THE PARASOL TAIL AND THERMOREGULATORY BEHAVIOR OF THE CAPE GROUND SQUIRREL XERUS INAURIS[1]

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The Cape ground squirrel, *Xerus inauris,* a diurnally active inhabitant of hot arid regions of southern Africa, reduces environmental heat load by using its bushy tail as a portable parasol. During late spring in the southern Kalahari, operative environmental temperature (T_e) was measured on thermal mannequins of differing posture and tail orientation. Simultaneously, the thermoregulatory behavior of a free-living colony of squirrels was observed. The tail is raised to shade the body and the squirrels turn their backs to the sun whenever T_e exceeds approximately 40 C. The shade provided by the tail reduces T_e by over 5 C and allows squirrels to extend greatly their periods of continuous surface foraging (up to 7 h instead of 3 h). At midday, squirrels must frequently retreat to their burrows as T_e of tail-shaded animals then also exceeds 40 C.

INTRODUCTION

Most small mammals living in deserts are nocturnal and thereby avoid exposure to heat during the hottest times of the day. Nevertheless, a few species, such as ground squirrels, are diurnal. Living in open areas on the desert floor, they may be exposed to intense environmental radiation, particularly solar radiation, and high soil temperatures. Here we report observations on the thermoregulatory behavior of the Cape ground squirrel (*Xerus inauris*), a species widespread throughout the arid regions of southern Africa (Smithers 1971; Herzig-Straschil 1979; de Graaff 1981). This squirrel reduces its environmental heat load by using its bushy tail as a portable parasol during the hottest period of the day, thereby greatly increasing its foraging time.

Cape ground squirrels spend their day foraging for small plants and seeds around their burrow entrances (Zumpt 1968; Herzig-Straschil 1978). They dig large burrow systems with multiple entries and tunnels that usually are 60–70 cm below ground surface (Zumpt 1970; Herzig-Straschil 1978). These ground squirrels are very social, with generally six to 10 individuals inhabiting one colony (Nel 1975; Herzig-Straschil 1978). In the Kalahari semidesert, the site of our study, these colonies are usually located in open pans, river beds, or river banks (Smithers 1971; de Graaff 1981). Because these areas are generally without shade, foraging animals are often exposed to very high ambient temperatures.

The most conspicuous anatomical feature of this animal is its large, bushy tail, which is dorsoventrally flattened and nearly as long as its body (Herzig-Straschil 1978; de Graaff 1981). The tail gives rise to the animal's common name in Afrikaans: "waaierstert meerkat" or "fan-tailed meerkat" (Synman 1940; de Graaff 1981). Its use for creating shade for the squirrel has been noted previously (Powell 1925; Smithers 1971; Marsh, Louw, and Berry 1978; Herzig-Straschil 1978, 1979). A sit-

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ting animal holds its tail erect behind its back; when horizontal, animals hold their tails over their bodies (fig. 1). The squirrels often orient their backs to the sun, thus completely shading their bodies from direct solar radiation. Changes in tail position and orientation appropriate to thermoregulation at different times of day have also been noted (Marsh et al. 1978; Herzig-Straschil 1979). We have made the first measurements of the actual effectiveness of the tail as a heat shield in reducing environmental heat load on these animals and have correlated changes in patterns of behavior with specific levels of operative environmental temperature.

MATERIAL AND METHODS

A colony of at least 11 *Xerus inauris* was observed during late November (spring) 1981 in the dry bed of the Nossob River in Kalahari Gemsbok National Park on the border of the Republic of Botswana and the Republic of South Africa (12 km northeast of Twee Rivieren, R.S.A.). The number of squirrels active and their posture and tail position and orientation with respect to the sun were surveyed with binoculars every 15 min from sunrise to sunset on a 400 × 110-m quadrat. Animals in transit are excluded from reported census data. The area had no trees or other objects to provide shade and was exposed to full sun throughout the day. Soil temperatures at the ground surface and 10 and 50 cm below ground were measured every 30 min with buried thermocouples and a Wescor thermocouple thermometer.

