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Temperature selection and activity of the Norwegian Lemming *Lemmus lemmus* (L.) in a temperature gradient apparatus

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Tested in a temperature gradient apparatus the Norwegian lemming seemed to show a seasonal trend in temperature selection ranging from 21.6°C ±10.5 in summer, over 18.6°C ±10.9 in autumn to 15.9°C ±12.8 in winter. Different activities such as voiding, grooming, attacking and resting were recorded during the experiments. Possible relationships between the selected temperature (ST) and the selected temperature zone (STZ) found experimentally and the natural habitat of the Norwegian lemming, together with some physiological aspects, are discussed. Both ST and STZ are higher than the temperature regime prevailing in lemming habitats during the year. The coincidence of such physiological parameters as the critical temperature and the temperature pertaining to the lowest and most stable rate of oxygen consumption seems to indicate that ST is in the temperature zone with the lowest energy expenditure for maintenance of a constant body temperature.

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INTRODUCTION

The Norwegian lemming *Lemmus lemmus* (L.) was tested in a temperature gradient apparatus in order to investigate a possible temperature selection. Since temperature conditions in lemming habitats, i.e. alpine and arctic areas in Fennoscandia and the Kola peninsula of USSR show great variation through the year, the aim was to investigate whether lemmings show a seasonal variation with respect to temperature selection. Further, whether this temperature selection, performed as a single factor analysis in an artificial and highly simplified environment, could be used to reveal information on the animal's temperature relations to its natural environment.

Earlier experiments on temperature selection in small rodents indicated that it is mediated by stimulation of the thermoreceptors on the soles of the feet when these are in constant touch with the substratum (Herter 1934, Bodenheimer 1941, Stinson & Fisher 1953). Lemmings, however, have very densely furred foot soles, and Smith & Fisher (1956), in a similar experiment with the Varying lemming *Dicrostonyx groenlandicus,* thought that this insulation may interfere with the temperature selection in preventing thermoreceptor stimulation by the substratum. Two series of experiments were therefore run, one with normal feet and one where the fur was shorn from soles and toes. Lemming behaviour during the experiments was studied and the distribution and frequency of some activities noted in the gradient recorded.

MATERIAL AND METHODS

The lemmings were caught in different highland and mountain areas of South Norway in the four seasons, spring, summer, autumn and winter. The spring animals, 2 ♀♀, were caught at Vauldalen, Sør-Trøndelag county, ultimo May 1964. The summer animals, 2 ♂♂ and 2 ♀♀, were caught at Finse, Hordaland county, medio July 1966. The autumn animals, 4 ♂♂ and 2 ♀♀, were caught at Tynset and Ytre Rendalen, Hedmark county, at Nøsen, Oppland county, and at Kongsvoll, Sør-Trøndelag county, medio September 1963. The winter animals, 3 ♂♂ and 1 ♀, were caught at Ytre Rendalen, primo December 1963. Due to scarcity of the test material of spring animals, the test material from the other three seasonal categories form the main base for this study.

Within 1—2 days of capture the animals were transported to the animal quarters at the Zoological Institute, University of Oslo, and kept at approximately 10°C. As a rule most were tested within two weeks of capture. Tests with normal feet were always made within the first week. All animals were fully grown, since young animals usually show a selection for higher temperatures than adults (cf. Herter 1952, Maurus 1958, Ogilvie & Stinson 1966, Kalkowski 1966).

Experiments were performed in a temperature gradient apparatus, earlier described by Østbye (1970). Shortly described this is an rectangular arena of 15 mm thick aluminium plates welded together; length 98 cm, width 12 cm and height 14 cm, covered by a 13 mm thick transparent plexiglass plate. A rheostatically controlled heating element is drilled into an aluminium block which forms one end of the apparatus. The other end extends into a container with the same width and height as the main box, in which cooling is accomplished with a mixture of 96% alcohol and crushed solid carbon dioxide (dry ice). With the exception of the portion surrounding the heating element, all of the bare metal sides are covered with sheets of polystyrene. Temperature determinations were made using a potentiometer and copper-constantan thermoelements attached directly to the metal floor in five positions 20 cm apart lengthwise in the apparatus. The arena was divided into 98 sections each 1 cm long and numbered from 1 at the cold end to 98 at the warm end.

