DEVELOPMENT OF THERMOREGULATION AND TORPOR IN THE GOLDEN-MANTLED GROUND SQUIRREL *SPERMOPHILUS SATURATUS*

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ABSTRACT.—Small mammals ectothermic at birth become endothermic when they weigh only 20–50% of adult body mass. Juveniles of several species show torpor shortly after endothermy is reached, and it appears that they conserve energy during food shortages to avoid starvation. We became interested in whether juveniles of a species with a marked annual cycle of hibernation and activity can enter torpor during the season in which adults remain homeothermic. Neonatal *Spermophilus saturatus* were ectothermic, and development of endothermy and thermoregulation required about 36 days. In summer, withdrawal of food and water did not induce torpor in endothermic juveniles. Only in fall, 2 weeks before all juveniles began hibernation with surplus food and water, could torpor be induced in some individuals by food and water deprivation.

Most small mammals are ectothermic at birth. Endothermy and thermoregulation develop in the following days or weeks in conjunction with increase in body mass and growth of fur (Morrison and Petajan, 1962). Weaning generally occurs when the young are able to maintain a constant high body temperature by internal heat production. At weaning, young weigh only 20–50% of adult body mass, and heat loss to the environment is high because of the large relative surface area. Because of their smaller body mass, juveniles may face a greater stress by food shortage and cold temperature than adults.

Adults of many species of small mammals confront seasonal energy shortage by periodically becoming torpid. Torpor may occur on a daily basis as, for example, in deer mice (*Peromyscus*—Tannenbaum and Pivorun, 1984) or on a yearly basis as in ground squirrels (*Spermophilus*—Kenagy, 1986). Metabolic rate at these low body temperatures is greatly reduced and food intake declines. The potential exists for juveniles to conserve energy during short-term emergency food shortages by becoming torpid. This probably would have a negative impact on growth, but represents nonetheless a potential for increasing survival under emergency circumstances.

Torpor in juvenile mammals has been observed in white-toothed shrews (*Crocidura russula*—Nagel, 1977), and in several small insectivorous and carnivorous marsupials of the family Dasyuridae that as adults also show torpor throughout the year (Geiser, 1988; Geiser et al., 1986). Torpor has not been observed in juvenile rodents. We studied the golden-mantled ground squirrel (*Spermophilus saturatus*) which has a strong, endogenously controlled seasonal pattern of 4.5-months aboveground activity alternating with a 7.5-month hibernation season (Kenagy, 1986; Kenagy et al., 1989*a*). We became interested in whether juveniles of a rodent species with such a marked annual cycle of hibernation and activity could enter torpor during development, in the season of homeothermy in adults.

METHODS

Four pregnant female *S. saturatus* were caught on 1 May 1986 near Fish Lake, Chelan Co., Washington and maintained individually at the University of Washington in cages provided with wood shavings. Air temperatures were kept at 8°C from 2–31 May, 12°C from 1–30 June, 16°C from 1 July–31 August, and 12°C from 1–30 September. These temperatures approximate soil temperatures at 50-cm depth in the underground burrows where *S. saturatus* raises its litters (Kenagy et al., 1989*a*). The photoperiod in the laboratory was adjusted to natural day length in the field. Rodent laboratory chow and water were available ad lib.

Litters of four, four, three, and two young were born between 6 and 26 May. To determine the development of endothermy in these 13 juveniles, they were removed from their mothers and exposed individually to an air temperature of 8 or 12°C for 30 min in a bucket on a 5-cm layer of sawdust but without a nest. The

