LABILITY OF TAIL LENGTH OF THE WHITE-FOOTED MOUSE, *PEROMYSCUS LEUCOPUS NOVEBORACENSIS*

RICHARD W. THORINGTON, JR.

ABSTRACT.—White-footed mice raised at 25°C have significantly longer tails at maturity than do mice raised at 15°C. The length of distal caudal vertebrae is more affected by temperature than that of proximal caudal vertebrae, suggesting a direct effect of temperature on tail growth. The results may be invoked to explain variation observed in nature, but extrapolations to free-ranging mice involve unverified assumptions.

The effect of environmental temperature on the tail length of rodents was first investigated by Sumner (1909). He demonstrated that white mice (*Mus musculus*) raised at warmer temperatures had longer tails than did those raised at cooler temperatures. Przibram (1925) demonstrated the same effect with *Rattus rattus* and albino *Rattus norvegicus*. A number of other workers subsequently documented this phenomenon (Ogle 1934; Ashoub 1958; Harrison *et al.*, 1959; Knudsen 1962; Barnett, 1965) with different strains of *Mus musculus*.

The present investigation was undertaken to determine if the white-footed mouse, *Peromyscus leucopus noveboracensis*, also exhibits a temperature dependent lability of tail length. This is of interest for at least three basic reasons. First, *P. leucopus* is a cricetid rodent, whereas all previous investigations were carried out on murid rodents. Thus the results presented here permit a somewhat broader evaluation of the significance of this phenomenon among rodents. Second, the animals used were not inbred or laboratory strains. Przibram's work with *Rattus rattus* is the only other investigation in which this is the case. The investigations of Harrison *et al.* (1959) with inbred and "hybrid" *Mus musculus* demonstrated the relevance of the amount of inbreeding in studies of the lability of tail length. Third, the geographic variation of tail length of the white-footed mouse is of a complex and interesting nature. Over its range, *P. leucopus* exhibits little subspecific variation of size or tail length, in striking contrast to *P. maniculatus* (Osgood, 1909). It does not exhibit the geographic variation of Allen's rule. Within any geographic area, however, *P. leucopus* is a highly variable species, and the differences between local populations may be as great as the described differences between subspecies. Dice (1937) investigated this variation in *P. l. noveboracensis* by raising animals from different populations under uniform conditions in the laboratory. By showing that interpopulation differences still exist among animals raised in the laboratory, he demonstrated that there is a genetic basis for the variation observed in the wild. He did not investigate nongenetic variation of characters, *per se*, but, in fact, such variation is evident in his data and was noted by him. Specifically, the tails of mice raised in the laboratory were characteristically and significantly shorter than the tails of the parents, which had been trapped in the wild. Both this nongenetic variation and the considerable variation of neighboring populations in the wild may be due in part to an effect of temperature on tail growth.

METHODS

Specimens of *Peromyscus leucopus noveboracensis* were trapped at several localities in Massachusetts and southern New Hampshire. The animals were paired and placed in cages 6 by 12 inches with a height of 3½ to 7 inches, one pair per cage. For nesting material, each pair was given one paper towel. Each breeding pair was placed in one of two experimental groups. Both experimental groups included animals from several different localities, but the averages of tail lengths of the mice in the two groups were the same.

One group of mice was kept in a cold room, which ranged in temperature from 15 to 17°C. The other group was kept at room temperature, which varied from 25 to 30°C during the experimental period. In the cold room there was no seasonal fluctuation of temperature, although there was a difference between shelves, so that some cages were at slightly warmer temperatures than were others. There was little diurnal fluctuation in temperature in the warm room, and a better circulation of air assured in that all cages were at the same temperature. However, there was a distinct seasonal fluctuation in temperature, which affected the results, as will be noted. Photoperiod was controlled so that both rooms were dark for 8 hours per day. Humidity was not controlled, as it was reported by Przibram to be relatively unimportant (but note the suggestion to the contrary made by Knudsen, 1962).

Two series of measurements were taken on mice born and raised under these experimental conditions. First, a series of 35 mice that were 12 weeks old was measured; the standard field measurements of length of tail, total length, and weight were taken. Subsequently, 76 adult mice (including most of those in the first series) were X-rayed, and the second series of measurements was taken from these X-rays. The mice in this second series varied in age from 2½ to 8½ months but none of the mice raised in the cold room was less than 5 months old, an age beyond which little additional growth may be expected.