The temperature of the apparatus can be regulated to the desired range by the heater thermostat and the proportions of dry ice and alcohol used in the cooling compartment. The horizontal gradient during the experiments could range from - 39°C to + 55°C. The vertical temperature gradient was, in general, very small, the maximum difference in temperature from floor to cover being 2°C, whether determinations were made on the metal wall or in the air.

By altering the temperature gradient the animals can be compelled to change their position in relation to the shift in gradient. The intention was that the temperature at each end of the arena should be repellent to the experimental animals (too high/low). This procedure was meant to partly eliminate the «edge effect» at the ends of the apparatus, which is an inherent problem in such studies. However, it appears that some animals in addition display a second type of «edge effect» in that they tend to squeeze themselves into the angle between the floor and walls at the long sides of the apparatus.

During experiments the apparatus is covered with a dark cloth and the room protected against sunlight. When readings are taken, the cloth is lifted just enough to permit quick and accurate readings.

Humidity was not regulated during these tests apart from blowing an air current directed into the apparatus, alternatively from the cold and warm ends in order to cause the animal to move when it remained in any position for more than five consecutive minutes. Otherwise the animal could stay at the same position for a considerable time.

During each experiment there was one lemming in the apparatus for one hour. Prior to observation time, the animal was admitted to the apparatus for 15 minutes to familiarize itself with the new surroundings. Different tests were tried with observation times ranging from one to three hours, and with recording times ranging from one to five minutes. The most convenient procedure was found to be one hour observation time with recordings each minute, the same as used by Smith & Fisher (1956) in similar experiments.

Animals in movement at the moment of observation were not recorded. The non-locomotory activity performed by the animal and its position in the apparatus at the time of recording were always registered. The animal's snout was taken as the recording point in the apparatus. During experiments the lemmings spent much of their time running back and forth from end to end, and when not running, were usually engaged in four major categories of non-locomotory activity, all easily distinguished by the observer. All this paralleled observations made by Smith & Fisher (1956). The four categories were: voiding, grooming, attacking and resting. Of these the first three are here used as activity groups, while resting is expressed as the selected temperature (ST) and selected temperature zone (STZ). The definition of these categories are as follows:

Voiding: urination or defecation; the presence of urine and faeces after the experiment was taken as evidence of this behaviour, and the number of splashes and droppings were counted.

Grooming: the animal rubs its face with the forefeet, especially after rapid running or having been frightened, or licks, scratches or strokes its pelage.

Attacking: includes biting (or attempting to bite), and scratching the floor, walls, and cover of the apparatus.

Resting: the animal stayed quiet in the same position for five consecutive minutes. Each of the five observations in the five minute series counted as a separate recording.

RESULTS

Orientation in the gradient

In both series of experiments, lemmings tested with normal feet and lemmings tested with naked feet, control experiments were carried out during which the apparatus ran with no temperature gradient. This was in order to investigate «edge effect», i.e. the tendency of the animals to seek towards the ends of the apparatus (corner attraction behaviour) (Fig. 1). Both with normal and with naked feet a clear tendency to stay in one or the other end of the apparatus was observed.

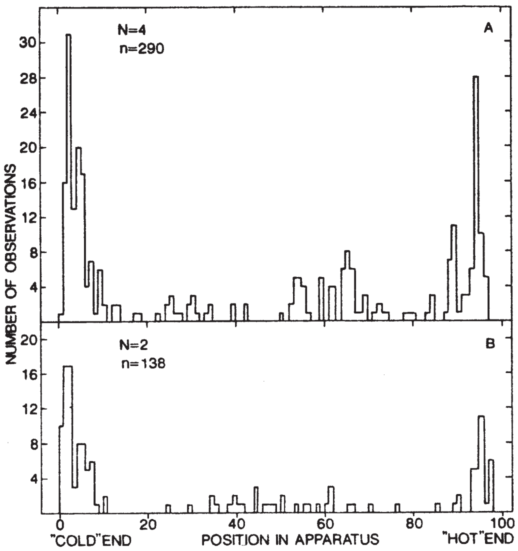

Fig. 1. The number of lemmings observed in the gradient apparatus at a uniform temperature of 20°C. (Combined data). A. Animals with normal feet. B. Animals with naked feet. N = number of animals tested. n = number of observations.

