SOCIAL BEHAVIOUR AND TELEMETRIC ASSESSMENT OF THERMOREGULATION IN HIBERNATING MARMOTS

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1. Introduction

Identifying the selective forces responsible for the evolution or maintenance of social life has been a primary interest of ethologists. Do animals live socially and cooperate in order to cope with environmental conditions that are, in the long run, unbearable for solitary animals? To answer this question it is necessary to understand how physiology limits or constrains the environmental conditions tolerable for an organism. Hence a study of the fitness consequences of sociality must address physiological questions. Physiological research is not typically conducted using free-living animals. Yet, we cannot solely rely on laboratory results when dealing with evolutionary questions for two reasons. First, it is necessary to measure critical environmental parameters in the natural habitat. Without this we will not be able to simulate natural conditions with sufficient accuracy in the laboratory. Second, the animals may not show their typical behaviour in the laboratory forcing us to measure the relevant physiological parameters in free-living animals in their natural habitat.

With the availability of advanced telemetry technology and the computerised recording of large data sets, it is now possible to collect physiological measurements in free-living animals found in remote areas. This paper describes the development and preliminary results from such a study: a physiological investigation of social thermoregulation in alpine marmots *(Marmota marmota)* hibernating in their natural habitat. The study was initiated because long-term demographic results suggested that advantages of group hibernation were crucial for understanding marmot sociality [8, 10]. In the following sections, I will review the history of this study and the observations that led me to employ telemetric assessment of thermoregulation in hibernating alpine marmots.

2. The Problem

Marmots are a closely related group of species ideally suited for the study of the adaptive significance of social life. The genus is of recent phylogenetic origin [42]. The 14 marmot species are very similar physiologically and morphologically although they occur from lowlands to high alpine regions and from semi-deserts to Arctic tundras. However, marmots differ enormously in their social organisation and these differences seem to reflect the wide range of environmental conditions in the species' habitats. Variation in social organisation

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seems to be associated with variation in a single factor - the age of natal dispersal. For example, in *Marmota monax*, a solitary species inhabiting low elevations, offspring typically leave their natal area after weaning when only two months old. Many of them, particularly females, reproduce the following year [17, 18, 21, 22, 26, 37]. Yellow-bellied marmots (*M. flaviventris*), occurring from medium elevations to high altitudes [25] are moderately social. Here, dispersal typically occurs after the first hibernation [3]. Offspring of marmot species inhabiting high altitudes or latitudes, like the alpine, hoary or olympic marmot disperse at either sexual maturation after the second hibernation, or even years later [7, 15, 29]. Delayed dispersal leads to the formation of large social groups containing several adult individuals. Group members share a common home range and burrows. However, in each group only a single female reproduces a maximum of once per year. Available information suggests that the social organisation of all other marmot species appears to resemble this latter type [7, 16].

A first hypothesis explaining the apparent correlation between delayed dispersal and environmental harshness in a species' habitat assumed that offspring remained in the natal unit if there was insufficient time in one season to reach a body size to ensure successful dispersal [1, 2, 13, 14]. Prolonged tolerance of offspring by the parents was viewed as "continued parental investment", increasing an offspring's chance of becoming reproductive [1, 2]. This hypothesis offered a plausible explanation for different dispersal ages and hence for different levels of sociality. However, there were virtually no data available about the fitness consequences of delayed dispersal that would permit testing the hypothesis. A second problem was that only information from Nearctic species was used to develop the hypothesis.

Now there is detailed information available for one of the highly social Palearctic species, the alpine marmot (see [7] for a description of field methods). These animals live in groups of up to 20 individuals on alpine meadows in altitudes from 600 to 3,200 m [8, 24]. Typically, there is a dominant, territorial pair in each group. Only the territorial female breeds; subordinate females never reproduce, even if the territorial female fails to litter. Monopolisation of reproduction by territorial males is less stringent. Territorial males apparently tolerate reproduction of their sons with the territorial female [34] (Arnold and Dittami, unpublished data). However, reproductive success of subordinate males is lower than that of territorial males [7]. This difference in reproductive success leads to intense competition for territory ownership. About 10% of the territory owners are replaced each year, either because they have died or were evicted by a stronger competitor. The new owners may be offspring of the former territorial animal, may come from neighbouring territories, but mostly are unrelated individuals from distant groups [7]. Offspring of former territorial animals are typically tolerated in the group by new territory owners. It is mainly because of this tolerance that we find about 30% of alpine marmot groups containing subordinate adults that are not offspring of the territorial pair.

Given that there is delayed dispersal in alpine marmots, the critical question is why a marmot remains in its natal area despite little, if any, reproductive success. In other words, what are the fitness benefits compensating for the apparent lack of direct fitness that delayed dispersers forego?

Data from my study on alpine marmots provide equivocal support for the "parental investment" hypothesis: on average, juveniles had at weaning only 18% of adult mass (SD

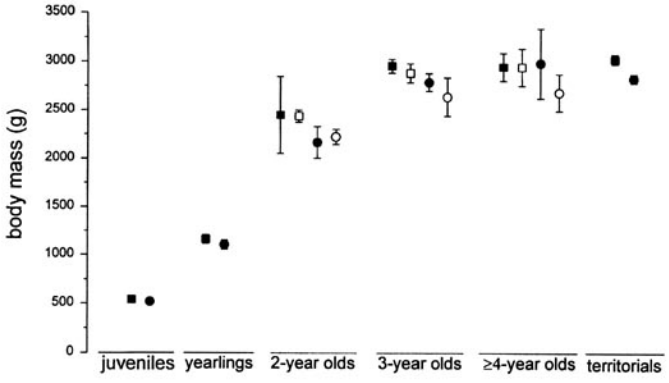

Figure 1. Body mass of alpine marmots of various individual classes after emergence from hibernation, of juveniles after emergence from the natal burrow (means, 95% confidence intervals). Gray symbols indicate individual classes that have never been found to disperse [7]. Open symbols indicate individuals that remained another year at the natal site, filled symbols indicate dispersers. Male results are shown as squares, female results as circles.