Tail lengths were measured to 0.1 millimeter with vernier calipers from the X-rays. The measurements taken were the total length of the caudal vertebrae, the length of the first five, and the length of the next 10 vertebrae. The length of the terminal nine to 12 vertebrae was determined by subtraction. This subdivision of the tail vertebrae into three groups approximates the morphologic changes of the vertebrae. Of the first five caudal vertebrae, two to four are within the body and tend to be fairly short. The next 10 (vertebrae six to 15) are the longest vertebrae of the tail. The vertebrae then become progressively shorter toward the tip of the tail. The number of caudal vertebrae of each mouse was counted or estimated. In young animals, and in some of the mice raised in the cold room, the terminal vertebrae were difficult to count, and it was necessary to base an estimate on both the noted rate of shortening of successive vertebrae and the total length of the caudal vertebrae.

RESULTS

At 12 weeks of age, mice raised in the warm room had longer tails than those raised in the cold room. As shown in Table 1, the mean of the tail lengths of the five litters raised in the warm room was 78.8, whereas that of three litters raised in the cold room was 61.1 millimeters. The difference is significant ($P < .001$). The difference between the means of the relative tail lengths is also significant ($P < .001$). The tails of mice from the warm room averaged 87.8 per cent of the body length, whereas those of mice from the cold room averaged 70.3 per cent.

The results of the second series of measurements are presented in Figs 1 and 2. The mean lengths of the caudal vertebrae (82.7 and 66.3 millimeters) for the two groups are

TABLE 1.—*Tail lengths of* Peromyscus leucopus *at 12 weeks of age.*

Animals raised at 25–30° C			Animals raised at 15–17° C		
Litter	Tail length	Tail length / Body length	Litter	Tail length	Tail length / Body length
A	79	0.88	F	56	0.65
	78	0.83		68	0.79
	82	0.89		60	0.71
	84	0.92		60	0.66
	69	0.71		61	0.67
	81	0.89			
	81	0.84	G	62	0.67
				60	0.65
B	74	0.86		60	0.67
	78	0.87		63	0.76
	73	0.80			
	80	0.86	H	59	0.71
				59	0.68
C	69	0.85		64	0.77
	70	0.84		60	0.69
	76	0.93			
			Mean =	61.1	0.703
D	82	0.92	SD =	2.9	0.047
	90	0.97	SE =	0.8	0.013
	83	0.93			
	81	0.93			
E	90	0.97			
	77	0.93			
	77	0.87			
	80	0.83			
Mean =	78.8	0.878			
SD =	5.6	0.060			
SE =	1.2	0.013			

significantly different ($P < .001$). The overlap between the two groups and the greater variation of tail lengths of mice raised in the warm room may be ascribed to the seasonal variation of temperature in that room, because the mice with the shortest tails were raised at a time when the temperature ranged lower than 25°C. Due to this variation in temperature, the apparent correlation between the tail lengths of the parents and their progeny cannot be considered valid.

The lengths of basal, medial, and terminal groups of vertebrae are plotted in Fig. 2 as percentages of the total length of caudal vertebrae for mice of both groups. The length of the basal five vertebrae was relatively unaffected by temperature and they contributed proportionately less, therefore, to the length of the longer tails. The medial group of 10 vertebrae constituted a constant percentage of tail length, independent of the total length. The terminal vertebrae constituted a larger percentage of the length of longer tails. This is due to the increased length of the constituent vertebrae, not to an increase in the number of vertebrae in the longer tails. Thus the terminal vertebrae are relatively the

