The Role of Energy Availability in Mammalian Hibernation: A Cost-Benefit Approach

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ABSTRACT

Hibernation is widely regarded as an adaptation to seasonal energy shortage, but the actual influence of energy availability on hibernation patterns is rarely considered. Here we review literature on the costs and benefits of torpor expression to examine the influence that energy may have on hibernation patterns. We first establish that the dichotomy between food- and fat-storing hibernators coincides with differences in diet rather than body size and show that small or large species pursuing either strategy have considerable potential scope in the amount of torpor needed to survive winter. Torpor expression provides substantial energy savings, which increase the chance of surviving a period of food shortage and emerging with residual energy for early spring reproduction. However, all hibernating mammals periodically arouse to normal body temperatures during hibernation. The function of these arousals has long been speculated to involve recovery from physiological costs accumulated during metabolic depression, and recent physiological studies indicate these costs may include oxidative stress, reduced immunocompetence, and perhaps neuronal tissue damage. Using an optimality approach, we suggest that trade-offs between the benefits of energy conservation and the physiological costs of metabolic depression can explain both why hibernators periodically arouse from torpor and why they should use available energy to minimize the depth and duration of their torpor bouts. On the basis of these trade-offs, we derive a series of testable predictions concerning the rela-

tionship between energy availability and torpor expression. We conclude by reviewing the empirical support for these predictions and suggesting new avenues for research on the role of energy availability in mammalian hibernation.

Introduction

Mammalian hibernation has been the subject of intense research attention for many decades, and the resulting advances have been thoroughly summarized in several books (Kayser 1961; Lyman et al. 1982; Hochachka and Guppy 1987), reviews (Davis 1976; Wang 1989; Nedergaard and Cannon 1990; French 1992; Geiser and Ruf 1995; Guppy and Withers 1999), and a series of conference proceedings (Lyman and Dawe 1960; Suomalainen 1964; Fisher et al. 1967; South et al. 1972; Wang and Hudson 1978; Musacchia and Jansky 1981; Heller et al. 1986; Malan and Canguilhem 1989; Carey et al. 1993; Geiser et al. 1996; Heldmaier and Klingenspor 2000). Although alternative hypotheses about the ecological role of hibernation have been proposed (Grigg and Beard 2000; Lovegrove 2000*a*), hibernation is most typically regarded as a physiological and behavioral adaptation that permits survival during seasonal periods of energy shortage via a combination of prehibernal energy storage and hibernal metabolic depression (referred to here and elsewhere as "torpor"). Considerable research attention has been paid to energy storage by hibernators, and much more has focused on the metabolic depression during hibernation itself, but surprisingly little has examined the interaction between the two. The paucity of data on how hibernation patterns are influenced by energy availability means that the widespread explanation of hibernation as an adaptive response to energy shortage remains largely an untested hypothesis. Better understanding of the ecological implications of mammalian hibernation (i.e., how hibernation influences the distribution and abundance of organisms) requires that the phenomenon be studied in the context of the energetic responses of individuals and populations to fluctuations in resource abundance (Hall et al. 1992).

The presumed benefits of metabolic depression for hibernators have led some authors to interpret factors that lead to increased torpor expression as eliminating constraints that prevent torpor from being expressed at its ideal, maximal level (e.g., Frank et al. 2000; Harlow and Frank 2001). Although some energy conservation through metabolic depression is

likely essential for surviving prolonged periods of resource shortage, more may not necessarily be better if surplus energy is available. High rates of metabolism are frequently speculated to be beneficial for endotherms when resources are abundant (Ruben 1996; Hammond and Diamond 1997; Speakman 2000). Because torpor expression requires a complete cessation of behavioral activity as well as relatively severe physiological disruption (Lyman et al. 1982; Guppy and Withers 1999), even mammals sequestered in a hibernaculum may benefit from maintaining elevated rates of metabolism if sufficient energy is available (French 1988, 2000). If reduced torpor expression by hibernators typically reflects an absence of energetic necessity rather than a lack of physiological capability, many interpretations about the ecological implications of variation in torpor expression will be reversed or qualified (e.g., Geiser et al. 1990; Frank et al. 1998, 2000; Grigg and Beard 2000).

In this review, we develop a general hypothesis postulating that torpor expression by hibernating mammals reflects an optimization problem between costs and benefits of metabolic depression and that this trade-off is mediated by variation in energy availability. As a result, we argue, differences in energy availability may account for variation in both the torpor patterns of different hibernating species and, given sufficient plasticity in torpor expression, the torpor patterns of populations and individuals within the same species. In this article, we examine torpor expression by hibernating mammals within this context by considering the form and extent of energy accumulation in autumn, the potential costs and benefits associated with torpor expression during winter, and the importance of reserves for spring reproduction. We conclude by proposing a series of testable predictions regarding the influence of energy availability on torpor expression and reviewing the current empirical support for these predictions.

Acquiring an Autumn Energy Reserve

Most mammalian hibernators do not actively forage between autumn immergence and spring emergence (Lyman et al. 1982; but see Avery 1985; Park et al. 2000). Because this period typically exceeds 5 mo and hibernators can reduce but not eliminate maintenance metabolic requirements (Guppy and Withers 1999), surviving the hibernation period requires considerable preimmergent energy storage in the form of body fat or hoarded food (body protein can also serve as a minor hibernation energy source in some circumstances [e.g., Harlow 1995], but we do not consider it further in this review; see discussion of fat vs. protein storage in Speakman 2000). Most hibernation research has been conducted on fat-storing species (e.g., ground squirrels, *Spermophilus* spp.; bats, Vespertilionidae and Rhinolophidae; marsupials), but species from at least four rodent families (Cricetidae, Gliridae, Heteromyidae, Sciuridae) show no or little prehibernation increases in body mass and instead support hibernation requirements primarily with stored food (Vander Wall 1990). We evaluate whether the two storage strategies are associated with differences in body size or food habits. We then compare the maximum reserve sizes of food- and fat-storing hibernators and conclude by briefly considering what determines the timing of autumn immergence. This establishes the extent of energy accumulation by different hibernators, which in turn determines the energetic necessity of torpor during winter and the prospects of successful reproduction in spring.

