Comparative winter thermoregulation and body temperature in three sympatric *Apodemus* species (*A. alpicola, A. flavicollis,* and *A. sylvaticus*)

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Abstract

When living in sympatry with *Apodemus sylvaticus* and *A. flavicollis, A. alpicola* dominates numerically at higher altitudes. A more efficient winter thermal isolation or a higher winter thermogenic capacity procuring a physiological advantage could explain at least part of this domination. We therefore measured body temperature (Tb), oxygen consumption (VO_2), wet minimal thermal conductance (C) and non shivering thermogenesis (NST) at different ambient temperatures (Ta) on winter acclimated mice of the three species, and this for the first time in *A. alpicola*.

NST was high and C low in the three species. No significant difference could be noticed either in Tb between 5 and –10 °C, in VO_2 measurements at a Ta of –10 °C or in C. The NST measurements represent, respectively, 135.2% for *A. sylvaticus*, 142.8% for *A. flavicollis* and 140.5% for *A. alpicola* of the expected values, the values for *A. sylvaticus* being significantly lower than for the other two species. The basal metabolic rates (BMR) represent 169.4% for *A. sylvaticus*, 161.6% for *A. flavicollis* and 138.3% for *A. alpicola* of the expected values. Having removed the effect of body weight, the BMR value was significantly lower in *A. alpicola* than in *A. flavicollis*, but no difference could be noticed between *A. sylvaticus* and the other two species.

In conclusion, the three species of mice have very similar acclimated thermoregulatory characteristics, well adapted to cold ambient conditions. One discriminating and advantageous factor could be the lower basal metabolic rate measured in *A. alpicola* compared to the other two species.

Key words: *Apodemus*, rodents, thermoregulation, metabolism

Introduction

Mountain populations of small mammals are confronted with various limiting factors, the main ones being a short warm season, either for reproduction or constitution of winter reserves, and severe cold winter ambient temperatures. The temperatures in the Alps reach mean values between –1 and –8 °C during the winter period, with mean minimal values between –5 and –10 °C and extreme monthly mean minimal values of –11.5 °C beneath 2 000 m and –15 °C at 2 500 m (Swiss Meteorological Institute, data covering at least 20 years for the region presently investigated). These low temperatures require a high capacity for heat production, the main pathway for this production being NST, non shivering thermogenesis (Heldmaier et al. 1989). Seasonal acclimation of NST has now been well studied (Haim 1982; Haim and Yahav 1982; Cygan 1985; Feist and Feist 1986; Klaus et al. 1988; Heldmaier et al. 1981, 1989; Haim et al. 1995). This acclimation occurs

through a response to cold and/or to changes in photoperiod. Differences in NST level may be correlated to ecological speciation and adaptation to climatic conditions (Haim et al. 1984, 1993). For instance, rodents from desert areas with cold periods are characterized by high values of NST (Haim and Borut 1976; Haim and Fourie 1980). Wet thermal conductance is also a factor of importance in these conditions, even if the fur of small animals must remain short and light compared to larger forms (Scholander et al. 1950). The fur isolation properties change nevertheless between summer and winter (Hart 1956; Bolshakov 1984; review in Grodzinski 1985). Even at very low ambient temperatures, rodents may exploit actively atenuate climatic conditions by foraging under the snow cover and adjusting thermal isolation by adequate nest construction (Dufour 1972, 1978; review in Montgomery and Gurnell 1985). However, they must also be able to survive direct exposure to cold in spite of the high rate of heat loss due to their small size.

The Alpine mouse (*Apodemus alpicola*) with its distribution between 800 and 2 000 m is without doubt regularly exposed to severe climatic conditions. Described as an alpine subspecies of *A. flavicollis* by Heinrich (1952), its specific status was recognized by Storch and Lütt (1989) on morphological criteria. A biochemical confirmation was given by Vogel et al. (1991) and Filippucci (1992) for Italian, Austrian, and Swiss populations. The general distribution of this species was not known until recently for Austria (Spitzenberger and English 1996). Therefore, many biological data reported for "*A. flavicollis*" may in fact have been observed on *A. alpicola*.

