

The fasting endurance hypothesis: the case of two rodent species from central Chile

La hipótesis de resistencia a la privación de alimento:
el caso de dos especies de roedores de Chile central

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ABSTRACT

Recently, Millar and Hickling (1990) have restated a model in which the interplay between food requirements, fasting endurance, and food availability would explain the evolution of both large and small body size in mammals in either unpredictable or unproductive environments. One main assumption of the model is that within species, large individuals have greater fasting endurance capacities than small ones. Evidence supporting such an assumption is only indirect. Field experiments, using two sigmodontine rodents (*Abrothrix longipilis* and *Phyllotis darwini*) from central Chile, whose food resources fluctuate temporally, provide a preliminary test for evaluating the realism of this assumption and the applicability of the model itself. Different sized adult animals were left individually in wired-mesh cages during 12-h periods (20:00-08:00 h), without food, in the microhabitats currently used by them. The fraction of body weight loss during these periods was inversely correlated to body weight in *P. darwini*, suggesting that fasting endurance is greater in larger animals. Large and small sized individuals of the syntopic species, *A. Longipilis*, exhibited similar losses of body weight, suggesting no relationship between fasting endurance and body size. Although part of present results supports Millar and Hickling's model, other suggest that the role of fasting endurance during the evolution of mammalian body size might be limited even in environments having fluctuating food resources for the focal species. Some drawbacks of the model as well as ways to test it further are discussed.

Key words: Chile, energetics, fasting endurance, body size, sigmodontines.

RESUMEN

Recientemente, Millar & Hickling (1990) han replanteado un modelo en el que la interacción entre los requerimientos alimenticios, la resistencia a la privación de alimento y la disponibilidad de alimento explicarían la evolución del tamaño corporal de mamíferos en ambientes impredecibles o improductivos. Un supuesto del modelo es que dentro de una misma especie los individuos grandes tendrían mayor resistencia a la privación de alimento que individuos de menor tamaño. La evidencia que apoya tal afirmación es sólo indirecta. Experimentos de campo realizados con dos especies de roedores sigmodontinos (*Abrothrix longipilis* y *Phyllotis darwini*) de Chile central, cuyos recursos alimenticios fluctúan temporalmente, proporcionan una evaluación preliminar del realismo de este supuesto y de la aplicabilidad del modelo mismo. Animales adultos de diferentes tamaños corporales fueron mantenidos individualmente en jaulas durante períodos de 12 h (20:00-08:00 h), sin alimento, en los microhábitats usualmente utilizados por estos roedores. La pérdida de peso corporal medida durante estas observaciones estuvo correlacionada inversamente con el peso corporal en *P. darwini*, lo cual sugiere que la resistencia a la privación de alimento es mayor en individuos grandes. En el caso de *A. Longipilis* la correlación entre la pérdida de masa corporal y el tamaño corporal no fue estadísticamente significativa, lo cual sugiere una ausencia de relación entre la resistencia a la privación de alimento y el tamaño corporal. Aunque una parte de estos resultados apoya el modelo propuesto por Millar & Hickling (1992), otra sugiere que su aplicabilidad podría ser limitada aun en ambientes con fluctuaciones en la base de recursos alimenticios de la especie en cuestión. Se discuten algunos problemas del modelo así como vías adicionales para someterlo a prueba.

Palabras clave: Chile, energética, resistencia a la privación de alimento, tamaño corporal, sigmodontinos.

INTRODUCTION

Based on previous analyses (Lindsey 1966, Rosenzweig 1968, Brodie 1975, Searcy 1980, Lindstedt & Boyce 1985), Millar & Hickling (1990) have restated a model in which the interplay between fasting

endurance and the temporal distribution of food would explain the evolution of mammalian body size in either unpredictable or unproductive habitats. Since large sized individuals are expected to have greater fasting endurance capacities than small ones, large animals will be favored when periods

of food abundance are interrupted by food-shortage episodes in an unpredictable way (Millar & Hickling 1990). In contrast, small sized individuals will be favored if food is generally in short supply, but never unavailable (Millar & Hickling 1990).

