

A test of two hypotheses explaining the seasonality of reproduction in temperate mammals

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Summary

1. Two proposed hypotheses about energy allocation were tested to explain the patterns of seasonal reproduction found in temperate mammals. The two hypotheses predict either that total demand for energy is greater during reproduction than during winter (when thermoregulatory costs are high) (Increased Demand Hypothesis) or that total costs during winter are greater than or equal to total costs during reproduction (Reallocation Hypothesis).

2. Data were compiled from the literature on summer (non-reproducing) and winter metabolic rates of temperate mammals, and were used on litter sizes and a published equation to predict metabolic rates during lactation.

3. All three measures of metabolic rate scaled to body mass with slopes significantly less than one. Metabolic rates during winter averaged ≈ 2 times greater than those of non-reproducing mammals during summer. On average, predicted metabolic rates during lactation were not significantly greater than during winter, but for some individual species they clearly were.

4. It is suggested that neither the Reallocation nor the Increased Demand Hypothesis can fully explain seasonal reproductive patterns in temperate mammals.

Key-words: Comparative method, mammals, reallocation of energy, seasonal reproduction

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Introduction

Few things characterize temperate regions more than the rapid initiation of breeding by birds and mammals to coincide with the spring flush of vegetation. Two contrasting ecological and energetic strategies might explain this extreme seasonality of reproduction in temperate endothermic homeotherms. The most commonly proposed explanation is that they have evolved to time the provisioning of growing young, which entails high energetic costs, to coincide with the spring and early summer peak in primary production (Lack 1950). This explanation implicitly assumes that reproduction results in the greatest total energy expenditures that animals can sustain (Fig. 1a).

Alternatively, cold winter temperatures might impose on winter-active homeotherms such high thermoregulatory energy costs that total energetic costs during winter are greater than or equal to total costs during reproduction in spring/summer (Fig. 1b). Thus,

reproduction during winter would be energetically impossible, because total energy costs would exceed the highest possible rate of sustained energy expenditure.

These alternative possibilities were formally presented by Masman *et al.* (1986) as the Increased Demand Hypothesis and the Reallocation Hypothesis, respectively. Weathers & Sullivan (1993) compared seasonal energy allocation patterns from field metabolic rate data in species of birds for which such information was available, and they found that different species vary in which pattern they exhibit. To date, no critical test of these alternatives has been performed with mammals.

Because, with only a single exception (Francis *et al.* 1994), female mammals assume the majority of the energetic cost of reproduction through the production of milk, they permit a relatively simple test of the Increased Demand and Reallocation hypotheses. Although other costs may be involved in reproduction, such as gestation or parturition, we limited our analyses of reproductive costs to lactation because it has been suggested to be the major cost involved in mammalian reproduction (Oftedal 1984b). In addition,

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information on costs of gestation, parturition, etc., are less available.

For the Reallocation Hypothesis to be applicable to mammals, the difference between the energetic cost of thermoregulation in winter and in summer would have approximately to equal the energetic investment that females make in the production of milk (as shown in Fig. 1b). If this is the case, then the reduction in thermoregulatory costs associated with spring and summer temperatures could permit a reallocation of energy to reproduction without necessitating an increase in energy intake. If, however, the energetic costs of thermoregulation in winter are less than the sum of reproductive (lactation) costs plus summer thermoregulation (as shown in Fig. 1a), then a pure reallocation strategy would be impossible, thus providing support for the Increased Demand Hypothesis.

The specific predictions of the Reallocation Hypothesis are that energy expenditures in winter are greater than during summer, and greater than or equal to total energy costs during reproduction (Fig. 1b). The Increased Demand Hypothesis predicts that expenditures during winter are greater than during summer, but that total metabolic costs during reproduction surpass winter costs (Fig. 1a). In this paper, we draw on the extensive literature on metabolic rates of mammals during summer and winter, and the somewhat less extensive literature on the energetic cost of lactation to test the Increased Demand and Reallocation Hypotheses for non-hibernating mammals.