As in Austria (Storch and Lütt 1989), *A. alpicola* may occur in the Swiss Alps forests in sympatry with *A. sylvaticus* and *A. flavicollis* (Vogel and Reutter, unpubl.), dominating numerically at higher altitudes. This domination may be explicited by many factors, either demographic, such as a possible higher natality for *A. alpicola*, or behavioral, such as a potential higher competition success for this species resulting in a lower mortality. Many of these factors are currently being investigated in the course of a PhD thesis by B. Reutter. According to Spitzenberger and English (1996), the fur of *A. alpicola* is particularly soft. This raises the question whether the Alpine mouse has a more efficient thermal isolation. In the present study we therefore investigated some energetic parameters under winter conditions. A lower thermal conductance or a higher thermogenic capacity may procure a physiological advantage, which could explain at least in part the domination of one of the three congeneric species.

Material and methods

Animals

All mice (24 individuals) were trapped during November 1996 in mountainous regions of Switzerland at altitudes ranging from 1 000 m to 1 400 m above sea level, thus accounting for a possible adaptation to altitude and harsh climates. Due to trapping hazards, the sex ratio of each species could not be controlled. The females were in no case pregnant. Depending on which experiment, the animals were held in captivity in outdoor conditions for 2 weeks to 5 months prior to measurements. They were housed in Macrolon® cages (type II: 40×25×15 cm), with a wire roofing, a sawdust floor and were fed ad libitum with apples, seeds, and water.

Experiments

Body temperature regulation (Tb)

5 *A. alpicola* (4 males, 1 female) and 5 *A. flavicollis* (5 females) were fitted with implanted thermodependant radio transmitters (Mini-Mitter X, Sunriver, Oregon, USA). Surgery was performed by a veterinary surgeon under total anaesthesia (Halothane, Halocarbon Laboratories, River Edge, U.S.A.). The signal sent by the transmitter was received by a loop antenna placed under the housing cage of the

subject. The period was measured by a high resolution timer-counter (Philips PM 6671). It was then recorded continuously on a recorder (W + W Elektronik AG., Basel, Switzerland) and was compared to a calibration curve established previously to the implantation.

Each measurement lasted 22 hours, 16 hours of which (2.00 pm to 5.00 am) were used in the analysis in order to avoid periods during which the animals were potentially disturbed or stressed. Four ambient temperatures were experienced (+5 °C, 0 °C, –5 °C, and –10 °C), the cages being placed in a cold chamber (±1 °C) (Frigorex, Villars-Ste-Croix, Switzerland or Weiss Technik AG., Kirchberg, Switzerland). The animals were fed ad libitum.

Hourly fluctuations of Tb over time, amplitude (as the difference between minimum and maximum body temperatures occurring at least 10 times during the 22 hours that the measurements lasted, REFINETTI 1996) and maximum amplitude (as the maximum amplitude occurred during the 22 hours of measurement) were observed.

Oxygen consumption (VO$_2$)

Oxygen consumption of 5 *A. alpicola* (all males), 5 *A. flavicollis* (1 male, 4 females) and 5 *A. sylvaticus* (all males) was measured in an open circuit respirometer (SPARTI and GENOUD 1989). Five ambient temperatures (Ta) were experienced (5 °C, 10 °C, 15 °C, 20 °C, 30 °C). The animals were placed in a Plexiglas chamber (3.8 litres) in a thermostatized water bath (±0.1 °C). No food was offered.

The minimal values obtained at 30 °C are considered to be basal metabolic rates (BMR), within the thermoneutral zone (CYGAN 1985; Haim et al. 1993). They are compared to the allometric equation BMR = 3.45 m$^{-0.287}$ (McNAB 1988; BMR in ml O$_2 \cdot$ g$^{-1} \cdot$ h^{-1} and m in g).

Some additional data were obtained at a Ta of –10 °C with the 10 implanted individuals (5 *A. alpicola*, 5 *A. flavicollis*) used in the first experiment. The animals were housed in a larger metabolic chamber (15 litres) located in a cold chamber (Weiss Technik AG., Kirchberg, Switzerland).

The experiments lasted 4 hours. The resting metabolism at different temperatures was obtained over a stable minimum period of 5 minutes at least.

Thermal conductance (C)

The simultaneous measurements of body temperature and metabolism obtained at the lowest tested ambient temperature (–10 °C) allowed a precise calculation of the wet thermal conductance of *A. flavicollis* and *A. alpicola*, following the formula C = VO$_2$/(Tb–Ta) (McNAB 1980). C is considered minimal at this temperature. A second set of measurements of Tb was made on the other set of non-implanted individuals of the three species at the end of each measurement of oxygen consumption between 5 and 30 °C. Tb was this time measured by means of a rectal probe (Bat-12, Sensortek, Bailey, USA). C was calculated following the same formula and the minimal values for each individual chosen. These results were then compared to the allometric equation C = 0.76 m$^{-0.426}$ (BRADLEY and DEAVERS 1980; C in ml O$_2 \cdot$ g$^{-1} \cdot$ h^{-1} °C^{-1} and m in g).

