

Exploring Ecology and Its Applications



Readings from **American Scientist**

Edited by Peter Kareiva

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EDITED BY

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The Cover

Migrating western sandpipers forage on an intertidal flat. The predation of such migratory shorebirds on soft-bodied intertidal invertebrates is intense but brief; their influence on the ecology of the intertidal zone is usually temporary. See "Intertidal Zonation of Marine Invertebrates in Sand and Mud" by Charles H. Peterson, page 142. (Photograph by T. Leeson/Photo Researchers.)

Exploring Ecology and Its Applications: Readings from *American Scientist*

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"Adaptive Strategies of Coral-Reef Invertebrates"
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PREFACE

Ecology has never been a more exciting science than it is today. Challenged with everything from guiding society toward a sustainable biosphere to passing judgment on conservation plans for spotted owls, ecology is attracting the best and brightest students. To meet its challenges, ecology draws inspiration from economics, chemistry, physics, and atmospheric sciences, while remaining firmly grounded in the natural history of organisms. And professional scientists are not the only ones who must struggle with ecological questions and think in interdisciplinary terms; environmental debates commonly find their way into courtrooms, legislatures, and voting booths. The task of nurturing our biosphere demands economic sacrifices and hard political choices; this means we all need to have some familiarity with ecology, if only so that we can distinguish false prophets of ecological doom from those justified calls to political action in the service of our environment. The twentieth century was marked by the industrial and computer revolution; the next century will likely see an environmental revolution. We need sound, yet provocative, information—such as that developed by the contributors to this volume—that adds to our basic understanding of both general ecological principles and specific environmental crises.

Exploring Ecology and its Applications is a collection of articles in which leading researchers explain their personal approaches and points of view regarding ecological problem-solving. It is not intended to be a comprehensive textbook. Too often textbooks homogenize science into a bland soup of principles and examples, as though all participants in a field have agreed on one common pathway to the truth. Such is never the case in any science, and it is less the case in ecology than in most other sciences. Ecology is a fractious field. Approaches to the subject range from the painstaking observation of organisms in their natural environments, to clever manipulations of populations in small experimental settings, to computerized interpretation of satellite images. The articles in *Exploring Ecology and Its Applications* expose students to the many different ways of doing ecology by encompassing the major questions that ecologists are currently tackling.

This book is designed to provide vivid supplementary readings for courses in ecology or environmental sciences. Because the authors have been selected for their skill at communicating with a wide audience, this collection could profitably be used by students who are not science majors. At the same time, the research reported here is sufficiently topical and “cutting edge” that the articles can introduce the novice scientist to a richly rewarding technical literature.

Seattle, January 1998

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PART I

The Ecology of Individuals: Adaptations and Strategies of Organisms

The study of ecology begins with the organism and makes little progress without a solid understanding of plant and animal adaptations to their environment. Although understanding such adaptation has long been a goal of ethologists, physiologists, and morphologists, recent developments in optimization theory have revitalized this branch of evolutionary ecology. By studying adaptations with an aim toward predicting how organisms “should behave or should be designed,” we gain much more than knowledge about specific plants or animals; we often uncover patterns that allow us to predict what we might expect to see in different environments, or we identify the constraints that press most severely on an organism’s evolutionary success. The articles in this section display the range of insights delivered by studies of adaptations and life histories, as well as the diversity of research approaches that deliver these insights.

We lead off with what might at first seem like “old-fashioned” physiology: an article by French that discusses hibernation in mammals. However, instead of simply recounting adaptations to cold, French explores the thermoregulatory implications of how metabolism scales nonlinearly with body size, whereas the capacity for fat storage scales linearly with body size. The result is that large hibernating mammals face a strikingly different set of constraints than do small hibernating mammals. Whereas small animals are precariously balanced between the energy savings provided by hibernation and the possibility their fat reserves may run out, large hibernators are constrained primarily by the possibility of too little time for growth and reproduction should they hibernate for too long. This is just one of many cases of evolutionary physiology identifying those aspects of the environment that present the greatest risks to organisms.

Being “too cold” is something countless organisms must face, not just hibernating mammals. As the article by Seeley shows, the risk associated with freezing temperatures often translates into a question of whether an animal can get enough food to stay warm. Seeley makes this risk vivid by pointing out that in our North American temperate climate, as many as 90% of wild honeybee colonies die each winter from starvation; therefore, much attention has been given to the thermoregulatory abilities of honeybees in temperate regions. But overlooked in our fascination with honeybee heating sys-

tems is the fact that honeybees evolved in the tropics, which remain their center of diversity. And in the tropics, cold winters are not a problem—rather, predation on nests is the greatest problem the bees face. The major adaptations of tropical honeybees often take the form of antipredator defenses that range from concealment, to sticky traps, to aggressive stinging behavior. Seeley synthesizes physiology and ecology to obtain predictions about broad patterns of social and nesting traits in honeybees as a function of the climate in which the bees live.

A second venue for studies of individual ecology is behavior. The past 20 years have been golden ones in behavioral ecology, with enormous advances in our understanding of foraging behavior, mating behavior, and fighting behavior. Three papers in this section deal with the fundamental decisions individual animals must make about when to disperse, when to fight, where to lay their eggs, and how to hunt for food. Reichert examines encounters among territorial grass spiders and asks what determines whether spiders back off from their disputes as opposed to engaging in escalating and potentially lethal battles. A modern development in behavioral ecology, called evolutionary game theory, is used to successfully predict frequencies of “retreats” versus “engaged battles” as a function of environmental circumstances. Game theory, with its concept of evolutionary stable strategies (ESS), has captured the imagination of behavioral ecologists because it focuses on the fact that the outcome of an organism’s behavior depends on what other animals in the population are doing—a realization that is probably a simple fundamental truth of interactions among organisms.