Materials and methods

Although the total energy cost of free-living individuals (field metabolic rate, FMR), as measured with the doubly labelled water method (in winter and summer), would be the most appropriate measure to use in this analysis, not enough FMR studies of temperate species in different seasons are available to permit such an analysis (Nagy 1994). Therefore, we based our analyses on published laboratory measurements of non-hibernating eutherian temperate and arctic mammals as measured by oxygen consumption in metabolic chambers.

Metabolic rates, expressed as $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, were transformed into units of kJ day^{-1} by assuming energy equivalents of $4.8 \text{ kcal l}^{-1} \text{ O}_2^{-1}$ and $4.184 \text{ kJ kcal}^{-1}$. The studies were separated into summer (31 species) and winter (12 species) metabolic rates according to the time of year that measurements were made, thus allowing for seasonal acclimatization (Table 1). For 10 of these species, data were available in both summer and winter, thus allowing a direct comparison across seasons (Table 2). The difference between 'summer' and 'winter' metabolic rates represents the maximum amount of energy that could possibly be reallocated to reproduction (Table 2). Metabolic rates were used for a 'summer' temperature of 20°C and a 'winter' temperature of -10°C . Any study where

20°C was above the upper critical limit of the species' thermal neutral zone was excluded, since this would result in an overestimate of summer thermoregulatory costs.

The energetic cost of reproduction includes both the energy transferred to the young via milk as well as the increased foraging, digestive and anabolic costs required for milk production. Because estimates of these direct costs of reproduction were not available for most of the species, the cost of lactation was estimated using the allometric equation derived by Oftedal (1984b). This regression predicts the energy output of the mother based on litter size and mean mass of littermates at weaning (litter metabolic mass; LMM). Weaning represents the most energy-demanding stage of lactation for the mother and therefore represents peak cost (Oftedal 1984a). Litter sizes and masses at weaning for 28 species (Table 3) were taken

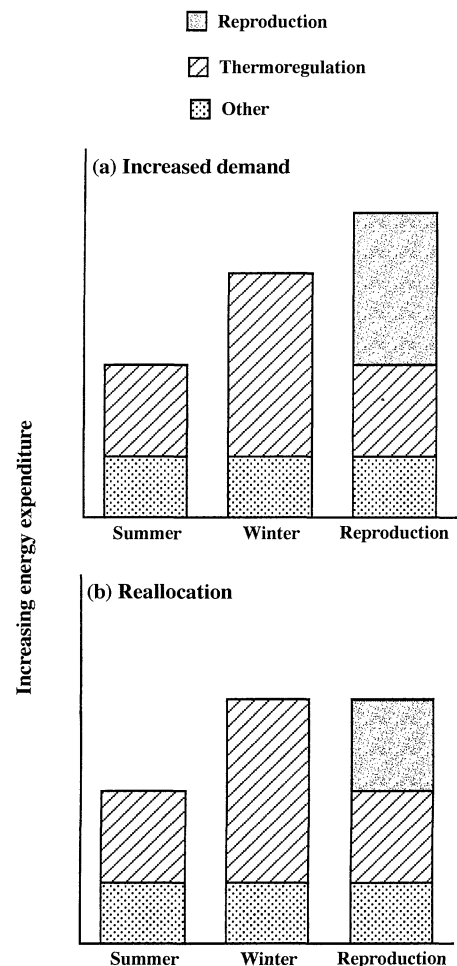


Fig. 1. Schematic representation of both hypotheses for a hypothetical mammal. (a) For the Increased Demand Hypothesis to be supported, the total energetic costs during reproduction must exceed total costs during winter. (b) For the Reallocation Hypothesis to be supported, the difference between summer and winter metabolic costs must approximately equal the energetic investment that females make in milk production during the peak demand just prior to weaning.