= 3.8, n = 229), yearlings 39% (SD = 8.3, n = 188) (Fig. 1), and both were never found to disperse [7]. Two-year old marmots had reached on average 81% of adult mass (SD = 10.4, n = 147) (Fig. 1) and dispersed less frequently than older marmots (Fig. 2). Yet there was no body mass difference between dispersers and non-dispersers in any age-class (Fig. 1). Hence insufficient body size could explain the failure of the small juveniles and yearlings to disperse but fails to explain why individuals remain in the natal group for longer periods of time.

Marmots increase their body mass considerably throughout the active season. To compare body masses of different individual classes, it was necessary to control seasonal mass variation. In juveniles, I analysed only body masses that were obtained within 10 days after first emergence from the natal burrow. Similarly, data from older marmots were only used when measured within 10 days after emergence from hibernation or within 10 days after the home range became snow free in spring, respectively. Marmots typically emerge from hibernation through an extant snow pack and do not gain mass as long as their home range is snow covered [5]. The body mass of an animal after emergence from hibernation is also the relevant mass for dispersal. Most dispersers leave their natal area immediately after emerging from hibernation or during the subsequent three or four weeks before they gain a substantial amount of mass.

Dispersal may come about via two non-mutually-exclusive routes. Offspring may leave voluntarily, or be evicted by the territorials. However, parents cannot prevent dispersal if an offspring really wants to leave. Thus, before discussing why it is in the interest of territorials to tolerate delayed dispersal of subordinates, we need to understand why it is in the offspring's interest to remain in its natal group.

Dispersal is a strategy that bears a high mortality risk [7]. It might be therefore more safe to remain at the natal site and wait for a breeding opportunity nearby, or to inherit the territorial position in an area of proven quality. On the other hand, dispersers travel long distances and encounter and investigate more marmot territories in the same time than non-

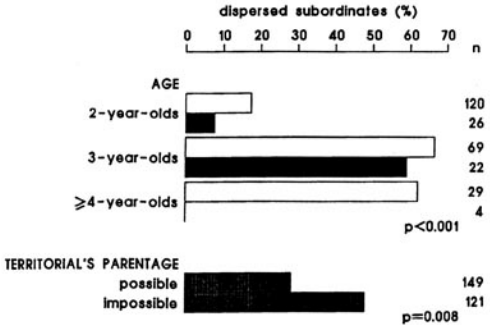

Figure 2. The influence of group composition on dispersal. Open bars: juveniles absent, solid bars: juveniles present, none of the four ≥4-year old animals living in groups with juveniles dispersed. Two-year old alpine marmots dispersed less frequently than did older ones. Less dispersal occurred in all age-classes if young were born in the group, but this trend was most pronounced among two-year old animals (hierarchical log-linear analysis, three-way-interaction of factors dispersal, age, juveniles presence, $c2 = 16.7$, $p < .001$, upper graph). Subordinates dispersed less frequently if both territorial animals of the group were their parents ($c2 = 7.0$, $p = .008$, lower graph). Modified after [10], courtesy of proceedings of the German Zoological Society.

dispersers [10]. During the entire study about 9% of the marmot territories were not occupied in the spring [7], mostly because the former residents had died during the winter. Hence the chance of finding an abandoned territory or of meeting a marmot group with a weak territorial animal that can easily be expelled is much higher for dispersers then for non-dispersers. We should expect dispersal to occur when the fitness of dispersers exceeds that of phylopatric individuals [35]. However, the fitness pay-offs of both options are not simply constant. They change with age, with the quality of the natal site, the quality of territories that can be obtained by dispersal, the number of animals competing for territory ownership, and an individual's competitive abilities. As far as age is concerned, it may well pay for a young animal with a high residual reproductive value to adopt a less risky strategy in order to maximise lifetime reproductive success. The older an animal becomes the more beneficial it is to take greater risks and to scan a large area thus increasing the immediate chance of obtaining a territory. The dispersal age maximizing lifetime reproductive success is basically determined by three factors:

1) the relationship between the probabilities of becoming territorial without or with dispersal
2) the relationship between the survival chances of dispersers and phylopatric individuals
3) the fitness gains possible while remaining at the natal site in subordinate rank [10].

If older siblings care for juveniles then they might gain indirect fitness and this should delay dispersal. In each age class, but particularly among two-year old marmots, a larger proportion of potential dispersers remained for an additional year in their natal group when juveniles were present (Fig. 2). This suggested that older offspring may care in some way for juveniles. Furthermore, subordinate alpine marmots dispersed more frequently if the territorial animals of their group were not their parents and the group's juveniles therefore were not their full sibs (Fig. 2). Thus, more dispersal from groups with unrelated territorials and from groups without juveniles might have occurred for the same reason: the impossibility of indirect fitness gains.

