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Solitude versus gregariousness: do physical benefits drive the choice in overwintering meadow voles?

Dominique Berteaux, Jean-Marie Bergeron, Donald W. Thomas and Hélène Lapierre

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Winter group formation has been described for many small rodent species living in temperate environments. Physical benefits (e.g. energy and water conservation) of huddling are generally considered to be the ultimate cause of these aggregations. We manipulated group size of meadow voles (1 versus 4 individuals) in a field experiment involving 40 individuals (5 replicates, each including 4 solitary-living and 4 group-living individuals) to test the validity of the physical benefits hypothesis. Energy expenditures and water flux were measured using the doubly labelled water method. Group size had no effect on field metabolic rate, water turnover, body mass changes, body composition, and survival. The role of physical benefits as the driving force behind winter aggregations should thus be reevaluated. Future studies should concentrate on specific time periods characterized by extreme climatic conditions. Alternative benefits of aggregations, such as decreased predation risk or social transmission of information, should also be considered.

D. Berteaux, J.-M. Bergeron and D. W. Thomas, Groupe Recherche en Écologie, Nutrition et Énergétique, Département de Biologie, Univ. de Sherbrooke, Sherbrooke, PQ, Canada J1K 2R1. – H. Lapierre, Lennoxville Research Station, Agriculture Canada, Box 90, Lennoxville, PQ, Canada J1M 1Z3.

Alexander (1974) proposed that only three fundamental selective forces underlie the evolution of sociality: predation risk, foraging efficiency, and resource patchiness. This list has since been extended to include e.g. social transmission of information (e.g. Barash 1982, Brown 1986) and "physical benefits", such as reduced energy and water requirements that might accrue to individuals living in groups (Madison 1984). These benefits would occur when temperature is low and individuals aggregate in communal nests, thereby decreasing their energy and water expenditures. A number of laboratory studies show that huddling does indeed reduce thermoregulatory costs in small mammals, either by reducing exposed surface areas (Vickery and Millar 1984) or by heating the local environment (Hayes et al. 1992) (see references in Hayes et al. 1992 and Madison et al. 1984). Huddling in communal nests may also reduce pulmocutaneous water loss by increasing humidity and reducing respiratory rates (e.g. Punzo 1975). Because of these laboratory results, and also due to the virtual absence of studies analyzing the cost/benefit equation of winter grouping in terms of other currencies (e.g. predation risk or social transmission of information), physical benefits have been progressively adopted as the major evolutionary force driving winter aggregations of small mammals, particularly microtine rodents (Madison 1984, 1990, Madison et al. 1984, West and Dublin 1984, Wolff 1985, Cockburn 1988).

Understanding the factors that promote social living in microtines is important because some species of the family (e.g. the pine vole, *Microtus pinetorum*) may become good models to understand the evolution of very elaborate forms of sociality, such as eusociality (Solomon 1994). Before physical benefits can be ac-

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cepted as an ultimate cause of grouping, they should, however, satisfy two conditions. First, laboratory results must remain valid under natural conditions. Second, physical benefits must translate directly into fitness benefits. Despite their crucial importance, these conditions have never been tested in the field.

Here, we present a field experiment in which we manipulated group size of overwintering meadow voles, *Microtus pennsylvanicus*, to test whether group living results in measurable physical benefits (reduction of energy and water fluxes) and an increase in survivorship. We consider demonstration of these two elements as a prerequisite to accepting physical benefits as the selective force driving winter sociality in small mammals.

Methods

Forty adult female meadow voles used in this experiment originated from a captive colony that was periodically outbred with wild voles. For details on rearing of voles, see Berteaux et al. (1994). We acclimatized voles to natural photoperiod and temperatures for 11 to 18 weeks before they were released into adjacent pens built in an old-field community on the campus grounds of Sherbrooke Univ. Québec, Canada (45°15′N, 72°00′E). Pen walls were made of polyethylene paneling that extended 90 cm above and 30 cm below ground.

We manipulated group size by releasing 8 voles into 8 separate 25-m^2 pens (solitary voles) and two groups of four voles into two 100-m^2 pens (social voles). Vole densities were equivalent for solitary and social voles (1 individual/25 m^2) and the available home range reflected that found under natural conditions at that time of the year. For social voles, group size reflected that found naturally (Webster and Brooks 1981a). Voles were released on 12 January, 4 February and 16 March, 1994 for a total of 20 solitary and 5 groups of 4 social voles. Voles were allowed to habituate to the enclosures during two weeks before they were captured to assess survival, estimate daily energy expenditure and body water turnover, and measure changes in body mass since their introduction.