Table 1. Summary of body mass and metabolism data for non-hibernating, non-reproductive temperate mammals

Species	Mass (g)	Season ^a	Total energy expenditure (kJ day ⁻¹)	Reference
<i>Sorex minutus</i>	2.91	S	20.9	Gebczynski (1971)
<i>Sorex cinereus</i>	3	S	15.9	Morrison, Ryser & Dawe (1959)
<i>Sorex araneus</i>	8.08	S	45.4	Gebczynski (1965)
	7.21	W	63.5	Gebczynski (1965)
<i>Micromys minutus</i>	8.71	S	31.7	Gorecki (1971)
<i>Neomys anomalus</i>	13.21	S	37.9	Gebczynska & Gebczynski (1965)
<i>Neomys fodiens</i>	14.05	S	39.6	Gebczynska & Gebczynski (1965)
<i>Peromyscus maniculatus</i>	17	S	31.5	Brower & Cade (1966)
<i>Blarina brevicauda</i>	20.3	S	49.8	Neal & Lustick (1973)
<i>Napaeozapus insignis</i>	21.6	S	47.8	Brower & Cade (1966)
<i>Clethrionomys glareolus</i>	23.7	S	57	Gorecki (1968)
	19.8	W	109.1	Gorecki (1968)
<i>Clethrionomys gapperi</i>	24	S	50.2	McManus (1974)
<i>Microtus longicaudus</i>	26.1	S	45.8	Beck & Anthony (1971)
<i>Myopus schisticolor</i>	26.4	W	96	Saarela & Hissa (1993)
<i>Clethrionomys rutilus</i>	28	S	40.6	Rosenmann, Morrison & Feist (1975)
	15	W	79.5	Rosenmann <i>et al.</i> (1975)
<i>Microtus montanus</i>	30.8	S	54.8	Packard (1968)
<i>Microtus oeconomus</i>	32	S	55.4	Casey, Withers & Casey (1979)
<i>Mustela nivalis</i>	43	S	72.5	Casey <i>et al.</i> (1979)
<i>Dicrostonyx groenlandicus</i>	47	S	56.03	Casey <i>et al.</i> (1979)
<i>Eutamias minimus</i>	49.3	S	57.2	Jones & Wang (1976)
<i>Microtus ochrogaster</i>	50	S	48.2	Wunder, Dobkin & Gettinger (1977)
	36.3	W	105	Wunder <i>et al.</i> (1977)
<i>Glaucomys volans</i>	61.5	S	50.4	Stapp (1992)
	67	W	157.9	Stapp (1992)
<i>Lemmus sibiricus</i>	64	S	92.6	Casey <i>et al.</i> (1979)
<i>Ochotona princeps</i>	109.3	S	79	MacArthur & Wang (1973)
<i>Tamiasciurus hudsonicus</i>	224	S	127.3	Pauls (1981)
	231	W	261.7	Pauls (1981)
<i>Sciurus carolinensis</i>	630	S	340	Ducharme, Larochelle & Richard (1989)
<i>Ondatra zibethicus</i>	869	S	369.5	Fish (1979)
<i>Martes americana</i>	900	S	429.4	Worthen & Kilgore (1981)
	900	W	793.3	Buskirk, Harlow & Forrester (1988)
<i>Lepus americanus</i>	1581	S	662.9	Hart, Pohl & Tener (1965)
	1479	W	749.1	Hart <i>et al.</i> (1965)
<i>Lepus arcticus</i>	3004	W	725	Wang <i>et al.</i> (1973)
<i>Alopex lagopus</i>	3600	S	658.7	Casey <i>et al.</i> (1979)
<i>Vulpes vulpes</i>	4433	S	1176.9	Irving, Krog & Monson (1955)
	5010	W	1207.4	Irving <i>et al.</i> (1955)
<i>Erethizon dorsatum</i>	5530	S	1146.8	Irving <i>et al.</i> (1955)
	6210	W	1754.1	F. Fournier, unpublished observations
<i>Castor canadensis</i>	16000	S	2699.2	MacArthur (1989)

^aSeason: S = summer (20 °C), W = winter (-10 °C).