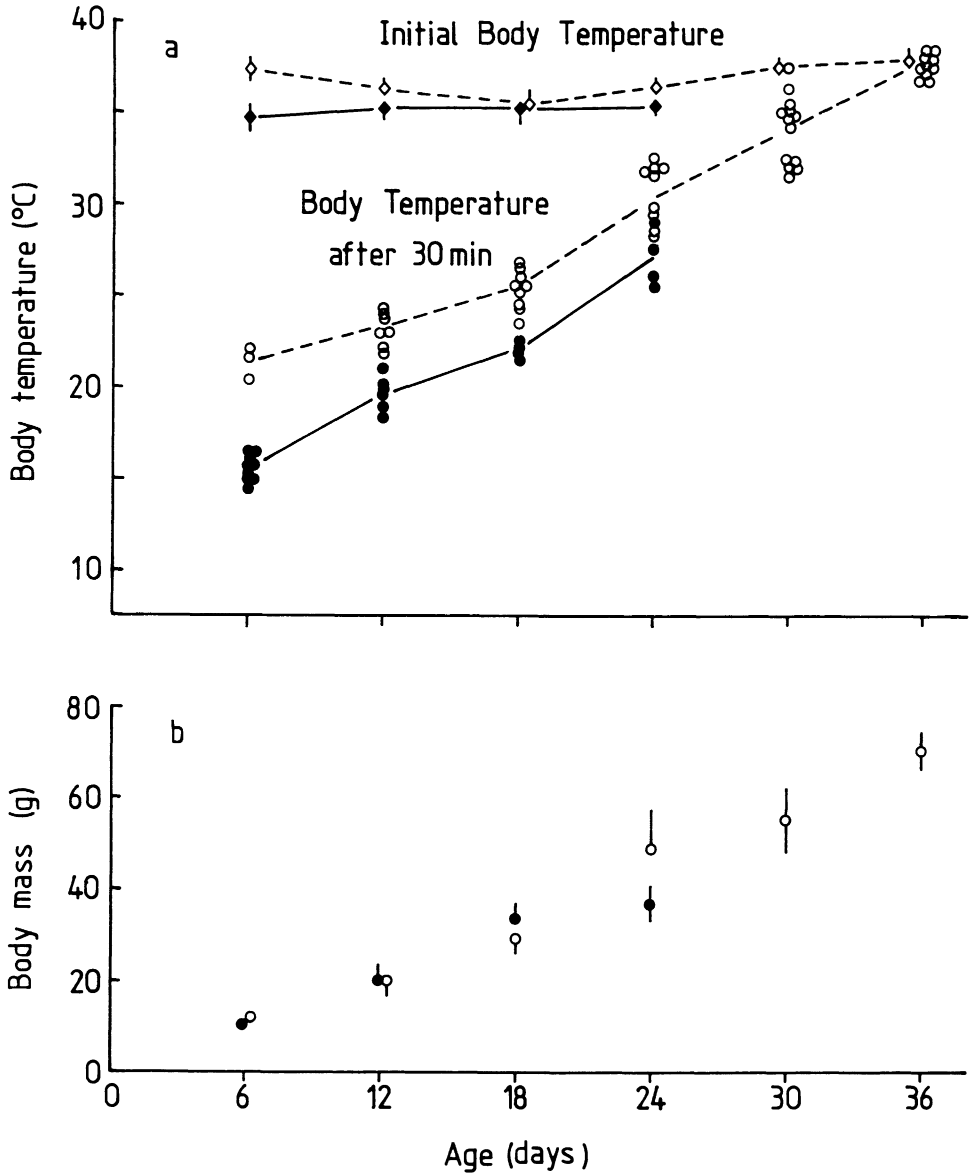

FIG. 1.—Occurrence of torpor in 10 juvenile *S. saturatus* (a) and (b) their mean body mass with *SD* (vertical bars) before and after the 2-day withdrawal of food.

ability to maintain body temperature also was investigated in whole litters in the nest. Body temperature was measured rectally with a calibrated thermocouple probe. After all juveniles had become endothermic, they were separated from their mothers and kept with litter mates until 1 July, after which they were kept individually. Beginning in late June, food and water were withdrawn from these juveniles for 2 days at intervals of about 2 weeks throughout the summer to ascertain whether torpor could be induced by food and water deprivation as in other heterothermic mammals. Rate of oxygen consumption was measured continuously in some individuals for 1-day periods to determine whether torpor occurred during the daily cycle. Food and water were not provided during measurements of oxygen consumption (open-flow system; Applied Electrochemistry S-3A, Pittsburgh, PA). Air temperature during experiments always matched that of the prevailing holding conditions of each litter.

