TEMPERATURE REGULATION IN THE OPOSSUM, *DIDELPHIS MARSUPIALIS VIRGINIANA*

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ABSTRACT.—The opossum, *Didelphis marsupialis virginiana*, was able to maintain body temperature close to the normal value of $35.46 \pm 0.66°C$ (measured at T_a 25° C) at ambient temperatures ranging from 3 to 35° C. At colder ambient temperatures a drop in body temperature was observed in caged animals, but body temperature was usually kept above 33° C. Over T_a 35° C, body temperature rose rapidy. Subjects appeared to experience heat stress when ambient temperature rose much above 37° C. Temperature regulation at high temperatures depends mainly on evaporative heat loss from saliva spreading coupled with vasodilation, while at lower ambient temperatures postural responses, vasoconstriction, piloerection, and avoidance of extreme temperatures by denning are most important for thermoregulation.

Previous reports on thermoregulation in the opossum, *Didelphis marsupialis virginiana*, indicated that it is an effective homeotherm with an average deep body temperature of about 35° C (Enders and Davis, 1936; Morrison and Petajan, 1962; Higgenbotham and Koon, 1955; Nardone *et al.*, 1955). First signs of temperature regulation are found in 60-day-old pouch young and at 95 days of age deep body temperatures are held constant at ambient temperatures as low as 5° C (Morrison and Petajan, 1962). Morrison (1946) found no indication of a daily temperature cycle in the South American opossum, *D. m. etensis*. When subjected to rising ambient temperatures, *D. m. virginiana* exhibits striking behavioral responses, and elevated body temperatures are found at ambient temperatures above 35° C (Higgenbotham and Koon, 1955). Generally similar body temperatures and thermoregulation have been reported for other marsupials (Robinson, 1954; Robinson and Morrison, 1957; Bartholomew, 1956). This study provides further information on temperature regulation in the opossum, with particular emphasis on the behavioral adaptations to changes in ambient temperature.

METHODS

Opossums were captured in the vicinity of Ithaca, Tompkins Co., New York, in 1966 and 1967. Body temperatures and behavioral observations were recorded for 36 individuals during the course of this study. The animals ranged in body weight from 1.7 to 5.3 kilograms. They were housed separately out of doors in cages $4 \times 4 \times 3$ feet and were maintained on a diet of dry dog food and table scraps; water was available in open pans and straw was provided for nesting material.

Rectal temperatures of caged opossums were recorded at various times of the day and night during June, July, August, November, and December, using a mercury thermometer inserted to a depth of 2 inches. Observations were also made on postures, nest construction, and salivation responses. During July, August, and September, controlled temperature experiments were performed on 16 individuals: eight males (four adults and four young of the year) and eight adult females, two of which were carrying pouch young. In these experiments, animals starved for at least 24 hours were considered post-absorptive; water was always available. The opossum was placed in the chamber (18 × 18 × 18 inches) of a refrigerated incubator lighted with a 15-watt bulb and fitted with an observation window. Deep body and tail surface temperatures were monitored with a multichanneled telethermometer, using small animal probes held in place with tape. A probe was inserted rectally to a depth of 6 to 10 inches, bringing the tip of the probe near the liver and to one side of the stomach. No detectable differences in deep body temperature were noted using this technique or the insertion of a mercury thermometer to a depth of 2 inches. Additional probes were fastened to the surface of the tail 1 and 5 inches from the base and, if the tip had not been lost due to frostbite, another probe was fastened 8 inches from the base. The leads were long enough to allow the individual to move about the chamber. An ambient temperature of 25° C was maintained for 60 minutes to allow the animal to adjust to its surroundings, after which the temperature was slowly and continuously raised to 42 or dropped to 3° C (the rate of change was approximately 1° C every 6.8 minutes). Body and surface temperatures and behavioral responses were recorded at 10-minute intervals. The time required to reach a desired high or low final ambient temperature differed slightly among tests, and some tests had to be curtailed because the animals chewed or climbed the probe wires. Using 16 individuals, a total of 20 tests (10 with males and 10 with females) was performed at each temperature regime.