Non shivering thermogenesis (NST)

NST measurements of the same individuals used for the oxygen consumption experiments were made following the methods of HELDMAIER (1971) and SPARTI (1992). The amount of noradrenalin (NA) injected was calculated following the formula given by HELDMAIER (1971), plus an amount of 0.004 mg NA after preliminary control experiments, in order to have a maximum response. The NA (Arterenol, Hoechst) was injected intraperitoneally and the animal placed immediately in the respirometer. Oxygen consumption was measured following the procedure explained above, at a Ta of 15 °C in order to avoid a possible overheating of the animal.

Two successive measurements were realized for each individual in order to control the validity of the data. The first were made at the end of March, the animals being kept under a natural photoperiod and temperature. The second session took place one month later, after acclimation to a controlled short photoperiod (8 L : 16 D) and low regulated temperature.

The results were compared to the expected values according to NST = 30 m$^{-0.454}$ (HELDMAIER 1971; NST in ml O$_2 \cdot$ g$^{-1} \cdot$ h^{-1} and m in g).

Results

Body temperature (Tb)

In order to ensure independence of the data, measurements of body temperature at one hour intervals over a period of 16 hours were used (Fig. 1). Body temperature decreased slightly with ambient temperature in *A. alpicola*, but not in *A. flavicollis* (Fig. 2).
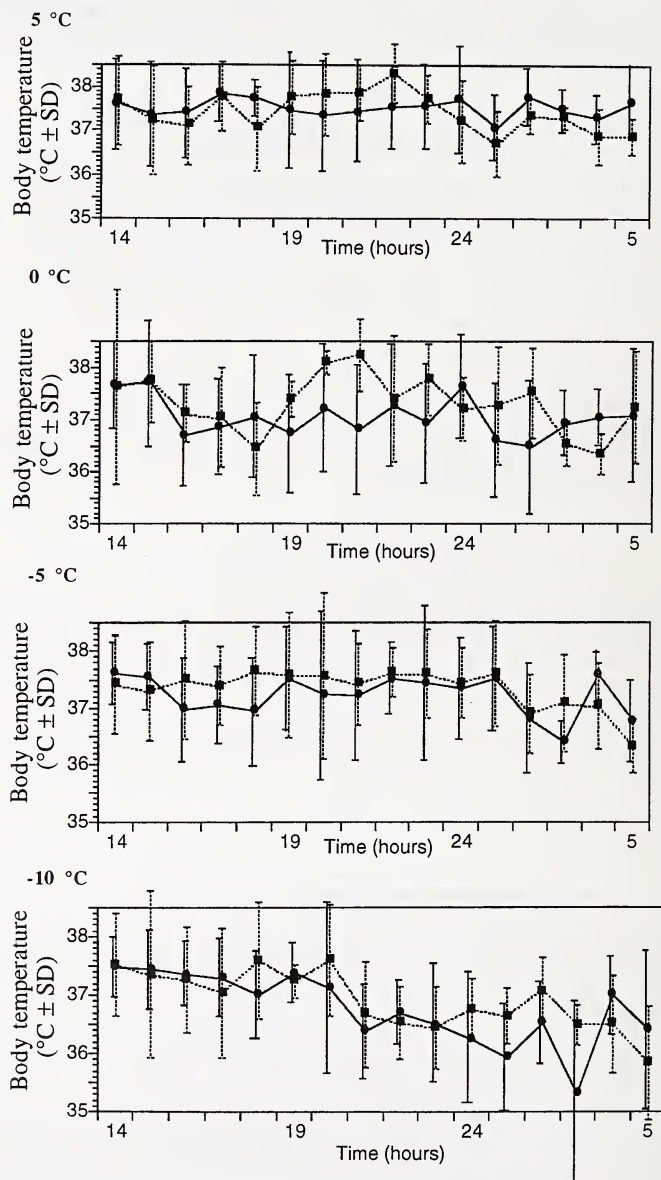

Fig. 1. Daily fluctuations in body temperature (°C ± SD) at four ambient temperatures (N = 5 for *A. flavicollis* - - -■- - - and N = 5 for *A. alpicola* —●—).