Each vole was radiocollared with one-stage transmitters (Custom Electronics of Urbana, Inc.) weighing 2.55–3.45 g or 6.4–11.7% of body mass ($\bar{x} = 8.4 \pm 1.3\%$ of body mass). Carrying a radiocollar has no measurable effect on daily expenditure of energy of individuals (Berteaux et al. 1996). Telemetry allowed us to assess survival of individuals more easily and to enhance trapping success by opening only the traps nearest to the nests. Two or 3 d after voles were introduced in the enclosures, individuals were located 4–6 times at one-h intervals to find nests. After that, 1–3 locations of each individual were obtained every other day to verify that the nest remained at the same place and that group-living individuals did not split into smaller groups.

Rates of CO_2 production were measured using doubly labelled water ($H^3H^{18}O$) (Lifson and McClintock 1966). Animals were captured with Sherman traps baited with apple slices and protected by trap shelters (Iverson and Turner 1969). Voles were transported within a few minutes after capture to a building located near the study site, weighed to the nearest 0.1 g, and given an intraperitoneal injection of 4 μl/g body mass of water containing 77.9 atom % ^{18}O and 94 mCi ^3H per ml. After 1 h, a 150-μl blood sample was taken under light anesthesia (methoxyfluorane) from the suborbital sinus using heparinized glass capillary tubes. We released animals at their point of capture and tried to recapture them at the same time of day 24 and/or 48 h later for collection of second and third blood samples. We aimed to measure daily energy expenditure of individuals more than once because intraindividual variation in measures is generally high in free living animals, possibly due to individuals not balancing their energy budgets over the time-scale of single days (Speakman et al. 1994, Berteaux et al. in press). Blood samples were also taken before isotope injection in 5 individuals for measurement of natural abundance levels of ^{18}O. Blood samples were stored refrigerated before being vaccuum distilled in pasteur pipettes to recover the water fraction (Nagy 1983). We analyzed for ^3H using liquid scintillation in a Beckman LS 6000 counter and for ^{18}O using the guanidine hydrochloride method to prepare CO_2 gas (Dugan et al. 1985, Wong et al. 1987) which was analyzed with a VG-Isogas Sira 12 isotope ratio mass spectrometer. All samples were analyzed in duplicate and a triplicate sample was run when the coefficient of variation exceeded 2%. We calculated CO_2 production for voles using eq. 1 in Nagy (1983) and estimated energy expenditure by assuming an energy equivalence of 21.7 J ml^{-1} CO_2 (Nagy 1983).

Water flux rates were calculated using eq. 4 in Nagy and Costa (1980). For each individual, the volume of water in the body at the time of initial capture was estimated as the dilution volume of injected ^{18}O (Nagy 1983). Total body water volumes at recaptures were estimated from body mass assuming that the water fraction remained constant.

In the course of this study we measured CO_2 production and water flux 19 times from 11 solitary voles and 16 times from 13 individuals living in groups. When two measures were obtained on the same individual, they were averaged to maintain independence of data. Survivorship for 16 solitary and 18 social voles was assessed over the 14–16 d of the experiments.

Minimum, maximum and mean temperatures (°C) at ground level and 1.5 m above ground, and mean snow depth (cm) were measured daily during the experiment. Statistical analyses were carried out with STATVIEW for Macintosh (Abacus Concepts, 1987) and Super-

ANOVA (Abacus Concepts, 1989). Values are mean ±S.E.

Results

During the study, mean snow cover varied from 10 to 48 cm ($\bar{x} = 38 \pm 9$ cm) and mean daily temperature 1.5 m above ground level varied from −25.4 to 11.9°C ($\bar{x} = -9.9 \pm 9.3$°C). Because of the buffering effect of snow, temperature at ground level ranged only between −5.7 and 0.1°C ($\bar{x} = -2.6 \pm 1.9$°C) (Fig. 1). During the days ($n = 6$) when field metabolic rate and water flux of individuals were measured, the mean daily air temperature varied significantly between measurement periods (January -24.9 ± 0.7°C, February 1.9 ± 4.0°C, March 2.0 ± 2.1°C). However, ground level temperature remained at -1.3 ± 1.4°C.

A few days after individuals were introduced into the enclosures, nests of both solitary and social voles were easily located because individuals returned consistently to specific points after foraging bouts. In large enclosures, group cohesion was shown by the constant use of one nest by all members of the group. Trapping did not break down group cohesion.