Of course, “game theory” is not the only way to understand behavior, as Holekamp and Sherman eloquently show with their analysis of dispersal in male ground squirrels. The beauty of Holekamp and Sherman’s research is that it addresses both proximate (physiological) and ultimate (evolutionary) explanations for dispersal behavior in squirrels. Finally, studies of individual behavior lend themselves to elegant experiments, something exemplified in the research reported by Prokopy and Roitberg. Ingenious arrays of “model lures” are used to isolate the cues flies use when laying their eggs on fruit such as apples. This represents a case in which fundamental understanding of a pest’s behavior yields practical, environmentally sound methods for pest control.

The final two papers in this section explore the life history strategies of organisms. Cook analyzes the demography of ramets (genetically identical modules of the same genetic unit) to understand why clonal growth in plants is so extraordinarily successful, leading in some cases to single clones that occupy almost half a million square meters. Cook's perspective introduces a way of looking at clones that raises questions of "clonal foraging behavior" and "developmental decisions." Jackson and Hughes meld Cook's perspective with quantitative data on lifetime success to contrast clonal versus sexual reproduction among invertebrates, espe-

cially corals. The result is striking evidence for the great advantage of rapid clonal expansion in disturbed environments. The central idea in Jackson and Hughes' analysis is that fundamental "investment strategies"—trade-offs in the allocation of resources to growth, maintenance, and sexual reproduction—underlie the life history patterns we observe among invertebrates. This notion of critical trade-offs is one of the unifying ideas in evolutionary ecology, and underlies most predictions about how organisms should develop, behave, or be designed in different environments.

The Patterns of Mammalian Hibernation

Alan R. French

Most of the food eaten by mammals is used for generating heat to maintain their relatively high and constant body temperatures. Obviously the advantages of this internal heat production offset its energetic costs—mammals would not be so successful if it were otherwise. However, strongly seasonal environments may present formidable thermoregulatory challenges to small mammals. Energy demands increase during cold winters at the same time the productivity of the environment declines, and snow cover frequently prevents foraging well into the spring (Fig. 1). In such habitats, many mammals that do not migrate must temporarily rely on stored energy supplies. Should these energy stores be inadequate for the continuous maintenance of high body temperatures—a thermoregulatory state known as euthermy—a mammal's survival depends on its ability to reduce energy consumption by allowing itself to cool and hence become torpid. Some of the smaller hibernators are capable of reducing their rates of metabolism as much as a hundredfold.

Even though the energy savings of torpor can be substantial, no mammalian hibernator remains continuously at low body temperatures all winter. All hibernators rewarm and then briefly maintain high body temperatures at periodic intervals throughout the dormant season. The universal occurrence of these arousal episodes suggests that, even within the confines of a secluded cave or underground burrow, high body temperatures are somehow adaptive.

It seems reasonable to assume that natural selection would favor a compromise between these opposing selection pressures, between the presumed advantages of the euthermy common to all mammals and the necessity for torpor in the face of energy shortages. Accordingly, hibernators would be expected to remain torpid no more than necessary to ensure survival. If so, then the total amount of time spent in torpor should be correlated with the energetic constraints on an individual during

Figure 1. (Next page) This adult male ground squirrel (*Spermophilus beldingi*) has emerged from hibernation through the snowpack at a high elevation in the Sierra Nevada well before green vegetation is available. Such an early emergence in anticipation of the appearance of the females is an energetic gamble, which requires that the males have ample post-hibernation stores of fat. (Photo courtesy of P. Sherman.)

the winter. As will be elaborated below, these energetic constraints are a function of the size of the hibernator and its method of storing energy.

Hibernators can be classified as either those that store energy in the form of body fat or those that rely predominantly on stored food, a fundamental distinction that is usually unambiguous. Although some hibernators that become obese also occasionally cache food, such stores do not appear to be necessary for successful hibernation, are usually small when found in natural areas away from agricultural development, and may not be consumed until hibernation is terminated in the spring (Shaw 1925). Likewise, species that rely on stored food also may deposit some fat, but such internal stores usually represent a minor component of the total energy available.

The physical limitations of fat storage permit a theoretical analysis of the energetic problems facing hibernators that store fat. This in turn provides a framework for understanding the observed differences among their patterns of thermoregulation during dormancy.

Energetic consequences of size

In general, large mammals can fast for a longer period of time than can small ones, a phenomenon governed by the fact that the capacity to store fat and metabolic rate are related differently to body size (Morrison 1960). The capacity to store fat is directly related to mass (mass^1). In contrast, the rate at which energy is used to maintain euthermy is proportional to $\text{mass}^{3/4}$ at warm temperatures where metabolic rates are at basal or minimal levels (Kleiber 1947); the rate varies approximately with $\text{mass}^{1/2}$ at colder temperatures where resting metabolism is elevated above basal levels (Herreid and Kessel 1967). Therefore, as body size increases, the ability to store fat increases faster than the rate at which fat is metabolized. Small mammals will starve within a few days unless they become torpid, but large mammals can remain warm for many months without eating. In fact, although many large mammals have long dormant seasons, no mammal over approximately 5 kg in mass has evolved the capacity to reduce its body temperature more than a few degrees. This observation reinforces the idea that it must be very important for mammals to maintain high body temperatures if they can possibly do so.