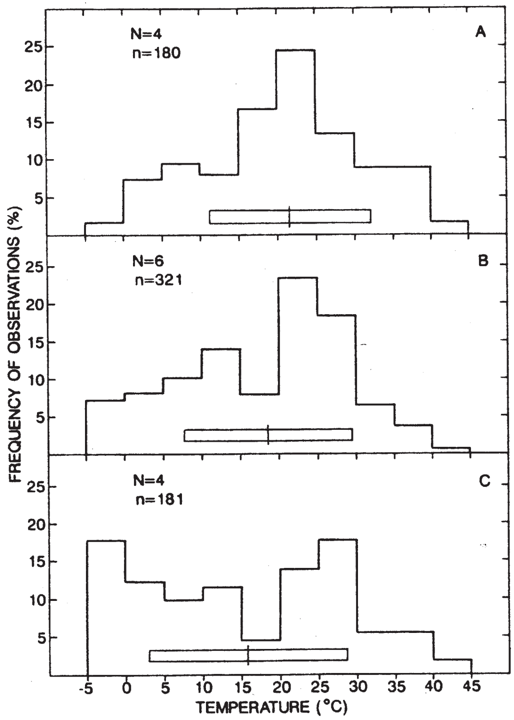

Fig. 2. The frequency with which lemmings with normal feet were observed in the apparatus when it was run with a temperature gradient. A. Summer animals. B. Autumn animals. C. Winter animals. Other symbols as in Fig. 1. ST and STZ are denoted.

Run with a temperature gradient, summer and autumn lemmings showed a tendency to select a certain temperature zone. This in contrast to winter animals which seemed less selective (Fig. 2). With naked soles, summer, autumn and winter animals all showed a more definite tendency to select restricted temperature zones under their orientation in the gradient (Fig. 3). All edge visits in these tests were eliminated from the calculation of the mean selected temperature (ST). The number of eliminated observations out of the total per group of data was approximately 18% (range 11% to 22%) for animals with normal feet, and approximately 9% (range 6% to 12%) for animals with naked feet.

Data from all experiments are given in Table 1. The mean of the observed temperature recordings is used to denote the animal's selected temperature (ST) together with the zone restricted by ± the standard deviation

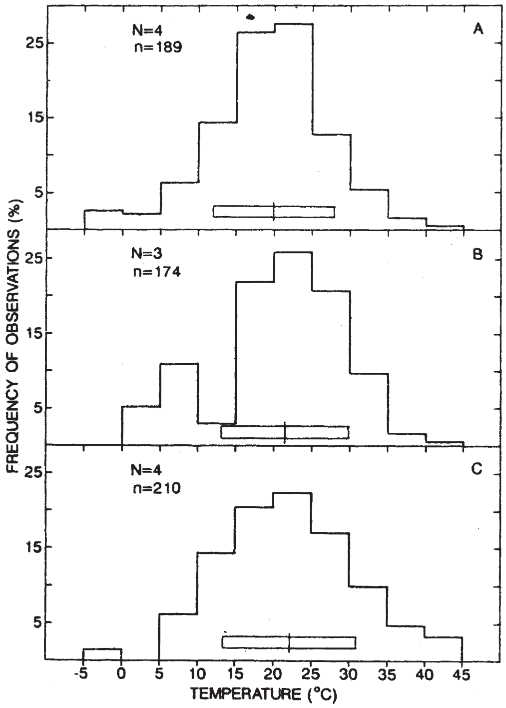

Fig. 3. The frequency with which lemmings with naked feet were observed in the apparatus when it was run with a temperature gradient. Symbols as in Fig. 2.

comprising 67% of the readings, referred to as the selected temperature zone (STZ). Significant differences are calculated by t-test.