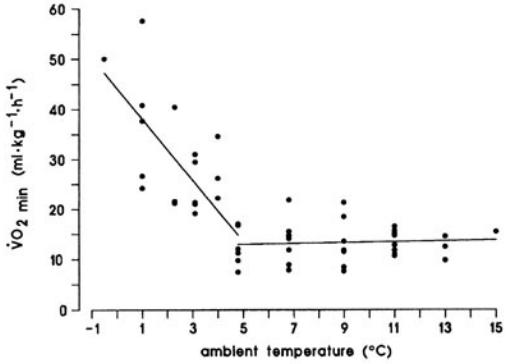

Figure 3. Minimal oxygen consumption of singly hibernating alpine marmots at different ambient temperatures. Regression analysis for 5° C ≤ Ta ≤ 15° C: y = 12.45 + 0.093x, n = 32, R2 = 0.01, n.s.; for -0.5° ≤C Ta≤5° C: y = 44.18 - 6.13x, n = 23, R2 = 0.59, p <.001. Reprinted from [11], courtesy of the Journal of Thermal Biology.

Could the "parental investment" hypothesis explain these results as well? The "parental investment" hypothesis indeed predicts more dispersal of subordinates unrelated to territorials, but it implies that subordinate dispersal would be forced by territorials. Again, there is equivocal evidence from observational data: some dispersers apparently left their natal group because they were chased away, but in many other instances subordinates dispersed in the absence of observed overt aggressive behaviour. The second result, reduced dispersal due to the presence of juveniles, is inconsistent with the "parental investment" hypothesis. Why should parents benefit from investing more in older offspring (i.e., tolerate them longer) when juveniles were present?

The most important question is now whether subordinates help the territorials in raising young and which fitness consequences arise from such help. To date, I have detected no evidence for alloparental care during the summer, but the presence of older siblings was advantageous during the winter. For 11 years I studied about 25 groups of individually known alpine marmots and found only once that not all group members entered the same burrow for hibernation, although many groups used different hibernacula in various winters and hence had the opportunity to disband [7]. This suggested that there might be benefits to communal hibernation and that physiological data would be important.

The first series of physiological investigations employed laboratory studies. During winter, marmots rely entirely on body fat to fuel their metabolism [16, 20]. Hibernating marmots do not allow their body temperature (T_b) to drop below a certain threshold. A decrease of T_b below the hypothalamic set point of thermoregulatory response evokes a gradual increase of metabolic heat production or complete arousal from hibernation [23, 28, 41]. Our laboratory measurements of oxygen consumption at different ambient temperatures showed that this threshold was about 5° C in singly hibernating alpine marmots (Fig. 3).

To better understand natural hibernating conditions, I determined the temperature regime in natural winter burrows of alpine marmots by measuring the temperature in or close to the nest. Access to a burrow system was possible through flexible water pipes. These pipes were

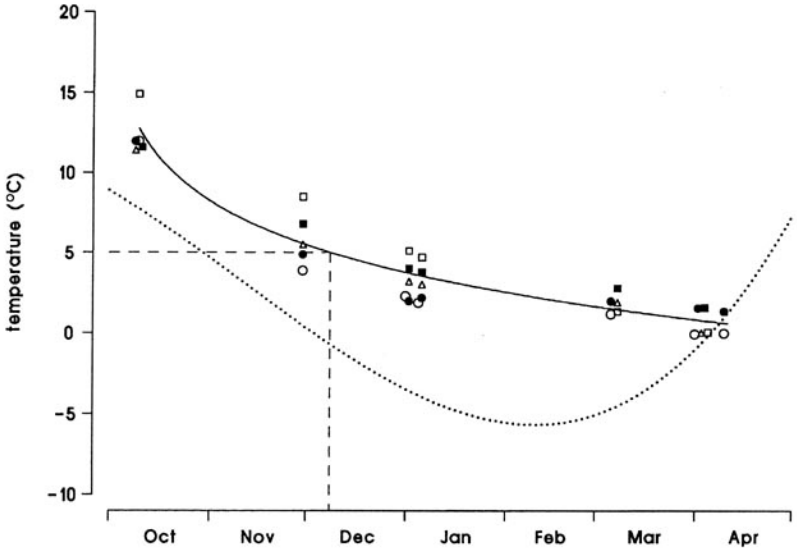

Figure 4. Burrow temperatures in natural hibernacula of alpine marmots and air temperature during winter. Different symbols are plotted for each of the five burrows measured. The solid line indicates the best logarithmic fit on the data from burrows occupied by marmots (R2= 0.92). The dotted curve is the cubic regression on the air temperature data (R2= 0.57, higher order polynomials did not substantially improve the fit). The dashed line indicates the estimated mean date when temperatures in the occupied hibernacula fell below the threshold of thermoregulatory response of laboratory animals (see Fig. 3). Reprinted from [11], courtesy of the Journal of Thermal Biology.

introduced into the hibernacula several weeks before the animals plugged the entrances from the inside. A marmot was trapped and the end of a pipe was loosely mounted with adhesive tape to its tail. The animal was then released into its winter burrow. Typically, the animals stopped moving after 6-8 m of the pipe had been carried into the burrow. Then, the pipe was either pulled off of the marmot's tail or the animal was left undisturbed to gnaw off the tape. I assumed that their reluctance to move further indicated that the animals had reached the nest chamber. The outer ends of the pipes were sealed to prevent unnatural movement of air through the burrow.

Ambient temperatures in natural hibernacula (T_{bur}) were measured by introducing thermocouples through the pipes at regular intervals during winter. T_{bur} dropped continuously from about 12° C in autumn at the onset of hibernation to almost 0° C in spring (Fig. 4). The critical threshold of 5° C was reached in the beginning of December. Thus single animals could maintain minimal metabolism during deep torpor only during the first third of the hibernation season, the remainder of the winter they had an increasing energy expenditure.