Table 2. Comparison of energy expenditures in summer, in winter, and during lactation, in non-hibernating temperate mammals

Species	Body mass ^a (g)	Total energy expenditure (kJ day ⁻¹)		
		Summer	Winter	Lactation
<i>Sorex araneus</i>	7.6	45.4	63.5	75.1
<i>Clethrionomys rutilus</i>	21.5	40.6	79.5	110.4
<i>Clethrionomys glareolus</i>	21.8	57.0	109.1	89.8
<i>Microtus ochrogaster</i>	43.2	48.2	105	101.2
<i>Glaucomys volans</i>	64.3	50.4	157.9	138.6
<i>Tamiasciurus hudsonicus</i>	227.5	127.3	261.7	430.5
<i>Martes americana</i>	900	429.4	793.3	505.9
<i>Lepus americanus</i>	1530	662.9	749.1	727.7
<i>Vulpes vulpes</i>	4722	1176.9	1207.4	-
<i>Erethizon dorsatum</i>	5870	1146.8	1754.1	1998.1

^aBody mass is an average of summer and winter masses.

from Farrell & Christian (1987); Nowak & Paradiso (1983); Millar (1977); Banfield (1974).

STATISTICAL ANALYSES

To test the two hypotheses of seasonal energy allocation patterns, the energy expenditure among seasons was compared in 10 or 9 species for data were available. Because metabolism is highly correlated with body mass, the data were first corrected using the 0.75 exponent of body mass, and then log-transformed. Significant differences in seasonal expenditure were tested for with pairwise comparisons using paired *t*-tests (Zar 1984).

To compute allometric equations, Felsenstein's (1985) method of phylogenetically independent con-

trasts was used to regress log metabolic rate on log body mass. This is the most widely used and best understood of available phylogenetically based statistical methods (e.g. Ricklefs, Konarzewski & Daan 1996; Sparti 1992; review in Garland, Midford & Ives, 1999). The two polytomies shown in Fig. 2 were treated as hard as described in Purvis & Garland (1993). All equations with independent contrasts were computed by forcing them through the origin, as required by the method. To compute confidence intervals about the y -intercept, we used the new procedures described in (T. Garland & A. R. Ives, personal communication) and implemented in version 5.0 of the PDTREE program (available from T. G.).

The composite phylogeny shown in Fig. 2 was assembled from a variety of sources (Brownell 1983; Catzeflis, Aguilar & Jaeger 1992; Catzeflis, Dickerman, Michaux & Kirsch 1993; Degen, Kam, Khokhlova, Krasnov & Barraclough 1998; George 1988; Ricklefs *et al.* 1996; Sparti 1992). Relationships within the Sciuridae are based on an unpublished DNA sequencing study (V. L. Roth, personal communication). The 33-species tree shown in Fig. 2 was pruned as required to match the sample sizes for the three different metabolic traits (summer $N = 31$, win-

ter $N = 12$, lactation $N = 28$), and branch lengths (next paragraph) were then reset.

Reliable information on branch lengths (e.g. divergence times) was not available for all parts of the phylogeny, so Pagel's (1992) arbitrary branch lengths was used (e.g. as shown in Fig. 2 for all 33 species) for all analyses (branch lengths were reset for each of the three analyses). The adequacy of these branch lengths was checked by testing for correlations between the absolute values of the standardized contrasts and their standard deviations (Díaz-Uriarte & Garland 1996, in press): in no case were correlations statistically significant.

Results

The difference between winter and summer metabolic rates is greater for small mammals than for large ones because of their small mass and large surface area (Fig. 3). This is reflected by the slope of the winter allometric relationship being significantly shallower than that for the summer relationship. The allometric relationship between body mass and metabolic rate during lactation had the highest elevation, followed by winter and summer, respectively (Table 4, Fig. 3).