Lemmings with normal feet show a trend to seasonal shift in the mean selected temperature. Summer animals have the highest ST at 21.6°C, autumn animals 18.6°C and winter animals are lowest at 15.9°C. Spring animals seen to be intermediate between summer and autumn animals. With naked feet the same animals seem to select somewhat higher temperatures than with furred soles. Winter animals now have the highest ST at 22.5°C, autumn animals 21.5°C, and summer animals the lowest at 19.9°C. The one spring animal tested had ST close to the ST of summer animals.

Activities

In the following, all data are arranged into two groups, animals with normal feet, and animals with naked feet. Urination tended to occur towards both ends of the apparatus in gradient experiments, while in control tests it was more uniformly spaced, or showed a slight tendency towards one end (Fig. 4).

Even if dropping of fecal pellets occurred over the whole apparatus, the tendency was towards a higher frequency at either end. Animals with naked feet however, deposited in gradient experiments more pellets at the cold end than at the warm end (Fig. 5).

Grooming seemed to take place over the whole apparatus, though with a slight preference for one end in two of the groups: naked feet with no gradient, and naked feet with gradient (the cold end) (Fig. 6).

Although attacking occurred over the

Table 1. The seasonal temperature selection of the Norwegian lemming. Edge effect excluded. Only significant differences are denoted.

Season	Feet	Number of animals tested	Number of observations	Mean selected temperature ($\bar{x}$ = ST)	Standard deviation (SD)	Selected temperature zone (STZ)	t-test P
Summer	Normal	4	180	21.6	10.5	11.1-32.1	0.01>p>0.001
Autumn	Normal	6	321	18.6	10.9	7.7-29.5	0.02>p>0.01
Winter	Normal	4	181	15.9	12.8	3.1-28.7	p<0.001
Spring	Normal	2	66	20.5	8.7	11.8-29.2	
Summer	Naked	4	189	19.9	8.0	11.9-27.9	0.01>p>0.001
Autumn	Naked	3	174	21.5	8.4	13.1-29.9	
Winter	Naked	4	210	22.5	8.8	13.7-31.3	0.01>p>0.001
Spring	Naked	1	15	19.6	3.6		

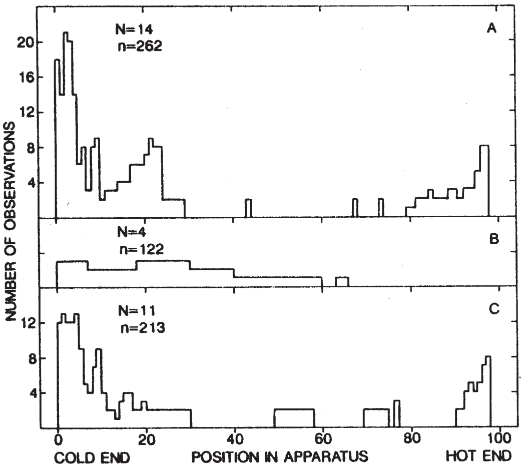

Fig. 4. The number of urine spots in the different sections of the apparatus. (Combined data). A. (gradient present). Animals with normal feet. B. (no gradient) & C. (gradient present). Animals with naked feet. Other symbols as in Fig. 1.

whole apparatus it showed a clear tendency for all groups to occur at the ends of the apparatus (Fig. 7).