Results

Deep Body Temperatures Under Seminatural Conditions

Although daily variation in mean deep body temperature of caged opossums was not detected, seasonal variation was observed. The average body temperature of 18 animals exposed to an ambient temperature range of 18 to 32° C during June, July, and August was 35.55° C, with a standard deviation of 0.57° C, agreeing with the reports of other workers (Higgenbotham and Koon, 1955; Morrison and Petajan, 1962). Correlation of body temperature with ambient temperature was weak over this range.

The mean body temperature of 11 opossums exposed to an ambient temperature range of 7 to –10° C during November and December was 33.76 ± 0.67° C. The difference between this value and the mean body temperature during the summer is significant at the .01 level of confidence on the basis of a *t*-test. The lowest recorded body temperature was 30.8° C for a female at T_a –10° C.

Deep Body and Tail Surface Temperatures Under Experimental Conditions

Trends in deep body and tail surface temperatures with increasing and decreasing ambient temperature are shown in Fig. 1. During the summer opossums were able to maintain a reasonably constant body temperature at ambient temperatures ranging from 3 to 35° C. Increasing ambient temperature from 35 to 42° C resulted in a rapid rise in body temperature. The mean body temperature (35.46 ± 0.66° C) for males and females at T_a 25° C differed significantly from that of T_b 38.58 ± 1.14° C at T_a 42° C at the .01 level of confidence using the *t*-test. The average body temperature recorded at T_a 25° C was 35.65 ± 0.46 for females, 35.31 ± 0.79° C for males, and 35.46 ± 0.66° C for both sexes combined. The difference in body temperature between sexes was not significant ($P > .05$) at any ambient temperature

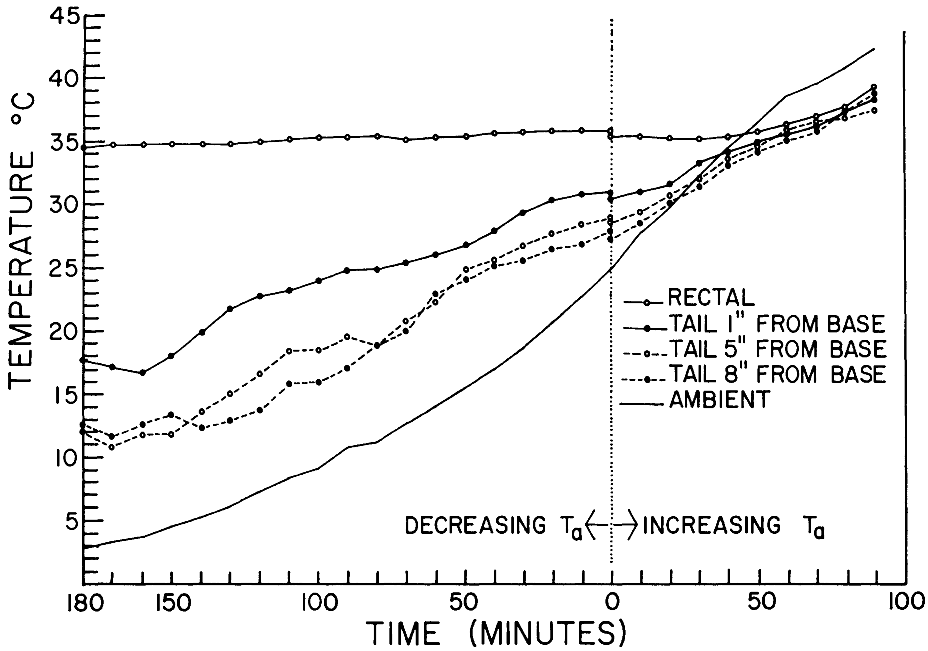

FIG. 1.—Influence of varying ambient temperature on deep body and tail surface temperatures of *Didelphis*. Data to the left of zero time represent averaged values for 20 separate tests at low temperatures; data to the right are averages for 20 separate tests at high temperatures. High and low temperature data are plotted as a continuum for convenience.

tested. Body temperatures of both males and females were more variable at extreme temperatures, but males were more variable at high ambient temperatures whereas females were more variable at low ambient temperatures (Fig. 2).