Operative environmental temperature (T_e) (Bakken 1976, 1980), an integrated measure of radiant and convective thermal input to an organism, was measured with pelt-covered taxidermic mannequins (Bakken et al. 1981; Chappell and Bartholomew 1981*a*) during the squirrels' active period. The T_e is the equilibrium temperature a squirrel would attain if it lacked metabolic heat production and evaporative water loss. Thus T_e serves as a measure of environmental heat loads. Two mannequins were constructed, one in the tail-up (shaded) position and the other in the tail-down (unshaded) position. Mannequins were prepared by mounting the skins of two adult female squirrels on frames fashioned from baling wire. The mannequins were the same size and shape as live squirrels and were modeled into a sitting position, the most common posture of foraging squirrels. Thermocouples were mounted in the thoracic region of the hollow internal cavity, and temperatures were monitored with a Wescor thermocouple thermometer. The mannequins were thoroughly dried and placed in full sun in an area directly adjacent to the observed colony. During the middle of the day, tail positions of the models were exchanged: temperatures of the mannequins rapidly reversed and attained the same level as the other mannequin prior to the change. When both mannequins were in the same tail posture and position, their T_e's were less than 1 C different.

The tendency of squirrels to orient their position (front, back, right side, or left side) with respect to the sun was computed using two-tailed χ^2 tests (adjusted for continuity), assuming an expected ratio of 1:3 for squirrels orienting randomly to the sun. Probability of nonrandom orientation is indicated in the text.

RESULTS

Observations were made on a warm, dry, and cloudless day, typical for late spring in the Kalahari. Air temperature in the shade at 1 m above ground level rose from 15 C at 0600 hours to a maximum of 33 C at 1530 hours (local time); intermittent breezes blew from the south. Soil surface temperatures exceeded 50 C from 1100 to 1600 hours, peaking at 61.7 C at 1230 hours, but temperatures at burrow depth remained at 27 C for the entire day.

The first squirrel emerged at 0748 hours local time, well after sunrise (0549 hours). The number of active animals, their tail position, and temperatures of the mannequins at each census period are shown in figure 2. The daily behavior pattern of the squirrels can be separated into a temporal series of five relatively discrete postures: tail down on soil surface, tail up on surface, tail up and burrow shuttling, tail up on surface, and tail down on surface.

From the 0800 to the 0915 hours census, squirrels foraging on the soil surface had

FIG. 1.—Use of the tail as a sun shade by the Cape ground squirrel (*Xerus inauris*). *Top,* The erected tail covers the entire dorsal surface of a sitting animal. *Bottom,* The tail is held erect over the back of a horizontal squirrel. Note the shading of the body and head.

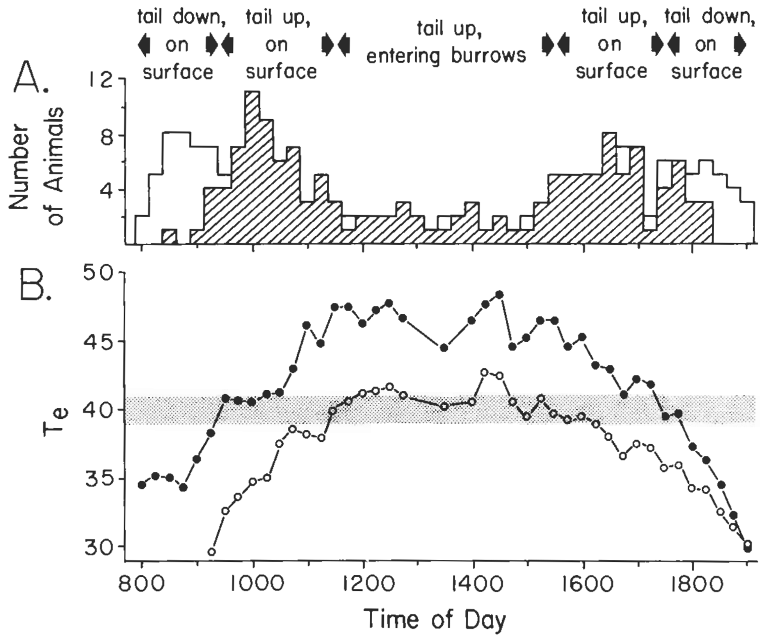

FIG. 2.—Thermoregulatory behavior and operative environmental temperature in the Cape ground squirrel. *A*, The number of individuals active above ground at each 15-min census interval. Open areas indicate animals with tails down; shaded areas, individuals with tails up over their backs. *B*, Operative environmental temperatures of two thermal mannequins of ground squirrels. ● = the model with the tail down, ○ = the model with the tail up. The shaded band indicates the approximate range of ambient temperatures that begins to elicit a rise in body temperature and salivation in this species.

their tails down, and their orientation with regard to the sun was random (14 of 34 observations with back to sun, $P > .05$). Between 0915 and 0930 hours, the T_e of the tail-down (unshaded) mannequin exceeded 40 C. Temperatures in this range in still air impose severe heat loads on this species: exposure of these squirrels to 40–41 C in a dry, controlled temperature cabinet causes a rise in body temperature from a normal value of 37.9 C and profuse salivation (Bolwig 1958). Field behavior changed dramatically at this time: squirrels erected their tails over their backs and sat with their backs toward the sun (46 of 58 observations between 0930 and 1130 hours, $P < .001$). This posture and tail orientation reduced T_e by 6–8 C (fig. 2).