DISCUSSION

The intention of introducing the lemmings to this long narrow apparatus was to simulate an enlarged «small rodent tunnel» with approximately even temperatures on all sides. The small vertical temperature gradient will supposedly have little effect on temperature orientation, in that throughout the entire experiment the animals generally remain down along the floor, in direct control with the metal. Tests conducted by Herter (1934, 1952), Bodenheimer (1941), Stinson & Fisher (1953) and Smith & Fisher (1956) imply that the temperature selection of the experimental animals results from the stimulation of thermoreceptors on the foot pads. These must be in contact with a substrate which is a good heat conductor to permit temperature gradient orientation. In contrast Kreiner

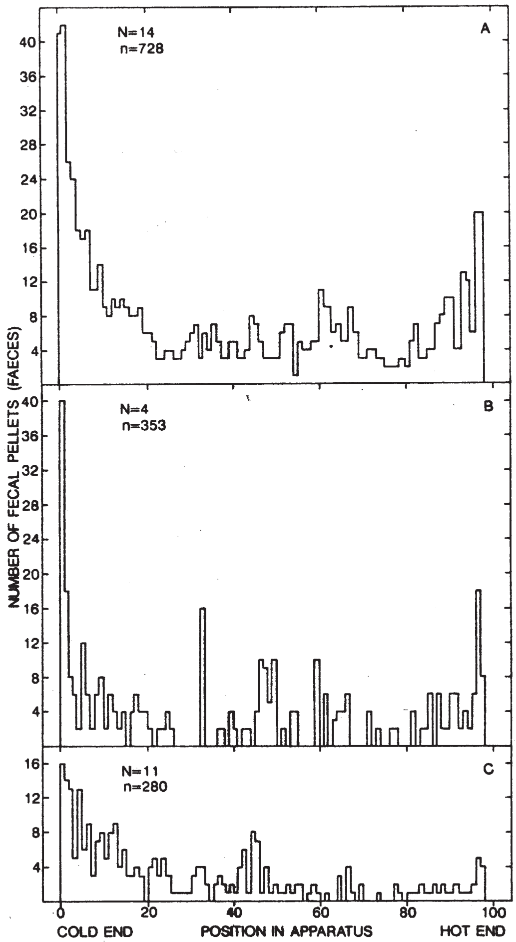

Fig. 5. The number of fecal droppings in the different sections of the apparatus. (Combined data). A. (gradient present). Animals with normal feet. B. (no gradient) & C. (gradient present). Animals with naked feet. Other symbols as in Fig. 1.

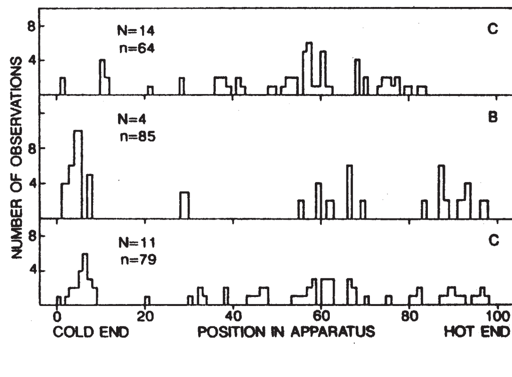

Fig. 6. The number of grooming observations in the different sections of the apparatus. (Combined data). A. (gradient present). Animals with normal feet. B. (no gradient) & C. (gradient present). Animals with naked feet. Other symbols as in Fig. 1.