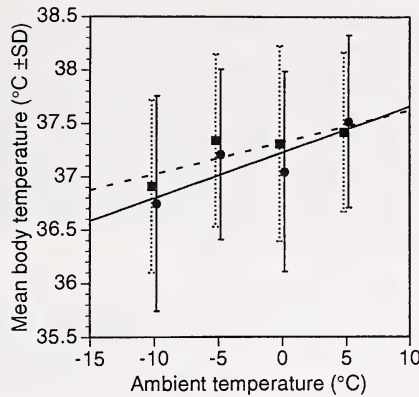**Fig. 2.** Mean body temperatures (±SD) over a period of 16 hours at four ambient temperatures (N = 5 for *A. flavicollis* - - -■- - - and N = 5 for *A. alpicola* — ● —). Regression lines are: Tb = 37.32 + 0.03 Ta (r^2 = 0.19; p = 0.058) for *A. flavicollis*, and Tb = 37.24 + 0.04 Ta (r^2 = 0.30; p < 0.05) for *A. alpicola*.

Repeated-measurements ANOVAs applied to each ambient temperature showed no statistical differences either between the level of body temperatures over 16 hours (between 2.00 pm and 5.00 am) between *A. alpicola* and *A. flavicollis* or in the fluctuations of body temperatures over time (all interactions Time × Species: NS). Tb was independent of the hour of the day at all ambient temperatures except −10 °C ($F_{(15/120)}$ = 3.83, P < 0.0001), the lower body temperatures being recorded during the night, at the end of the measurement.

The largest amplitudes and extreme amplitudes were determined with the data of all ambient temperatures pooled for every individual (Tab. 1). No statistical difference could be observed between the two species (Student t-test: NS). The especially large standard deviation (±2.44) of the extreme amplitude in *A. flavicollis* is due to an individual who experienced a short torpor bout during one experience at −10 °C.

Table 1. Mean amplitude (±SD) and extreme amplitude (±SD) of Tb for *A. flavicollis* and *A. alpicola*. All Ta are pooled.

	N	Amplitude (°C)	Extreme amplitude (°C)
A. flavicollis	5	4.61 ± 1.05	6.26 ± 2.44
A. alpicola	5	5.88 ± 1.52	6.64 ± 1.14

Oxygen consumption (VO₂)

Oxygen consumption was measured at 6 different ambient temperatures (Fig. 3). The results at Ta = −10 °C are treated separately because these measurements were made on a different set of individuals. Between 5 and 30 °C, oxygen consumption increased with decreasing ambient temperature (Tab. 2). The lines intercept the ambient temperature axis at, respectively, 49 °C for *A. sylvaticus*, 46 °C for *A. flavicollis*, and 48 °C for *A. alpicola*. These temperatures are higher than the observed body temperatures. This shows clearly that the wet thermal conductance is not independent of ambient temperature.

Having removed the influence of body weight, the basal metabolic rate (BMR) values are significantly different for the three species (ANCOVA, $F_{(2/12)} = 7.85$, $p < 0.01$) and significantly lower for *A. alpicola* than *A. flavicollis*. (Scheffé Post Hoc Test: *A. alp.* – *A. flav.*: $p = 0.01$). No significant difference is observed between *A. sylvaticus* and the other two species. The measured oxygen consumptions represent for *A. sylvaticus* 169.4%, for *A. flavicollis* 161.6% and for *A. alpicola* 138.3% of the expected values.