Effect of group size on survival and body mass changes

When individuals in which survival or mortality could be ascertained are considered, 14 of 18 (78%) voles living in groups survived the 14–16 d experimental period, which was not significantly different (G-test: $G = 0.56$, $p > 0.10$) from the 87% (14 of 16) survival rate of solitary voles. For 2 of the social voles and 4 of the solitary voles, survivorship could not de determined because during the experiment they either lost their transmitter (3 individuals), escaped from the enclosure (2 individuals) or were killed accidentally (1 individual).

Body mass of voles when introduced in the field enclosures did not differ significantly according to treatment (solitary 39.3 ± 4.3 g, $n = 20$; social 37.0 ± 3.8 g, $n = 20$; unpaired two-tailed t-test: $t = 1.72$, $p = 0.10$). During the period when the voles were in the enclosures, both voles living in groups and voles living singly lost weight, but body mass changes were not affected by group size (solitary 0.26 ± 0.06 g d^{-1}, $n = 14$; social 0.28 ± 0.09 g d^{-1}, $n = 14$; one-tailed t-test: $t = 0.17$, $p = 0.433$).

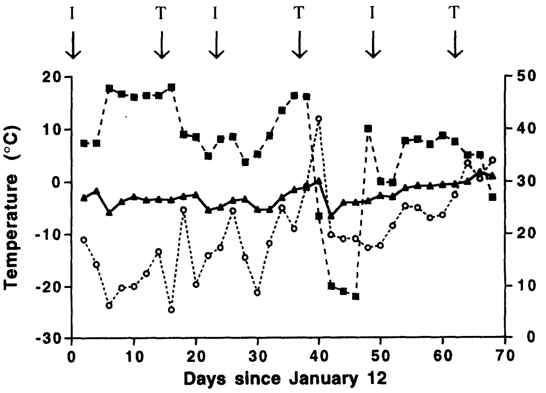

Fig. 1. Mean snow cover (squares), mean daily temperature at ground level (triangles), and mean daily temperature 1.5 m above ground (circles) during the study period. For each experimental period, arrows identified by "I" indicate when voles were introduced in the enclosures and arrows identified by "T" indicate when voles were trapped to be injected with doubly labelled water.

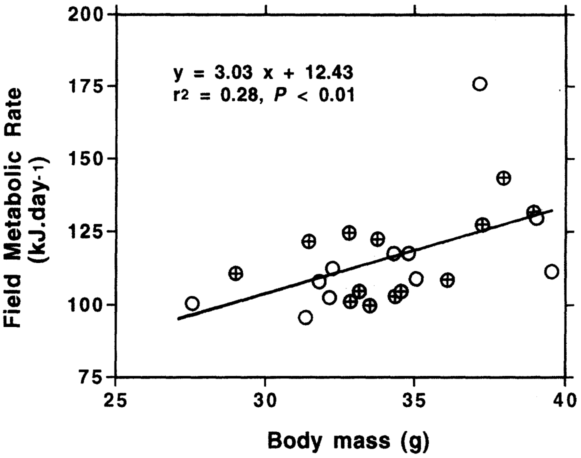

Fig. 2. Daily field metabolic rate of wintering meadow voles, as a function of body mass. Open symbols are solitary voles and closed symbols, social voles.

Effect of group size on energy expenditures

Across all individuals, field metabolic rate was positively related to body mass ($F_{1,22} = 8.728$, $p = 0.0073$; Fig. 2). When field metabolic rate was corrected for body mass (mass specific metabolic rate), a two-way ANOVA of mass specific daily field metabolic rate, with group size and measurement period as the main effects, revealed no significant effect of group size ($F_{1,18} = 0.017$, $p = 0.897$), measurement period ($F_{2,18} = 0.221$, $p = 0.804$) or interaction between group size and time ($F_{2,18} = 0.059$, $p = 0.943$; Fig. 3). Body mass changes over the 1 or 2-d duration of measurement did not explain variations in mass specific field metabolic rates ($F_{1,22} = 1.013$, $p = 0.325$). Overall means for mass specific daily field metabolic rates were 3.38 ± 0.10 kJ (g d)$^{-1}$ ($n = 13$) for group-living individuals and 3.42 ± 0.16 kJ (g d)$^{-1}$ ($n = 11$) for solitary-living individuals.