Table 3. Summary of data used in estimating total energy expenditure during lactation in non-hibernating temperate mammals

Species	Maternal mass (g)	MMM ^a (kg ^{0.75})	Litter size	Mass of young at weaning (kg)	LMM ^b	Metabolic mass ratio ^c	Gross energy output ^d (kJ kg ^{-0.75} day ⁻¹)	Total energy expenditure (kJ day ⁻¹)
<i>Sorex cinereus</i>	3	0.0128	4.4	0.0023	0.029	2.23	2187.03	27.99
<i>Sorex minutus</i>	4.9	0.0185	9	0.0032	0.077	4.14	4063.89	75.18
<i>Sorex araneus</i>	8.08	0.0269	6.9	0.0047	0.081	3.03	2969.45	79.88
<i>Micromys minutus</i>	8.71	0.0285	5	0.0050	0.062	2.16	2111.51	60.18
<i>Neomys anomalus</i>	13.21	0.0390	5	0.0068	0.080	2.04	1993.58	77.75
<i>Neomys fodiens</i>	14.05	0.0408	5	0.0071	0.083	2.02	1977.38	80.68
<i>Peromyscus maniculatus</i>	17	0.0470	4.2	0.0087	0.082	1.74	1701.39	79.97
<i>Blarina brevicauda</i>	20.3	0.0538	4.5	0.0093	0.093	1.72	1682.13	90.50
<i>Napaeozapus insignis</i>	21.6	0.0563	4.4	0.0097	0.094	1.66	1624.47	91.46
<i>Clethrionomys glareolus</i>	23.7	0.0604	5	0.009	0.100	1.66	1615.56	97.58
<i>Clethrionomys gapperi</i>	24	0.0610	5.6	0.0105	0.127	2.09	2040.16	124.45
<i>Microtus longicaudus</i>	26.1	0.0649	5.4	0.0111	0.129	1.99	1944.34	126.19
<i>Clethrionomys rutilus</i>	28	0.0684	5.9	0.0117	0.147	2.15	2101.55	143.75
<i>Microtus montanus</i>	30.8	0.0735	5.8	0.0126	0.154	2.09	2045.61	150.35
<i>Microtus oeconomus</i>	32	0.0757	7.5	0.0129	0.203	2.68	2622.15	198.50
<i>Mustela nivalis</i>	43	0.0944	5	0.0160	0.162	1.71	1670.04	157.65
<i>Dicrostonyx groenlandicus</i>	47	0.101	4.5	0.0171	0.153	1.52	1480.95	149.58
<i>Eutamias minimus</i>	49.3	0.105	5.5	0.0177	0.193	1.84	1796.2	188.60
<i>Microtus ochrogaster</i>	50	0.106	3.4	0.0179	0.121	1.14	1105.11	117.14
<i>Glaucomys volans</i>	61.5	0.123	3.4	0.0208	0.137	1.11	1078.00	132.59
<i>Lemmus sibiricus</i>	64	0.127	7.3	0.0214	0.300	2.36	2313.48	293.81
<i>Ochotona princeps</i>	109.3	0.190	2	0.0560	0.183	0.96	931.80	177.04
<i>Tamiasciurus hudsonicus</i>	224	0.326	4.5	0.0600	0.436	1.34	1300.15	423.85
<i>Sciurus carolinensis</i>	630	0.707	2.7	0.1139	0.446	0.63	602.96	426.29
<i>Ondatra zibethicus</i>	869	0.900	6.4	0.1055	0.992	1.1	1069.11	962.20
<i>Martes americana</i>	900	0.924	2.6	0.1477	0.530	0.57	547.56	505.95
<i>Lepus americanus</i>	1581	1.410	3	0.2000	0.789	0.56	533.29	751.94
<i>Erethizon dorsatum</i>	6000	3.83	1	2.5	2.14	0.56	532.7	2040.24

^aMMM: maternal metabolic mass = maternal mass (kg^{0.75}).

^bLMM: litter metabolic mass = litter size × mass at weaning (kg^{0.83}).

^cMetabolic mass ratio = LMM/MMM.

^dGross energy output estimated by the following equation (Oftedal 1984b): ($y = 236(\text{metabolic mass ratio}) - 4.6$) × 4.184.

On the arithmetic scale, winter energy expenditures averaged ≈ 2 -fold higher than summer costs, ranging from 1.2-fold for medium-sized mammals (10 kg) to 3.1-fold for mammals weighing 10 g.

