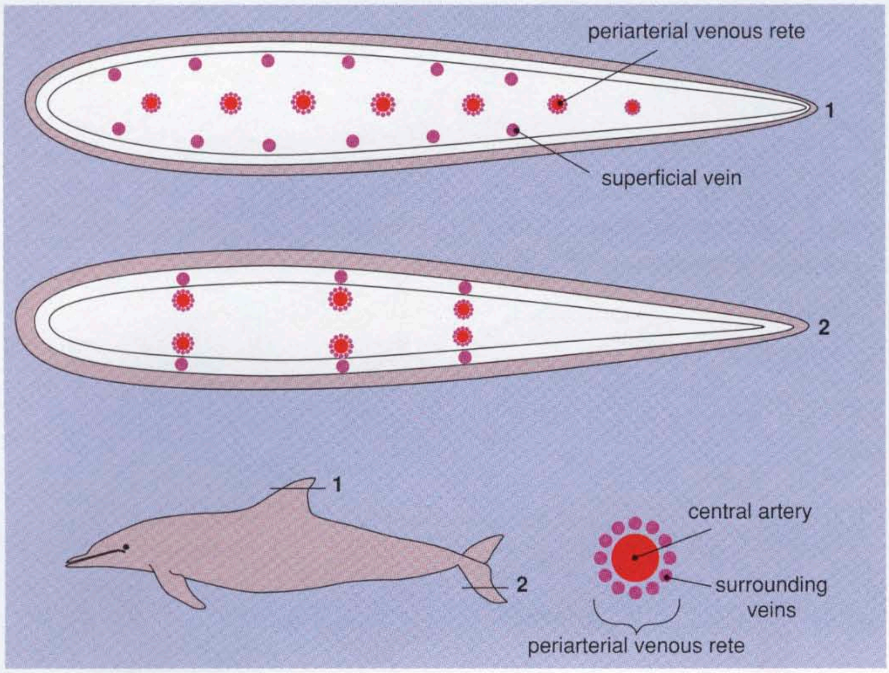

Figure 5. Sections through the dorsal fin *(1)* and fluke *(2)* of a common dolphin show the locations of the *periarterial venous retia (violet)* surrounding arteries *(red)* deep within the extremities of these animals. This countercurrent heat exchange mechanism serves to retain body heat. A collateral venous return system is found near the surfaces of both extremities. These superficial veins are used by the dolphin to regulate the temperature of its reproductive organs.