Food or Fat Storage

The distinction between reliance on body fat and hoarded food during hibernation has been recognized as potentially important (Davis 1976; French 1988, 1992), but there are few explanations for why the different storage strategies occur and what consequences these strategies have on hibernation energetics. French (1988) proposed that reliance on stored food rather than body fat permits small mammals to circumvent size-related constraints on maximum reserve size. Because fat storage capacity is expected to increase directly with body mass ($mass^1$), while resting metabolism scales according to $mass^{0.75}$ (Kleiber 1947; Lovegrove 2000b), euthermic endurance of fat-storing mammals should increase with body mass$^{0.25}$ (Lindstedt and Boyce 1985). Thus, in the absence of torpor, large mammals should be able to survive on stored energy reserves for much longer than small mammals (Morrison 1960; Millar and Hickling 1990; Nedergaard and Cannon 1990). Potential costs associated with fat storage include increased locomotory costs and reduced mobility leading to increased predation risk (Witter and Cuthill 1993). Although these costs are unlikely to apply during the hibernation period, they may influence the relative benefits of fat storage for hibernation because of the occurrence of costs before and after the inactive season.

Davis (1976, p. 484) suggested that because food stores could be pilfered and were not as "readily available" as fat stores, storing food would be a "less efficient" form of energy storage for hibernation. Stated more explicitly, potential negative consequences associated with relying on hoarded food during hibernation include ingestive and digestive requirements during hibernation and the risk of hoard pilferage and perishability. We have recently shown that digestive efficiency is enhanced by torpor expression in hibernating eastern chipmunks (*Tamias striatus*; Humphries et al. 2001); thus, an incompatability of torpor and digestion does not appear to be a cost associated with the food-storage strategy. Nevertheless, food ingestion is prevented by the loss of muscular coordination during torpor (Choi et al. 1998); thus, constraints on maximum rates of food ingestion and stomach clearance during euthermy could force food-storing hibernators to express longer and/or more frequent arousals (Humphries et al. 2001). Furthermore, unlike fat-storing species that are characterized by pronounced gut atrophy during hibernation (Carey 1990, 1992, 1995; Hume et al. 2002), food storers must pay the additional energetic cost

of maintaining a functional digestive tract throughout winter (Cossins and Roberts 1996). Food perishability may be another major constraint associated with the food-storage strategy because food hoards need to last many months until spring emergence. Furthermore, because of the possibility of pilferage, hoards may need to be stored in close proximity to the hibernator, where environmental conditions may be better suited to the physiological requirements of the hibernator than to the minimization of hoard perishability (Vander Wall 1990).

To evaluate whether the food- and fat-storing strategies are associated with variation in body size or diet, we gathered literature on the food habits, body mass, and mode of energy storage of hibernating mammals. The pattern that emerges is that reliance on hoarded food coincides with granivorous diets but not small body size (Table 1). Four of five granivorous groups are food-storing hibernators, and all 11 nongranivorous groups are fat storers. Dormice pursue a mixed fat and food storage strategy, and some hibernators listed as predominantly fat storers also supplement their energy reserves with hoarded food (e.g., *Spermophilus*, *Burramys*). Even in these cases, seeds are the major food item found in hoards (Vander Wall 1990),

despite comprising a relatively small portion of the active-season diet. Granivory also predominates among the nonhibernating, long-term (i.e., multimonth) food hoarders discussed by Vander Wall (1990). The association between granivory and food hoarding reflects the profitability of storing seeds relative to other food types. Seeds are adapted to persist for long periods in a dormant state (Smith and Reichman 1984) and thus are among the least perishable food items eaten by hibernating mammals (Vander Wall 1990). Because seeds are energy rich and highly digestible (Robbins 1993), they yield a larger energy return per volume stored than other food types. Furthermore, because their energy reserves are dominated by carbohydrates or lipids rather than protein, seeds do not impose any substantial water stress by requiring the elimination of nitrogenous wastes. In contrast to expectations based on allometric patterns in euthermic endurance, small hibernators are not more likely to store food than large hibernators (Table 1). Bats and jumping mice are among the smallest nongranivorous and granivorous hibernators, respectively, and both groups rely exclusively on body fat as an energy source for hibernation.

Table 1: Diet, size, and energy storage form in hibernating mammals

Diet and Group[a]	Hibernating Genera[b]	Body Mass[c] (g)	Total Species in Genera[d]	Confirmed Hibernating Species[b]	Principle Storage Form[e]
Gramnivores:					
Ground squirrels	*Cynomys, Spermophilus*	600	43	9	Fat
Marmots	*Marmota*	5,000	14	3	Fat
Granivores:					
Pocket mice	*Perognathus*	12	9	2	Food
Jumping mice	*Napaeozapus, Zapus*	25	4	2	Fat
Chipmunks	*Tamias*	75	25	2	Food
Dormice	*Eliomys, Muscardinus, Myoxus*	125	4	3	Fat/food
Hamsters	*Cricetus, Mesocricetus*	225	5	3	Food
Insectivores:					
Vespertilionid bats	*Barbastella, Eptesicus, Myotis, Nyctalus, Pipistrellus*	10	193	8	Fat
Horseshoe bats	*Rhinolophus*	10	62	2	Fat
Hedgehogs	*Erinaceus, Setifer, Tenrec*	600	5	4	Fat
Echidnas	*Tachyglossus*	4,000	1	1	Fat
Omnivores:					
Gliders	*Acrobates*	12	1	1	Fat
Pygmy possums	*Burramys, Cercartetus*	30	5	4	Fat
Lemurs	*Cheirogaleus*	300	2	1	Fat
Badgers	*Meles*	10,000	1	1	Fat
Bears	*Ursus*	100,000	6	1	Fat

[a] Dietary categories based on McNab (1988).
[b] Geiser and Ruf 1995.
[c] Intermediate body mass of group from Silva and Downing (1995).
[d] From Nowak 1999.
[e] Based on Vander Wall (1990) and a generic BIOSIS literature search for 1989–1999.