As predicted by both hypotheses, winter metabolic rates were significantly greater than summer ones (paired $t = -13.8$, $df = 17$, $P < 0.0001$; Table 2). However, considering all nine species for which data were available, winter and lactation metabolic rates do not differ significantly (paired $t = 0.035$, $df = 17$, $P > 0.9$; Table 2).

Discussion

The Increased Demand Hypothesis predicts that the cost of reproduction should be greater than the energetic cost in winter while the Reallocation Hypothesis predicts that total energy expenditures between winter and reproduction should be equal (Fig. 1). Our analysis revealed that there was no statistical difference between the total amount of energy expended among winter and reproduction. The latter result is inconsistent with the Increased Demand Hypothesis (see

Table 4. Allometric regression equations computed with phylogenetically independent contrasts between total energy expenditure (kJ day^{-1}) and body mass (g)

Energy expenditure	<i>N</i>	Slope \pm 95% CI	<i>y</i> -intercept \pm 95% CI	r^2
Lactation	28	0.469 \pm 0.086	1.39 \pm 0.31	0.830
Winter	12	0.429 \pm 0.099	1.47 \pm 0.30	0.904
Summer	31	0.632 \pm 0.068	0.778 \pm 0.28	0.926

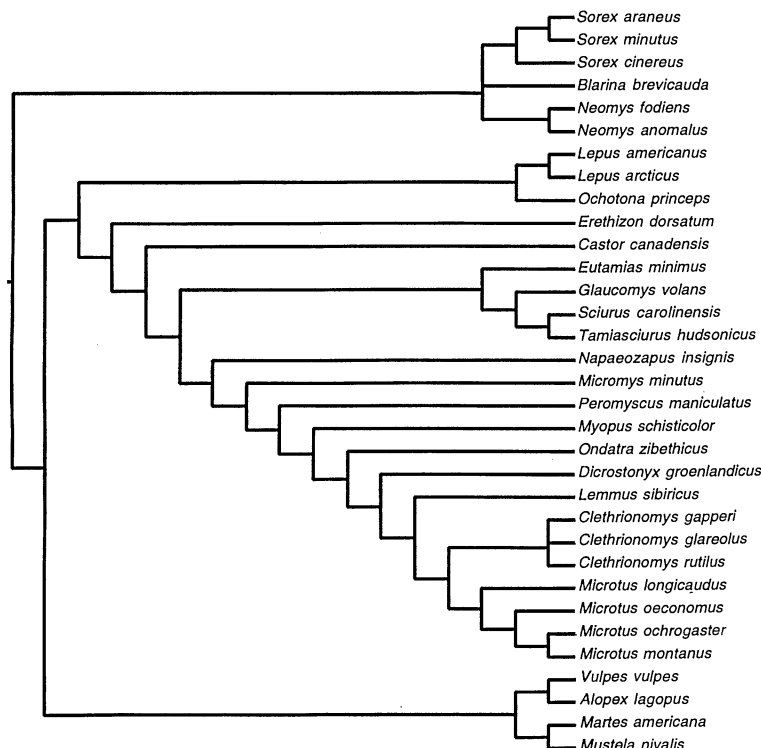


Fig. 2. Phylogeny of the 33 species included in this study.

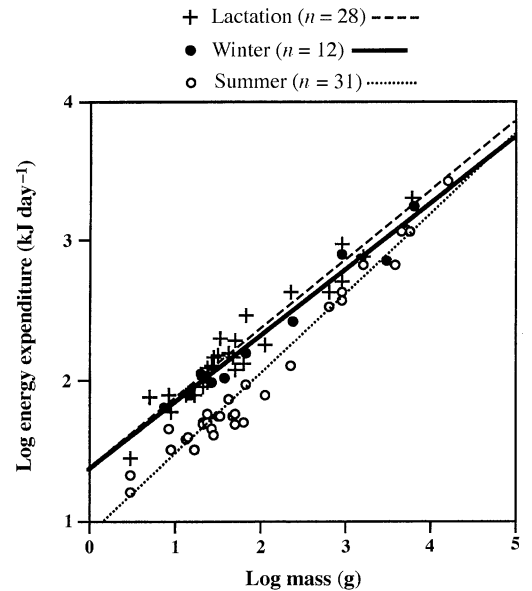


Fig. 3. Allometric relationships computed by phylogenetically independent contrasts (see Table 3) between body mass and energy expenditures in non-hibernating temperate-zone mammals.