Hence it seems reasonable to assume that the energetic demands of long and cold winters at high altitude or latitude jeopardise survival of singly hibernating marmots and force the formation of larger winter groups in order to reduce individual heat loss. Indeed, all social marmot species hibernate in groups [7, 9]. Only *Marmota monax* hibernates alone and this may reflect the relatively moderate winter conditions in its typical habitat [26, 40]. Low T_{bur}

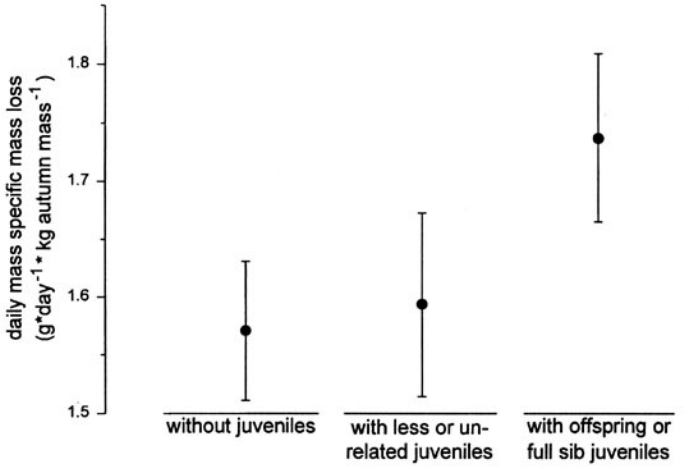

Figure 5. Daily mass specific mass loss of yearling and older alpine marmots (means, 95% confidence intervals) and the influence of juveniles presence in the hibernating group and relatedness to the juveniles ($F(2,273) = 7.07$, $p = .001$). Post-hoc comparisons of means demonstrated significant differences ($p < .05$) between animals hibernating together with offspring or full sib juveniles and animals from the two other categories.

may not only require group hibernation but also active warming of juveniles. Juvenile marmots suffer considerably higher winter mortality than adults [4, 7, 12, 13, 30, 31]. They possess less body fat reserves than adults [16, 32, 39], and should lose relatively more heat because of their less favourable surface area/volume ratio. If juveniles must be warmed during winter, non-dispersing marmots could gain indirect fitness by helping their parents if such help improved the survival of juveniles or that of parents.

2.1. INDIRECT EVIDENCE FOR SOCIAL THERMOREGULATION AND WARMING JUVENILES

The analysis of mass loss during winter indicated that group hibernation influenced energy expenditure and provided indirect evidence for the occurrence of social thermoregulation. Individual mass loss was lower when more animals hibernated together, presumably because of reduced thermal conductance due to huddling. However, this was true only for groups hibernating without juveniles. When juveniles were present, the opposite trend was observed: the larger the group, the higher the individual mass loss [8]. Further analysis showed that the presence of juveniles in a hibernating group actually caused higher mass loss in the juvenile's parents and full sibs. Individuals unrelated or distantly related to juveniles lost the same mass as individuals hibernating without juveniles (Fig. 5).

Hence increased energy expenditure due to the presence of juveniles was apparently not an inevitable cost, but was rather the result of active parental and alloparental care. Such care must have been more than mere huddling since huddling should have been beneficial for every participating individual. However, it was completely unknown what actually happened during social hibernation. The next step was therefore the direct investigation of individual thermoregulatory behaviour during winter.

3. Measuring Body and Burrow Temperatures During Winter in the Natural Habitat

I began to study individual thermoregulatory behaviour during social hibernation in the natural habitat during the winter 1990/91 by recording core T_b of 37 alpine marmots (27 adults, 4 yearlings, 6 juveniles) with implanted temperature-sensitive transmitters. These animals hibernated in eight social groups. One male was evicted from its territory in late autumn and wintered alone. In three of the groups, each individual was equipped with a transmitter. In the remaining groups the relation between animals with and without transmitters was 10/12, 6/7, 2/7, 3/4 and 1/3, respectively.

3.1. TRANSMITTERS

For recording temperatures I used two-stage CMOS-transmitters with a loop antenna, constructed in SMD-technique (ÖKOKART, Munich, FRG). The disk-shaped transmitters were 11 mm high and 26 mm across. Loop antennas had the same diameter as the transmitter. When operating, a transmitter was switched on and off by an unstable multivibrator and emitted a VHF-signal of approximately 12 ms duration. The pulse rate was temperature dependent with the addition of a resistor in the circuit having a negative temperature coefficient (thermistor). Each transmitter with antenna was embedded in epoxy synthetic resin to protect the electronic parts from shock and moisture. For easy replacement, the batteries (3 V lithium disks, 24 mm diameter, 7 mm high, 950 mAh) were not imbedded in resin. One battery provided a transmitter life-time of about one year. Transmitters with attached batteries were encased in shrink tubes and heat-sealed at both ends. The entire package was coated with a mixture of beeswax and paraffin to reduce irritation of animal tissue after implantation and to provide an additional protective layer against moisture for the transmitter and batteries.

For recording T_{bur}, I used the same type of transmitter, except that the temperature-dependent resistor was attached to the transmitter with wires, and a longer antenna (approximately half the wave length of the emitted signal) was used instead of the loop antenna. The wires with the resistor mounted on top were introduced into winter burrows in the same way as described above for thermocouples. Each transmitter was put into a water-proof case filled with silica gel to bind moisture. Both transmitter cases and antennas were buried at the respective burrow entrance.

Transmitters' frequencies were between 150.00 and 150.99 MHz and individual transmitters were separated by at least 10 kHz. A unique frequency was used for each marmot and burrow. Under optimal conditions (clear sight line, transmitter located about 1 m above ground), signals from transmitters with loop antennas were detectable up to *ca.* 5 km. The signals from transmitters used for recording T_{bur} were a magnitude stronger. If these transmitters were located close to the receiving antenna it was necessary to reduce the signal power by clipping the transmitting antenna in order to avoid interference with transmitters having adjacent frequencies.