At the other extreme of the range of measurements, the comparison of the metabolic rates at –10 °C between *A. flavicollis* and *A. alpicola* shows no significant differences between both species (ANCOVA, $F_{(1/7)} = 0.87$, NS).
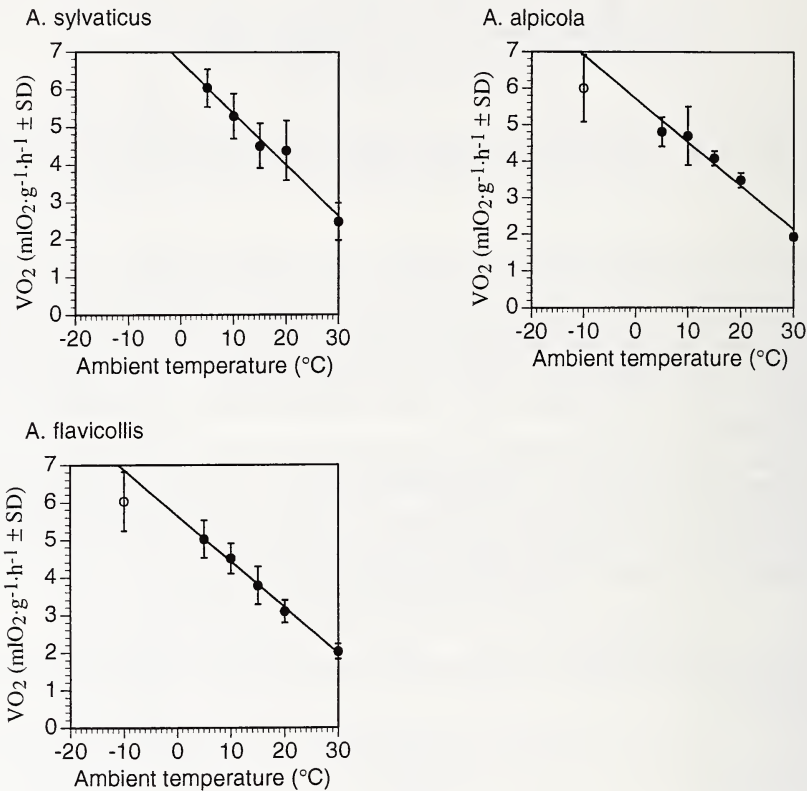

Fig. 3. Mean relative oxygen consumption (VO_2, ml $O_2 \cdot g^{-1} \cdot h^{-1} \pm SD$) at different ambient temperatures. The equations of the regression from 5 to 30 °C are given in table 2. (N = 5 individuals for each species. A different set of individuals was used at Ta = –10 °C).

Table 2. Relation between ambient temperature (Ta, °C), body weight (m, g) and oxygen consumption (VO_2, $mlO_2 \cdot h^{-1}$) between 5 and 30 °C.

	N	Regression	r^2	p
A. sylvaticus	5	$LogVO_2 = 1.87 + 0.32 \, Log \, m - 0.02 \, Ta$	0.915	$p < 0.0001$
A. flavicollis	5	$LogVO_2 = 1.76 + 0.36 \, Log \, m - 0.02 \, Ta$	0.943	$p < 0.0001$
A. alpicola	5	$LogVO_2 = 2.06 + 0.16 \, Log \, m - 0.02 \, Ta$	0.959	$p < 0.0001$

Thermal conductance (C)

Two methods were used to assess Tb: implantation and rectal probe (Tab. 3). A significant difference exists between the two values of C for *A. alpicola* (ANCOVA, $F_{(1/7)} = 8.41$, $p < 0.05$) and for *A. flavicollis* (ANCOVA, $F_{(1/7)} = 8.56$, $p < 0.05$). The relative values are inferior to the expected values in all cases. No significant statistical difference was observed either between the two species measured by implantation (ANCOVA, $F_{(1/7)} = 0.000$, NS) or between the three species measured by rectal probe (ANCOVA, $F_{(2/11)} = 0.99$, NS).

Table 3. Mean absolute ($C \pm SD$, $mlO_2 \cdot h^{-1} \cdot {}^{\circ}C^{-1}$) and relative ($Crel \pm SD$, $mlO_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$) thermal conductance measured for *A. flavicollis*, *A. alpicola*, and *A. sylvaticus* with two sets of individuals and two methods used to measure Tb: implantation or rectal probe; m is the body mass (g) and $\Delta\%$ is the difference between Crel and the expected values.

		N	C	Crel	m	$\Delta\%$
A. flavicollis	Implant.	5	3.36 ± 0.44	0.13 ± 0.02	28.81 ± 7.31	71.6
A. alpicola	Implant.	5	3.46 ± 0.31	0.14 ± 0.02	25.03 ± 3.57	72.6
A. flavicollis	R. probe	5	4.93 ± 0.39	0.15 ± 0.02	33.26 ± 3.66	87.8
A. alpicola	R. probe	5	4.57 ± 0.50	0.15 ± 0.01	31.08 ± 3.25	85.3
A. sylvaticus	R. probe	5	4.60 ± 0.41	0.18 ± 0.02	25.56 ± 2.03	94.2

Non shivering thermogenesis (NST)

All individuals reached a high oxygen consumption within minutes following the NA injection (Fig. 4). The consumption remained at a maximum level for a variable length of time, between 5 and 30 minutes. The metabolic rate then diminished progressively.