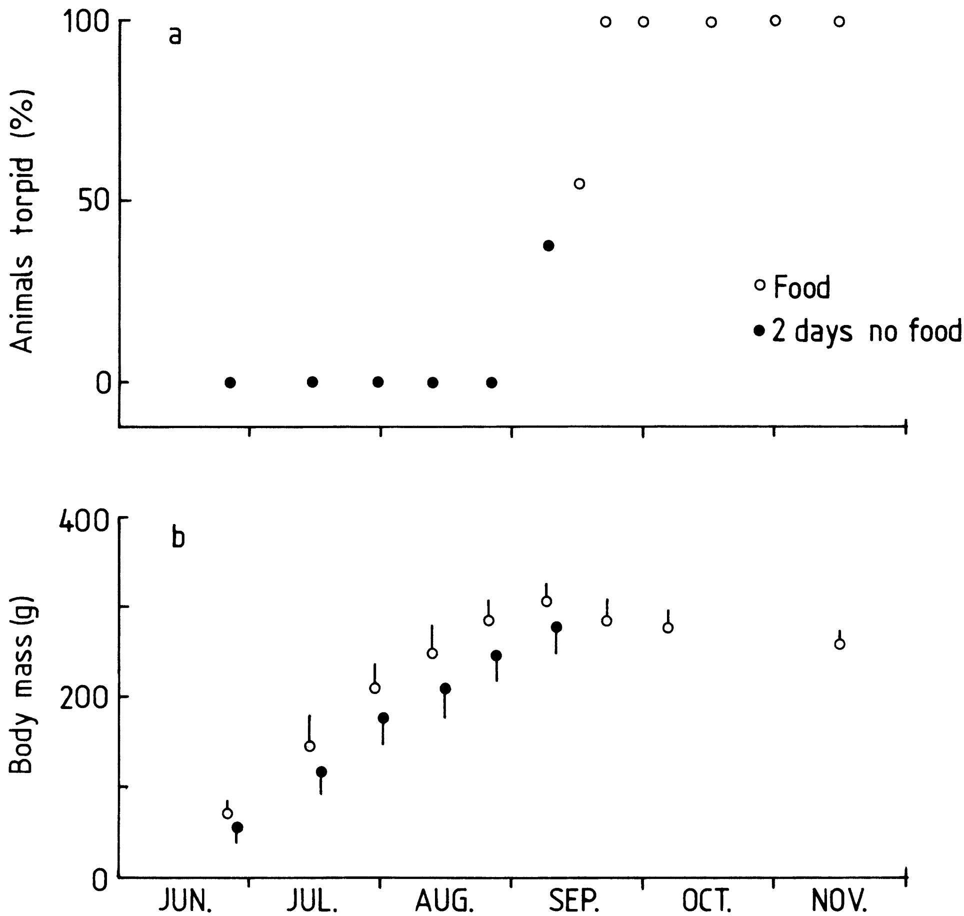

FIG. 2.—Body temperature (a) and body mass (b) of juvenile *S. saturatus* as a function of age. Initial body temperatures (diamonds) are $\bar{X}$ with *SD* (vertical bars) of animals in the nest with their mothers. Body temperatures after 30 min isolated exposure to 8 or 12°C (circles) are individual values for each animal. Sample size for initial body temperature is identical to that shown for body temperatures after 30 min. Closed symbols indicate air temperature of 8°C, open symbols 12°C.

RESULTS

Development of endothermy and thermoregulation in *S. saturatus* was gradual (Fig. 1). At 6 days, when body mass was about 11 g, body temperature of individual juveniles fell rapidly during the 30-min exposure to an air temperature of 8 and 12°C. Body temperatures of individuals at 8°C ($\bar{X} \pm SD$, 15.6 ± 0.7°C, $n = 10$) were lower ($P < 0.0001$; *t*-test) than those at 12°C ($\bar{X} = 21.4 \pm 0.9$°C, $n = 3$). The rate of cooling was reduced gradually during the next 30 days of development, and at 36 days (body mass about 70 g) all individuals were able to maintain a constant, high body temperature.

