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Thermoregulation as a limit to habitat use in alpine marmots (*Marmota marmota*)

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Summary. The body temperature (T_b) of free-living alpine marmots rose with activity; the higher the effective environmental temperature (T_e), the higher the rise. Maximum T_b of 40° C was reached at the time of greatest activity in late afternoon or evening. The activity pattern was strongly influenced by the microclimate. Up to an T_e of 25° C the animals spent more time above ground and were more active the higher T_e was, but above 25° C this trend was reversed, and the animals withdrew increasingly into their burrows. On warm days the activity pattern was therefore bimodal and above ground presence was reduced, in contrast to cool days. Hence behavioural thermoregulation limits the available time for above ground activity on days with high T_e in this strictly diurnal species. We suggest that the alpine marmots' preference for south oriented slopes is due to the better conditions for hibernation there, the microclimate during summer is more favourable on northerly slopes. Thermoregulatory constraints could also keep alpine marmots away from lower elevations.

Key words: Thermoregulation – Habitat use – Alpine marmots

Alpine marmots (*Marmota marmota*) inhabit elevations from 800 to 3200 m (Forter 1975) and experience extreme climatic conditions. They are considered thermophilic (Müller-Using 1951; Bopp 1964), and reported to be more active on warm sunny days (Zelenka 1965). They like basking in the sun and larger marmot colonies occur in areas exposed to the south (Forter 1975). On the other hand, a marmot's fur strongly absorbs solar radiation and the animals have only poor abilities to rid themselves of excessive heat (Pattie 1967; Hayes 1976). Hence in summer temperatures may sometimes become intolerably high. As alpine meadows, the typical marmot habitat, offer little shade, the diurnal herbivorous marmots are nearly always fully exposed to solar radiation whenever they leave their burrows. Yellow-bellied marmots (*Marmota flaviventris*) reduce foraging if equivalent black body temperature exceeds 25° C (Webb 1980). Therefore, heat stress in addition to daylength and the length of plant growing season limit the total annual foraging time available to individuals of this species (Webb 1980). Similarly, alpine marmots apparently avoid the noon heat and emerge only rarely on very hot days (Wüthrich 1982), and consistently gain less weight during summer on south oriented slopes (Arnold, unpublished work).

Inadequate physiological thermoregulation is often compensated by behaviour (Sale 1970; Bartholomew and Rainy 1971). In this paper, we investigate links between microclimate, body temperature and behaviour in order to understand how the daily activity pattern of alpine marmots is influenced by thermoregulation.

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Material and methods

Study sites and animals

The investigations were carried out in 1984 on two alpine meadows (Krautkaseralm and Büchsenalm) on the northern border of the Alps in the Berchtesgaden National Park, SE Germany.

Krautkaseralm. Three adult marmots living on a 29° SW slope, 1400 m above sea level were caught on 27 July 1984, marked with Nyanzol D fur dye and weighed (female no 1 4450 g; male no 3 4950 g; female no 5 4300 g). Temperature transmitters embedded in synthetic resin and coated with a mixture of paraffin and beeswax (2.9 × 3.3 × 1.5 cm; 20 g) were implanted in the abdominal cavity under anaesthesia. Body temperature (T_b) and behaviour were recorded from 31 July to 30 September between 0500 and 2000 h for a total of 133 h, and between 2000 and 0500 h for a total of 32 h. Signals were received with a H-antenna (maximal range ca. 300 m), and the impulse interval, coding T_b to 0.1° C, was read digitally from a portable multichannel receiver. In order to get a time budget we tried to observe the three animals continuously (focal subgroup sampling, Altmann 1974).

Data were evaluated, however, only up to the date, when the animals' daily mean T_b began to decrease steadily, which was considered a sign of transition into hibernation. This was August 18 for female 1, September 9 for male 3 and August 31 for female 5.