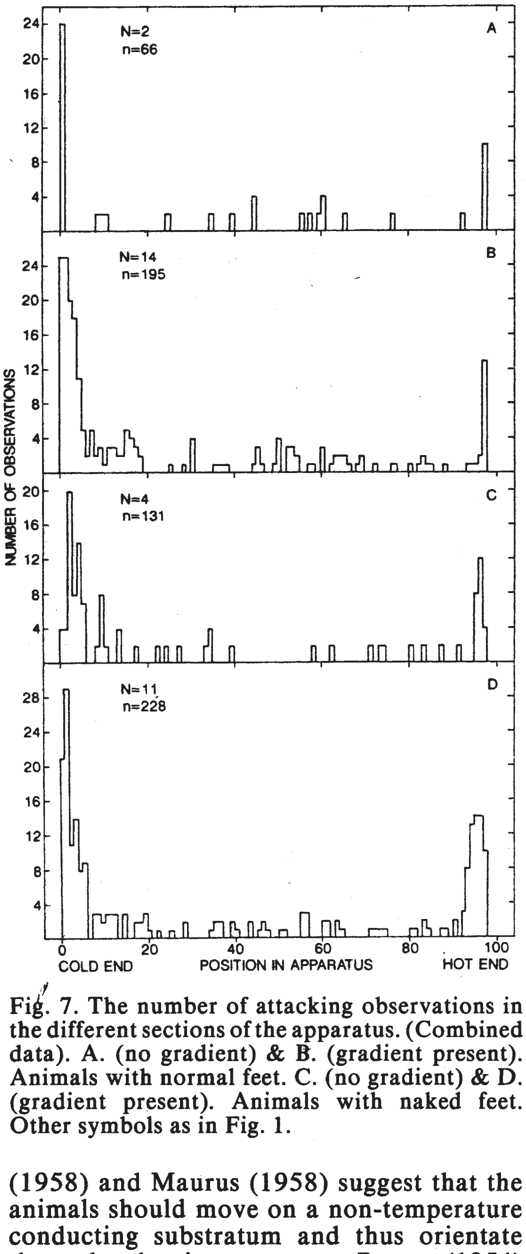

Fig. 7. The number of attacking observations in the different sections of the apparatus. (Combined data). A. (no gradient) & B. (gradient present). Animals with normal feet. C. (no gradient) & D. (gradient present). Animals with naked feet. Other symbols as in Fig. 1.

(1958) and Maurus (1958) suggest that the animals should move on a non-temperature conducting substratum and thus orientate themselves by air temperature. Prosser (1954) remarks that temperature selection in an ecological gradient need not necessarily involve specific thermoreceptors. Pain receptors cannot be entirely excluded in gradients with temperatures from below zero and up to 50°C (Hensel et al. 1973). Experiments with lemmings (Smith & Fisher 1956) indicate that close contact with the substratum leads to a better orientation, as revealed in experiments with animals tested first with normally furred feet and later with naked feet.

Animals with less dense fur on foot soles, i.e. summer and autumn animals, thus showed a stronger selective power than winter animals with a denser hair cover on the foot soles. Significant differences between the seasonal groups when tested with normal feet may indicate a shift in ST from higher in summer to lower in winter. A similar trend should then perhaps be expected when animals are tested with naked feet. A very slight, but significant reverse trend, was however observed. It is still an open question whether the trend observed in tests with normal feet is due to a real change in temperature selection or simply to the seasonal change in the fur density on the foot soles, i.e. denser fur permits an animal to tolerate lower temperatures. Summer animals with less dense foot fur tested with naked feet should be more adapted to lower temperatures than winter animals under the same conditions.

Since the microclimate in lemming habitats undergoes great daily as well as seasonal variation, and since the animals are moving from one location to another following different microclimates for short time intervals, it seems appropriate to use the selected temperature zone (STZ) for comparison of the experimental results with the microclimatic regime of a natural habitat.

For lemmings tested with normal feet there seems to be a seasonal change in the STZ. The trend appears to parallel the seasonal changes in temperature. Seasonal changes in selected temperatures have been found in some small rodents, but the broad variance in some of these tests makes them of questionable significance (see Hart 1971).

Both the ST and the STZ are higher than the daily seasonal temperature range of the normal habitat. The same phenomenon has been described for several small rodents (e.g. Herter 1952, Ivlev & Leizerovich 1960). However, when comparing habitat temperatures and ST, one should bear in mind that in many ST experiments it is the substratum temperature which is measured, and most recorded habitat temperatures are air measurements. Besides we lack knowledge of how temperature selection on a short-term basis affects the distribution of animals in nature (Smith & Fisher 1956).

In their study of the Varying lemming,

Smith & Fisher (1956) found no distinct ST for animals with normal feet; they had a clear tendency to stay at the ends of the apparatus (edge effect/corner attraction behaviour). In contrast the Norwegian lemming showed a fairly distinct ST (winter animals excepted), ranging from 21.6°C in summer, over 18.6°C in autumn to 15.9°C in winter. In experiments on animals with naked feet Smith & Fisher (1956) found a ST in the range of 28° -35°C. This is considerably higher than values from the Norwegian lemming in similar tests which show a ST ranging from 19.9°C in summer, over 21.5°C in autumn to 22.5°C in winter. Curiously, the Arctic fox *Alopex lagopus* was found to have a ST of 18.8°C in winter and of 23°C in summer (Kalabuchov 1950). These values lie in the range found for the Norwegian lemming.