Two main assumptions of the Millar & Hickling's model include that within populations, large individuals have greater energy requirements and greater fasting endurance than small individuals (Millar & Hickling 1992). Although there is abundant interspecific (Hayssen & Lacy 1985, McNab 1983) and some intraspecific (Derting & McClure 1989) evidence supporting the former assumption, there is no direct evidence for the second statement in mammals. In fact, most of the evidence supporting that large individuals do better than small ones when dealing with periods without food is only indirect. Following Millar & Hickling (1990), interspecific comparisons show that large mammals consume more food, but at less frequent intervals than small mammals, suggesting that large animals may resist longer periods without eating than small ones. There are at least two problems with this kind of evidence. First, it comes from interspecific scaling and not from intraspecific comparisons, which are not necessarily comparable (Speakman 1992). Second, large animals may be eating less frequently than small animals for reasons other than fasting endurance. Since large predators tend to consume large prey (Vézina 1985, Fisher & Dickman 1993), and animal abundance tends to decrease with body size (Damuth 1981, Peters 1983, Blackburn et al. 1993), the time between meals for some large sized animals may result simply from a low rate at which they find relatively large prey.

A second line of evidence supporting a positive relationship between fasting endurance and body size comes from the use of allometric relationships between body weight and metabolic rates, and between body weight and metabolic reserves. According to Millar & Hickling (1990), a positive relationship between fasting endurance and body weight would support their model; it may be obtained through subtracting the exponent derived after regressing

metabolic reserves and body weight to that resulting from a regression between food intake and body weight. After applying this protocol to data sets from unstarved animals of five rodent species, Millar & Hickling (1990) derived a positive exponent between fasting endurance and body weight (mean = 0.40), which was considered a satisfactory piece of evidence for their model's assumption. Assumptions using this approach include that metabolic reserves depend only on the animals' fat reserves, and that food intake accurately reflects the animals' metabolic requirements. Although the first assumption appears to be met among mammalian species (Pitts & Bullard 1968), energy reserves may also include gut (and other organs) tissue, blood sugar, and liver and muscle glycogen (Calder 1984), which might vary with body size and play a role during fasting. Regarding the second assumption, resting metabolic rates of starved animals may differ from unstarved animals (Westerterp 1978, Harlow 1981). Although the way in which metabolic rate changes with body size during fasting is unknown, it may potentially affect the energy cost exponent.

Although the Millar & Hickling's (1990) model has been strongly criticized on the grounds that their predictions would be ambiguous (Speakman 1992, 1993; see replies by Millar & Hickling 1992, 1993) or overly simplistic (Dunbrack 1993), I know of no formal test of the model's predictions and assumptions. In particular, observing the animals' capacity to overcome periods of food shortage might provide more direct evidence to the Millar & Hickling's (1990) assumption that fasting endurance is positively correlated with body size. If large animals do better than small ones during periods without food, large individuals should be able to lose proportionately less body weight than small animals during similar periods of food shortage. By monitoring individual variations in the body weight of two sigmodontine rodents of central Chile, I provide some preliminary evaluation of this Millar & Hickling's (1990) assumption.

Sigmodontine rodents of central Chile tend to be nocturnal (Iriarte et al. 1989), and no evidence is available showing that these

rodents may hibernate or become torpid at any time during their life cycle (Bozinovic & Rosenmann 1988a). In this area, syntopic sigmodontines use the same microhabitats (Simonetti 1989), and they are generally omnivorous, consuming shrub and herb seeds and fruits, and arthropods (Glanz 1977, Meserve & Glanz 1978, Meserve 1981a). Since the abundance of these food resources show both spatial (Vásquez 1992) and temporal fluctuations, including both within (Atkins 1977, Fuentes et al. 1984, Simonetti 1989, Vásquez 1992) and between years (Hoffmann et al. 1977, Saiz 1977, Meserve 1981b, Jiménez & Armesto 1992), these rodents are likely to experience variable periods of food shortage (Péfaur et al. 1979). Thus, mice from central Chile are potentially a good model for testing the influence of fasting endurance on the evolution of mammalian body size.