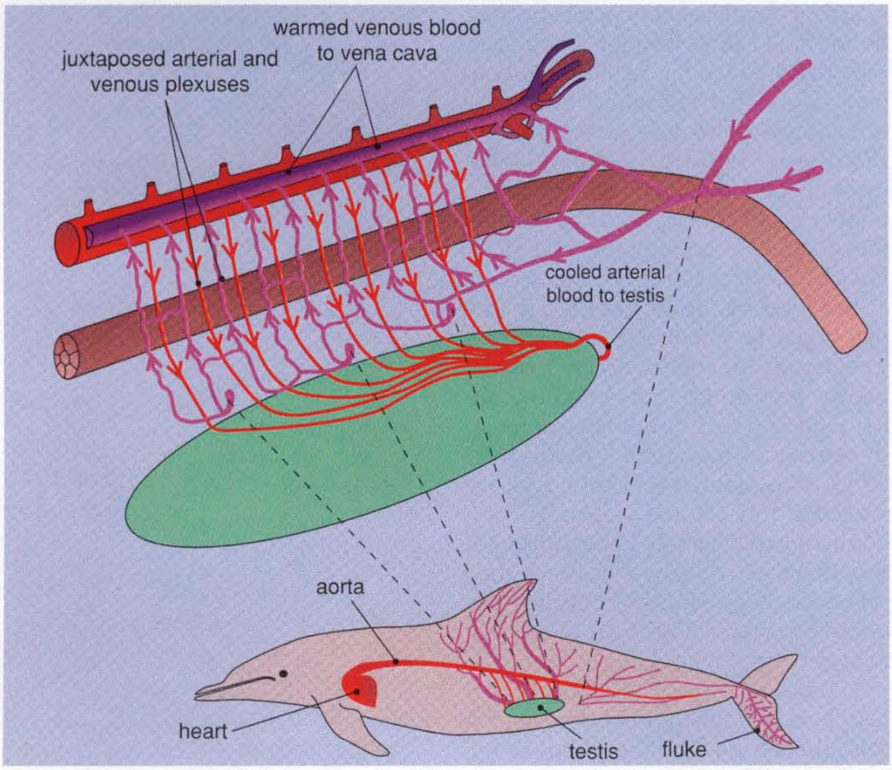

Figure 6. Vascular countercurrent heat-exchange network near each dolphin's testis helps to prevent thermal insults. Veins *(violet)* returning from the dorsal fin and the flukes carry relatively cool blood and form a flat array, the *lumbo-caudal venous plexus.* Arteries *(red)* carrying warm blood from the aorta form a flat *testicular arterial plexus* before coalescing into a single artery that enters the caudal pole of each testis. The juxtaposition of the two plexuses and the flow of warm and cold blood in opposite directions results in an exchange of heat that provides relatively cool arterial blood to the testes.

the abdominal cavity may cause the thermal gradient to flow from the surrounding tissues toward the fetus. Thermoregulation of the fetus may be further complicated during a dive when the flow of blood is diverted away from the abdominal viscera and locomotory muscles. Although the effects of high temperatures on developing cetaceans and phocid seals is still unknown, it seems likely that there are limits to the amount of excess heat a fetus can tolerate.

Our anatomical explorations of female cetaceans reveal vascular structures that are similar to the vascular countercurrent heat exchanger in the male *(Figure 9)*. In this instance, the arterio-venous plexuses are even larger in pregnant dolphins than they are in sexually mature male dolphins. The general form of the lumbo-caudal venous plexuses are similar in both sexes. A *uterovarian arterial plexus* in females corresponds to the testicular arterial plexus of males. The life history of these structures is also consistent with their role in the pregnant female. The arterial and venous plexuses are small in juvenile females, and they increase in size and complexity as pregnancy develops and then regress in postpartum females. Cooled blood from the dorsal fin and flukes appears to provide the pregnant dolphin with the functional equivalent of the abdominal-wall thermal window of terrestrial mammals.

Observations by others on a Weddell seal during a simulated dive suggest no net change in blood-flow rates through the uterus. However, we have found two sites—the *pelvic anastomosis* and the *pudendo-epigastric anastomosis*—where cooled superficial venous blood from the hind flipper can be shunted to two deep venous plexuses (the abdominal and pelvic plexuses) that surround the female seal's reproductive system *(Figure 10)*. The cooled venous blood has substantial thermal mass with a large, direct cooling potential. Cooled blood in the deep plexuses would lower the temperature of the region occupied by the pregnant uterus, thus providing the functional equivalent of an abdominal thermal window.

Physiological Evidence

Our anatomical investigations of dolphins and seals suggest the presence of vascular mechanisms that could keep reproductive structures cool in both males and females. But do these mechanisms actually work in the living animal? How would one go about testing these hypotheses? It turns out that we can assess the temperatures of the blood in the vicinity of the reproductive organs with a relatively safe and noninvasive method—by measuring colonic temperatures.

In dolphins and seals the colon passes directly through the region occupied by the arterial and venous structures described in our work. If these blood vessels do carry relatively cool blood, then colonic temperatures adjacent to these plexuses should be less than those in regions in front of and behind the plexuses. To test this possibility we designed a rectal probe with the capacity to take temperature readings simultaneously at several points along the length of the colon. It consisted of a linear array of thermocouples enclosed in thin flexible tubing that allowed us to record temperatures at five to seven sites along the colon depending on the configuration of the probe *(Figure 11)*.

An opportunity to measure dolphin temperatures presented itself when we were invited to work with Terrie Williams, then at Naval Oceans Systems Command (NOSC), Kailua, Hawaii, who was studying the metabolic physiology of bottlenose dolphins. We measured colonic temperatures on peripubescent and sexually mature males at 10-second intervals for periods ranging from four minutes to 120 minutes. As predicted from the vascular anatomy, there were marked differences in temperature along the length of the colon. Colonic temperatures on either side of the countercurrent heat-exchange plexus were indeed higher than those in the region of the plexus.