Büchsenalm. An adult territorial male and female, one 3-year-old male, three 2-year-old females, one 2-year-old male and one male yearling, all belonging to one family group, were caught in April 1984 and individually marked with Nyanzol; their home range was located on a 22° slope, flattening out below, facing ENE, 1190 m above sea level.

The animals were observed on 17 days between 12 June–12 July 1984 between 0430–2000 h for a total of 135 h. Behaviour was noted every 5 min to construct a time budget (scan sampling, Altmann 1974).

Climatic variables

The effective environmental temperature (T_e) gives a direct idea of an animal's thermal environment and is best measured using an animal model as "T_e-thermometer" (Bakken and Gates 1975; Bakken 1976). We measured T_e every 10 min inside a standing wire model-marmot, covered with a marmot hide, to within 0.1° C with a NiCr-Ni-thermocouple. Simultaneously, air temperature (T_a) was measured in the shade, 10 cm above the ground, and wind velocity (v) 30 cm above the ground with a mechanical anemometer. Air temperatures in the burrows were measured occasionally with a NiCr-Ni-thermocouple inserted in the burrow entrance. The surface temperature of boulders or mounds, used by the marmots for resting, and as look-out posts, was determined by means of an infrared radiation thermometer.

Data analysis

Recorded behaviours were grouped into categories: Feeding, running, carrying hay into a burrow, fighting, playfighting and digging under "active behaviour", sitting, lying and sitting up alert under "inactive". A third category was "staying in the den". The sum of min a given animal could be located within a 30 min observation interval was set to 100%. The proportion of this time spent above ground was then calculated for each individual, summed over all animals at an Alm and divided by their number. The proportions of active behaviour on above ground presence were calculated and averaged in the same manner. These half-hourly means entered statistical analysis, performed according to Sokal and Rohlf (1981) and Siegel (1976), as independent events.

During rain and mist the animals stayed for long periods in their burrows regardless of T_e. Therefore, we excluded times with bad weather from further analysis.

Days with an average T_e, during the entire observation time, above or equal to 25° C were regarded as warm, those with average T_e below 25° C as cool days. The distributions of observation hours over days did not differ significantly between warm and cool days ($X^2 = 17.5$, df = 14, $P > 0.2$).

Results

Climatic setting

On the easterly slope of the Büchsenalm maximum T_e was reached between 1100 and 1200 h, whereas on the southwest-exposed Krautkaseralm T_e reached its maximum towards 1500 h. T_a and T_e were higher on the Büchsenalm than on the Krautkaseralm for most of the day; wind velocity was very low at both sites (Table 1).

Body temperature

Mean body temperature was 37.7° C for female no 1 and male no 3, and 37.9° C for female no 5. T_b showed a circadian rhythm. At night T_b was usually lower than by day, the average daily range was 1.7° C in female no 1, 2.2° C in male no 3 and 2.1° C in female no 5. There was a plateau or even decrease of T_b during noon and a peak at 1800 h (Fig. 1). On hot days T_b climbed steeply from about 1700 h until dusk, when activity was highest, while on cold and rainy days T_b decreased from about 1700 h, because the animals retreated earlier into their burrows.

The apparent influence of various behaviours on T_b (Table 2) was examined in detail with multiple regression analysis. Bouts of behaviour which lasted at least 10 min were considered as independent events. Short intermitting episodes of other behaviours up to 1 min were neglected. We took the difference in T_b between beginning and end of a certain behaviour (ΔT_b) as dependent variable and the initial T_b ($T_b i$), the duration of the behaviour (t) and T_e as independent variables.