By the 1130 hours census the T_e of the tail-up (shaded) mannequin also exceeded 40 C, and even squirrels with tails up thus encountered high heat loads. During this period, squirrels began to disappear from the surface (fig. 2) and to shuttle to and from their cool burrows, emerging for only brief foraging bouts on the surface. Because temperature in these burrows was only 27 C, environmentally acquired heat loads could thus be unloaded in the cool burrow tunnels, a situation very similar to that observed in the antelope ground squirrel, *Ammospermophilus leucurus* (Bartholomew 1964; Chappell and Bartholomew 1981*b*). Foraging bouts between 1130 and 1530 hours averaged only 9.6 min in duration ($n = 24$; SE $= 0.92$). During surface activity at midday, tails were usually held erect.

When T_e of the tail-up mannequin declined below approximately 40 C during midafternoon, the squirrels stopped shuttling in and out of their burrows and remained on the surface. They again oriented with backs toward the sun (46 of 50 observations, 1530–1730 hours, $P < .001$) and continued to shade their backs with erected tails. At 1730 hours, T_e of the tail-down mannequin also declined below 40 C. The squirrels soon began to lower their tails, and their orientation with backs to the sun was much less striking (10 of 20 observations, 1800–1900 hours, $P > .05$).

The sun set at 1904 hours, and the last squirrels entered burrows at 1911 hours.

DISCUSSION

The tail of the Cape ground squirrel is a highly effective parasol, significantly reducing environmental heat loads. Tail elevation decreased T_e by an average of 5.6 C between 0930 and 1730 hours (maximum decrement = 8.3 C) (fig. 2).

The activity and behavior of the squirrels are highly correlated with environmental heat load. Squirrels show no orientation to solar position and do not erect their tails early in the morning and late in the afternoon when T_e is low. When T_e exceeds about 40 C, they erect their tails and turn their backs to the sun, reducing heat input considerably. This behavioral use of the tail as a heat shield more than doubles the time available to squirrels for continuous surface foraging, adding 4 h to the 3 h sustainable with tail-down behavior alone (fig. 2). The use of the parasol tail, sun-orientation behavior, and burrows as thermal retreats should also considerably reduce water loss by these animals, which rarely have access to drinking water. Shading by the tail and burrow shuttling are also used by the antelope ground squirrel, *Ammospermophilus leucurus*, during hot weather (Hudson 1962; Bartholomew 1964; Chappell and Bartholomew 1981*a*, 1981*b*). The tail of *Ammospermophilus* is less bushy and is much shorter, extending less than half the body length and reducing T_e by a maximum decrement of only 3 C. These observations and those of Golightly and Ohmart (1978) provide empirical support for the suggestion (Muchlinski and Shump 1979) that the sciurid tail may be an important thermoregulatory organ, not only in cold but also in hot environments.

Diurnal surface activity varies seasonally in Cape ground squirrels. They forage actively throughout the day during the winter (Herzig-Straschil 1979), engage in burrow-shuttling behavior at midday during the spring, and remain underground during the hottest parts of the day in the summer (Bolwig 1959). The suite of thermoregulatory adjustments outlined here (parasol tail, sun orientation, and burrow shuttling) greatly increases time for foraging and social behavior for this species. But environmental heat loads during the hottest parts of the year are apparently too great for these behaviors to be completely effective. These behavioral and morphological adjustments can lessen but not eliminate thermoregulatory difficulties in the intensely hot deserts that these squirrels inhabit. They reinforce the notion that the behavior and morphology of organisms (Bartholomew 1964; Porter and Tracy 1974), not just their physical environment, must be considered in analysis of adaptations of organisms to climate.

This is the first study to report simultaneous measurements of operative environmental temperatures and continuous observations of thermoregulatory field behavior. The correlations between T_e and behavior in *Xerus inauris* are very striking: sun orientation, tail carriage, and timing of surface activity appear to be highly predictable with reference to this single measurement. T_e is an integrated measure of heat load that can easily be estimated in remote field situations with minimal equipment (Bakken 1980; Bakken et al. 1981; Chappell and Bartholomew 1981). We anticipate that the use of thermal mannequins will provide many opportunities in natural contexts for the interpretation of thermoregulatory behavior as well as for the documentation of environmental restriction of activity.

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