This result was exciting not only because it supported our hypothesis, but also because it helped to explain certain concerns of health-care specialists who use colonic temperatures to assess dolphin health. These clinicians discovered that colonic temperatures often vary between measurements and are not reliable predictors of an animal's health. But our findings show that the variation might be explained if the standard rectal probe (with a single thermocouple) was placed in different positions within the colon or if it was placed in a region that was influenced by the countercurrent heat exchanger. Our work may ultimately provide better ways of understanding

Figure 7. Histological section through the countercurrent heat-exchange system of a male dolphin *(Delphinus delphis)* shows the proximity of the testicular arterial plexus *(here represented by three thick-walled arteries)* and the lumbo-caudal venous plexus *(here represented by a single venous channel below the arteries)*. The arteries that form the plexus are approximately 0.5–1 millimeter in diameter. (Photomicrograph courtesy of the authors.)

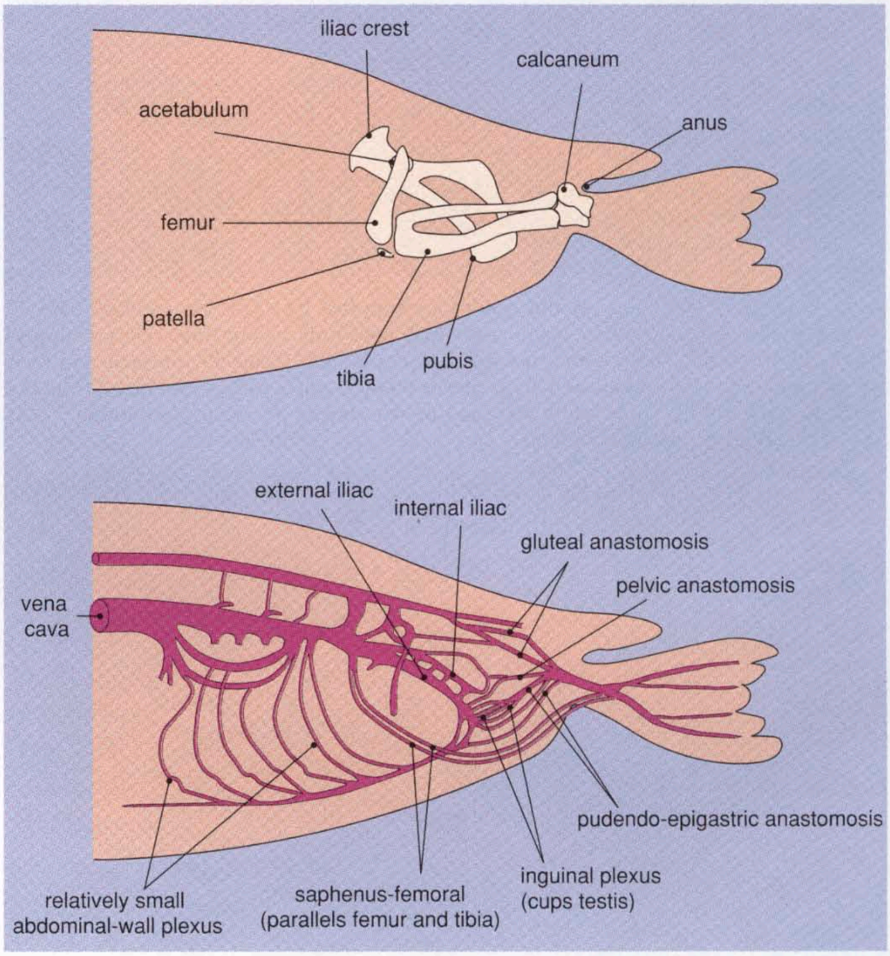

Figure 8. Close relation between the bones of the hind limb and the pelvis of the harbor seal *(top)* provides the opportunity for venous blood vessels to form shunts or anastomoses *(bottom)* that are not present in terrestrial mammals. Three of these shunts—the *gluteal, pelvic* and *pudendo-epigastric anastomoses*—allow cool blood from the hind flipper to be carried directly into the pelvic and abdominal cavities. Part of the pudendo-epigastric anastomosis forms the *inguinal plexus,* which surrounds and directly cools each testis.