The rise in T_b during active behaviour was greater the higher T_e was (standardized partial regression coefficient (b') = 0.263, $P = 0.003$), and the longer the activity lasted ($b' = 0.217$, $P = 0.012$). $T_b i$ had the strongest influence on ΔT_b: the higher $T_b i$, the less T_b increased ($b' = -0.574$,

Table 1. Climatic conditions during the observation periods on Büchsenalm (12 June–12 July) and on Krautkaseralm (31 July–9 September), between 0500 and 2000 h

	T_a (° C)		T_e (° C)		v (m/s)	
	mean	range	mean	range	mean	range
Büchsenalm	15	5–33	27	6–54	0.7	0.0–4.0
	***		*			
Krautkaseralm	13	5–24	23	5–50	0.2	0.0–1.5

Differences between both sites were tested by comparing corresponding half-hourly means which had been averaged over all observation days (Wilcoxon tests, *** $P < 0.001$, * $P < 0.02$, $n = 30$)

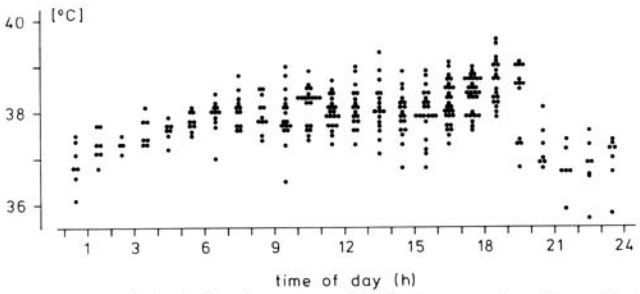

Fig. 1. Hourly individual means of body temperature from all observation days (5 days with average $T_e < 25°$ C, 11 days with average $T_e \geq 25°$ C)

Table 2. Bouts of different behaviours during which the body temperature from start to finish increased, decreased, or did not change

	T_b increase	T_b decrease	no change	P*
activity	57	13	6	<0.001
sitting	31	23	10	n.s.
lying	2	13	2	0.008
in the den	11	32	6	0.002

* Differences between increases and decreases were tested with binomial tests (H_0: $P = q = 0.5$)

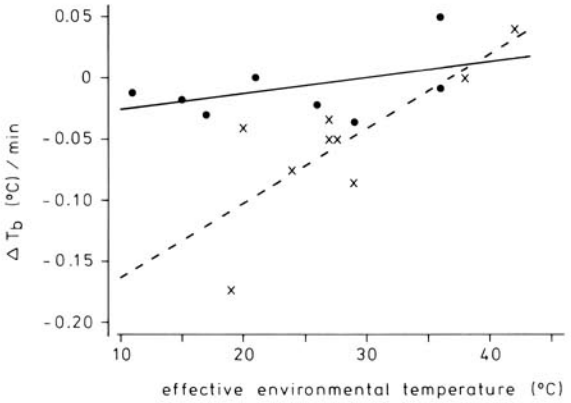

Fig. 2. Rate of change in body temperature, calculated as the difference in T_b from beginning to the end of a lying bout divided by its duration in min, versus effective environmental temperature of animals lying on a boulder (*xx*, broken line; $y=-0.23+0.006\,x$, $P<0.02$), or lying on a mound (.., continuous line; $y=-0.04+0.001\,x$, n.s.)

$P=0.001$). The three independent variables explained 50.6% of the ΔT_b variability in bouts of active behaviour.

When sitting, T_b rose less, the higher $T_b i$ ($b'=-0.362$, $P=0.005$) and increased more the higher T_e ($b'=0.316$, $P=0.018$).

When lying, T_b decreased in most instances (Table 2), but we could not find a significant influence of $T_b i$, T_e or t, presumably due to the additional effect of the substrate beneath the animal. Contrary to soil, the surface temperature of boulders correlated strongly with T_e ($r=0.925$, $P=0.001$, $n=21$). Hence the rate of change of body temperature (ΔT_b/min) was only influenced by T_e in animals lying on boulders, but not when lying on the mound in front of a burrow (Fig. 2).