Body temperature of juveniles in the nest with their mothers ranged from 34.7 to 37.5°C between days 6 and 30, and was more stable than in individuals removed from the nest. At 36 days, body temperature in the nest was 37.8 ± 0.5°C and after 30 min of individual exposure to an air temperature of 12°C (without nest) body temperature was 37.7 ± 0.6°C ($n = 10$). When mothers were removed and litters remained in the nest for 30 min, body temperature fell less than when pups were removed from the nest and kept individually. Under these conditions, all juveniles were able to maintain their body temperature above 37°C at 30 days, when body mass was about 55 g.

Removal of food and water generally did not induce torpor in endothermic juvenile *S. saturatus* (Fig. 2). When food and water were withheld for 2 days at about 2-week intervals (or 1 day during measurement of oxygen consumption) from late June to early August, most individuals remained homeothermic. In June, some individuals with low body masses became hypothermic; they could not arouse from their low body temperature and required exogenous heat, provided by returning them to the mother's nest, for rewarming. In early September, withdrawal of food and water resulted in torpor in about 40% of the animals. However, just 2 weeks later all individuals began to enter torpor spontaneously and regularly, despite access to surplus food and water, indicating onset of the hibernation season. Thus, it was only possible to induce torpor by food and water restriction at a brief transitional interval of change in the pattern of thermoregulation.

Discussion

Our study shows that *S. saturatus* is ectothermic at birth like many other small mammals and birds (Dawson and Hudson, 1970; Morrison and Petajan, 1962). Endothermy develops with the increase in body mass and growth of fur. Individual *S. saturatus* were homeothermic at an age of 36 days (Kenagy et al., 1989*b*), the age of emergence from the natal burrow in nature (Kenagy et al., 1989*a*). Our results on development of thermoregulation also are similar to those reported for other species of ground squirrels (Dolman, 1980; Maxwell and Morton, 1975). This is somewhat surprising because our animals were raised and investigated at environmental conditions similar to those experienced by animals in their underground burrows in the field, low air temperatures of 8–12°C, rather than at about 20°C, as in the other studies (Dolman, 1980; Kenagy et al., 1989*b;* Maxwell and Morton, 1975). Our observations, therefore, indicate that differences in air temperature over the range of 8–20°C do not affect development of thermoregulation in *S. saturatus* when food is freely available.

Endothermic juvenile *S. saturatus* did not enter torpor during summer, even when food and water were withheld for 2 days. This contrasts with observations on small dasyurid marsupials, which show torpor upon 1-day food restriction shortly after endothermy has been achieved. Furthermore, torpor in juvenile dasyurids was deeper and longer than in adults (Geiser, 1988; Geiser et al., 1986). Torpor in endothermic juveniles also has been observed in a shrew (Nagel, 1977) and in birds, such as storm-petrels (*Oceanodroma furcata*—Boersma, 1986) and house martins (*Delichon urbica*—Prinzinger and Siedle, 1986). Most species that show juvenile torpor are insectivorous, therefore, must cope with unpredictable fluctuations in prey availability. Postnatal mortality may be reduced by employing torpor during food shortages.

In contrast to the described instances of apparently adaptive use of torpor by juvenile endotherms, juvenile *S. saturatus* maintained a high body temperature even when withdrawal of food and water resulted in a dramatic decrease in body mass (Fig. 2). The circannual rhythm of *S. saturatus* (Kenagy, 1986) apparently directs a postnatal pattern of growth and uninterrupted homeothermy that fits into the limited season of trophic production (Kenagy et al., 1989*a*). During this limited productive period the animals must increase their mass and energy reserves for the long hibernation season. Food is abundant during the season of reproduction and early postnatal growth (Kenagy et al., 1989*a*). Thus, torpor during this period seems unlikely and would be counterproductive as it would slow growth and decrease the chance of surviving the first hibernation season.

Acknowledgments

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