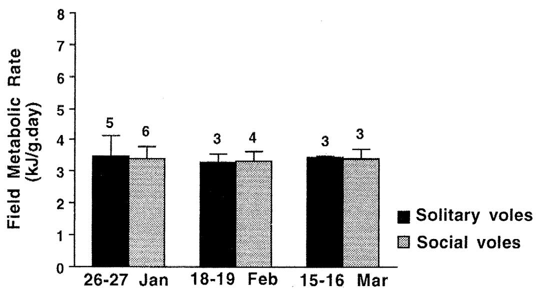

Fig. 3. Daily field metabolic rate (corrected for differences in body mass) of solitary versus social meadow voles, for each of 3 measurement periods. Means are given +SE. Numbers indicate sample size.

Effect of group size on water flux

Across all individuals, there was a strong positive relationship between total body water volume and body mass ($F_{1,22} = 94.43$, $p = 0.0001$; Fig. 4). Total body water volume as a percentage of body mass did not differ according to group size (solitary 73.27 ± 0.8%, $n = 11$; social 72.15 ± 0.81%, $n = 13$; two-tailed Mann-Whitney U test, $z = -1.42$, $p > 0.10$). This suggests that body fat reserves were not lower in solitary animals as a result of increased thermoregulatory costs, since lipids are mostly anhydrous, and per cent lipid content varies more or less inversely with per cent water content in small mammals (Kodama 1971, Fleharty et al. 1973).

We analyzed the water flux data in the same way as field metabolic rate data to identify the sources of the observed variations. Across all individuals, water flux rate was not related to body mass ($F_{1,22} = 0.913$, $p = 0.350$; Fig. 5). However, water flux rates were corrected for body mass in subsequent analyses in order to present values that are easy to compare with data previously published in the literature. Using a two-way ANOVA of mass specific daily water flux with group size and measurement period as the main effects, we obtained a non-significant effect of group size ($F_{1,18} = 0.771$, $p = 0.391$) and no interaction between group size and time ($F_{2,18} = 0.076$, $p = 0.927$). There was, however, a significant effect of measurement period ($F_{2,18} = 11.3$, $p < 0.001$; Fig. 6). Body mass changes over the 1 or 2-d duration of measurement did not explain mass specific water flux rates ($F_{1,22} = 0.315$, $p = 0.580$).

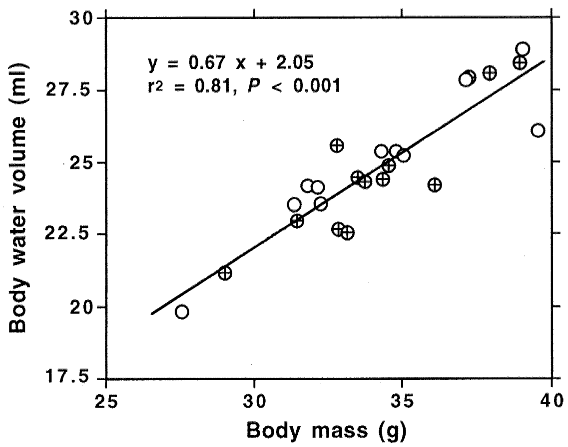

Fig. 4. Body water volume of wintering meadow voles as a function of body mass. Open symbols are solitary voles and closed symbols, social voles.

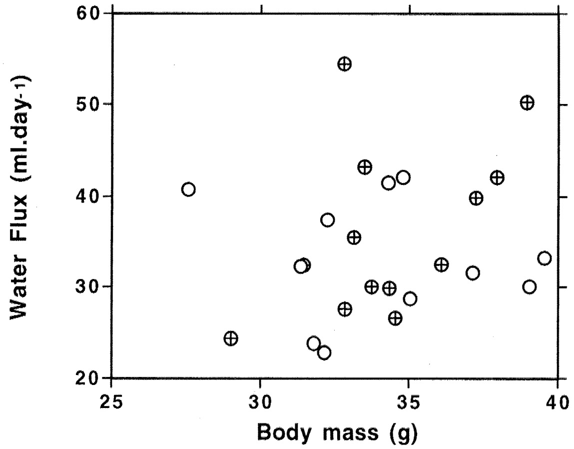

Fig. 5. Daily water flux rate of wintering meadow voles as a function of body mass. Open symbols are solitary voles and closed symbols, social voles.