The T_b changes of animals retiring to their dens during the day were negatively related to $T_b i$ ($b'=-0.587$, $P=0.001$). The dens provided a rather uniform thermal environment where the marmots could cool down. Minimal T_a 60 cm down the burrow entrance was 10° C (measured during the night, when T_a outside was 12° C), and maximal T_a was 14.6° C (during the day, T_a outside was 23° C) with a mean of 11.9° C (SD = 1.7, $n=8$). 150 cm down, T_a varied only between 12.4° C (T_a outside was 10° C) and 13.5° C (T_a outside was 16° C) with a mean of 12.9° C (SD = 0.4, $n=15$). As we did not measure T_e inside the burrows, this variable was not included in the multiple regression analysis. Length of stay in the den did not detectably influence ΔT_b. How long an animal would stay in the burrow was not predictable from T_e or $T_b i$, as the animals entered the burrows not only because of heat, but also because of rain and danger.

Activity pattern

The first animals emerged from the burrows as early as 0500 h, the last disappeared towards 2000 h (Fig. 3). They stayed on average 7 h above ground, of which about 50% was spent feeding, 10% in other activities and 40% in inactive behaviour.

The proportion of time the animals spent above ground in a 30 min interval correlated positively with T_e for $T_e<25$° C (Spearman rank correlation coefficient (r_s) = 0.63, $P<0.001$, $n=130$), but negatively with T_e for $T_e \geq 25$° C ($r_s=-0.41$, $P<0.001$, $n=236$). On cool days, time spent above ground increased almost continuously to a maximum in the late afternoon, whereas on warm days two peaks were evident (Fig. 3, bottom). The marmots retired again into their dens during the hot midday hours. From late afternoon until dusk there was a second peak of above ground presence which the animals preferentially spent in the sunny part of the territory. The animals spent more time above ground on cool than on warm days (Fig. 3, bottom).

We found similar trends in the animals' behaviour outside their burrows. The proportion of this time above ground spent active also increased with T_e for $T_e<25$° C ($r_s=0.34$, $P<0.001$, $n=124$), and decreased with T_e for $T_e \geq 25$° C ($r_s=-0.13$, $P<0.03$, $n=224$). However, these effects were weak. Thus the animals neither spent significant higher proportions of their above ground presence in active behaviour on cool than on warm days, nor differed the distributions of these proportions detectably between cool and warm days (Fig. 3, middle).

Discussion

Marmots have little physiological capacity for heat loss; they do not pant and have hardly any sweat glands (Pattie 1967). Salivation, a sign of heat stress, could often be observed on warm days in live-trapped marmots, but this is an ineffective method of cooling and seems to be used only in emergencies (Schmidt-Nielsen 1979). Dense fur, and the thick subcutaneous fat layer accumulated as energy-depot for hibernation (Müller 1986) also hinder loss of excess body heat. Thus behavioural thermoregulation via choice of location and body posture is to be expected.

A marmots ventral fur is shorter than the dorsal fur, and 2–3 times less dense, so that insulation is poorer (Bibikow 1968) and conduction is enhanced when lying. In sitting marmots a rise in T_b was approximately as frequent as a decrease and could already be observed for relatively low T_e (20° C), while T_b in lying marmots sank in most cases (Table 2). The T_b of marmots lying on soil sank up to a T_e of ca. 30° C and of marmots lying on a boulder even up to a T_e of ca. 37° C (Fig. 2). The rate of T_b change was significantly influenced by T_e for marmots lying on boulders but not for animals lying on soil (Fig. 2). Thus boulders provided a better substrate for conductive heat loss and for a wider range of T_e. Especially on warm and hot days the marmots often stretched out on a boulder, but this conspicuous posture of marmots is obviously the reverse of a thermophilic "basking" behaviour. Similar thermoregulatory behaviour is known for hyraxes (Sale 1970). An alternative and certainly more efficient way to escape heat stress is to retreat into the cool and stable thermal environment of a burrow.