Thermoregulatory strategies of hibernating mammals balance the need to conserve energy over the winter and the demands of springtime reproductive success



These relationships demonstrate that even among those mammals that must hibernate, large species are less constrained by energy requirements than are small ones. The deficit between the energy available and the energy needed to maintain high body temperatures during a dormant season of fixed duration is inversely proportional to body size (Fig. 2). This theoretically presents large hibernators with several options. In comparison with small individuals, they potentially can have longer hibernation seasons, deposit proportionately less fat prior to hibernation, spend more time at high body temperatures, or finish hibernation with proportionately more fat unused.

There is no evidence that large hibernators either have longer dormant seasons or put on proportionately less fat than small hibernators. Variations in the duration of dormancy appear to be related to climatic conditions and not to body size. For example, jumping mice and marmots differ by two orders of magnitude in mass, but they frequently live together in montane meadows, where they may go without eating for eight months or more out of the year (Cranford 1978; Andersen et al. 1976). Fat content is also variable but unrelated to body size. Small jumping mice may enter hibernation with

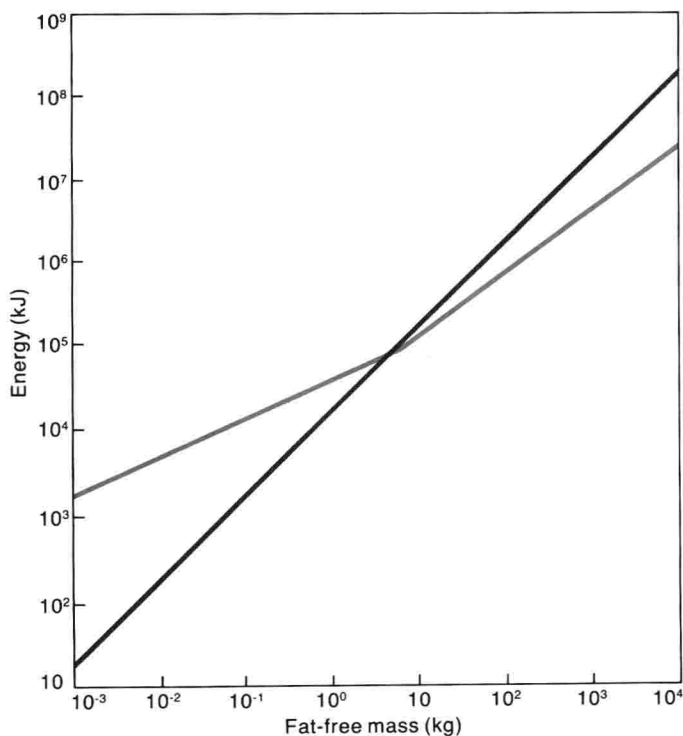


Figure 2. The energy available to mammals when fat is 50% of body weight (gray line) and the energy necessary to maintain high body temperatures (red line) are related differently to body size. Energy requirements were calculated for mammals resting for a period of six months at a temperature of 5°C; the slope of the line changes because large mammals metabolize at basal levels at this temperature but small mammals do not. These relationships indicate that although large mammals consume more food each day, they can also go without eating for much longer periods of time than can small mammals. As lean body weight falls below about 5 kg, the energy available from body fat becomes increasingly inadequate for the continuous maintenance of high body temperatures, and the selection pressures for the use of torpor increase commensurately.

50% of their weight as fat (Cranford 1978), but equally small or smaller bats often deposit only half that percentage (Kruhin and Sealander 1972). This range of values is similar to that found in some of the largest marmots (Andersen et al. 1976).

In contrast, the amount of time spent at high body temperatures during dormancy is directly related to size. Large hibernators arouse only slightly more frequently in midwinter than do small ones, but the duration of their euthermic intervals is much greater (French 1985). Small bats usually remain euthermic for only one or two hours, whereas large marmots maintain high body temperatures for about a day at a time (Fig. 3). The duration of these euthermic episodes increases with size at about the same rate that mass-specific rates of metabolism decrease (French 1985). This means that the longer arousal episode of a large hibernator costs proportionately the same amount as the shorter one of a small hibernator. It also means that large and small hibernators starting with the same percentage of body fat can have hibernating seasons of about the same length, despite their differing rates of metabolism.

In addition, large hibernators are more likely than small ones to terminate their hibernation seasons spontaneously before food becomes available and, as a result of this early termination, to start their active seasons with relatively large fat reserves. Often such individuals remain euthermic for several weeks before feeding (Snyder et al. 1961); their energy stores are necessary for survival after hibernation and, in some cases, for reproductive activities during the spring. This thermoregulatory strategy is associated with an early onset of breeding, the selective advantage of which is also related to body size.

Reproductive consequences of size

Large hibernators should resume activity and begin breeding earlier in the spring than small hibernators, because both the need for an early emergence and the ability to overcome the energetic risks involved with such behavior increase with increasing size. Time, like energy, is at a premium for hibernators. The longer they are forced to remain dormant, the less time they have for reproduction and preparation for the next hibernation season. These time constraints increase with increasing body size, because gestation and juvenile growth are slower in large species than in small ones (Western 1979). However, there are energetic risks associated with an early emergence, because environmental conditions in the spring can be unpredictable. Obviously if hibernators become active before food is available, they run the risk of starving, especially in years when springtime conditions are delayed. Even the synchronization of emergence with the first appearance of food is perilous, because those resources may prove to be ephemeral in the face of late-season storms (Morton and Sherman 1978). The longer a hibernator waits to emerge, the more it will be assured that the environment will be hospitable, but the less time it will have to breed.