Maximum Reserve Size

Maximum fat and food reserves observed in nature could result from limitations on resource availability, diminishing returns associated with large energy reserves, or absolute structural constraints on maximum reserve size. Whatever the cause, comparison of maximal reserve sizes provides evidence concerning the amount of energy available for hibernation.

Field data on the maximum reserve sizes of fat- and food-storing hibernators are presented in Table 2. For fat-storing species, maximum reserves are consistently 40%–50% of total body mass and thus scale to body mass with approximate unity (fat mass = 0.43 body mass$^{1.04}$, $r^2 = 0.99$). As a result, euthermic fasting endurance increases with body size from approximately 25 d in the smallest hibernators to 250 d in the largest (euthermic endurance = 1.1 body mass$^{0.26}$, $r^2 = 0.90$). Maximum reported reserve sizes of food-storing hibernators are an order of magnitude larger than those of similar-sized fat-storing species and do not vary consistently with body mass (Table 2). The estimated assimilated energetic value of food hoards translates into multiple years of euthermic endurance, far exceeding the potential duration of seasonal energy shortages and, in some cases, exceeding the probable life span of the hoarder. Hoard perishability and pilferage likely result in much lower levels of realized euthermic endurance in the field than those predicted in Table 2, but the general point remains: small endotherms that store food can accumulate much larger energy reserves than those that store fat.

The Timing of Autumn Immergence

We might expect hibernators to remain active in autumn as long as additional reserve accumulation is possible. Alternatively, they might immerge as soon as a reserve of a given size has been accumulated. These responses might relate to overall availability of food or energy storage capacity. Available evidence suggests that hibernators often immerge when conditions would permit additional reserve accumulation. Asynchronous immergence by different age and sex classes of fat-storing ground squirrels generally corresponds to differences in energy accumulation schedules (e.g., Davis 1976; Michener 1984; Buck and Barnes 1999a; Strijkstra 1999) and clearly demonstrates that many individuals initiate hibernation while environmental conditions still permit conspecifics to achieve highly positive energy budgets. Similarly, our quantification of the energetics of autumn hoarding in food-storing eastern chipmunks suggests that most individuals terminate aboveground activity while ambient temperatures and food availability would have permitted additional hoard accumulation (Humphries et al. 2002a). The extremely large hoards of several food-hoarding species reported by Vander Wall (1990; Table 2) suggest that accumulation is not always terminated when a fixed reserve size is reached. But the frequent tendency of both food- and fat-storing hibernators to terminate reserve accumulation while resources remain abundant suggests that the timing of autumn immergence is influenced by some combination of the following: limited storage capacity (especially in fat-storing species),

Table 2: Maximum energy reserve size and fasting endurance of food- and fat-storing hibernators

Storage Form and Species	Body Mass (g)	Resting Metabolic Rate (kJ/d)	Maximum Reserve Size			Euthermic Endurance (d)
			g	(g)/Body Mass (g)	kJ[a]	
Fat:						
Little brown bat, *Myotis lucifugus*[b]	10	6	3.8	.39	151	25
Jumping mouse, *Zapus princeps*[c]	36	26	14.6	.40	580	23
Arctic ground squirrel, *Spermophilus parryii*[d]	985	251	473	.48	18,800	75
Woodchuck, *Marmota monax*[e]	4,900	578	2,840	.40	112,884	195
Brown bear, *Ursus arctos*[f]	237,400	22,408[g]	135,600	.44	5,389,829	241
Food:[h]						
Pocket mouse, *Perognathus parvus*	24	19	4,400	1,342	32,217	1,703
Long-tailed hamster, *Cricetulus triton*	73	43[g]	35,000	3,511	256,270	5,955
Eastern chipmunk, *Tamias striatus*	100	70	12,200	893	89,328	1,276
European hamster, *Cricetus cricetus*	362	109	90,000	1,092	395,388	3,616

[a] Assuming 37.3 kJ/g fat and 7.3 kJ/g food (Robbins 1993).

[b] Kunz et al. 1998.

[c] Cranford 1978.

[d] Buck and Barnes 1999a (C. L. Buck, personal communication).

[e] Snyder et al. 1961.

[f] Hilderbrand et al. 2000 (G. V. Hilderbrand, personal communication).

[g] Estimated from order-specific allometric equation (McNab 1988).

[h] Vander Wall 1990.

diminishing returns on the benefits of large energy reserves (Houston and McNamara 1999), and costs of additional foraging (e.g., predation; Lima and Dill 1990; Lima and Bednekoff 1999).

Torpor Expression during Hibernation

We consider the benefits and costs of torpor expression during the prolonged winter period between the commencement of torpor expression in autumn and the onset of preparation for spring emergence. For most hibernators, this period comprises at least one-third to one-half of their total lifetime. We briefly review the energetic benefits of torpor and then refer back to data on maximum energy reserve size (Table 2) to evaluate the energetic necessity of torpor for different hibernators. We then review the recently expanding literature on the costs of torpor and conclude by questioning the validity of the assumption that hibernators should generally benefit from maximizing torpor expression.

Benefits of Torpor

Clearly, the major proximate benefit of torpor expression is a profound reduction of energy requirements. Rates of metabolism during deep torpor are typically less than 3% of euthermic rates at the same ambient temperature (Geiser 1988; Heldmaier and Ruf 1992). The basis of this metabolic reduction involves an elimination or substantial reduction of thermoregulatory requirements, Q_{10} effects on reaction rates, and probably metabolic inhibition through respiratory acidosis (Wang and Lee 2000). Small hibernators are generally characterized by a larger proportional reduction in metabolism than large hibernators (Geiser 1988), and this appears at least partially because of increased metabolic inhibition (Song et al. 1997). Thus, while euthermic metabolism scales with mass$^{0.75}$, minimum torpor metabolism scales approximately with mass^1 (Geiser 1988). This difference partially explains why fat storage is a feasible energetic strategy for even the smallest hibernators (Table 2).