At T_a 25° C, distinct differences between deep body and tail surface temperatures were evident, as was a temperature gradient along the tail itself. Tail surface temperatures recorded 1, 5, and 8 inches from the base differed from body temperature by an average of 4, 7, and 8° C, respectively. As ambient temperature dropped the magnitude of these differences increased markedly, with the exception of the temperature differential between the tail surface at 5 and 8 inches. Variation in tail surface temperature increased sharply with a decrease in ambient temperature because tail surface temperature depended largely on the degree to which the tail was curled under the body. In several individuals, surface temperatures at 8 inches from the base of the tail dropped as low as 4.0° C in ambient temperatures of 2 to 3° C, but this occurred only when the tail was completely exposed.

With rising ambient temperature, temperature differentials along the tail and between the tail and the body diminished rapidly. Surface temperatures of the tail closely followed ambient temperature between 28 and 35° C, above

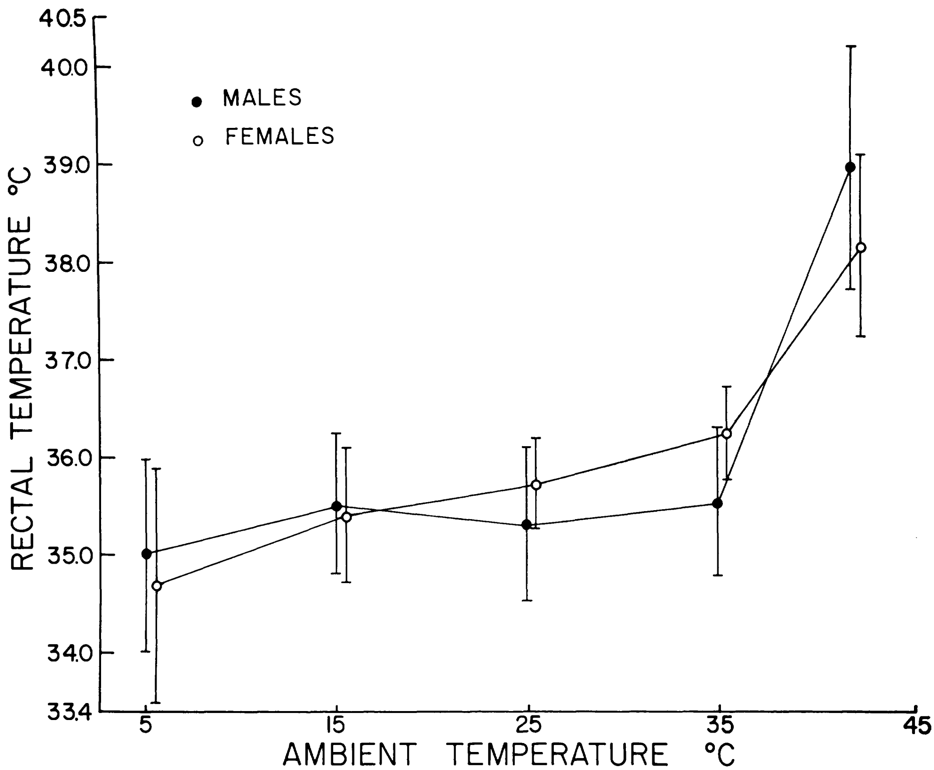

FIG. 2.—Comparison of the mean deep body temperatures and variability of males and females at different ambient temperatures. Vertical lines equal one standard deviation above and below the mean.

which they remained at or slightly below body temperature, but never greater than body temperature. Variability in the surface temperatures of the tail was reduced sharply above T_a 35° C, the deep body temperature and behavioral responses presumably limiting the extent to which the surface temperatures of the tail could rise. Through the high and low temperature tests, definite color changes occurred in the lightly pigmented tail, nose, feet, and rims of the ears. Vasodilation produced a flushed appearance above T_a 30° C, but at lower temperatures the extremities became progressively more pallid, indicating reduced peripheral blood flow. These changes are common in other mammals and serve to increase and decrease amounts of heat lost to the environment from body surfaces at high and low ambient temperatures, respectively.

Behavioral Responses

Immediately after introduction to the observation chamber, most opossums exhibited mild exploratory behavior. Following this they almost invariably assumed a sitting or lying posture and remained quiet or went to sleep.

Body postures while resting were quite variable and no characteristic position of the tail was noted.