MATERIALS AND METHODS

The nocturnal rodents *Abrothrix longipilis* (Waterhouse 1837), and *Phyllotis darwini* (Waterhouse 1837) were livetrapped (using Sherman traps) in two localities of central Chile: Fundo El Pangué (33°17' S, 71°11' W), and Quebrada de La Plata (33°29' S, 70°54' W). Upon capture, mice were transported to the lab and maintained during one week before being tested back in the field. Animals were caged individually; food (rabbit pellet and fresh vegetables) and water were provided ad libitum, as well as material for nest construction. In the lab, temperature and photoperiod were natural.

At each of the above localities, I selected representative sites of the three kinds of microhabitats currently used by these animals: patches with high shrub cover (over 90%), and patches with small to medium values (20% to 60%). The later was further divided into sites under the shrub canopies and open spaces between bushes (Ebensperger 1992). Experimental microhabitats were never more than 50 m apart in the same locality. During field experiments, different sized animals were individually and simultaneously placed into wired-mesh cages and left at one particular microhabitat during

one night between 20:00 and 08:00 h. This period roughly corresponds to the animals' period of activity (Iriarte et al. 1989). Dimensions of experimental cages (30 x 25 x 25 cm) enabled the animals to move freely. During experiments, no food and thermal refuge was provided to the animals. Mice were maintained fasting during a 6-h period before the beginning of each experiment (only water was provided). By doing so, experimental results were not influenced by previous changes in gut content. I used animals of both sexes (only females with no external signs of pregnancy were included) in roughly equal sex ratios among microhabitats. After each experiment, animals were fed ad libitum and all of them were able to recoup their body weight (no animals died during the experiments). Each animal was used just once.

I calculated individual losses of body weight as the difference between the animal's body weight at the beginning of each experimental night and the weight in the morning. During experiments, nocturnal air temperature was measured using a Data-logger (Li-1.000) and max/min thermometers. I adjusted the Data-logger to record air temperature every 30 min between 20:00 and 08:00 h. To do so, two thermistors (probe 3 cm long) were located 5 cm above the ground and within 1-3 m from the animals' cages. I used data on temperatures along with species-specific regressions between ambient temperature and metabolic rate (Bozinovic & Rosenmann 1988a) to compute an expected energy expenditure and the fraction of the individuals' metabolic scope that this expenditure represented. For each species, metabolic scope (the total energy an individual has available to be allocated to different physiological processes and activities) was computed by subtracting basal metabolic rate (Bozinovic & Rosenmann 1988a) to maximum metabolic rate (Bozinovic & Rosenmann 1989).

A total of four experiments were carried out during late winter and spring time between mid October 1990 and September 1991. Experimental dates and the number of individuals tested (Table 1) were largely determined by abundance of these species at the trapping sites. For each species, I

TABLE 1

Experimental dates, mean body weight (g) and number of individuals (N) of *P. darwini* and *A. longipilis* during field measurements of body weight loss. Figures are mean \pm 1SE. Small letters indicate statistically significant differences after comparing mean body weight among experimental dates (Kruskal-Wallis tests and non-parametric tests for multiple comparisons, $P < 0.05$).

Fechas experimentales, peso corporal promedio (g) y número de individuos (N) de *P. darwini* y *A. longipilis* utilizados durante mediciones de pérdida de peso corporal en terreno. Los datos se muestran como promedio \pm 1EE. Las letras pequeñas indican diferencias estadísticamente significativas después de comparar los valores de peso corporal promedio entre fechas experimentales dentro de cada especie (pruebas de Kruskal-Wallis y pruebas no paramétricas para comparaciones múltiples, $P < 0,05$).