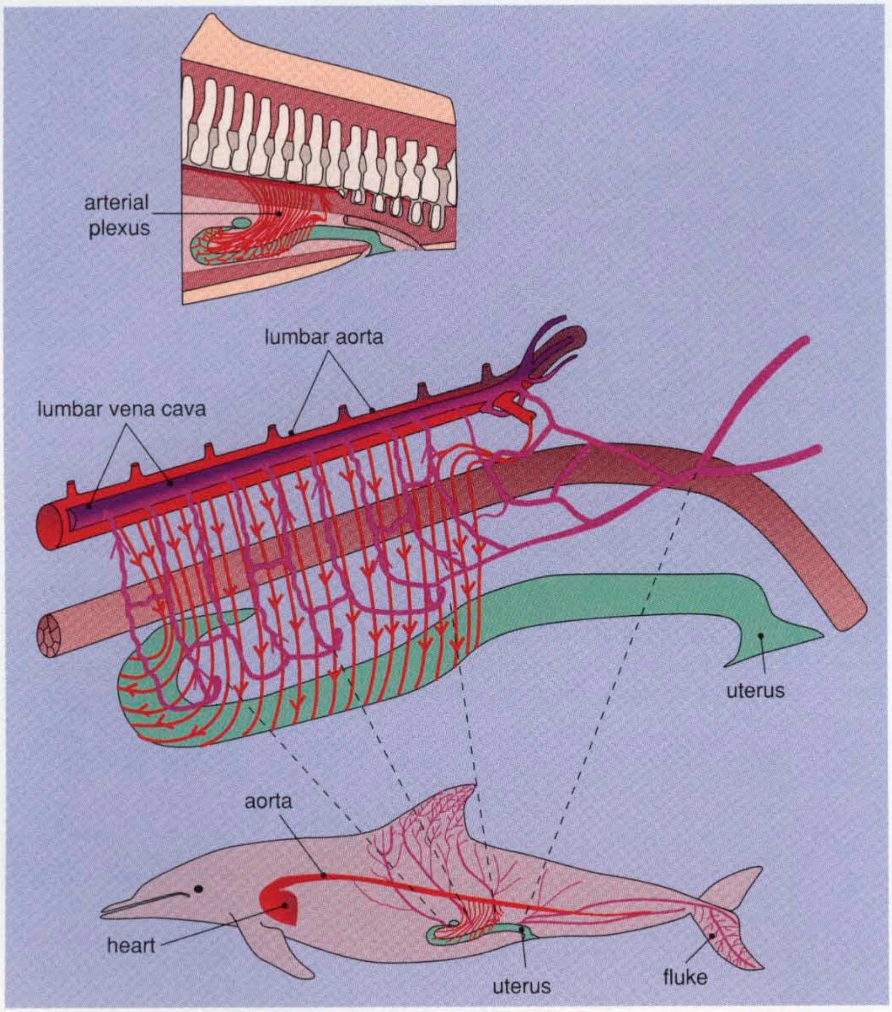

Figure 9. Dolphin uterus *(green)* and ovaries are supplied by a rich plexus of perhaps 40 arteries—unlike most terrestrial mammals, which have only two or three arteries supplying these structures. This *uterovarian arterial plexus (red)* forms a countercurrent heat exchanger with the lumbo-caudal venous plexus *(violet)*, which carries cool blood from the dorsal fin and flukes. This system increases in size during pregnancy, providing a cool flow of blood for the developing fetus.