The primary fitness advantage of reducing expenditure through prolonged torpor expression is widely assumed to involve enhancement of survival during predictable periods of resource shortage or reproductive inactivity (French 1992; Grigg and Beard 2000) and associated enhancement of reproductive success following these periods (Kunz et al. 1998; Michener 1998). This presumed advantage forms the conceptual basis of much hibernation research; given that energy is in limited supply and is necessary for winter survival and spring reproduction, hibernators should benefit from minimizing winter energy requirements by maximizing torpor expression. Thus, hibernation research has focused on identifying the nutritional and environmental factors that permit maximum torpor depth and duration (e.g., Geiser et al. 1990; Geiser 1993) and the physiological constraints that force hibernators to reg-

ularly arouse from torpor to the energetically costly euthermic state (e.g., Daan et al. 1991; Thomas and Geiser 1997). Factors that lead to increased torpor expression are concluded to improve "hibernation ability" (Harlow and Frank 2001, p. 83), lead to "optimal hibernation patterns" (Carey et al. 2000, p. 552), or permit "proper hibernation" (Frank et al. 2000, p. 207).

An additional benefit of torpor expression could involve delayed aging if the reduced metabolism associated with torpor results in reduced lifetime accumulation of somatic damage (Lyman et al. 1981). A similar argument has been invoked to explain why euthermic endotherms usually maintain levels of metabolism well below physiological limits (Speakman 2000). Consistent with this hypothesis, caloric restriction has been shown to enhance longevity in a wide diversity of taxa (Shanley and Kirkwood 2000; Speakman 2000). However, Shanley and Kirkwood (2000) recently suggested that this enhancement may not result from reduced metabolism per se but, rather, from an adaptive response to resource shortage involving a shift in allocation away from growth and reproduction and toward somatic maintenance. Thus, at present, there is little direct empirical support for the hypothesis that reduced metabolism delays the onset of aging, either among hibernators or among endotherms in general (Speakman 2000). Furthermore, torpor expression appears to be associated with increased, rather than reduced, somatic damage.

Energetic Necessity of Torpor

Because winter length exceeds the maximum euthermic fasting endurance of small, fat-storing hibernators (Table 2), surviving until spring requires torpor. As argued earlier, food hoarders and larger fat storers are not necessarily constrained to the same extent by energy availability (Table 2). Interspecific variation in average or maximum torpor expression generally conforms to these differences in energetic necessity; small fat storers express longer and deeper torpor bouts than food-hoarding and larger fat-storing species (French 1988; Geiser and Ruf 1995; Humphries et al. 2001). Most hibernation research has focused on small, fat-storing species and has emphasized the extent of the energetic constraints hibernators face and the importance of deep torpor expression for winter survival (Lyman et al. 1982; Nedergaard and Cannon 1990; French 1992).

Nevertheless, the pronounced metabolic savings offered by torpor provide even small, fat-storing species with considerable potential scope in the amount of torpor they need to express. Minimum hibernation energy requirements (including costs of periodic arousals) in little brown bats (*Myotis lucifugus*) are approximately 6.5 mg fat/d (Humphries et al. 2002b). Thus, an individual with maximum energy reserves (3.8 g; Table 1) could theoretically survive 585 d without acquiring any additional energy. Alternatively, the same individual could survive a fixed, 6-mo period while expending 3.2 times more energy

than its minimum requirements (resulting from maximum torpor expression). Similarly, minimum hibernation energy requirements of arctic ground squirrels (*Spermophilus parryii*), again including the costs of arousals, are 0.7 g fat/d (estimated from Buck and Barnes 2000); thus, an individual could use maximum reserves (473 g; Table 1) to fast for 670 d or for a fixed period of 6 mo while expending 3.4 times more energy than minimum requirements. Under natural circumstances, many individuals, whether food or fat storers, may possess energy reserves much smaller than those indicated in Table 2 and may not have access to optimal hibernaculum temperatures. In these situations, deep torpor expression may be essential for surviving even relatively short winters (e.g., Arnold 1993; Humphries et al. 2002*b*). But under more favorable ecological circumstances, many hibernators are likely to have considerable scope in the amount of torpor needed to survive winter.

The Costs of Torpor

Recent research reveals that many diverse physiological phenomena may be negatively affected by the extreme metabolic suppression and hypothermia associated with torpor. In general, the adaptations that permit hibernators to survive body temperatures that would be fatal for nonhibernators do not involve circumvention of the fundamental effects of temperature on biological processes (Hochachka and Guppy 1987; Davenport 1992). Instead, they confer an increased tolerance for, and capacity to recover from, the consequences of this thermal dependency (Lyman et al. 1982; Nedergaard and Cannon 1990). During torpor, sensory and motor capabilities are severely reduced (Choi et al. 1998), protein synthesis ceases (Frerichs et al. 1998; Van Breukelen and Martin 2002), mitosis is arrested (Kolaeva et al. 1980), and active transport across cell membranes is inhibited (Marjanovic and Willis 1992). But, owing to the specialized capacity of hibernators to spontaneously rewarm from torpid to euthermic body temperatures (Nedergaard and Cannon 1990) and to up-regulate the processes inhibited by torpor while euthermic (e.g., Carey et al. 1999), most of the negative consequences arising from torpor are thought to be reversed during the brief, periodic arousals characteristic of all species studied to date (Grigg and Beard 2000).

Because of the universal occurrence of periodic arousals and their high energetic cost, considerable research effort has been dedicated to identifying the specific physiological processes that necessitate repeated returns to euthermy. Because most hibernators arouse for only a few hours at a time and remain relatively inactive in the hibernaculum throughout the arousal (Lyman et al. 1982), periodic euthermy is thought to be necessary for restoration of some aspect of physiological homeostasis (e.g., Daan et al. 1991; Thomas and Geiser 1997). The widespread occurrence of periodic arousals suggests torpor is

associated with important, negative consequences that cause energetically costly arousals to be beneficial (Willis 1982; French 1988; Carey 1993).