Activity led to an increase in body temperature except when T_b was already close to the upper limit (Table 2). T_b rose more at higher T_e and during longer activities. It reached a maximum of 40.0° C on a hot day during the evening main activity period. Thus, the marmots seem to store a certain amount of excess heat to prolong their surface activity and get rid of it inside a burrow. The average daily T_b range of our study animals lay above the 95% prediction zone of the regression on the range of body temperatures of 17 small mammalian species with body weights below 10 kg (Aschoff 1981). Unfortunately, we were not

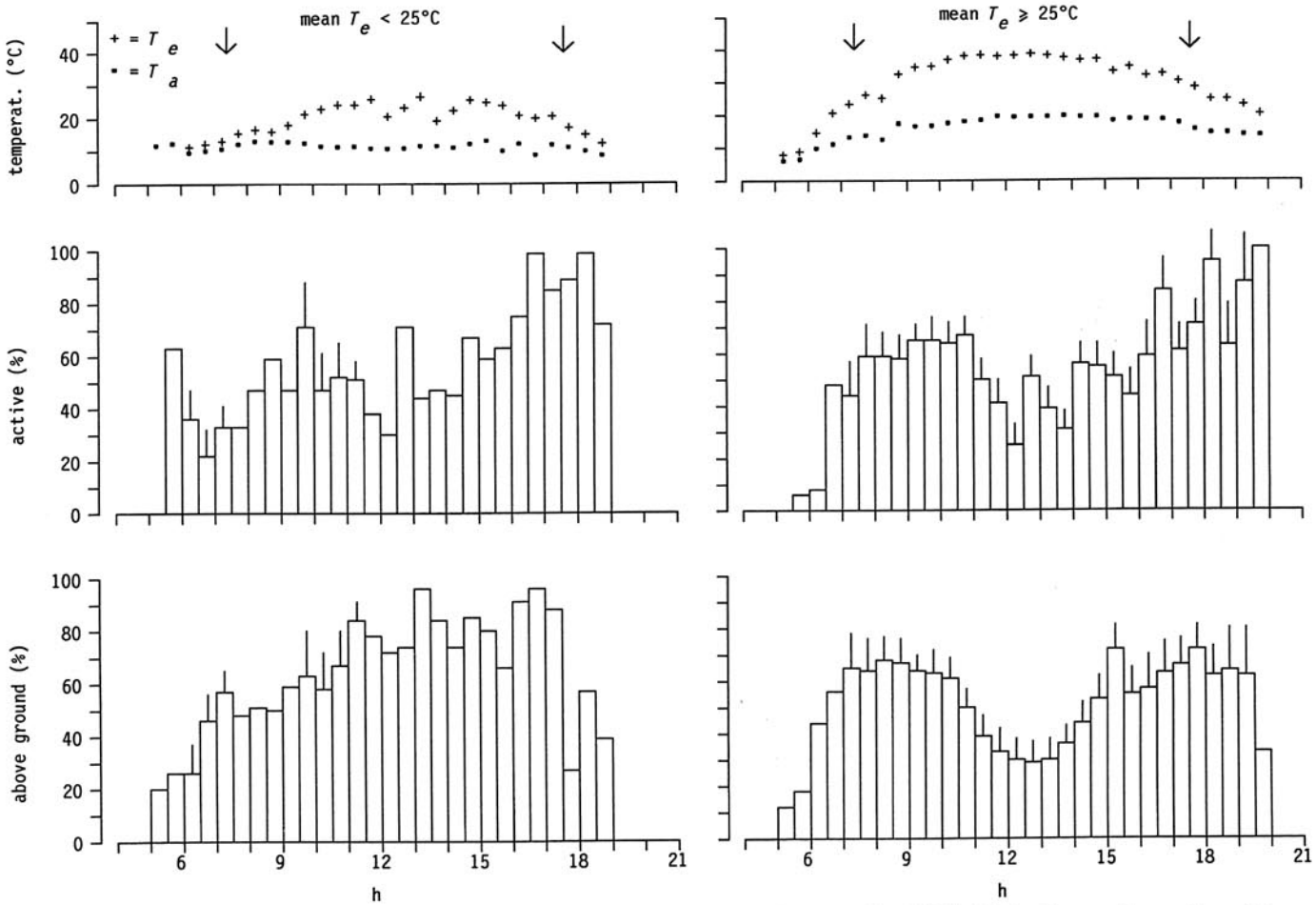

Fig. 3. Differences between cool days (average $T_e < 25°$ C, left) and warm days (average $T_e \geq 25°$ C, right). *Bottom:* Proportion of time spent above ground during half hour observation periods. *Middle:* Proportion of time spent in active behaviour while above ground. *Top:* Average half hourly means of air temperature (T_a) and effective environmental temperature (T_e). Arrows point to average sunrise and sunset at the study sites. The numbers of half-hourly means used for calculating the plotted means for the 30 min intervals range from 1 to 6 on cool days (mean = 4) and from 2 to 15 on warm days (mean = 10). If sample size was greater than 4, SEM is indicated by vertical lines in the lower and middle graph. Mann-Whitney U-tests: n cool days = 90, n warm days = 276, bottom $P = 0.002$, middle, n.s.; Kolmogorov-Smirnov tests for difference of distributions: $n = 30$ corresponding 30-min-intervals from 500 to 2000, bottom $P < 0.01$, middle n.s.

able to determine a threshold T_e for retreat into the burrow. The animals entered burrows also because of rain, disturbance by tourists, or danger from predators and it was in too many instances not reliably possible to recognize the true reason for a retreat.

Our study animals became less active and spent more time in their burrows with increasing T_e above 25° C, but this trend was reversed at T_e below 25°. During rain, the animals were almost entirely inactive. Alpine marmots obviously prefer bright weather but a narrow range of T_e and this might explain the contradictions in the literature. Whether they behave thermophilic (Müller-Using 1951; Bopp 1964; Zelenka 1965) or avoid sun radiation (Wüthrich 1982) depends on T_e, and the microclimate can be very different