Isotope rebreathing within and between individuals could potentially limit the differences in metabolic or water flux rates observed between individuals sharing a common nest (Nagy 1983) and so artificially reduce variance among social voles. We tested whether this bias had any effect by considering a group as a single measure and taking the mean for the group. This reduced sample size substantially (the 13 individuals sampled belonged to 5 groups) but had no effect on the conclusions. Group size still did not affect daily field metabolic rate or water flux (daily field metabolic rate:

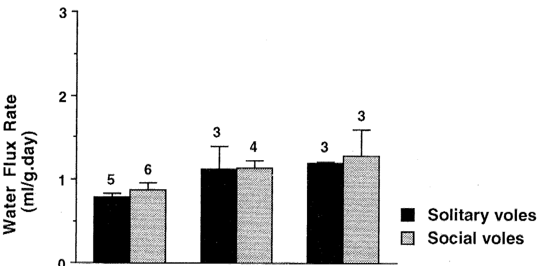

Fig. 6. Daily water flux rate (corrected for differences in body mass) of solitary versus social meadow voles, for each of 3 measurement periods. Means are given +SE. Numbers indicate sample size.

$t = 0.11$, $p = 0.46$; daily water flux: $t = 1.10$, $p = 0.143$; one-tailed t-tests).

Discussion

It is commonly assumed that group living in wintering small mammals is driven by physiological benefits that accrue to social animals. Energetic savings associated with huddling have been reported for more than 20 species of small mammals studied in laboratory experiments (references in Hayes et al. 1992). For example, Pearson (1960), Gebczynski (1969), Layne (1969) and Hayes et al. (1992) all found that small mammals huddling in groups of 2–5 individuals reduced energy expenditure by 20–30% when temperature was around freezing. Five lines of evidence from our study suggest that these laboratory-derived results do not apply to the field. We found no benefit of group living in our measures of 1) field metabolic rate, 2) body water turnover, 3) body mass changes, 4) body composition, and 5) survival.

Measurement imprecision or high inter-individual variation in field metabolic rates, that may have prevented us to detect any significant effect of group living because of statistical weakness and type II error, can be excluded by an analysis of least significant difference (Sokal and Rohlf 1981). Our sample size, indeed, would have allowed us to detect a 9% difference between means of metabolic rates of social versus solitary voles (t-test with $\alpha = 0.05$). Three main reasons may explain the contrast between the energetic benefits of huddling shown in the laboratory and the absence of benefits suggested by our field study.

First, time spent in the nest is known to be a critical variable determining energetic benefits of huddling (Vickery and Millar 1984). Wild meadow voles spend 50% of time huddled in the nest (Webster and Brooks 1981b). Although we did not quantify time spent in the nest in our study, this figure likely was similar since in a study of space use conducted in winter 1993 at the same site and with similar animals (Berteaux and Bergeron unpubl.) we found that half of the locations of individuals were at the nest. The energetic cost of activity in *Microtus* are largely unknown (Wunder 1985). However, a very conservative estimate is that active animals expend energy at least twice the rate of resting animals (Karasov 1992). With such a conservative assumption, one third of the daily energy expenditures should have been spent in the nest. Even if we assume a 25% energetic benefit of huddling when individuals are grouped, the maximal benefit of huddling should thus be $0.25 \times 0.33 \times \mathrm{FMR}$, or 8.25% of FMR. Thus, a 25% benefit of huddling as measured in the lab drops to a maximum 8.25% benefit when considered relatively to daily energy expenditure.

Second, in a majority of laboratory studies the energetic benefits of huddling have been observed while nest material was not provided to animals (e.g. Hayes et al. 1992). This probably led to an overestimate of the benefits of huddling. For example, Gebczynska and Gebczynski (1971) demonstrated a 13% energetic benefit of huddling for groups of 4 bank voles maintained at 4°C without nest, but this benefit became insignificant when a nest was available. Other authors have observed that with the proper insulation of a vole nest, one individual could warm up the nest chamber as well as several voles (S. McLean unpubl. in J. Wolff in litt.).

Finally, behavioral adaptations of voles with respect to changes of social structure may play an unknown but critical role. Size and construction of the nest, for example, may differ drastically with the number of animals utilizing it, as observed by Gebczynska and Gebczynski (1971). Voles living singly may also compensate for the absence of cohuddlers by reducing time spent out of the nest. Such adaptations may be favored by the frequent between-group movements of individuals (Madison et al. 1984, Cockburn 1988, McShea 1990) that probably expose voles to live singly at times.