Experimental Date	<i>Abrothrix longipilis</i>	<i>Phyllotis darwini</i>
19 October 1990 (mid spring)	58.5 \pm 3.7 ^a N = 12	60.5 \pm 3.1 ^a N = 12
10 August 1991 (late winter)	64.8 \pm 2.4 ^a N = 20	50.7 \pm 2.4 ^a N = 5
23 August 1991 (early spring)	66.0 \pm 3.7 ^a N = 11	46.0 \pm 3.0 ^b N = 2
7 September 1991 (mid spring)	67.5 \pm 3.7 ^a N = 11	60.0 \pm 6.0 ^a N = 2

attempted to keep animals' mean body weight between experimental dates the same. Only individuals of *A. longipilis* used on late August were smaller than those used in other tests (Kruskal-Wallis test and Non-Parametric Multiple Comparisons test, $P < 0.05$; Table 1).

RESULTS

Since the fraction of body weight loss did not differ among individuals in different microhabitats (Two-Factor ANOVA: $F_{2,76} = 0.38$, $P = 0.68$; Ebensperger 1992), data were pooled for each species. Overall, individuals of *A. longipilis* (body weight range = 43.0-78.0 g) lost a smaller fraction of their body weight compared *P. darwini* (body weight range = 43.0-89.0 g; Mann-Whitney test, $P < 0.009$). In the case of *A. longipilis*, a correlation analysis revealed that the percentage of body weight loss during one night fasting was similar between small and large in-

dividuals (Pearson $r = 0.28$, $P = 0.22$; Fig. 1). Statistical power for this correlation (Zar 1984) was 74%. For *P. darwini* however, the same analysis showed that small animals lost a greater fraction of their body weight compared to large individuals (Pearson $r = -0.47$, $P < 0.001$; Fig. 2).

Mean temperature did not differ between late winter and spring (Student t-test, $t_{52} = 1.69$, $P = 0.10$), as well as minimum temperature ($t_{52} = 0.35$, $P = 0.73$; Table 2). Only maximum temperature was higher in spring compared to late winter ($t_{52} = 2.86$, $P = 0.006$; Table 2). Since lower critical temperatures of *A. longipilis* (27.3°C) and *P. darwini* (27.5°C; Bozinovic & Rosenmann 1988a) are higher than those recorded during experiments, animals were well below their thermoneutral zone when measurements of body weight loss were taken. Computed minimum energy requirements and the fraction of the metabolic scope that these expenditures represented (Table 3) suggest that individuals of both species were exposed to relatively high energy-demanding conditions during measurements. On late winter experiments, individuals of *A. longipilis* spent about 52% of their scope to keep a stable body temperature; figure for *P. darwini* was even higher (69%). These costs were slightly lower in spring: 50%

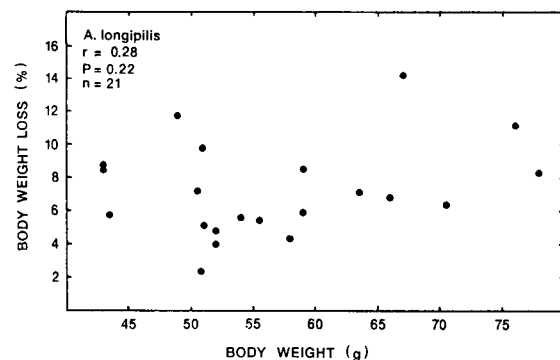


Fig. 1: Correlation between body weight (g) and the percentage of body weight loss in *Abrothrix longipilis*. Each data point represents one individual. Measurements were taken to animals kept individually in the field inside wire-mesh cages without food or nest during 1-night periods.

Correlación entre el peso corporal (g) y el porcentaje de pérdida de peso corporal en *Abrothrix longipilis*. Cada punto representa un individuo. Las mediciones fueron obtenidas de animales mantenidos individualmente en jaulas sin alimento o nido durante períodos de una noche.