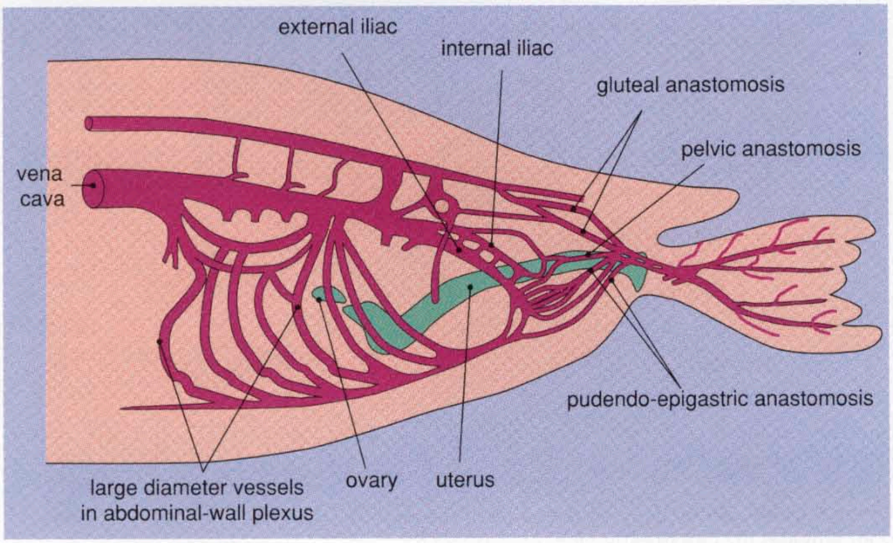

Figure 10. Seal uterus *(green)* is surrounded by pelvic and abdominal venous plexuses *(violet)*, which receive cool blood from the hind flipper by way of the pelvic and pudendo-epigastric anastomoses. These veins provide a large thermal mass that can directly cool the fetus in a pregnant animal.

the relation between colonic temperature and a dolphin's health.

When we measured colonic temperatures after the dolphins had been swimming vigorously, we found that temperatures decreased in the region adjacent to the vascular heat-exchange system, relative to when the animal was resting. This is the first report of a decrease in deep-core body temperatures during nondiving exercise. It suggests that the countercurrent heat exchanger has an increased ability to cool the arterial blood supply to the reproductive organs, providing thermal isolation from adjacent thermogenic muscles when the dolphin is swimming vigorously. As the animal swims faster, more water flows across the dorsal fin and the flukes, thereby increasing the amount of heat exchanged between the superficial veins and the environment. Thus, exercise increases the flow of cooled venous blood and brings about maximum cooling at the countercurrent heat exchanger.

Seal Physiology

Encouraged by our dolphin work, we hypothesized that there should be measurable differences in the temperature of tissues bordering the venous plexuses we found in seals. Our hypothesis is supported by the literature on seals, which contains numerous measurements of deep-body temperatures that range from 29.8 to 39 degrees. Testis temperatures have been reported to be 1–4 degrees lower than core temperatures in harp seals and 6–7 degrees lower than core temperature in elephant seals. And a number of scientists have shown that seals have a 2–3 degree drop in core temperature during a dive. These temperatures have been interpreted to be a result of either a modified flow of heat through the blubber or a lowered metabolic rate, or both. However, we believe that some of these temperature changes can be reinterpreted in the light of the seal's vascular anatomy.

Since the seal's colon traverses regions of the pelvis and abdomen bordered by the venous plexuses from the hind flipper, temperature differences along the colon may be a reflection of venous cooling potential deep within the body. An opportunity to conduct some preliminary experiments presented itself when an adult, female harbor seal at the New England Aquarium in Boston required a series of veterinary treatments for an ear problem. The treatments followed standard veterinary procedures with the exception that the single-thermocouple rectal probe routinely used in such procedures was replaced with a similar probe that had six thermocouples spaced 5 centimeters apart. During five times over the course of the next several weeks, we measured colonic temperatures at 10-second intervals for periods ranging from 4 minutes to 43 minutes.

Our observations show that there is indeed a range of temperatures along the length of the colon. Temperatures are lowest close to the anus and progressively increase deeper within the body. Occasionally, however, the deeper positions show some persistent low temperatures—as much as 10 degrees lower in the region of the kidneys. Although we need to conduct further studies, it is clear from these observations that measuring the temperature at a single site cannot represent the range of core body temperatures in a seal. We believe these temperature measurements show that cooled venous blood from the hind flippers is introduced deep into the body cavities and can be used to regulate the temperature of the seal's abdominal and pelvic cavities.

Conclusion

Dolphins and seals use two different vascular designs to regulate the temperature of their reproductive systems. Dolphins use cool, superficial blood in countercurrent heat exchangers to lower the temperature of arterial blood delivered to their reproductive systems. Seals use cool, superficial venous blood to directly cool their reproductive organs by surrounding the organ with a plexus filled with the cooled blood.

Other marine mammals, such as the Sirenia (manatees and dugongs), also face thermal stresses to their reproductive systems. Preliminary morphological and physiological studies of the Florida manatee suggest that they too may have vascular adaptations for regulating the temperatures of their reproductive tissues. These investigations are an ongoing part of our research.