During the last decade, it has been clearly established that hibernators do not sleep while in torpor and that, in fact, the majority of time during euthermic arousals is spent sleeping (Daan et al. 1991; Trachsel et al. 1991; Larkin and Heller 1999). Memory is hypothesized to be enhanced during sleep through a process called nonutilitarian dynamic stabilization (DS), which involves refreshment of memory circuits via slow-wave electrical activation (Kavanau 1997; Maquet 2001). During deep torpor, slow-wave activity ceases (Daan et al. 1991), and, concordant with this, synaptic contacts and dendritic branching decline substantially (Popov et al. 1992). Rapid regeneration of synapses and dendrites occurs during arousals (Popov et al. 1992), when sleep and slow-wave activity resume (Larkin and Heller 1999). Thus, the duration of torpor bouts has recently been speculated to represent "the longest period for which circuits for most memories can remain in functional states in the total absence of non-utilitarian DS" (Kavanau 1999, p. 639). This provides a clear example in which torpor may suppress a homeostatic requirement (DS), which could lead to somatic damage (declines in neuronal connectivity), which could in turn lead to a loss of function (memory). Early empirical evidence concerning the impairment of memory by torpor was contradictory (Mihailovic et al. 1968; McNamara and Riedesel 1972), but recent research on European ground squirrels (*Spermophilus citellus*) provides stronger evidence of a negative effect (Millesi et al. 2001). Nevertheless, a link between torpor-related damage to neural circuitry and subsequent influence on memory has yet to be firmly established.

Because torpor negatively affects so many different aspects of function, many physiological phenomena could necessitate periodic arousals. In addition to DS, other potential candidates include the inhibition of lymphocyte proliferation leading to reduced immunocompetence (Burton and Reichman 1999; Maniero 2000; Prendergast et al. 2002), dehydration leading to compromised circulation and ionic balance (Thomas and Geiser 1997), and the production of reactive oxygen species (Buzadzic et al. 1990) leading to lipid peroxidation (Carey et al. 2000; Harlow and Frank 2001). An important, shared characteristic of all these physiological costs is that they have the potential to become increasingly severe over the duration of a torpor bout, but this awaits empirical confirmation.

The physiological suppression associated with torpor likely also leads to ecological costs for hibernators in their natural environment. The severely limited sensory capacity and motor function of torpid animals makes them highly susceptible to predation; even when provoked into an emergency arousal, they require several minutes to hours of rewarming before having any capacity for coordinated activity (Lyman et al. 1982; Choi et al. 1998). Torpor expression may also increase the risk of

hoard pilferage for food-storing hibernators (Vander Wall 1990).

Optimal Torpor Expression

Overwinter mortality of hibernators is usually attributed to total hibernation requirements, E_h, exceeding energy reserves at immergence, R_i (Murie and Boag 1984; Karels et al. 2000). If the expected energy requirements resulting from maximum torpor expression, $E_{h\text{-}min}$, exceed R_i, the hibernator faces little choice but to minimize expenditure and hope for an early spring. But if $R_i > E_{h\text{-}min}$, then optimal torpor expression, $E_{h\text{-}opt}$, could lie anywhere in the interval

$$E_{h\text{-}min} \leq E_{h\text{-}opt} < R_i, \tag{1}$$

depending primarily on (1) costs associated with reducing E_h toward $E_{h\text{-}min}$, (2) uncertainty regarding $E_{h\text{-}min}$, and (3) the relationship between energy reserves at emergence, R_e, and reproductive success, *RS*. We consider the first of these issues here and the latter two in the next section.

Total hibernation energy requirements, E_h, could be reduced toward $E_{h\text{-}min}$ by increasing the proportion of winter spent in torpor and the depth of torpor when it is expressed. The duration and depth (i.e., reduction in body temperature) of torpor bouts are positively correlated in all hibernators studied to date (e.g., French 1985; Geiser and Kenagy 1988; Geiser et al. 1990; Michener 1992; Waßmer and Wollnik 1997; Buck and Barnes 2000; Park et al. 2000). The significance of this relationship is not well understood, but the interdependency of these variables may provide insight into the function of periodic arousals and the dichotomy in the torpor patterns of daily heterotherms and hibernators, and it thus warrants a more detailed theoretical and empirical examination. For present purposes, we simply accept that torpor bout depth and duration are interrelated and collectively are the primary determinants of total hibernation energy requirements (Geiser and Ruf 1995). Furthermore, the reduction in body temperature and energetic savings associated with torpor are not always correlated (Song et al. 1997), especially when hibernaculum temperatures are colder than optimal (Buck and Barnes 1999*b*, 2000). Thus, although we follow many other studies in using body temperature as an index of torpor depth, we acknowledge that metabolic rate is a more direct and energetically relevant measure.

We use the specific example of the hypothesized implications of sleep deprivation to illustrate that the same physiological requirements that necessitate periodic arousals can result in general benefits of using available energy to minimize, rather than maximize, the depth and duration of torpor bouts. Although Kavanau (1999) speculated that the DS requirement should cause hibernators to remain in torpor as long as "most" circuitry remains in a functional state, the timing of arousals represents an optimization problem between the DS benefits

of shorter torpor bouts and the energetic benefits of longer torpor bouts. The solution should depend not only on the effect of torpor on neural integrity and the importance of memory during hibernation and spring reproduction but also on the energy reserves available to the hibernator and the importance of reserves in supporting spring reproduction. Hibernators with small energy reserves may need to sacrifice some neural integrity to ensure their reserves will last until spring, while hibernators with large reserves may benefit from sacrificing some of their potential spring reserves for enhanced neural integrity. Thus, DS offers the possibility of a single phenomenon that could cause hibernators to periodically arouse from torpor and to benefit more generally from using available energy to minimize the depth and duration of torpor bouts. Our argument also provides an explanation for contradictions in the reported effects of hibernation on memory (Mihailovic et al. 1968; McNamara and Riedesel 1972; Millesi et al. 2001). The extent of memory impairment incurred by hibernators is likely to vary according to the depth and duration of their torpor bouts, which should, in turn, be influenced by the energetic necessity of expressing prolonged torpor as determined by energy availability.