3.2. IMPLANTATION

Animals were trapped with single-door TOMAHAWK live traps and kept in wooden boxes until surgery and afterwards during recovery from anaesthesia. Surgery was conducted in a cabin located in the middle of the study area. Transmitters were implanted into the abdominal cavity under narcosis with 25 mg ketamine and 31.25 mg xylazine per kg body

mass. This anaesthesia completely immobilised the animals for about 40 min and was prolonged, if necessary, with pure ketamine (supplementary doses of 40 mg). A 2-3 cm incision was made along the linea alba caudal to the navel to implant the transmitter. The transmitter was sterilised before introduction with 70% ethanol and then rinsed with sterile normal saline solution. The abdominal cavity was closed with three layers of stitches using resorbable material (DEXON® metric 2). One layer of stitches pulled muscle and peritoneum together, a second subcutaneous tissue, and the last the epidermis. I chose this conservative stitching because the animals were released in their natural habitat approximately five hours after surgery when recovery from anaesthesia was completed. As a precaution against infections, the marmots received a subcutaneous injection of 0.3 ml of a long acting suspension of penicillin and streptomycin (TARDOMYOCEL®).

Transmitters were implanted not later than four weeks prior to the onset of hibernation as healing and resorption of threads is substantially impaired in hibernating animals. Juvenile animals received transmitters with one battery (*ca.* 20 g), yearlings and adults transmitters with two paralleled batteries (*ca.* 35 g). Juveniles were not implanted before the end of August by which time they had reached a mean body mass of 1,625 g (SD = 88.03, n = 6).

3.3. AUTOMATIC RECORDING OF TEMPERATURE DATA

Signals from implanted transmitters and from 12 transmitters used for measuring T_{bur} were recorded automatically and continuously at three different stations (19 transmitters at station A, 16 at B, 14 at C). Stations A and B were set up in a cabin in the centre of the main part of the study area. Station C was located at a remote part of the study area, about 5 km away from the cabin. All equipment (except antennas and preamplifiers) was enclosed in wooden boxes insulated with 6 cm styrofoam. Air temperature inside each box was maintained above 5° C with a small battery powered electric thermostat in order to guarantee correct performance of electronic parts.

Figure 6 shows the configuration of devices at a station. Transmitter signals from burrows located 400-600 m from recording station B were received with an highly directional 8-element VHF-yagi-antenna (PHILIPS IRELAND, Ltd., gain 9.5 dB) mounted 4.5 m up on a pole. Signals from burrows located in other directions but closer to a station (A and C) were received with an omnidirectional antenna (2 m long, gain 6.8 dB) mounted on top of the pole. All signals between 150 and 151 MHz were preamplified by 16-17 dB with a HF-amplifier before further processing with an 100-channel telemetry receiver (ROHDE, D-79232 March, FRG). An Epson HX-20 computer, chosen because of its low (40 mA) power requirement, was used to systematically select a frequency on the receiver. The analogue receiver output triggered in an interface a digital signal passed on the computer's serial port. A computer program measured the time lag between signals during 30 s for each frequency. After filtering and storing the data on the Epson's microcasette (see below), the computer selected the next programmed frequency and switched the receiver to that channel. Each transmitter was sampled repeatedly every 10 to 15 min from August 1990 until the transmitter stopped transmitting because of battery drain.

A serious problem with automatic recording was fine tuning (frequency and gain) of individual channels. With the standard equipment of the receiver there was only one fine tuning possible for all channels. However, the signals emitted from transmitters implanted

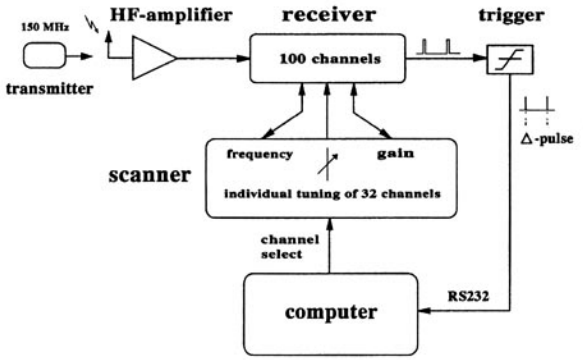

Figure 6. Configuration of devices used for automatic recording of body and burrow temperatures.

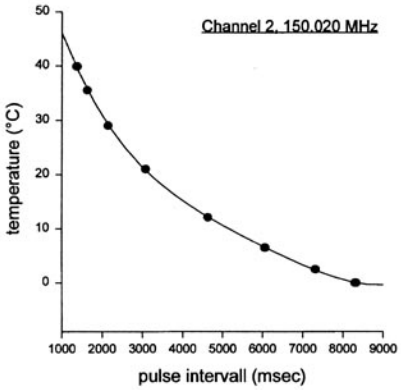

Figure 7. Calibration curve of a temperature coding telemetry transmitter. Pulse intervals (ms) are plotted against temperature in the water bath used for calibration. The parameters of a third order polynomial fitted to the calibration values were used for calculating temperatures from the pulse interval of a transmitter.

in animals hibernating in burrows several metres below the surface and under a heavy snow pack were so weak that greater individual fine tuning was necessary for each channel. The problem was solved with the addition of a separate potentiometer for frequency and for gain for each channel. This allowed independent fine tuning for each channel. By switching the receiver to a particular channel, the controlling program also selected automatically the potentiometers with the pre-set fine tuning for this frequency.