No significant statistical difference was observed between the two series of measurements for each species taken separately (ANCOVA, NS). The consumption of *A. sylvaticus* was significantly lower than the other two species in the first NST measurements (ANCOVA, $F_{(2/10)} = 7.97$, $p < 0.01$, Scheffé Post Hoc Test: *A. sylv.* – *A. flav.*: $p < 0.05$, *A. sylv.* – *A. alp.*: $p < 0.05$) but no difference remained after the second series of measurements (ANCOVA, $F_{(2/10)} = 0.66$, NS).

The first series of NST measurements represent, respectively, 135.2% for *A. sylvaticus*, 142.8% for *A. flavicollis* and 140.5% for *A. alpicola* of the expected values.
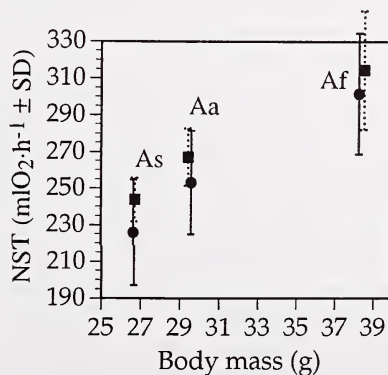

Fig. 4. Maximum mean NST consumptions (ml $O_2 \cdot g^{-1} \cdot h^{-1} \pm SD$) and body mass (g) for the 1st (- - -■- - -) and 2nd (—●—) series of measurements. (N = 5 for *A. sylvaticus* (As) and *A. flavicollis* (Af) and N = 4 for *A. alpicola* (Aa)).

Discussion

Oxygen consumption (VO_2) and body temperature (Tb) at various ambient temperatures (Ta), as well as non shivering thermogenesis (NST) values and minimal wet thermal conductance (C), were measured for the first time in *Apodemus alpicola*. These same measurements were also realized for the first time on a taxonomically controlled sample of *A. flavicollis*. All the experiments were made under winter conditions, the animals being kept outdoors under natural temperatures and photoperiod, and all animals having been caught at high altitudes. Furthermore, the individuals were subjected to cold conditions during the measurements without any kind of external structure procuring an isolated warmer microclimate, such as the one they should be expected to use in nature: padded nests, tunnels, passages under the snow, etc. The data obtained should therefore give a good indication of the physiological capacities these species, as well as *A. sylvaticus*, possess to survive winter in their mountainous habitat.

All three species are obviously well adapted to cold conditions. The winter NST values found are high (about 140%). This result is close to the data in the literature. Haim et al. (1995) found a value equal to 117% of the allometry for *A. sylvaticus* at an acclimation Ta of 24 °C and a short photoperiod. Heldmaier et al. (1989) found a value of 139% of the allometry for cold acclimated *A. flavicollis* under a short photoperiod. The differences between these values and ours are probably due to the samples, but also to the methods used. The temperatures and photoperiod during acclimation, as well as the length of the acclimation period, or the differences in Ta during the experiences may cause these discrepancies.

Wet thermal conductance values are low (between 72 and 94% depending on the method and the species) compared to the allometry of Bradley and Deavers (1980). Our values are similar to the data found in the literature for *A. sylvaticus*. Haim et al. (1995) found 0.186 ± 0.021 $mlO_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$ (m = 24.7 ± 2.9 g), i. e. 95.9% of the expected value. Literature data concerning the other species are missing. However, we consider that the results obtained employing the method of implantation are reliable. Oxygen consumption and Tb were measured simultaneously, the delay due to the respirometry system being negligible and thus allowing a precise calculation of C, and no handling of the individuals was necessary. Ambient temperature was also lower during the measurement, so that C was more likely to be at its minimal value. The data for *A. sylvaticus*, obtained using the rectal probe method, are therefore perhaps slightly overestimated.