during a sunny day according to site exposure, altitude and daytime. At high T_e behavioural thermoregulation was obviously necessary. Above ground presence became bimodal (Fig. 3), similar to behaviour shown by the closely related yellow-bellied marmot (Armitage 1962, 1965; Travis and Armitage 1972; Kilgore and Armitage 1978; Webb 1980), woodchuck, *M. monax* (Hayes 1976) and bobac, *M. bobac* (Bibikow 1968). The noon pause clearly decreased the total time spent outside burrows on warm days and hence the available foraging time (Fig. 3). Furthermore, a similar shift from an unimodal distribution on cool days to bimodality on warm days is indicated in the proportion of active behaviour on above ground presence (Fig. 3). However, the difference was not significant. When in heat stress, the animals obviously retreated in most cases into a burrow instead of staying inactive above ground.

At the elevation of our study site, a northern exposure apparently affords a more favourable microclimate during summer which is reflected in the higher weight gain of animals living there. On the other hand, these animals loose more weight during winter than animals living on south facing slopes (Arnold, unpublished work). But the number of offspring weaned by a mother is more strongly influenced by her weight loss during the last hibernation than by her previous summer's weight gain (Arnold 1986). Therefore, the reason for larger and obviously better thriving alpine marmot colonies on south-exposed slopes (Forter 1975) seem to be the winter and not the summer conditions. However, excessive temperatures during summer in low altitudes

could be responsible for limiting the alpine marmots' vertical distribution to the zone above 800 m (Forter 1975). Although local hunters claim that wandering marmots are sometimes seen in meadows at lower elevations, they never established stable colonies there. The higher T_e at low elevation presumably requires extreme extensions of the noon pause on too many days, thus preventing the accumulation of sufficient body fat during the summer to last through hibernation even under moderate winter conditions. Therefore, the needs of behavioural thermoregulation determine not only the daily activity pattern of alpine marmots, and hence limit the habitat use temporally, but perhaps also explain its vertical distribution.

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