The animals remained quiet and in the same position as ambient temperature rose from 25 to 35° C. When ambient temperature approached body temperature, however, a well defined series of behavioral responses was observed. At T_a 35 or 36° C, the subjects showed increased activity. Copious salivation and licking began at T_a 37° C, when body temperature averaged 35.81 ± 0.79° C. The forefeet, snout, and hind feet were usually licked first, then the abdomen, hind limbs, and tail. When ambient temperature approached 40° C, saliva spreading became more vigorous and continuous. The hindlimbs and tail received progressively more attention and in several instances the tail was even grasped with the hind feet and held while the tongue was drawn along it from base to tip. Almost without exception, urination and defecation occurred between T_a 36 and 40° C. As ambient temperature approached and rose above 40° C, the licking behavior often was interrupted, the opossums lying on their sides breathing deeply and rapidly; actual panting was not observed. Both females with pouch young (20 and 35 days old) spread saliva on the young as they licked the pouch region, but the young appeared to have been licked only by virtue of their position in the pouch and not by any directed effort on the part of the females, as both the young and the walls of the marsupium seemed to receive equal attention. Activity of the young also increased with rising ambient temperature. Above T_a 41° C, individuals appeared to be under severe temperature stress and spent more of their time on their sides breathing heavily, with brief but violent periods of licking. To prevent death of the subjects, the experiments were discontinued when body temperature reached about 40° C. The highest body temperature recorded was 40.80° C. Higgenbotham and Koon (1955) indicated that the lethal body temperature of *Didelphis marsupialis* is near 43° C.

Frequent observation of caged opposums during hot summer days suggested that the licking responses noted above are also common even below 35° C. Animals frequently saturated their forefeet, hind feet, hind limbs, and tails at temperatures of 27 to 32° C. Females with pouch young were often found with the marsupium relaxed and the young exposed and damp to the touch. Resting postures were quite variable at high temperatures and opossums commonly slept on the back, with the mouth open and tongue out. The scrotum became flaccid at high ambient temperatures.

Behavioral responses to lowered ambient temperature were neither as well defined nor as consistent as those at higher ambient temperatures. As the temperature dropped from 25 to 15° C, the subjects usually remained quiet, either sitting or lying on their sides. At about 15° C some indication of mild discomfort was noted and the animals tended to curl more tightly and to pull the feet closer to the body. Below 15° C activity increased and grooming was common; the forefeet and hind feet were licked, but the major activity was scratching and combing the back with the hind feet. The fur appeared to be more erect at ambient temperatures below 15° C, particularly around the head and shoulder regions. With further decrease in the ambient temperature, behavior became more erratic. Some animals assumed a sitting position with the tail curled tightly alongside the body and the head tucked beneath the thorax. Others became hyperactive, trying to climb the walls of the chamber or dig through the mat on the floor. Visible shivering was observed, but varied markedly in its intensity, duration, and ambient temperature at which it was first noted. Surface temperatures of the tail when exposed dropped as low as 4 or 5° C, whereas surface temperatures of the tail might be as high as 25° C if protected by the body.

In contrast with observations in the experimental chamber, opossums under caged conditions were never seen to shiver at temperatures above freezing and gave no indication of discomfort at these temperatures. Nest building activity, described by Pray (1921), Smith (1941), and Layne (1951), became more common when temperatures fell below 10° C and nests made of straw were larger and more tightly constructed at lower ambient temperatures. General activity was sharply reduced at temperatures below freezing; individuals spent almost all of their time lying tightly curled in the nest boxes, coming out only for brief periods to eat or drink.

Discussion

Didelphis marsupialis virginiana appears to have about the same homeothermic ability as many placental mammals and is able to maintain a body temperature of about 35° C over a wide range of ambient temperatures. No indication of large daily fluctuations in body temperature was noted, nor was torpor ever observed, although such phenomena have been reported in other didelphids. Morrison (1946) noted cyclic fluctuations in the body temperature of *Metachirus nudicaudatus*, with amplitudes of 2° C. Cycles of similar magnitude were found in active *Marmosa microtarsus*, whereas torpid animals might decrease body temperature by as much as 16° C (Morrison and McNab, 1962). Morrison (1965) showed the body temperature of the dasyurid, *Dasycercus cristicaudata*, to fluctuate daily by as much as 4.1° C, and torpor in the phalangerid, *Cercaertus nanus*, was found to be common (Bartholomew and Hudson, 1962). Cade (1964) suggested that torpidity in rodents may be a primitive characteristic, but whether the same situation applies to marsupials is uncertain.