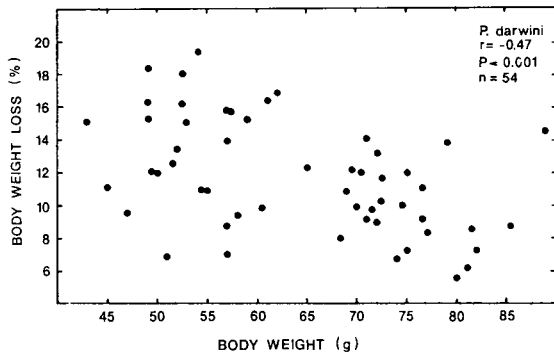


Fig. 2: Correlation between body weight (g) and the percentage of body weight loss in *Phyllotis darwini*. Each data point represents one individual. Measurements were taken to animals kept individually in the field inside wire-mesh cages without food or nest during 1-night periods.

Correlación entre el peso corporal (g) y el porcentaje de pérdida de peso corporal en *Phyllotis darwini*. Cada punto representa un individuo. Las mediciones fueron obtenidas de animales mantenidos individualmente en jaulas sin alimento o nido durante períodos de una noche.

TABLE 2

Air temperature (°C) taken 5 cm above ground during night in late winter and spring 1991 in microhabitats of central Chile. Observations were made between 20:00 to 08:00 h. In the case of mean temperature, each data point represents an average obtained during the above time period. All figures are mean \pm 1SE (N = number of measurements). Statistically significant differences between seasons (using unpaired Student t-tests, $P < 0.001$) are indicated with double asterisks.

Temperatura del aire (°C) tomada a 5 cm sobre el suelo durante la noche en invierno y primavera de 1991 en microhábitats de Chile central. Las observaciones se realizaron entre las 20:00 y las 08:00 h. En cuanto a la temperatura media, cada dato representa un promedio obtenido durante el período anterior. Todos los datos se muestran como promedio \pm 1EE (N = número de mediciones). Las diferencias estadísticamente significativas entre estaciones (evaluadas mediante pruebas t de Student para muestras independientes, $P < 0,001$) se indican con asteriscos dobles.

Season	Mean Temperature	Minimum Temperature	Maximum Air Temperature
Late winter	8.1 \pm 0.5 N = 15	6.6 \pm 0.5 N = 15	10.4 \pm 0.5** N = 15
Spring	9.2 \pm 0.4 N = 39	6.4 \pm 0.3 N = 39	12.9 \pm 0.5** N = 39

and 66% for *A. longipilis* and *P. darwini*, respectively. If differences in maximum temperature between late winter and spring

are considered, energy expenditure of spring animals was only 4.6% (for *A. longipilis*) and 6.1% (for *P. darwini*) lower than late summer animals.

DISCUSSION

Although severely criticized (Dunbrack 1993, Speakman 1992, 1993), the Millar & Hickling's (1990) model provided a mechanism by which energetics would play a role during the evolution of mammalian body size. Their model assumes that within populations, large individuals have greater food requirements and greater fasting endurance than small individuals. Among species, it is well established that large mammals have higher energy requirements than small species (Hayssen & Lacy 1985, McNab 1983). Within species, the available evidence is much more scarce but it tends to point toward the same (Derting & McClure 1989). In relation to the second assumption, only a study by Threlkeld (1976) on planktonic crustaceans has reported an interspecific correlation between body size and survival time during fasting. However, there is no direct evidence showing that within a population large individuals do better during periods without food compared to small sized animals. After using two sigmodontine species from central Chile for testing this assumption, my study showed conflicting results. During one-night periods without food, large individuals of *P. darwini* lost a lesser fraction of their body weight compared to small animals, suggesting that large animals do better than small ones when dealing with periods of fasting. Nonetheless, loss of body weight among individuals of *A. longipilis* did not vary with body weight, providing no support to the model's assumption.