DS is only one of several physiological functions hypothesized to be impaired during torpor, but the net accumulation of somatic damage incurred from other physiological impairments should be an outcome of an optimization problem similar to that suggested for the maintenance of neural circuitry. Thus, costs such as oxidative stress and reduced immunocompetence, either alone or in combination with DS, could lead to periodical arousals and general benefits of minimizing the depth and duration of torpor bouts. Indeed, according to the symmorphosis paradigm (Taylor and Weibel 1981; Weibel 2000), major physiological transitions like torpor arousals are unlikely to depend on a single, limiting process. Thus, a suite of negative physiological consequences may necessitate periodic arousals and result in benefits of general torpor avoidance. Furthermore, torpor may have important, negative consequences for many aspects of physiology, but because of the potential for euthermic restoration, detectable somatic damage and loss of function may only occur under circumstances of severe energy limitation.

Ecological costs associated with torpor expression, such as a risk of predation or hoard pilferage, seem less likely than physiological costs to result in torpor avoidance. Although euthermic individuals probably have a much higher probability of escaping an encounter with a predator than torpid individuals do, the risk of predation presumably does not increase with time in torpor. Thus, unlike physiological costs, substantial increases in energy expenditure would be required to marginally reduce predation risk. For example, if an eastern chipmunk (*Tamias striatus*) increased the duration of its euthermic intervals while keeping the depth and duration of its torpor bouts constant, doubling total hibernation energy requirements

would achieve only a 15% increase in the probability of being euthermic when a predator visited the hibernaculum (on the basis of parameters in Wang and Hudson 1971; see Humphries et al. 2001). Furthermore, hibernators are typically constrained to continuous occupation of a single hibernaculum, and predation attempts involve either excavation of the hibernaculum by large predators (e.g., Michener 2000) or entry into the hibernaculum by smaller predators (e.g., Jedrzejewski et al. 1992). Excavation would be likely to result in mortality of the hibernator whether or not it escaped the predation attempt (because of cold exposure, inability to locate another suitable hibernaculum, and so on), and smaller predators, having discovered an occupied hibernaculum, need only to continue revisiting it until they find the occupant in torpor. Euthermy may also facilitate defending food hoards from pilferage (Vander Wall 1990), but, as with predation, the energetic cost of torpor avoidance is sufficiently high and the probability that euthermic intervals will coincide with a pilferage attempt sufficiently low that protecting the food hoard via reduced torpor expression is not likely to be generally beneficial. Furthermore, although predation can occur in seconds, removal or consumption of an entire food hoard takes hours to days (C. L. Hall and M. M. Humphries, unpublished data). Thus, if a food-storing hibernator were in a position to detect the presence of a potential pilferer and was sufficiently responsive to tactile disturbance to arouse as a result, much of the potential hoard loss could be averted. Consistent with this, food-storing species often hibernate in burrow locations that block access to chambers containing food hoards (Elliot 1978) and, at least in the laboratory, appear more sensitive to tactile or auditory disturbance than fat-storing species (Wang and Hudson 1971; Waßmer and Wollnik 1997).

Clearly, additional research on the physiological and ecological consequences of torpor will facilitate better prediction of how and why torpor expression may vary according to energy availability. But recognition of the potential energetic flexibility of most hibernators and accumulating evidence for important and widespread costs of torpor seem clearly sufficient to question the assumption that "optimal hibernation" (sensu Frank and Storey 1995) necessarily involves maximizing the depth and duration of torpor bouts. Because torpor affects so many diverse aspects of function, it will be difficult to identify a single negative consequence of torpor that is responsible for periodic arousals or general torpor avoidance. Furthermore, because the relative importance of different consequences may vary according to environmental conditions (e.g., humidity or pathogen abundance), species (e.g., food vs. fat storers), and individual characteristics (e.g., males vs. females, adults vs. juveniles, large vs. small energy reserves), interpreting a single phenomenon as responsible for periodic arousals may also be misleading.

Emergence and Spring Reproduction

Here we consider some additional costs of torpor expression that pertain specifically to the preemergent period, before evaluating the influence of energy reserves at emergence on spring reproduction and the constraints hibernators face in maximizing reproductive success.

Preparing for Emergence

Many hibernators reproduce immediately following spring emergence (Kunz et al. 1998; Michener 1998), and early initiation of reproduction enhances the survival prospects of both offspring and parents during the subsequent winter (King et al. 1991; Millesi et al. 1999; Karels et al. 2000). Thus, emerging early and in a state of maximum reproductive preparedness is thought to be highly advantageous (Michener 1983). During hibernation, considerable muscle catabolism and atrophy can occur (Wickler et al. 1991; Buck and Barnes 1999a), and, in fat-storing species, the gut undergoes profound atrophy (Carey 1990, 1992, 1995; Hume et al. 2002). These negative effects of torpor are largely reversible, and hibernators may benefit from restoring them before emergence, especially if maximizing performance early in the season is important. In fact, the process of atrophy and restoration of tissues that are not required during hibernation could be considered as an adaptation rather than a cost (Piersma and Lindström 1997). Nevertheless, tissue restoration requires considerable protein synthesis and cell division, both of which are inhibited by torpor (Kolaeva et al. 1980; Frerichs et al. 1998; Van Breukelen and Martin 2002), and thus necessitates a period of preemergent euthermy. In the absence of additional costs of torpor, these effects are unlikely to cause hibernators to use available energy reserves to avoid torpor throughout the hibernation period. Instead, they may cause hibernators to benefit from switching to continuous euthermy at some point before emergence.

Perhaps the best elucidated cost of torpor, both in terms of demonstration of the physiological phenomenon and documentation of its consequences on field torpor patterns, involves an inhibition of spermatogenesis at torpor body temperatures (Barnes 1984, 1996; Barnes et al. 1986). In response to this constraint, males of several species are known to terminate torpor expression 10–30 d before emergence (Young 1990; Michener 1992; Nicol and Andersen 2000). The high energy cost of this extended euthermic period is often proposed as an explanation for why male but not female ground squirrels supplement fat storage with food hoarding (Kenagy 1989; Michener 1998). Follicular development in females also appears to be inhibited during torpor, but preemmergent follicular maturation likely eliminates the need for prolonged, preemergent euthermy (Millesi et al. 2000).