Body mass changes during our 2-week experiments were high since voles lost on average 10% of their body mass. These body mass losses may be the result of the natural mass dynamics of voles over winter (Bronson and Kerbeshian in press), food changes after voles were released into the enclosures and radiocollar attachment (Webster and Brooks 1980, Berteaux et al. 1994). It is important to note here that body mass loss of meadow voles in winter is associated with a decrease in the amount of body fat (Bronson and Kerbeshian in press). If the energetic stress incurred by solitary voles had been higher than that incurred by social voles, one would have expected solitary voles to be leaner than social ones. However, we did not find any effect of sociality on body composition, which again leads us to think that the energetic cost of living alone was not higher than that of living in groups in our study conditions.

Basal metabolic rate (BMR) of meadow voles has been measured by Thomas et al. (1988) and Bradley (1976). They found that BMR was 1.79 and 1.93 ml O_2 $(g\ h)^{-1}$, respectively. Taking the mean of these values and assuming an energy equivalence of 20.1 J per ml O_2 (Nagy 1983), field metabolic rate measured in our study (3.40 kJ $(g\ d)^{-1}$) was thus 3.8 times BMR. The total water flux rate of 1 ml $(g\ d)^{-1}$ that we report is similar to the values reported by McManus (1974), Deavers and Hudson (1979) and Grenot et al. (1983), but four times higher than the 0.24 ml $(g\ d)^{-1}$ reported by Holleman et al. (1982) in their winter study of free-living Alaskan voles. High metabolic rates coupled with a herbivorous diet may account for the generally high water turnover rate found in wintering microtines. To our knowledge, the only small mammal study showing a decrease in water loss due to social living is that of Punzo (1975) who found under laboratory conditions a 13.8% water economy in the desert-living cactus mouse, *Peromyscus eremicus eremicus*. We did not find such an economy. An analysis of least significant difference (Sokal and Rohlf 1981) shows that our sample size and observed variability only allowed us to detect a difference >20% between solitary and social voles. Type II error in our experiment should thus not be excluded. However, it is noteworthy that we failed to detect even a trend toward decreased water turnover in social voles. The general life conditions of wintering meadow voles are far from those of a desert rodent, since the observed water flux rates are at least 10-fold those reported for many desert rodent species (e.g. Punzo 1975, Degen et al. 1986). As a consequence, it seems unlikely that water economy is of great concern to wintering meadow voles. The increase of water turnover observed from January to March remains unexplained. It could be due to a progressive shift in food preferences, although Bergeron (unpubl.) found that green, and hence moist, biomass decreased from the beginning to the end of winter.

Living in a nest with a limited air circulation might tend to increase isotope rebreathing so that grouped voles would tend to exchange isotopes as H_2O or CO_2 among themselves. Because at least 3 of 4 nestmates were always injected with doubly labelled water in our experiments, one would expect grouped voles living in a communal nest to be exposed to higher levels of isotope-labelled water vapor and CO_2 than solitary voles, simply due to the greater metabolic activity generated by several voles in close proximity. Rebreathing labelled gas would tend to depress isotope turnover rates artificially and so underestimate water and CO_2 fluxes. This process would tend to enhance the predicted differences between solitary and social voles rather than reduce them. As a result, because no differences were detected, we feel that it is unlikely that isotope rebreathing introduced any bias in our study.

Our experimental design involved 2 plots for the group treatment and 8 plots for the solitary animals treatment. In our statistical analysis we treated the observational units (the individuals) as independent sample units, thus omitting the inherent structure of the experiment. One may point out that subtle habitat differences between plots may have obscured any treatment effect. With only 2 plots for the group treatment it is difficult to amend this problem analytically. Our perception of the field reality, however, makes it very unlikely that our general conclusions are affected by this potential bias.

The present study suggests that winter sociality confers no physical benefit to voles or that any immediate benefit, if too small to be detected through doubly labelled water measures, does not result in any fitness (survivorship) benefit. We cannot, however, exclude that energetic advantages of communal nesting may be of some importance if ground temperature is very low, such as in spring or autumn, when the snow cover is absent or minimal. These conditions, although temporally restricted, may induce transient benefits of high importance with respect to natural selection, since huddling may prevent voles from exceeding the maximal rate of energy metabolism compatible with survival (Sealander 1952, Karasov 1986). We could not test this hypothesis in our study because of the absence of variation in subnivean temperatures during our measurements. We can conclude, however, that group living does not confer a steady continuous physical benefit through winter. The physical benefit hypothesis explaining winter sociality in small mammals thus needs reevaluation. Efforts should also be made to estimate alternative benefits of winter grouping, such as decreased predation risk (Jedrzejewski et al. 1992) or social transmission of information (Lazenby-Cohen 1991).

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