NST and C are both essential adaptations allowing the presence of these species all year round in this type of habitat. *A. flavicollis* and *A. alpicola* were both capable of regulating their Tb at ambient temperatures between +5 °C and –10 °C. The mean Tb *A. alpicola* maintained was slightly influenced by Ta, but the slope of this relation is weak. *A. flavicollis* lost 0.5 °C and *A. alpicola* lost 0.7 °C between the mean body temperatures at 5 and –10 °C. Oxygen consumptions at –10 °C were high, but still well below the NST consumptions measured. Cygan (1985) measured the VO_2 sum of *A. flavicollis* in an He-O_2 atmosphere (thus at cooling conditions corresponding to –30 °C), finding 13.6 ± 1.6 $mlO_2 \cdot g^{-1} \cdot h^{-1}$ (m = 31.1 ± 5.7 g). This is also well above the oxygen consumptions obtained, in the present study, at –10 °C. No limitation seems then to arise from an eventual aerobic maximum reached at this temperature. It was, however, only at –10 °C that the time of the day had an influence on the measurements, Tb being minimum at the end of the experience. Low temperatures seem then to be a limiting factor at least when the animals are exposed during long periods, although it is difficult to explain the causes. The temperatures we tested do not, however, affect the survival of animals fed ad libitum, even when –10 °C represents an extreme in the temperatures that a small mammal can experience for long periods.

These results are not surprising. All three species are regularly found at high altitude

habitats subjected to cold winters. *A. sylvaticus* is the most wide spread. It is present at all altitudes and has been captured in Switzerland up to 2200 m. Data concerning *A. flavicollis* are more problematic: some or many of the observations made between 1400 and 2000 m should potentially be attributed to *A. alpicola*. An extreme observation has been made at 2450 m above sea level, but incertainty remains on the species determination between *A. flavicollis* and *A. alpicola* (YOCCOZ 1992). This third species has been found in Austria up to a height of 1900 m (SPITZENBERGER and ENGLISCH 1996). In conclusion, one of the corollaries of altitude, cold, seems to be a limitation in the home range, but the three species seem well armed against it. It is, however, difficult to have an exact idea of the microclimates that the small mammals must face in winter. They may be relatively well sheltered under the snow cover, under rocks, in crevasses or deep in the ground, and this even more so when they possess a well-isolated nest. What happens when they must leave these places? For instance, low temperatures might be present without snow covering the ground. More precise data on these microclimates are required.

Having established that all three species are relatively well adapted to mountainous conditions, what can be said about interspecific differences? No difference can be observed between *A. alpicola* and *A. flavicollis* either for NST values, C values, VO_2 at –10 °C or Tb (level, evolution, and amplitude) at any Ta. Less numerous comparisons have been made with *A. sylvaticus*, but NST values were significantly lower in this species than in the other two in the first series of measurements. This, added to the highest C value compared to the allometry, could reflect a different adaptation of this species. This result must, however, be taken with caution as no difference remained between species after the second series of measurements. An effective difference in the capacity to produce or use brown adipose tissue (BAT) may exist, but it must be slight, as attested by the almost similar percentages obtained when compared to expected values of NST.

A more important feature may be the basal rate of metabolism (BMR). *A. alpicola* has the lowest BMR of the three species. It is statistically different to *A. flavicollis* and is the smallest when compared to expected values. Literature data give even higher winter BMR values for *A. flavicollis* than ours, e. g. 175% (m = 35 g; KLAUS et al. 1988), 207% (m = 29 g; HELDMAIER et al. 1989) or 238% (m = 31.1 g; CYGAN 1985) of the allometry. A lower rate may be an adaptation to habitats susceptible to experience food or water shortages in the case of arid or semi-arid species (HAIM 1987). Food may also be more difficult to find and collect in the Alps during winter but an individual should find itself at a Ta situated in or very close to the thermoneutral zone to be able to benefit from this advantage on species of almost similar body weight and C. It should be noted that a low BMR is not directly linked to a low thermogenic capacity. At a specific level, BMR, maximum metabolism in the cold and NST are independent (SPARTI 1992). A high BMR is therefore not a direct advantage in cold conditions.

The few purely physiological differences between species pointed out are not of course sufficient to explain the predominance of one species over the others. Many other factors should be taken into account. Other physiological data are still missing, in particular in the case of *A. alpicola*. Many species experience a loss in body weight during winter (DEHNEL 1949), as in the case with *Clethrionomys glareolus* (KLAUS et al. 1988). *A. sylvaticus* seems to maintain a constant body weight throughout the year (KLAUS et al. 1988), while *A. flavicollis* is heavier during winter (CYGAN 1985 ; KLAUS et al. 1988). A body weight loss occurring in *A. alpicola* would perhaps represent an advantage if the food supply is precarious. The maximum rate of energy assimilation may also be a limitation. KOTEJA (1995) measured this maximum rate in *A. flavicollis* and found a value much smaller than the short-term maximum consumption measured previously (CYGAN 1985), thus indicating a limiting factor. This should also be investigated in *A. alpicola*. Torpor is another important means of saving energy or resources. Torpor bouts have been observed in several temperate Muridae, in particular in *A. sylvaticus* (MORRIS 1968; WALTON and ANDREWS 1981)