A final requirement associated with preparation for emergence involves properly timing the emergence itself. Synchro-

Table 3: Energy reserves and spring reproductive success in fat-storing hibernators

Species	Measure[a]	Effect[b]	Source
Little brown bat, *Myotis lucifugus*	Index	Probability of ovulation	Kunz et al. 1998
Uinta ground squirrel, *Spermophilus armatus*	Mass	Litter size, probability of weaning ≥ 1 young	Sauer and Slade 1987
European ground squirrel, *Spermophilus citellus*	Mass	Conception date, litter size	Millesi et al. 1999
Columbian ground squirrel, *Spermophilus columbianus*	Mass	Number of recruits	King et al. 1991
Arctic ground squirrel, *Spermophilus parryii*	Index	Probability of weaning ≥ 1 young, litter mass	Karels et al. 2000
Richardson's ground squirrel, *Spermophilus richardsonii*	Index	Litter mass	Dobson and Michener 1995
Alpine marmot, *Marmota marmota*	Mass	Probability of weaning ≥ 1 young	Häckländer and Arnold 1999
Black bear, *Ursus americanus*	Mass	Probability of parturition, litter size	Samson and Huot 1995

[a] Mass refers to total body mass; index refers to a condition measure that incorporates mass and structural size.

[b] All effects are positive (e.g., increased probabilities, advanced dates).

nizing emergence with suitable environmental conditions is critical to minimizing postemergent energetic stress and capitalizing on reproductive opportunities (Michener 1998; French and Forand 2000). Annual variation in the timing of emergence may be related to air temperature, soil temperature, or snow cover patterns (French and Forand 2000 and references therein). Torpid animals have extremely limited sensory capacity and are often isolated in sealed hibernacula. They are therefore unable to monitor environmental conditions other than soil temperature (French and Forand 2000). Thus, a pre-emergent period of euthermy may also be helpful in properly timing emergence.

Uncertainty regarding the timing of spring emergence also could have a direct effect on torpor expression throughout the hibernation season. Minimizing torpor expression for a given level of energy availability requires a precise estimate of the length of winter; overestimation results in more torpor expression than necessary, and underestimation results in depletion of reserves before emergence. Because the latter is likely to be much more detrimental than the former, uncertainty of estimation favors conservative strategies with margins of error (Bednekoff 1996). Although such projections could involve relatively complicated cognitive decisions, adherence to environmental cues or simple rules of thumb can result in optimal or near-optimal risk-sensitive behavior (McNamara 1996). For hibernators, variability in average hibernaculum temperatures (Geiser and Kenagy 1988; Buck and Barnes 1999b) and the timing of spring snowmelt (Murie and Harris 1982; Buck and Barnes 1999a) create considerable uncertainty in predicting winter energy requirements. As a result, hibernators should use more torpor than the average required to survive until emergence even if energy reserves do not contribute to reproduction.

Predicting how much more requires quantification of the degree of uncertainty in $E_{h\text{-}min}$.

Spring Energy Reserves and Reproductive Success

Because many hibernators mate shortly after emergence, often before any increase in resource availability (e.g., Armitage 1991; Kunz et al. 1998; Buck and Barnes 1999a; Hackländer and Arnold 1999), energy reserves remaining at emergence are likely to be an important determinant of spring reproductive success (Kunz et al. 1998; Michener 1998). Studies of female reproduction in fat-storing hibernators generally reveal positive associations between body mass or condition and various measures of reproductive success (Table 3). Less quantitative information is available for males, but they are speculated to be even more dependent on spring reserves because of pre-emergent spermatogenetic requirements and an earlier timing of their reproductive effort (Michener 1998). We are unaware of any documentation of the effect of energy reserves on reproductive success of male or female food-storing hibernators, but because food hoards can be larger (Table 2) and less costly to maintain than fat stores (Vander Wall 1990; Witter and Cuthill 1993), they have even greater potential to contribute to spring reproduction and postreproductive survival (Vander Wall 1990).

Successful spring reproduction may require some threshold reserve size (Kunz et al. 1998; Häckländer and Arnold 1999), and beyond this (but within the natural range of variation in spring reserve size), reproductive success could increase with R_e either linearly or according to diminishing returns. This is a critical distinction because if reproductive success asymptotes at relatively small R_e, then even minor costs of metabolic de-

pression could lead to torpor avoidance during winter, since large energy reserves will be of little benefit in spring. Asymptotic relationships could occur if, for example, reproductive success is also limited by ceilings on sustainable energy expenditure (Hammond and Diamond 1997) or number of available mates (Michener and McLean 1996), if fat reserves are associated with mobility or metabolic costs (Witter and Cuthill 1993), or if hoard perishability eliminates the benefits of large food reserves (Vander Wall 1990).

Maximizing Spring Reproductive Success

Available literature on the relationship between spring energy reserves and reproductive success in hibernators strongly suggests that, at least for fat-storing females, the utility of autumn energy reserves extends beyond the completion of hibernation. Given that somatic recovery and gametogenesis require prolonged preemergent euthermy and that even small reductions in the depth and duration of torpor bouts lead to substantial increases in energy expenditure, physiological preparedness for spring reproduction and R_e cannot be simultaneously maximized. Thus, individuals should be expected to emerge in prime condition only if their autumn energy reserves were exceedingly large or if energy reserves at emergence are rather unimportant. Because male mating activity typically interferes with or completely prevents feeding and, in hibernators, often occurs during periods of snow cover and low ambient temperature (Michener 1998), postemergent energy reserves should be essential. Food hoarding by males of some species of ground squirrels may help to alleviate this constraint (Kenagy 1989; Michener 1998), but even in these species some males are likely to have small total energy reserves. Thus, many male hibernators could be expected to have achieved submaximal spermatogenesis before the mating season and may pursue modified mating strategies or suffer reduced reproductive success as a result.