The timing of emergence should represent a balance between these constraints of time and energy. Large species need more time for reproduction, and by virtue of their large size they can afford to gamble more with their energy reserves to attain it than can small species.

On the other hand, small hibernators must employ a conservative thermoregulatory strategy in the spring, but they can afford to do so, and thereby to delay breeding, because their young reach adult size more quickly.

An accurately timed emergence is of value to hibernators of all sizes, and there are numerous examples to indicate that the resumption of activity in the spring is synchronized with relatively unpredictable changes in weather conditions (Michener 1984). In the most extreme case, members of a high-altitude population of Belding's ground squirrels (*Spermophilus beldingi*) emerged six weeks earlier in the year with the lowest snowfall and earliest snowmelt on record than they did in the year with the heaviest snowfall and latest snowmelt (Morton and Sherman 1978). The synchrony between emergence dates and climatic changes occurs despite the fact that hibernators spend the winter underground or in caves where they are insulated from most changes in the weather. Apparently many species assess environmental

conditions at or near the entrances to their dens, and it stands to reason that the more frequently this is done, the more accurately their emergence can be timed. Such assessment requires hibernators to be alert and mobile, and thus there are selective advantages in increasing the time spent at high body temperatures at the time of year when appropriate conditions for emergence are likely. In other words, the frequency and duration of arousal episodes should change during the course of the dormant season, because the benefits of euthermicity change relative to the costs.

The magnitude of this springtime increase in euthermicity should increase as body size increases, because large species accrue more reproductive benefits from an early and accurately timed emergence than do small species. A spontaneous termination of hibernation in the absence of food or environmental change can be viewed as the culmination of this trend. Furthermore, intraspecific differences should occur whenever there are large differences in size among individuals in a population, or when not all individuals breed.

Long-term hibernators

The ramifications of body size can be seen clearly in a comparison of the patterns of thermoregulation exhibited by three hibernators that live sympatrically in many mountainous areas of the western United States. Yellow-bellied marmots (*Marmota flaviventris*), Belding's ground squirrels, and western jumping mice (*Zapus princeps*) span two orders of magnitude in size, yet all face approximately the same climatic conditions and often must rely exclusively on stored fat for eight or more months out of the year. The intermediate-sized Belding's squirrels are one of the most thoroughly studied hibernators from

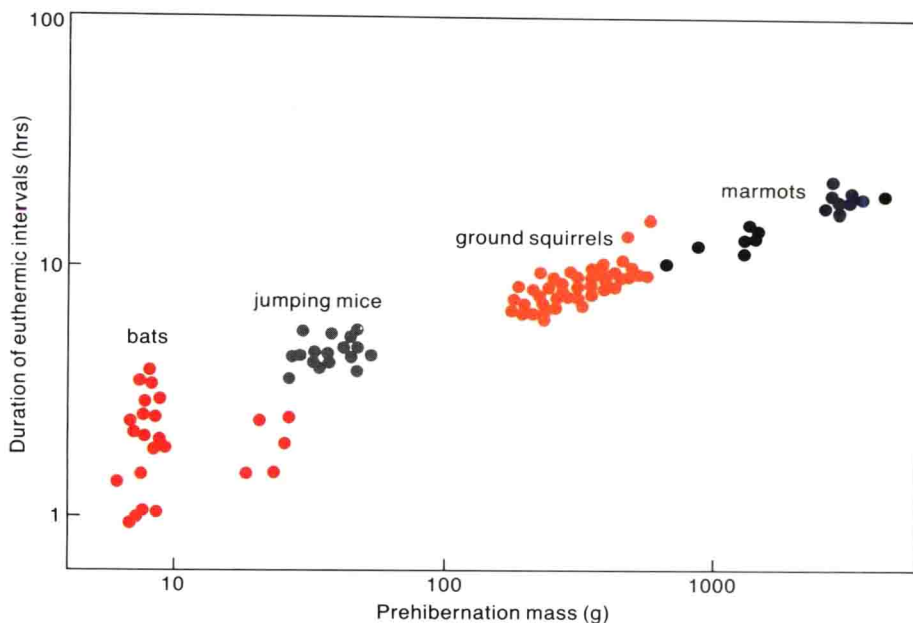


Figure 3. Large hibernators kept at 5°C spend more time at high body temperatures during each arousal episode in midwinter than do small hibernators. The duration of the arousal increases or decreases with mass^{0.38}, whereas the basal metabolic rate is proportional to mass^{-0.38} (French 1985; Kayser 1950). This match suggests that hibernators remain awake until they have completed a fixed amount of metabolism. Thus small and large hibernators with the same percentage of body fat can have hibernating seasons of equal length.

both physiological and ecological perspectives, and they provide a good basis of comparison for other species.

All Belding's squirrels increase the time they spend at high body temperatures toward the end of the dormant season, but the extent of this energetic gamble varies as a function of sex and age (French 1982). These animals are sexually dimorphic with respect to body size at maturity; large adult males spontaneously terminate hibernation, whereas females and small, nonbreeding males (yearlings) hedge their bets. These latter groups increase the frequency at which they arouse in the spring but do not stop hibernating until they are fed (Fig. 4).