and *A. flavicollis* (Cygan 1985). One *A. flavicollis* individual experienced three torpor bouts during two measurements we made at –10 °C. The torpors lasted 160 ± 34 min. Tb fell to 28.51 ± 0.25 °C and oxygen consumption to 6.4 ± 0.3 $mlO_2 \cdot g^{-1} \cdot h^{-1}$. Investigations should be made concerning the capacity of *A. alpicola* to experience torpors, both in the laboratory and in the field. Behavior can also have an essential impact on thermoregulation. Nest sharing, for instance, has been shown to reduce thermoregulatory costs. Such a behavior has been measured, for instance, in *A. flavicollis* (Fedyk 1971) and *A. agrarius* (Tertil 1972). If this sharing occurs in nature in *A. alpicola*, a difference in social habits between species may be of importance. Intra- or interspecific competition may also be a means of ensuring the possession of the best nesting sites or resources. *A. flavicollis* is the heaviest species and was found superior in interspecific encounters with *A. sylvaticus* (Cihakova and Frynta 1996). Montgomery (1980) stated that interspecific spatial segregation between these two species is maintained by *A. sylvaticus* avoiding the competitively superior *A. flavicollis*. The body weight difference is smaller between *A. alpicola* and the other two species, thus more or less aggression could make the difference.

In conclusion, the three species of mice tested in the present study have very similar acclimated thermoregulatory characteristics, well adapted to cold ambient conditions. One discriminating and advantageous factor could be the lower basal metabolic rate measured in *A. alpicola* compared to the other two species. Many other physiological, behavioral, and populational factors remain to be measured.

Acknowledgements

Zusammenfassung

Vergleichende Winterthermoregulation und Körpertemperatur bei drei sympatrischen Apodemus-Arten (A. alpicola, A. flavicollis und A. sylvaticus)

Bei sympatrischem Vorkommen der drei Waldmaus-Arten *Apodemus alpicola*, *A. sylvaticus* und *A. flavicollis* in höheren Lagen dominiert *A. alpicola* zahlenmäßig. Eine effizientere thermische Isolation im Winter oder eine erhöhte thermogenetische Kapazität, die einen physiologischen Vorteil mit sich bringt, könnten eine Erklärung für diese Dominanz sein. Hierfür wurden an winterangepaßten Waldmäusen der drei Arten die Körpertemperatur (Tb), der Sauerstoffverbrauch (VO_2), die Wärmedurchgangszahl (C), und die zitterfreie Wärmebildung (NST) bei verschiedenen Umgebungstemperaturen (Ta) gemessen. Für *A. alpicola* wurden diese Messungen erstmals durchgeführt.

Für die zitterfreie Wärmebildung fand man bei sämtlichen drei Arten hohe, für die Wärmedurchgangszahl tiefe Werte. Weder aus den Messungen der Körpertemperaturen bei Umgebungstemperaturen zwischen 5 und –10 °C, des Sauerstoffverbrauches bei einer Umgebungstemperatur von –10 °C noch der Wärmedurchgangszahlen resultierten signifikante Unterschiede. Die Messungen der zitterfreien Wärmebildung ergaben für *A. sylvaticus* 135.2%, für *A. flavicollis* 142.8% und für *A. alpicola* 140.5% des erwarteten Wertes, wobei die Zahlen von *A. sylvaticus* signifikant tiefer liegen als diejenigen der beiden anderen Arten. Der Grundumsatz (BMR) ergab für *A. sylvaticus* 169.4%, für *A. flavicollis* 161.6% und für *A. alpicola* 138.3% des erwarteten Wertes. Vernachlässigt man das Körpergewicht, liegt der BMR-Wert von *A. alpicola* signifikant tiefer als derjenige von *A. flavicollis*. Keinen Unterschied fand man hingegen zwischen *A. sylvaticus* und den beiden anderen Arten.

Abschließend sei erwähnt, dass die drei Waldmaus-Arten ähnliche thermoregulatorische Eigenschaften besitzen, die eine gute Anpassung an kalte Umgebungstemperaturen zulassen. Einzig der tiefere BMR-Wert von *A. alpicola* könnte sich, gegenüber den beiden anderen Arten, als vorteilhaft erweisen.

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