3.4. CALIBRATION

Each transmitter was calibrated by exposing it to at least six different temperatures in the range between 0° and 40° C in a glycerol/water bath (precision of the temperature regulation ± 0.5° C) and measuring its pulse interval for these temperatures. A third polynomial order was fitted to these data with an iterative computer programme (Fig. 7). The optimal parameters, estimated separately for every calibration curve, were used for converting milliseconds measured by the recording program (see below) into temperatures.

The precision of the temperature measurement was determined after calibration by recording 32 transmitters for about 20 hours. The transmitters were simply placed on the same spot and each was measured for 30 seconds. As the air temperature at this spot changed slowly, all transmitters were exposed to virtually the same temperature during a scan lasting 16 minutes. The 1,717 measurements obtained varied little around the mean temperature within a given scan round (SD = 0.4° C).

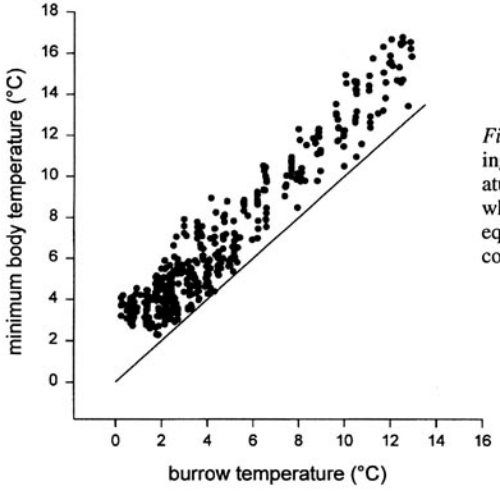

Figure 8. Minimum body temperature achieved during bouts of torpor as a function of burrow temperature. The diagonal line represents the isotherm where points would lie if body temperature were equal to burrow temperature. Reprinted from [10], courtesy of Westview Press.

3.5. DATA PROCESSING

The computer program measuring the transmitters' pulse intervals also contained a filter routine that detected most pulses triggered by signals from sources other than transmitters. A measurement was considered reliable if at least 30% of the measured time lags between pulses did not differ by more than 6%. This filter routine failed whenever a bad value was very close to a "true" pulse rate. Such outliers were detected later by another computer program fitting a polynomial to larger time segments of data from individual channels and removing all values outside a pre-set tolerance.

Only the mean of values sampled for a given channel within 30 s was stored on the Epson's microcasette (capacity about 500 KByte) in binary format together with the channel number. A time marker was stored after every scan round. This dense data storage allowed continuous recordings for about 14 days.

4. Patterns of Thermoregulation during Hibernation

Hibernating mammals remain torpid only for a certain period of time. In the studied alpine marmots these bouts of torpor lasted on average 303.0 h (SD = 86.4, range 100-643 h, n = 341). As in other hibernators, the first autumn and the last spring torpor bouts are shorter in alpine marmots and were excluded from analysis. After each bout of torpor the animals rewarmed within 9.5 h (mean of 357 rewarmings, SD = 3.5, range 4.0-25.5 h) to euthermy. Average T_b during euthermy was 34.3° C (SD = 0.9, range 29.9-36.9 h, n = 461), considerably lower then the T_b of marmots during the active season [43]. The animals remained in euthermy on average for 19.0 h (SD = 10.6, range 1.3-136 h, n = 351). During reentry into hibernation, T_b dropped exponentially until it approached T_{bur}. The lowest T_b ever achieved was 2.6° C. As long as T_{bur} remained above 1.5° C, T_b followed T_{bur} passively with an average distance of 2.0° C [9] (Fig. 8). Hence the onset of additional heat production in order to prevent a further decline of T_b apparently occurred at a considerably lower temperature in the field than in the laboratory (cf. Fig. 3 and 8). The animals were exposed to temperatures that definitely caused higher torpor metabolism in three of six hibernacula investigated [11].

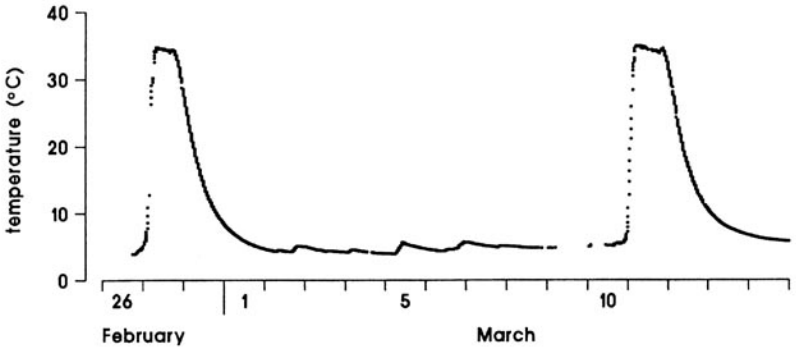

Figure 9. Body temperature of a solitary hibernating marmot during a hibernation bout in late winter at very low burrow temperature. Ambient temperature was not measured in this burrow but was 1.4° C at the same time in a burrow located about 100 m away.

Heat production during deep torpor occurs in cyclic bursts. The magnitude of these bursts depends on the difference between the actual ambient temperature and the central nervous set point for thermoregulation [27, 28]. The larger this difference is, the more heat must be produced in order to maintain T_b at or above the set point. Small bursts of heat production do not result in measurable peaks in the T_b-curve although they increase body temperature. Apparently, pronounced burst that became visible in the T_b-curve of the studied animals occurred only at low T_{bur} during late winter when a large differential between T_b and T_{bur} was maintained (Fig. 9).

5. Direct Evidence for Social Thermoregulation and Warming Juveniles

The most striking feature of social hibernation was the synchronisation of the arousal periods among group members (Fig. 10). Heat loss is most pronounced during the periods of euthermy when the gradient between T_b and T_{bur} is highest. Hence the decrease of individual mass loss with increasing group size [8] appears to be a function of synchronised euthermic intervals.