Because Belding's squirrels do not reach adult size in their first year, it is beneficial for females to breed as soon as possible and thereby to maximize the time their offspring have to grow and deposit fat before their first hibernation season. At high elevations in the Sierra Nevada, females hibernate in areas of the meadows that first become free of snow in the spring, and they synchronize their emergence with the snowmelt and the availability of green vegetation near their burrow entrances (Sherman and Morton 1979). Presumably the consumption of this food triggers the physiological termination of hibernation and the continued presence of the females above ground. The increasing frequency of arousal in the springtime most likely improves the accuracy with which they can time their emergence, but the benefits of a commitment to continuous euthermicity before food becomes available appear to be slight compared to the risks involved.

Adult males are active in the early spring, and at high elevations they regularly tunnel through the snowpack to reach the surface (Morton and Sherman 1978). It appears that the endogenously timed termination of their hibernation allows them to anticipate the emer-

gence of females. This is advantageous because female ground squirrels become sexually receptive a few days after they come above ground, and a male that is late to emerge would find females that had previously emerged already impregnated. However, because females time their emergence to coincide with the first availability of food, males are forced to fast while waiting for their potential mates to appear. This is a substantial energetic gamble, and the large size and concomitant fat storage capabilities of adult males are clearly adaptive. Nevertheless, males rarely survive as long as females (Morton and Parmer 1975).

Small yearling males do not have the energy stores necessary to undergo a prolonged fast at euthermic body temperatures; nor would they gain much by doing so, because sexual maturation and breeding do not usually occur until males are two years old (Morton and Gallup 1975). Their open-ended hibernation seasons and delayed emergence thus facilitate survival over the winter.

The differences between adult and immature males appear to be related to differences in their size and fat content rather than their age. Juveniles kept under ideal laboratory conditions attain adult weight in their first

summer, and they also spontaneously terminate hibernation and become reproductively active as yearlings the following spring. Conversely, males two years and older that fail to deposit normal quantities of fat have open-ended hibernation seasons and do not mature sexually (French 1982).

Intraspecific differences in the patterns of hibernation also occur in yellow-bellied marmots, which as adults are an order of magnitude larger than Belding's squirrels. Adult marmots of both sexes spontaneously stop hibernating, but the smallest juveniles do not (Fig. 4). Marmots grow more slowly than ground squirrels, and winter mortality of juveniles is inversely related to their weight at the start of dormancy (Armitage et al. 1976). To help compensate for this slow growth, marmots emerge and begin breeding early in the spring, well before there is food to eat (Andersen et al. 1976). In contrast to the smaller ground squirrels, the larger size of female marmots enables them to remain at high body temperatures and undergo the energy drains of early pregnancy while fasting. The smallest juveniles do not stop hibernating until they are fed, even though they are over twice as large as adult male ground squirrels.

Apparently there is little value for these large but immature mammals to make such an extreme energetic gamble, because neither sex breeds as a yearling (Andersen et al. 1976). In fact, yearlings usually emerge above ground a month after breeding adults (Carey 1985).

Western jumping mice are an order of magnitude smaller than Belding's squirrels, and all individuals have open-ended hibernation seasons (Fig. 4). However, males do arouse more frequently than females