Under the assumption that the fasting endurance model applies for sigmodontines in central Chile, the absence of a negative correlation between body size and loss of body weight in *A. longipilis*, compared to *P. darwini*, might be related to differences in the degree of predictability of their food resources. Although both species include seeds and arthropods in their diets, *A.*

TABLE 3

Expected energy expenditure ($J h^{-1}$) and the fraction (percentage) of the metabolic scope this expenditure represented for *A. longipilis* and *P. darwini* during field measurements of body weight loss. Energy expenditure was computed combining air temperature values (Table 2) along with species-specific regressions between ambient temperature and metabolic rate (Bozinovic & Rosenmann 1988a). For each species, metabolic scope was computed as the difference between species-specific maximum metabolic rate (Bozinovic & Rosenmann 1989) and basal metabolic rate (Bozinovic & Rosenmann 1988a). Energy expenditure per whole animal was computed considering mean body weights of 57.9 g ($N = 54$) and 64.2 g ($N = 21$) for *P. darwini* and *A. longipilis*, respectively. To convert milliliters of O_2 into Joules, a conversion factor of $1 \text{ ml } O_2 = 20.083 \text{ J}$ (Schmidt-Nielsen 1990) was used.

Gasto de energía esperado ($J h^{-1}$) y fracción (en porcentaje) de la expansividad metabólica que este gasto representó para *A. longipilis* y *P. darwini* durante la realización de mediciones de pérdida de peso corporal en terreno. Los valores de gasto de energía se obtuvieron a partir del uso combinado de los valores de temperatura del aire (Tabla 2) y regresiones especie-específicas entre la temperatura ambiente y la tasa metabólica (Bozinovic & Rosenmann 1988a). Para cada especie, la expansividad metabólica se calculó como la diferencia entre la tasa metabólica máxima (Bozinovic & Rosenmann 1989) y la tasa metabólica basal (Bozinovic & Rosenmann 1988a) especie-específicas. El gasto de energía por animal se obtuvo considerando valores de peso promedio de 57.9 g ($N = 54$) y 64.2 g ($N = 21$) para *P. darwini* y *A. longipilis*, respectivamente. Para convertir mililitros de O_2 a Joules, se usó la equivalencia de $1 \text{ ml } O_2 = 20,083 \text{ J}$ (Schmidt-Nielsen 1990).

Season and temperature	<i>Abrothrix longipilis</i>	<i>Phyllotis darwini</i>
Late winter		
Mean temperature	4,449.5 (52.1%)	5,033.7 (68.6%)
Minimum temperature	4,684.9 (54.9%)	5,302.5 (72.3%)
Maximum temperature	4,088.4 (47.9%)	4,621.5 (63.0%)
Spring		
Mean temperature	4,276.8 (50.1%)	4,836.5 (65.9%)
Minimum temperature	4,716.3 (55.3%)	5,338.3 (72.8%)
Maximum temperature	3,696.0 (43.3%)	4,173.4 (56.9%)

longipilis relies mostly on insects for most of its life cycle whereas *P. darwini* does on shrub and herb seeds (Meserve & Glanz 1978, Meserve 1981a). According to Millar & Hickling's (1990) model, the influence of fasting endurance on the evolution of body size is predicted to be unimportant whenever

food resources are permanently abundant. Thus, arthropods, the most preferred food item by *A. longipilis* in central Chile, are expected to be a more continuously abundant food item than seeds. Measurements of plant phenology (trees with fruits; Hoffmann et al. 1977) and soil insect biomass (Atkins 1977, Saiz 1977) made at Fundo Santa Laura (central Chile) show that arthropods tend to vary as much as seeds do. A similar pattern is shown by studies made at different localities and years (Meserve 1981b, Simonetti 1989, Jiménez & Armesto 1992, Vásquez 1992). Therefore, the available evidence suggests that even in fluctuating environments fasting endurance might not play a role in the evolution of body size within some mammalian species (i.e. *A. longipilis*).