Fig. 1a). However, adding further reproductive costs to the analyses, such as the cost of gestation or parental care (for which data are, unfortunately, not easily available), could potentially move things towards the direction that favours this hypothesis. Although our results suggest that mammals follow the Reallocation Hypothesis, a closer look at the data shows that some species exhibit substantial differences between winter and lactation metabolic rates (Table 2), and that which condition is higher varies among species.

Whether winter or lactation is more costly shows no obvious relationship to either body size or phylogenetic position. Thus, as suggested by Berteaux (1998), different species may fit along a continuum between Reallocation and Increased Demand, and some species may even use a mixed strategy that incorporates elements of the two hypotheses. Berteaux (1998) showed that reproducing female Meadow Voles (*Microtus pennsylvanicus*) had higher daily energy expenditures than both wintering females and non-reproducing females in summer. He developed a simple index that places species along a continuum of both energy allocation patterns, and his results for female voles suggest that they lie close to a pure Increased Demand strategy although they can reallocate part of the energy saved on lower thermoregulatory costs in summer to reproduction (Berteaux 1998). The same could also be true for the mammals included in our analysis.

For birds, the energetic cost of provisioning young in the nest is frequently shared by both parents, thus reducing individual costs. Nevertheless, the seasonal pattern of energy allocation may be similar to what we

report for mammals. Weathers & Sullivan (1993) indicated that data for Yellow-Eyed Juncos and Dark-Eyed Juncos support the Reallocation Hypothesis, but data for other species do not (Table 6 of Weathers & Sullivan 1993). They suggested that diets may be involved in the observed patterns of seasonal energy allocation. Birds that feed on difficult-to-capture prey, such as insects and vertebrates, adhered to the Increased Demand Hypothesis, whereas granivores and omnivores fitted the Reallocation Hypothesis. It is suggested that, in birds, reproduction is timed with peak food abundance not because parents are faced with an energetic bottleneck and that reproduction pushes them to their physiological limit, but because juvenile birds are inefficient foragers and they require enough available food resources to meet their energy needs (Martin 1987; Weathers & Sullivan 1993).

Diets could also be involved in mammalian patterns of seasonal energy allocation. One of the major winter energetic expenditure for mammals that consume hard-to-catch prey (carnivores) is the cost of foraging, and this may be the main reason why they time their reproduction to occur when prey is most abundant but also when foraging costs are lowest. For small herbivores, such as voles, they may have access to the same amount of plant biomass in summer and in winter but the quality of the latter is lower owing to the increase in dietary fibre. In this example voles would need to time their reproduction when food was most easily digestible and not simply when it was most abundant. It would therefore be of interest to examine the effect of diet on energy allocation patterns in mammals, but it is difficult to predict how these dietary habits would shape the patterns of seasonal energy allocation because of the great variation already seen in both birds (Weathers & Sullivan 1993) and the species included in this study. Our results are equivocal and do not show a clear pattern between diet and energy allocation (Table 2), and underscore the fact that the available data are not yet sufficient to carry out a detailed analysis.

Although conservative estimates of energy costs were used because of the paucity of cross-seasonal FMR data, if such information were available the difference in magnitude between seasonal energy expenditures would be greater and a better sense of the overall trends would be obtained. Our analyses outline the interspecific variability found in seasonal energy allocation patterns in mammals, and it is still unclear what their proximate or ultimate causes may be. Also, little is known whether there is a correlation between a species' seasonal pattern of energy allocation and its life-history traits, and this could be an interesting avenue for future research.

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