Summary and Predictions

Because most hibernation research has been approached from a physiological perspective and conducted in the laboratory, the influence of energy availability on hibernation patterns remains largely unexplored. The recent advent of inexpensive temperature dataloggers (e.g., Florant et al. 2000) offers an unprecedented opportunity for quantifying the torpor patterns of large numbers of individuals in the field. We hope the perspective presented here encourages more field research on the influence of energy availability on hibernation patterns. Therefore, we conclude by proposing several predictions based on our premise that torpor expression in hibernators will vary according to the costs and benefits of energy conservation. Our specific predictions follow.

1. Hibernators with large energy reserves at immergence should express less torpor during hibernation than individuals

with small reserves. Thus, food-hoarding and large, fat-storing hibernators should express less torpor than small, fat-storing hibernators because the former are capable of acquiring much larger reserves than the latter. Intraspecifically, individuals with large accumulated reserves should express less torpor than individuals with small reserves. Thus, winter reserve depletion should be positively correlated with initial reserve size, and the variability of reserve size at immergence should be larger than the variability at emergence.

2. Intraspecifically, the extent of observable somatic damage or loss of function following hibernation will be inversely related to immergent energy reserves and positively related to the depth and duration of torpor bouts expressed during winter.

3. Autumn energy reserves should be larger in situations where winter energy requirements are high because of either long winters or nonoptimal hibernaculum temperatures. For a given level of energy reserves at immergence, torpor expression will be positively related to expected total hibernation requirements and inversely related to the predictability of hibernation requirements. For example, hibernators in habitats with a late or highly variable snowmelt should express more torpor for a given level of energy reserves than hibernators in habitats with an earlier or less variable snowmelt.

4. Autumn energy reserves should be larger in situations where spring reserves are beneficial for reproduction. For a given level of autumn reserves, torpor expression will be higher for those accruing higher benefits of spring reproductive reserves. For example, if spring energy reserves are more beneficial for males than females, adults than subadults, or early breeding than late breeding species, the former should express more torpor for a given level of energy reserves than the latter.

5. Intraspecifically, hibernators with large immergent energy reserves should express longer intervals of preemergent euthermy and emerge in better condition as a result. For example, males with larger energy reserves at immergence should emerge with larger sperm reserves than males with smaller reserves.

At an interspecific level, there is general support for our first prediction but little evidence pertaining to the other four. French (1988) has argued previously that larger relative energy reserves permit food-storing and large, fat-storing hibernators to express shorter and shallower torpor bouts than small, fat-storing species. Indeed, the maximum torpor bout lengths of fat-storing hibernators (350 ± 48 h, $n = 8$ species) are nearly twice as long as those of food-storing species (178 ± 23 h, $n = 4$ species; Humphries et al. 2001). However, this difference may result from food-storing species needing to arouse more frequently to ingest food (Humphries et al. 2001). Among fat-storing species, small hibernators are characterized by more substantial metabolic reductions when in torpor than larger hibernators (torpor metabolism as a percentage of basal metabolism $= -2.5 + 3.6 \log_{10}$ BW, $r^2 = 0.60$, $n = 35$ species, $P < 0.0001$; Geiser and Ruf 1995). Our third prediction could be tested by amalgamating field data on the winter length,

hibernacula temperatures, energy reserves, and torpor patterns of different hibernating species, but to our knowledge this has not been done. Evaluating other predictions at the interspecific level will require additional data on the energy reserves, costs of torpor expression, and role of energy reserves in spring reproduction in a diversity of hibernating species.

At the intraspecific level, there is now empirical support for our first prediction in both major groups of North American food-storing hibernators (*Perognathus* spp. and *Tamias* spp.) but relatively little direct evidence from fat-storing species. Hibernating eastern chipmunks (*Tamias striatus*) dramatically reduce torpor expression in response to food supplementation in both the laboratory (French 2000) and the field (Humphries et al. 2003). Limited evidence also suggests pocket mice (*Perognathus amplus* and *Perognathus longimembris*) reduce torpor expression in response to increased food availability (French 1976, 1989; Reichman and Brown 1979). Evidence that fat-storing hibernators use available energy to minimize torpor is indirect. Some fat-storing hibernators require food deprivation or exposure to cold temperatures to initiate torpor in the laboratory (e.g., Harlow and Menkens 1986; Otsu and Kimura 1993). Furthermore, there is evidence from bats and ground squirrels that hibernation mass loss is positively correlated with the size of fat reserves at the onset of hibernation (Mrosovsky 1976; Ransome 1990), suggesting that animals adjust torpor expression and, hence, the rate of fat depletion to the size of the reserve. Our final prediction is supported by two captive studies on fat-storing ground squirrels showing that males with large preimmergent energy reserves emerge earlier in spring (*Spermophilus beldingi*; French 1982) and in better reproductive condition (Barnes 1984) than males with smaller reserves. To our knowledge, there is currently no direct intraspecific evidence relating to any of the other predictions. Additional experimental manipulations of the energy reserves of free-ranging hibernators, coupled with measures of their subsequent winter torpor expression and spring reproductive success, will provide the critical data needed to test these predictions. Comparisons of the torpor patterns expressed by different populations of the same species, along a gradient of ecological conditions (e.g., winter length, hibernaculum temperatures, predation risk) will provide additional tests of our predictions at an intermediate, interpopulation level.

In summary, mammalian hibernation is widely accepted as an adaptation to prolonged, seasonal periods of energy shortage (Lyman et al. 1982; French 1992; Griggs and Beard 2000), but surprisingly little attention has been paid to the actual effect of energy availability on hibernation patterns (French 1988, 2000). Because most hibernation research has been conducted in the laboratory (Geiser et al. 2000) and has tended to deemphasize interindividual variability in torpor use (Waßmer and Wollnik 1997), the generality and importance of torpor avoidance by hibernators may be underrecognized. This omission may simply reflect past emphasis of hibernation research

on physiological, rather than ecological, aspects of prolonged torpor. Nevertheless, differences in the energetic necessity of torpor may be a central determinant of both intra- and interspecific patterns of torpor expression, and these sources of variation form the basis of both physiological and ecological approaches to the subject. A more thorough examination of the role of energy availability in hibernation should improve understanding of the physiological and ecological consequences of this remarkable and widespread phenomenon.

Acknowledgments

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