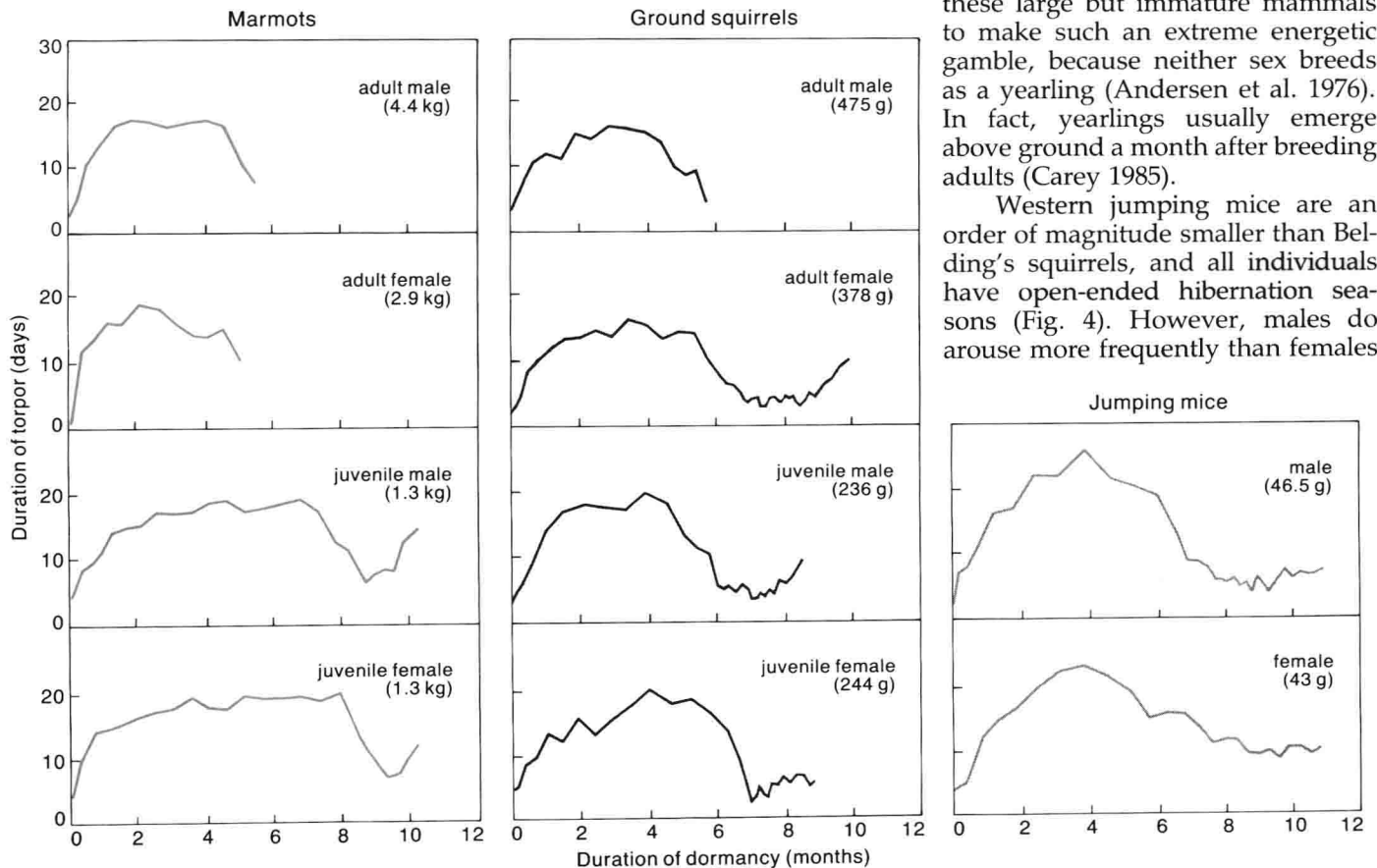


Figure 4. The duration of sequential episodes of torpor changes over the course of the hibernation season, as shown here for three representative mammal species kept at a temperature of 5°C over a period of months. These changes reflect the shifting balance between the benefits and costs of high body temperatures. For example, female and juvenile ground squirrels have briefer episodes of torpor and arouse more frequently in the spring than in the winter, enabling them to assess conditions near their burrow entrances and thus to time their emergence more propitiously. These squirrels continue to hibernate if spring is delayed, and their

torpor often lengthen as they begin to run out of fat reserves and energy conservation becomes more important than an accurately timed emergence. By contrast, adult male squirrels spontaneously terminate hibernation before their stores of fat are depleted in anticipation of the emergence of the smaller females, which become sexually receptive as soon as they appear above ground. In the experiment, bouts of torpor ended spontaneously in adult marmots of both sexes and in adult male ground squirrels; torpor ended in the other animals only when they were fed.

during the spring phase of hibernation, and like most other rodent hibernators, they emerge one to two weeks earlier as well (Brown 1967). Therefore, even in a species strongly constrained by energy, males gamble more with their fat stores than females. Nevertheless, the mice are conservative, emerging only after the snow has melted and the soil at the depth of their winter nests has begun to warm (Cranford 1978). The relatively rapid growth rates of jumping mice more than compensate for their late dates of emergence, and even at high altitudes youngsters grow to near adult size in the summer of their birth and breed the next spring.

Long-term hibernators at the extremes of body size mate prior to dormancy. For example, bears (family Ursidae) need to do so because the development time of their offspring is so long. They complete gestation and lactation during dormancy, and their young are mobile at the time of spring emergence and are ready to feed soon thereafter. Bears can do this because they are so large that they need not reduce their body temperatures during their winter fast (Hock 1960).

At the other extreme are many species of insectivorous bats, the smallest and most energetically constrained hibernators, which also are the only mammals that undergo delayed fertilization (Fig. 5). Mating occurs prior to or occasionally during dormancy, sperm is stored in the female reproductive tract over the winter, and ovulation and fertilization take place as soon as the females resume activity in the spring (Wimsatt 1969). This remarkable reproductive strategy helps to alleviate the delay in offspring development imposed by an insectivorous diet. Flying insects can be an ephemeral food resource early in the spring, and pregnant bats lower their body temperatures following nights of poor foraging, slowing gestation as a result. Pregnancy has been known to last over three months when the prevalence of torpor is high (Pearson et al. 1952).

The energetic constraints of their small size dictate that bats have a conservative hibernation strategy, but their prolonged gestation favors early conception in the spring. Bats cannot afford to resume activity until flying insects first appear. If copulation occurred in the spring, females would have to delay ovulation until males emerged and became reproductively competent. Autumn mating provides females with a source of sperm early in the spring, when the availability of competent mates would otherwise be at best unpredictable.

Patterns of thermoregulation have not yet been well documented for hibernating bats, but available data indicate that some species have relatively short torpors in the spring (Twente et al. 1985). It may turn out that female bats have more frequent arousals than males. Females must initiate pregnancy as soon as possible, but males, with females already inseminated, need not gam-



Figure 5. Many bats hibernate communally, like these cave bats (*Myotis velifer*), and winter aggregations may number in the thousands. This clustering may help tiny bats to conserve heat during their arousal episodes in much the way a nest helps insulate a rodent. Most females are inseminated before hibernation. Males store previously produced sperm, however, and during their brief arousals they will occasionally copulate with torpid females nearby. (Photo courtesy of T. H. Kunz.)

ble as much with their limited energy reserves in order to achieve an early emergence. In fact, among little brown bats (*Myotis lucifugus*), males have been known to remain hibernating in caves well after females have departed (Fenton 1970).