During winter, lemmings spend most of their time beneath the snow cover in the subnivean air space and visit the snow surface only for shorter periods. Even if the temperature regime of the Fennoscandian mountain areas shows temperatures down to -30°C and below, the temperature regime in the subnivean wintering habitats of lemmings in Norway is usually around 0°C, ranging from approximately + 2°C to -8°C once the snow cover has reached a certain depth (unpubl. data).

Lemmings usually build their winter nests in the subnivean air space, or even some distance above the ground in small bushes, still however under a thick cover of snow. The isolative value of a Varying lemming nest has been measured to be roughly 1.5 times that of lemming fur (Scholander et al. 1950 a). Huddling of small mammals in their winter nests, which may be built in colonies, may increase the inside temperature. Scholander et al. (1950 a) stated that it is reasonable to believe that the nests are warm enough to maintain an air temperature of around + 10°C or higher. The critical temperature for the Varying lemming is around + 15°C (Scholander et al. 1950 b), for the Ob lemming *L. obensis* and the Middendorf vole *Microtus middendorffi* it fluctuates around + 16°C (Schwartz 1963), and for the Norwegian lemming around + 10°C (Skar 1969). Below this temperature the animals have to raise their metabolic rate to maintain a constant body temperature.

Even in summer the microclimatic temperatures in their habitats are lower than their ST or STZ. In preferred habitats in peatlands and mossy areas, temperatures in superficial runways and burrows have been found to be in the range + 1°C to + 15°C, and in a burrow 25 cm deep in the range + 1°C to + 3°C (Hackman 1963). Herter (1952) found that the respiration count in small rodents showed a minimum at the selected temperature (Herter's Vorzugstemperatur), rising at both higher and lower temperatures. He further stated that the ST for mammals is the temperature giving the least thermal exchange between the animal body and the substratum with resulting least energy cost while maintaining constant body temperature.

Our observations on activities performed by the lemmings during experiments coincide largely with those of Smith & Fisher (1956). Without a gradient, most activities were performed at or towards the ends of the apparatus. With a gradient, more of the intermediate area of the apparatus was used, but still much of the activity took place at or towards the ends.

Smith & Fisher (1956) state that the tendency to deposit faeces at the ends of the apparatus appears to be identical with the habit of depositing faeces in relatively constant locations in nature. The Varying lemming have been found to deposit large piles of faeces at ends of short dead-end burrows branching off main underground tunnels, as well as outside winter nests. This habit is similar in the Norwegian lemming. In addition it could be mentioned that defecation is performed in much the same pattern around summer nests and along surface runways (unpubl. data).

The frequency of and the position in which grooming takes place along the temperature gradient coincides with the distribution of resting frequency, i.e. the STZ. It seems natural to display this activity in the zone of greatest thermal comfort. When grooming occurs at the end positions it can possibly be interpreted as a type of displacement activity following a series of unsuccessful attempts to escape through the ends of the apparatus, in other words, trying to escape through their «burrows» or «runways».

As a final remark on experiments on selected temperatures as ecological tools, I feel that they yield valid and useful information about the animal's thermal history, if one regards them critically as artificial one-factor experiments taken from a large complex of environmental factors. In addition we must be aware of the unsatisfactory state of our knowledge of the animal's behaviour both under these experimental conditions and under the conditions of the natural habitat. I share Hart's (1971) impression of the selected temperature, i.e. that it seems to be one of the factors in a small mammal's choice of suitable microclimate. Finally, the fact that the relatively high level of temperatures selected by most small mammals generally is close to the range of thermoneutrality, should undoubtedly indicate an important behavioural tendency to select warm microclimates and to avoid conditions leading to high rates of energy expenditure.

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