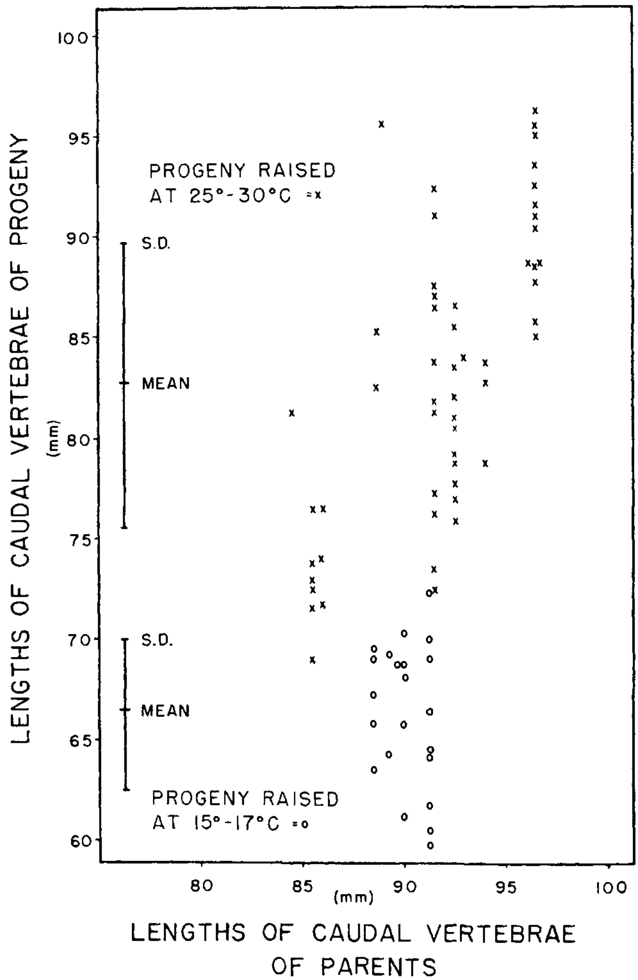

FIG. 1.—Tail lengths of *Peromyscus leucopus* raised at two different temperatures.

most labile—their lengths are the most affected by temperature. However, almost half of the total difference in tail length is accounted for by the lability of length of the 10 medial vertebrae.

DISCUSSION

Environmental temperature has been shown to affect the tail length of the cricetid, *Peromyscus leucopus*, and three murids, all of which have long, relatively naked tails. The effect of temperature on the tail length of short-tailed or hairy-tailed rodents is not known.

The mechanism of this temperature effect on tail growth has not been directly investigated. As first noted by Sumner (1909) in white mice and verified by several other authors, the temperature-induced differences of tail length reflect changes of lengths of vertebrae, not changes of the number of vertebrae. Barnett (1965) presented evidence of slight decreases in numbers of vertebrae in lab strains of *Mus*, but the major effect of temperature in his studies was also on the length of the vertebrae. I have presented evidence that the more distal vertebrae are the more labile in length. The simplest hypothesis to account for these facts is that the rate of cell division in the vertebrae is affected directly by the temperature of the vertebrae. Vertebrae at the base of the tail are little affected by the environmental temperature, whereas the rest of the caudal vertberae are affected both in temperature and in growth by the environmental temperature. The tail under many conditions is essentially poikilothermic. The temperature of the distal vertebrae should be most affected by environmental temperature and their growth was most changed by temperature. This hypothesis is incomplete, however, because there is no evidence to show what temperature is most significant: the average daily tail temperature; the average tail temperature when the mouse is in its nest; the highest tail temperatures experienced daily; or some other measure. An *a priori* case could be made for any of the three suggestions. Harrison (1963) obtained relevant but inconclusive data by raising *Mus musculus* under a daily temperature regime of 11 hours each at 21° and 32°C (allowing 1 hour for the change). The tail lengths of these mice more closely approximated those of mice raised at a constant 32° than at a constant 21°C, causing Harrison to suggest that the highest tail temperatures experienced daily are important.

The mechanism is obviously critical in any extrapolation from laboratory data to the wild. The tail length of an adult *P. leucopus* may be affected by the season of its birth and the microhabitats in which it lived. However, the effect would be less if nest temperature were more significant than the average or the maximum daily temperatures the mouse experienced. (Probably all *Peromyscus* modify nest temperature to some extent, as shown by Nicholson, 1941, for *P. leucopus*, by seasonally changing the place of the nest, the number of occupants, or the amount of nesting material; Selander, 1952, also noted seasonal changes in the thermal efficiency of nests made with the same material.) Therefore more laboratory studies involving fluctuating temperatures are required to determine precisely the parameters that are most significant in affecting tail length.