Short-term hibernators

The analysis so far has been restricted to long-term hibernators in order to illustrate the effects of body size. However, the costs and benefits of torpor also vary in response to environmental conditions. Species of similar size may have dissimilar reproductive strategies and patterns of thermoregulation if their dormant seasons are of substantially different durations.

This point is well illustrated by a comparison between thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), which remain underground for at least eight months out of the year (McCarley 1966), and round-tailed ground squirrels (*S. tereticaudus*), which are dormant for only half as long (Dunsford 1977). Both species are about half the size of Belding's squirrels, and thus one might predict that they would be energetically more conservative during dormancy than their larger cousins. This is true for the long-term hibernator *S. tridecemlineatus*; both males and females have open-ended hibernation seasons when kept at 5°C without food. In the desert-dwelling *S. tereticaudus*, however, females have open-ended hibernation seasons but males of all sizes and ages spontaneously terminate hibernation. A short dormant period allows these small male squirrels to start their active seasons with relatively large fat reserves, and thereby makes the risk of starvation before food becomes available relatively small.



Figure 6. An energetic strategy based on stored food rather than fat deposits is exemplified by this chipmunk (*Tamias striatus*), which has stuffed its cheek pouches with 93 ragweed seeds. The energy content of this animal's winter store is not limited by its size, and thus it need not spend as much time in torpor over the winter as a similar-sized hibernator that stores energy as fat. (Photo courtesy of K. Maslowski/Photo Researchers.)

Similarly, American badgers (*Taxidea taxus*) often live in environments with long winters, but because of their carnivorous diet, food is unavailable for a relatively short period and activity ceases for only two and a half to three months during the coldest years. Although badgers are not much different in size from the larger marmots, their patterns of thermoregulation during dormancy differ greatly; badgers allow their body temperatures to fall from 38°C to 29°C only during irregular torpors of about a day in duration (Harlow 1981). Again, we see that need and ability to reduce body temperatures are closely matched.

Hibernators that store food

The constraints of body size on energy availability during hibernation have been circumvented by species that store food (Fig. 6). For example, a bat weighing 8 g must survive all winter on less than 8 g of fat, but a pocket mouse weighing 8 g can easily store 25 to 50 times that amount of energy in the form of seeds. If high body temperatures are advantageous, then species that store food should not spend as much time in torpor as similar-sized species that deposit fat. Furthermore, if the energy content of food caches increases with body size in a

fashion similar to that of fat deposits, then large species that rely on stored food should be euthermic more than small species.

Data from both the smallest and largest hibernators that store food indicate again that high body temperatures tend to be maximized during dormancy. Many of the tiny pocket mice in the genus *Perognathus* are seasonal hibernators, and some remain underground ten months out of each year (O'Farrell et al. 1975). These mice may experience over a hundred arousal episodes, each lasting several hours, whereas a similar-sized bat may awaken for only an hour or two on fewer than two dozen occasions throughout the winter. The longest torpors in pocket mice are less than a week (French 1977); in bats they are over a month (Menaker 1959). Comparatively large chipmunks, *Tamias striatus*, also remain torpid for less than a week at a time, but torpor is infrequent in many individuals and may not occur at all in some, even though they remain underground for several months (Maclean 1981).

Differences between large and small species do exist and are similar to those observed in hibernators that store fat. Both male and female *Tamias* usually stop hibernating spontaneously after several months in the cold, but small pocket mice continue to hibernate until they run out of food or experience an increase in environmental temperature. However, pocket mice do increase the time they spend at high body temperatures in the spring, and the magnitude of this increase is greater in males than in females. Furthermore, the more food these mice store, the less time they spend in torpor (French 1976); this indicates both the importance of high body temperatures and the ability of the animals to adjust their physiology to match energetic demands.

It is tempting to speculate that the energetic principles derived for species that store fat also hold for those that rely on cached food. If, for ecological reasons, external energy stores do in fact increase with increasing body size, then energy availability should match the energy necessary for continuous euthermy at a much smaller body mass for species that store food than for species that store fat. This does not appear to be an unreasonable assumption. The largest mammals that rely exclusively on stored food and also reduce their body temperatures during dormancy are chipmunks and hamsters, which weigh between 100 and 140 g and are considerably smaller than the largest mammals, 5-kg marmots, that depend on stored fat and also reduce their body temperatures.

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The Ecology of Temperate and Tropical Honeybee Societies

Ecological studies complement physiological ones, offering a new perspective on patterns of honeybee adaptation

In his masterful synthesis of insect sociology, Wilson (1971) identified three overlapping stages in the history of research on social insects: a natural history phase, a physiology phase, and a population-biology or ecology phase. Until the mid-1970s, most students of the social insects focused on the first two stages, either describing the diverse societies of termites, ants, wasps, and bees or experimentally analyzing the physiological bases of their social systems. Quite recently, ecological studies of the social insects have also flourished. As a result, we are beginning to understand the properties of social insect colonies as adaptations fixed by natural selection.