The territorial male of the group shown in Fig. 10 died soon after spring emergence. This male was extremely emaciated at emergence. I assume that both an unusually low fat deposit at the beginning of hibernation (his autumn mass was 3,700 g, mean autumn mass of adult males is 4,500 g [9]) and a high mass loss during winter (40%) was due to the old age of this individual (12 years). Since his over winter T_b patterns appeared normal, I suspect the animal died of old age.

One subordinate adult male in this group showed several atypical long periods of euthermy. Why this happened remains open to question. Whenever this animal was still euthermic while its nest mates reentered hibernation, their cooling curves showed an irregular pattern with substantial rewarmings. Such irregular courses of T_b were found in other groups as well. They only occurred when at least one group member was euthermic. Hence incomplete rewarmings were most likely caused by passive warming due to body contact with euthermic nest mates and were unlikely the result of one's own heat production.

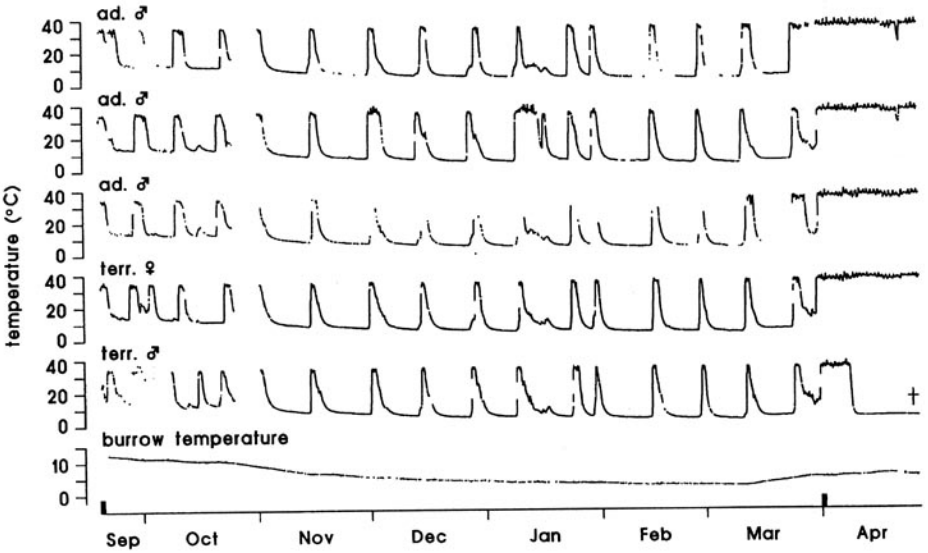

Figure 10. Body temperatures of five adult animals hibernating together and temperature course in their winter burrow. Black bars on the horizontal axis indicate the date when the hibernaculum was plugged from inside by the animals and the date of first emergence above ground in spring. Gaps in the temperature curve are due to missing data.

During winter 1990/91 we also measured oxygen consumption of the animals equipped with transmitters. Air was pumped out of a hibernaculum through the pipes and analysed with a portable oxygen analyser. The pipe in the burrow of the group shown in Fig. 10 was prepared for these measurements at the end of January. The noise inevitably associated with this preparation was responsible for the premature arousal of the whole group at this time after a very short torpor bout. This demonstrated that hibernating alpine marmots remain very sensitive to external stimuli even at very low T_b.

Figure 10 is a typical picture only for groups hibernating without juveniles. When juveniles were present in a group, the synchrony of arousals from deep torpor disappeared when T_{bur} became low. From approximately November onwards, marmots that were closely related to juveniles aroused prematurely from bouts of deep torpor and rewarmed their nest mates passively. Beside additional arousals I found two other mechanisms of care for juveniles during winter (Arnold, unpublished data). First, older marmots in groups without juveniles and juvenile marmots maintained a minimal gradient between T_b-T_{bur} during deep torpor that was about 1-2° C lower than that of animals hibernating with offspring or full sib juveniles. Hence this allowed for heat transfer that could help the energetically constrained juveniles to survive winter. Second, juveniles hibernating with older siblings cooled down more slowly than those without older siblings. This retarded heat loss during entry into hibernation suggested that juveniles might have been located in the centre of the hibernating group, surrounded by warmer older siblings [6].

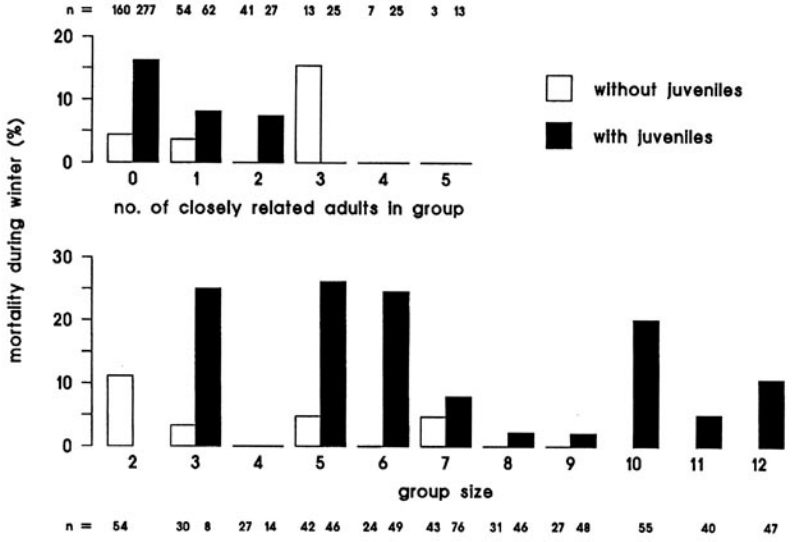

Figure 11. Winter mortality and the influence of the size of the hibernating group (lower graph) and the number of closely related adults in the group (upper graph, full siblings or offspring, for test statistics, see text). Sample sizes are given above and below each graph, respectively. Reprinted from [10], courtesy of proceedings of the German Zoological Society.