It is also necessary to know more about the thermal history of wild rodents. The techniques are available for studying the temperatures of nests, burrows, and runways when mice are in them (Nicholson, 1941; Pearson, 1959; Starck, 1963; Hayward, 1965), but the data are not yet adequate to permit precise comparisons of the thermal histories of mice at different seasons or in different habitats.

The tail temperature of *Peromyscus leucopus* and albino *Rattus norvegicus* is usually equal to the temperature of the environment (Thorington, 1966). Under two conditions this is not true: when the animals sit on their tails, which they do commonly in a cold environment, and when they are overheated or are exercising (Knoppers 1942, Rand *et al.*, 1965). Rand *et al.* showed that

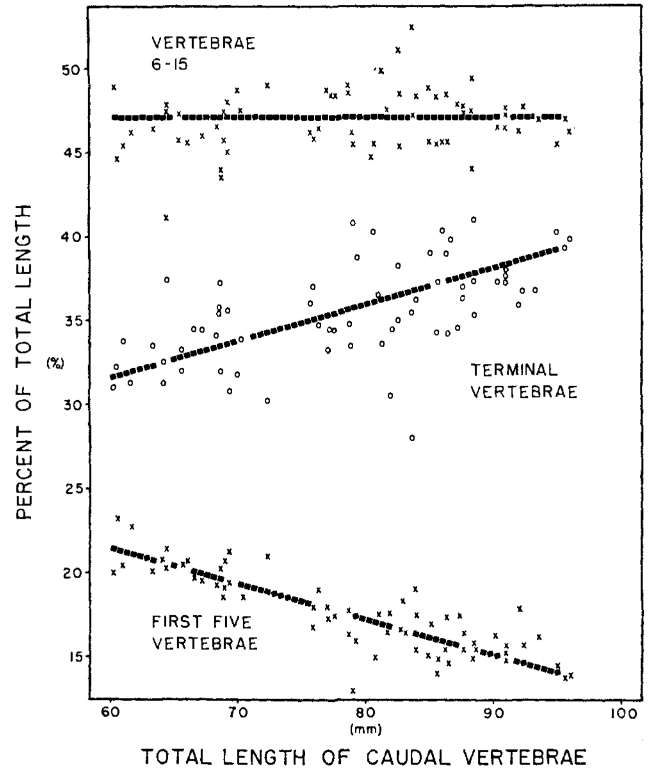

FIG. 2.—Relative lengths of proximal, medial, and distal caudal vertebrae of *Peromyscus leucopus.*

white rats not acclimated to heat, vasodilated their tails (and hence raised tail temperatures) at lower environmental temperatures than did rats that were acclimated to heat. Thus there are several factors other than environmental temperature that affect tail temperature and presumably tail growth.

For these reasons the relevance of the laboratory data for wild mice needs to be tested directly. Harrison (1963) stated that the tail growth of wild mice (presumably *Mus musculus*) is influenced by temperature, but I have not yet seen any data that unequivocally demonstrate this, either as a seasonal change in tail length within a population or as significantly different tail lengths between populations that are genetically similar.

Peromyscus leucopus exhibits little or no clinal variation of tail length (Osgood, 1909; Thorington, 1966), but this cannot be construed as evidence against a temperature effect on tail growth. In an artificial but analogous case (Barnett, 1965), different strains of *Mus musculus* grew equally long tails when raised at different temperatures. Although all strains exhibited lability of tail length, the rate of tail growth differed between strains raised at any particular temperature. Similarly, the lack of clinal variation in *P. leucopus* could result from differing growth responses to temperature, in spite of clinal changes in environmental temperatures throughout the range of the species. The significance of the uniform tail length of *P. leucopus*, in such striking contrast to the variation in *P. maniculatus*, is perhaps to be found in the use made of the tail in climbing. *P. leucopus* seems to be a scansorial animal throughout its range, and the tail is used considerably and effectively by the mice when they are climbing (Horner, 1954). In contrast, *P. maniculatus* is a scansorial species in some areas (where it generally has a long tail), and is more terrestrial in other areas (where it has a shorter tail). This correlation suggests that tail length of these mice is selected primarily for the role of the tail in locomotion. Therefore, any effect of temperature on the tail length of wild rodents can be recognized only in comparisons of genetically similar animals and it can be adduced as an explanation only of local geographic variation or seasonal variation.

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