Throughout the history of insect sociology the premier object of study has been a single species of social bee: *Apis mellifera*, one of four living honeybee species. Its preeminence stems from several factors. First, honeybee societies rank among the most complex of all insect societies, with such advanced features as strong dimorphism of queen and worker, elaborate division of labor by age, precise control of nest temperature, and a remarkable system of communication based on a dance language (Michener 1974). Ease of study also favors research on honeybees. Not only are their colonies easily maintained in man-made hives of the sort used by beekeepers, but they will even live in glass-walled observation hives, enabling humans

to peer into the heart of their society.

Still another factor is surely man's ancient fascination with the honeybee. The great insect sociologist William Morton Wheeler (1923) expressed this accurately when he wrote:

Its sustained flight, its powerful sting, its intimacy with flowers and avoidance of all unwholesome things, the attachment of the workers to the queen—regarded throughout antiquity as a king—its singular swarming habits and its astonishing industry in collecting and storing honey and skill in making wax, two unique substances of great value to man, but of mysterious origin, made it a divine being, a prime favorite of the gods, that had somehow survived from the golden age or had voluntarily escaped from the garden of Eden with poor fallen man for the purpose of sweetening his bitter lot. [p. 91]

When the human fascination with the honeybee turned scientific, man began to describe and experimentally analyze the interwoven phenomena of colony life cycle, caste structure, and communication codes that make up the social organization of bees. This approach gained strong impetus from the highly crafted studies of the Nobel Laureate Karl von Frisch (1967, 1971) and continues apace today. We now understand in fair detail such topics as honeybee caste determination, sensory physiology, nest micrometeorology, and communication among colony members. In stark contrast, the ecology of honeybee societies remains a largely uncharted area of study. In short, we know a great deal about how honeybee societies work, but remarkably little about the pressures of natural selection that have shaped them.

The honeybee's dance language

provides a clear example of this imbalance between mechanistic and functional knowledge. Over the past 60 years, aided by more than 40 graduate students, von Frisch (1967) has assembled a detailed picture of the physiological mechanisms of the behaviors that unfold when a scout bee discovers a rich patch of flowers, flies back to her nest, and recruits nestmates to gather the food by using the dance language. However, the precise ecological significance of this finely tuned system of communication has until recently remained a matter of speculation. Only in the past three years have researchers begun to analyze in a systematic way how the dance language helps colonies living in nature collect their food (Visscher and Seeley 1982; Seeley, in press).

In this essay I will describe some recent developments in the ecological study of honeybee social behavior, drawing in particular on a general program of behavioral-ecological research I have conducted over the past eight years. Most of my research deals with colonies of *A. mellifera* living in the northeast region of the United States. *A. mellifera* occurs as a native in Europe, western Asia, and Africa, but has been introduced throughout the world by man. A smaller portion of the research program considers the ecologies of the three other honeybee species: *A. florea*, *A. cerana*, and *A. dorsata*. Except for *A. cerana*, whose range extends north into China and Japan in eastern Asia, these three species are found only in southern Asia.

Colonies living in nature

Wild colonies of honeybees have been hunted by the peoples of Asia, Africa, and Europe for hundreds if not thousands of years (Crane 1975).

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Thus man has long had contact with honeybee colonies in nature, but with the intention of robbing them of their beeswax and honey, not studying them. When, in the 1500s, Europeans turned from exclusively plundering bees to also examining the fundamental facts of honeybee life, they observed bees living in man-made hives. To the present day, virtually all scientific research on honeybee biology has been conducted with colonies occupying beehives placed in locations that are convenient for scientists. For example, much of von Frisch's pioneering research on honeybee communication was carried out in the courtyard of the Munich Zoological Institute, a converted monastery in the heart of a city.

An important first step in studying honeybee ecology, therefore, was to describe the nests and life history of wild colonies of *A. mellifera*. This required turning away from colonies living in man-made hives in ecologically disturbed habitats and instead studying colonies inhabiting hollow trees in forests—in this case colonies found in the countryside near Ithaca, New York (Fig. 1). We located wild colonies either through information from local residents or by beelining, the old bee hunter's technique of inducing bees to forage from a comb filled with sugar water and then tracing the bees back along their flight lines until the bee tree is reached (Edgell 1949). Some of the bee trees were felled to collect the colonies and dissect their nests. Others were left standing for long-term observations of colony mortality. To determine the distinctive reproductive patterns of wild colonies, we simultaneously studied reproduction in colonies living in man-made hives the same size as the tree cavities occupied by wild colonies.

When allowed to remain in hollow trees in the forest, honeybee colonies live quite differently than they do when they inhabit a beekeeper's or bee researcher's standard beehives. Whereas a beekeeper desires a large, nonreproducing colony capable of stockpiling a vast quantity of honey (much more honey, in fact, than the colony would ever need), wild colonies grow to only one-third to one-half the population size, sequester only as much honey as they need, and devote their remaining



Figure 1. A knothole that serves as the entrance to an *Apis mellifera* nest is visible high up in the left fork of this intact bee tree in central New York State (above). A cross-section through a typical nest (right) shows what lies beyond the entrance. Layers of vertical comb nearly fill the tree hollow. Honey is stored in the upper region, pollen is packed in a narrow band directly below, and brood is reared in the lowermost portion of each comb. Queen cells house the new queens before swarming; drones occupy special cells at the edge of the nest. A polished layer of propolis, or tree resins, seals the nest cavity. Before a swarm occupies such a cavity, scouts carefully check its suitability by measuring the volume of the cavity and noting the size of the entrance opening, its compass orientation, and its proximity to the floor of the cavity. (All photographs by the author; sketch after Seeley and Morse 1976.)