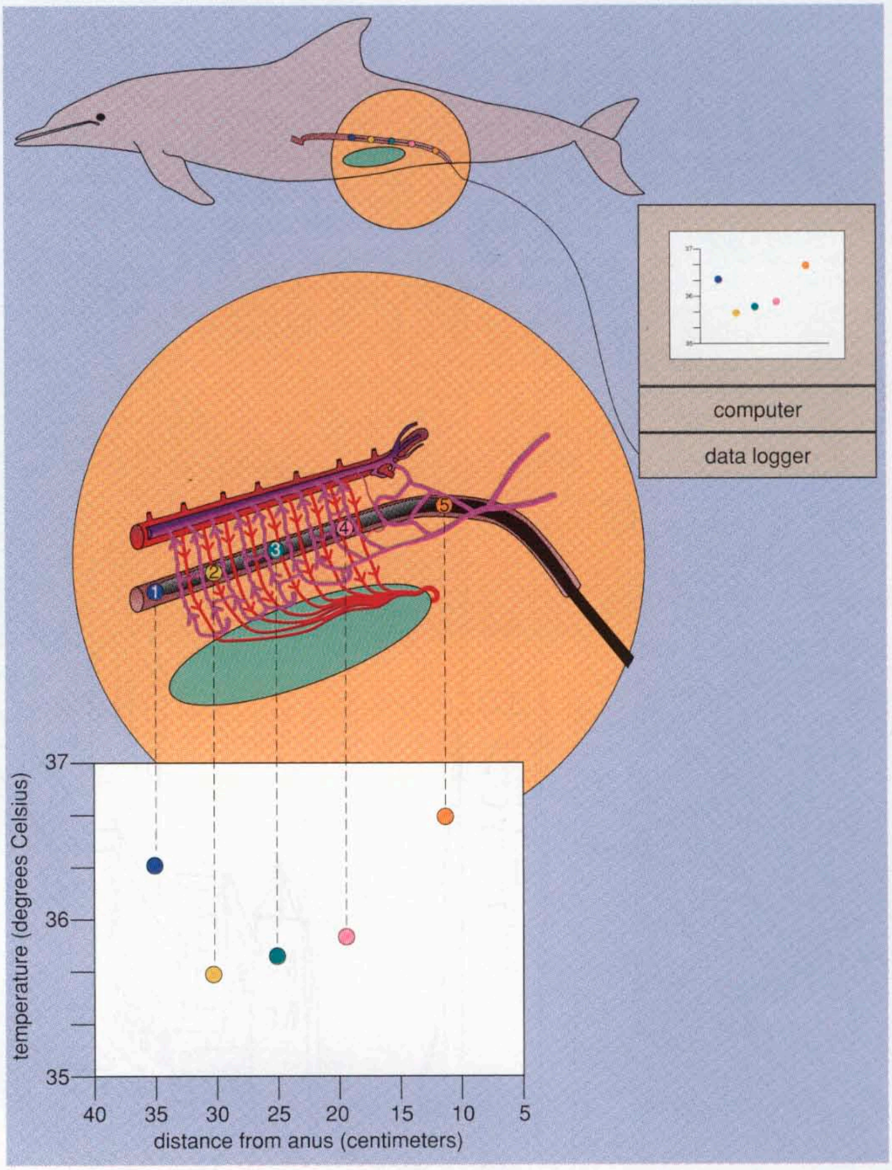

Figure 11. Deep-body temperatures at several sites within the dolphin's colon were measured simultaneously with a linear array of five thermocouples. Temperature readings in those regions of the colon adjacent to the vascular countercurrent heat exchanger *(sites 2, 3* and *4)* were consistently lower than colonic temperatures on either side of the cooling system *(sites 1* and *5)*. These experiments provide physiological evidence that cooled blood from the periphery may play a role in preventing hyperthermic insults to the animal's reproductive system.

Acknowledgments

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Most of the cetacean dissections and injections were performed at the NMNH in collaboration with James Mead and Charles Potter. The physiological observations on dolphins were performed at NOSC, Hawaii, in collaboration with Terrie Williams, Teri Rowles and William Friedl.

The injections and dissections of seals were carried out in the Necropsy Laboratory, Animal Care Center at NEA, Boston, Massachusetts in collaboration with Greg Early and Keith Matassa. Physiological observations on the adult female harbor seal were also done at the NEA.

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