All homeotherms use one or more of several physiological and behavioral mechanisms for maintaining body temperature within relatively narrow limits. These include changes in peripheral blood flow, shivering, varying the degree of piloerection, regulating evaporative heat loss by sweating, panting, and saliva spreading, postural responses, and behavioral avoidance of temperature extremes.

At high temperatures, vasodilation of peripheral blood vessels, particularly in the tail, feet, nose, and marsupium, interact strikingly with the response of saliva spreading to increase heat loss through evaporation. Sweat glands are lacking in the opossum (Higgenbotham and Koon, 1955), but Sorokin (1965) found the bronchial glands of *Didelphis marsupialis* to be highly developed, supplementing the amount of fluid available to the opossum for spreading over its body surfaces during heat stress. The licking response is common above temperatures of 27° C and must effectively limit the distance an opossum can be removed from an adequate supply of water. During the summer months, at least, it may in part explain why opossums are often found near streams or swamps.

Robinson (1954) and Robinson and Morrison (1957) described heat stress behavior in several Australian marsupials: above T_a 35° C, the dasyurids, *Sminthopsis crassicaudata*, *S. larapinta*, and *Antechinus flavipes*, licked the forefeet, hind feet, and base of the tail; *Satanellus hallucatus* licked the forefeet and hind feet only and began open mouthed panting at T_b 39° C. The peramelid, *Isoodon obesulus*, started panting at T_b 38.5° C and licked the forefeet and abdomen at T_b 39° C. The macropods, *Potorous tridactylus*, five species of *Wallabia*, and *Macropus major*, licked the forelimbs and hind limbs liberally, and Bartholomew (1956) showed that saliva spreading is the main thermoregulatory response to high temperatures of *Setonix brachyurus*. Saliva spreading was most extensive among the phalangerids, *Petaurus breviceps*, *P. norfolcensis*, *Schoinobates volans*, and *Trichosurus*. The forelimbs and hind limbs were licked at T_a 35° C and the abdomen, genitals, and tail as well at T_a 40° C. This last group closely resemles *Didelphis* in its responses to high ambient temperatures. With the exception of *Sarcophilus harrisii* (Dasyuridae) and *Thylacomys lagotis* (Peramelidae), all marsupials studied showed some dependence on saliva spreading as a means of regulating body temperature. It appears that this method of increasing heat loss through evaporation is characteristic of marsupials.

Although the temperature stresses placed on *Didelphis* at lower ambient temperatures were neither sharp nor of long duration, the nearly constant body temperature speaks well for an adequate temperature regulating mechanism. Vasoconstriction appears to play the major role in heat conservation, as evidenced by the sharply reduced surface temperatures of the tail and pallid condition of the nose, ears, feet, and tail. Piloerection may provide some increase in body insulation, but Scholander *et al.* (1950) showed the fur of *Didelphis* to be a poor insulating material. Temperatures at which shivering occurred were variable and often it was not observed. Simple avoidance of extreme low temperatures by denning probably enables *Didelphis* to survive the severe winters in the northern limits of its range. At temperatures below freezing the general activity of caged animals dropped sharply. However, Hamilton (1958) noted that opossums were sometimes seen to forage in subzero weather. They are apparently unable to remain inactive without food for long periods. In a sample of 124 opossums that survived a winter in New York State, 37.1 per cent showed frost damaged ears and 64.5 per cent had frost damaged tails. These data indicate the extent to which the temperature in the extremities may be reduced when *D. marsupialis* is exposed to low temperatures, as is suggested by the low surface temperatures of the tail recorded in this study.

Didelphis marsupialis virginiana is an effective homeotherm with temperature regulation comparable to that of many placental mammals. The main response to high ambient temperature is to increase evaporative heat loss by saliva spreading and vasodilation of peripheral blood vessels. At low temperatures, vasoconstriction and denning appear most important for conserving heat.

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