6. The Effect of Social Hibernation on Survival

The effect of group hibernation and care for juveniles on winter mortality was analysed by multiple logistic regression. It was necessary to control for two confounding variables that significantly affected winter survival. Winter mortality was positively associated with harsh winter conditions (indicated by the time of snow melt in spring at a hibernaculum, a strong correlate of soil temperatures at this location during winter [8]). Furthermore, winter mortality was higher if the time to accumulate fat reserves was short [10]. This period of fat accumulation was particularly crucial for juveniles.

The influence of group size and composition on winter mortality matched the results from the mass loss data. Winter mortality decreased with increasing size of the hibernating group in groups hibernating without juveniles (logistic partial correlation statistic $R = -0.168$, $p = .03$; Fig. 11, lower graph). In contrast, the number of closely related adult group mates had no significant influence (Fig. 11, upper graph). The reverse pattern was found in hibernation groups containing juveniles. Group size here had no detectable influence on overall winter mortality (Fig. 11, lower graph), but winter mortality decreased with the number of closely related adults supporting the parents in warming juveniles ($R = -0.133$, $p = 0.006$; Fig. 11, upper graph).

Hibernating with juveniles but without older subordinates was most hazardous for alpine marmots. Groups consisting of only parents and juveniles risked extinction during the winter (about 15% of such groups went extinct [8]). When the first litter survived, either because the hibernaculum was located at a site with favourable thermal conditions, or because the winter was mild, then the group did much better in subsequent years. Interestingly, the improvement of survival chances diminished with the number of helpers.

No further reduction of winter mortality occurred when four helping adult subordinates were already present (Fig. 11, upper graph). Hence, each additional helper could not gain indirect fitness.

7. Conclusions

Because of the extreme reduction of metabolism during torpor, hibernators expend most energy during the relatively short fraction of the total hibernation period when they maintain relatively high body temperatures [19, 33, 46]. Laboratory measurements showed that alpine marmots kept at an ambient temperature of 5° C expend 57% of the total energy required during hibernation to maintain euthermy, 15% was expended while rewarming to euthermy, and only 28% was expended during torpor. The total energy demand of a singly hibernating marmot during winter was estimated to be equivalent to about 1,300 g of body fat [27]. In the natural habitat, adult marmots lose on average about 1,400 g during winter [9]. This difference is small considering that thermal conductance in the damp nest of a natural burrow is several times higher than in the container used in the laboratory for measuring oxygen consumption (Jürgensmeier, Arnold and Heldmaier, unpublished data), and that temperatures in many natural winter burrows are lower than 5° C during most of winter.

So far there are no direct measurements available for marmots of the energetic effects of synchrony of euthermic intervals. Nevertheless, it seems reasonable to assume that the possibility to huddle with conspecifics having high T_b as well reduces individual energy expenditure considerably as it does in many small mammals (for review see [36]). Alpine marmots hibernating in the same burrow also huddle close together during torpor, at least when ambient temperatures are low [6, 38]. Theoretical [44] and empirical [45] studies show that huddling reduces the energy consumption during torpor as long as nest temperatures are below T_b. Such lower torpor metabolism due to huddling became apparent in this study when comparing the T_b-curves from the male that hibernated alone with those of communal hibernating individuals. Bursts of heat production could not be identified in the T_b-curve of group hibernators despite a T_{bur} between 0° and 0.5°C. In contrast, the adult male hibernating alone showed pronounced peaks of heat production during torpor already at an estimated T_{bur} of 1.4° C (cf. Fig. 9 and 10). Thus, the actual ambient temperature experienced in a huddle is most likely considerably higher than the measured T_{bur}.

Adult alpine marmots may survive winter when hibernating alone. However, their survival chances are higher when hibernating in a group (Fig. 11). The situation is more extreme for juveniles. Juveniles have considerably less time available for fattening than adults. Juveniles appear above ground at the beginning of July. During the following weeks they devote most energy uptake to growth and begin to accumulate substantial amounts of body fat only after mid-August (Arnold, unpublished data). Consequently, they achieve only 60% of the body fat deposits of adults (relative to body size [9]). Hence it is likely that juveniles of marmot species living at high altitude or latitude could not survive without being warmed by some conspecifics. Yet, the benefits from social thermoregulation are not only important for survival. Competitive abilities of alpine marmots in spring also depended on how much mass they lost during the previous hibernation [7].

Hibernating mammals appear to the naive observer as almost dead. This might have been the reason why little attention has been paid to the potential importance of long and cold

winters for social evolution in the genus *Marmota*. The telemetric study of communal hibernation in free-living animals demonstrated that hibernating alpine marmots are very sensitive to external stimuli and show elaborate social behaviour. While hibernating, marmots adjust their thermoregulatory behaviour in subtle ways according to group composition, relatedness to group members, and ambient temperature. It seems unlikely that these results would have been found in a laboratory study where social factors may have been viewed as a variable to be controlled rather than studied (see chapter by Queyras and Vitale, § 5.3., present volume). Even when focusing on social behaviour, control measurements in free-living animals would have been necessary. Important parameters like the conductance of the animals in a natural nest are difficult to simulate, and the artificial laboratory situation can disturb hibernating marmots preventing detection of the important influences of the social environment.

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