Even though fasting endurance may differ among different sized individuals, other factors may override its influence upon mammalian body size (Speakman 1992, Dunbrack 1993). Physiological mechanisms such as hibernation or torpor as well as behavioral adaptations including the construction of well isolated nests and group nesting (Bozinovic & Merritt 1991, West & Dublin 1984), may allow small individuals to decrease their energy expenditure and deal with periods of low food availability and low temperature. Among sigmodontine rodents, the influence of food deprivation in inducing torpor have been demonstrated in *Calomys musculinus* (Bozinovic & Rosenmann 1988b), *Calomys venustus* (Caviedes-Vidal et al. 1990), and *P. darwini rupestris* (Bozinovic & Marquet 1991). Since most of these species inhabit relatively xeric conditions (Redford & Eisenberg 1992), they do probably experience temporal fluctuations in their food supply. So, the possibility that these rodents may become torpid in response to periods of food shortage (i.e. overriding any selective effect that fasting endurance might have on body size), should be explored. Regarding *P. darwini* of central Chile, torpor has not been noted (Bozinovic & Rosenmann 1988a). However, individuals of this species may decrease their energy expenditure by 70% through a combined effect of group nesting (huddling) and nest construction (Bozinovic et al. 1988). Whether *P. darwini* normally uses these

strategies in the wild when food is in short supply is unknown. If so, these behavioral adaptations may undermine any potential influence that fasting endurance may have over body weight in this species.

Different alternatives may account for a lack of correlation between body weight and body weight loss in *A. longipilis*. First, it resulted from having a small data set for *A. longipilis* compared to *P. darwini*. However, statistical power allowed by data set on *A. longipilis* was relatively high (74%), and correlation in this rodent tended to be positive instead of negative. Second, a lack of correlation may have resulted from using thermally unstressed animals. *Abrothrix longipilis* lost significantly less body weight than *P. darwini* during experiments, which is in agreement with a lower energy expenditure expected for the first species. Nonetheless, energy expenditure of *A. longipilis* still compromised over 50% of its metabolic scope, suggesting that thermal environment for *A. longipilis* during experiments was indeed energetically demanding. Third, during late winter and spring experiments, animals were exposed to different conditions of ambient temperature (i.e. to different energy requirements) leading to an increase in the variance of body weight loss measurements. Differences in mean and minimum temperature between late winter and spring were not statistically significant. Even if maximum temperatures are considered, energy expenditure of *A. longipilis* would have been only 5% larger in late winter compared to spring. Finally, smaller individuals may have relied on brief episodes of undetected torpor to decrease their energy expenditure. No torpor has been recorded in *A. longipilis* (Bozinovic & Rosenmann 1988a) and I never observed torpid animals when they were checked every morning. However, since animals' behavior and body temperature were not monitored through experiments, I can not discard the occurrence of such a phenotypic plasticity in this species.

Millar & Hickling (1990) suggest that an allometric coefficient for fasting endurance greater than zero is a good piece of evidence in support of their model's assumption that fasting endurance should increase with body

size. Using data sets from unstarved animals of five rodent species, they recorded intra-specific values about 0.4 which is similar to the 0.44 value obtained by Lindstedt & Boyce (1985) from interspecific comparisons. However, an exponent greater than zero but smaller than one means that even though large individuals have a greater absolute fasting endurance capacity than small individuals, as an animal increases in size its fasting endurance capacity increases at a decreasing rate. So benefits from increasing body size, due to a greater fasting endurance to cope with periods of food shortage, will eventually decrease as an individual becomes bigger. This in turn might result into selective pressures, initially leading to a bigger body size, becoming progressively weaker. Thus, in addition to potential limitations imposed by the particular life history of the species involved, the applicability of this model might be restricted to some body size ranges. In particular, the model would be more likely to apply to relatively small mammals, in which increasing body size would result into a relatively high increase in fasting endurance.

Finally, my results give partial support to Millar & Hickling's (1990) assumption that fasting endurance in mammals increases with body size. However, they also suggest that even in environments in which food resources are expected to be relatively unpredictable, the model may not apply. Strategies involving torpor or group nesting, as well as the relative body size of the focal species, may limit the influence of fasting endurance on the evolution of mammalian body size. Using two or more mammal species (e.g. differing in body size and/or in their capacities for using torpor or group nesting) to record variations in their body weight during experimental manipulations of the temporal abundance of their food, would help to test the Millar & Hickling's (1990) model further.

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