DORMANCY

Contact Information

Professor Philip C. Withers
Zoology, School of Animal Biology M092
University of Western Australia
Crawley, Western Australia
6009 AUSTRALIA
pwithers@cyllene.uwa.edu.au
telephone: +61 8 6488 2235
facsimile: +61 8 6488 1029

Dr Christine E. Cooper
Environmental Biology
Curtin University of Technology
PO Box U1987
Perth, Western Australia 6845
AUSTRALIA
e-mail C.Cooper@curtin.edu.au
Telephone: +61 8 9266 7965
Facsimile: +61 8 9266 2495

Keywords

Hibernation, aestivation, dormancy, torpor, metabolic depression, diapause, ectotherm, endotherm, arousal, Q_{10}, circadian, circannual, cryobiosis,

Synopsis

Dormancy or torpor is a widely-recognized behavioral and physiological state of both animals and plants that generally indicates inactivity and reduced metabolic rate. It can involve very different physiological states in response to a variety of environmental stimuli, including temperature, water, or food. It can last < 1 day, may occur for a few consecutive days, or may last an entire season or even many years. Torpor involves physiological changes related especially to body temperature, metabolism and water balance. Hibernation is when an organism spends the winter in a state of dormancy; it is long-term multi-day torpor for survival of cold conditions. Estivation is summer dormancy, for survival of hot and dry periods. The general roles of torpor, hibernation or estivation are avoidance of unfavorable or lethal short- or long-term (seasonal) climatic conditions and conservation of energy during this period of inactivity. Seasonal dormancy allows species to exploit ephemeral environments and colonize habitats that would otherwise be unsuitable for growth or survival at certain times of the year. There are costs to dormancy and torpor, but the advantages contribute to the fitness of individuals and species that use it.

Article:
503 Dormancy

Dormancy

P C Withers, University of Western Australia, Crawley, WA, AUSTRALIA

C E Cooper, Curtin University, Bentley, WA, AUSTRALIA

Introduction

Dormancy is a widely-recognized behavioral and physiological state of both animals and plants that generally involves inactivity and reduced metabolic rate (Figure 1). Torpor is a similar term to dormancy, meaning inactivity or lethargy. Dormancy or torpor can involve very different physiological states, in response to a variety of different stimuli, including low temperature, high temperature, lack of water, or lack of food. It can be a short-term event (< 24 hours), can occur for a few consecutive days, or may last an entire season or even many years. Dormancy can also involve a developmental arrest (diapause). Cryptobiosis, which literally means 'hidden life', is a more extreme state than dormancy, with almost no detectable activity or metabolism. It is most prevalent in lower vertebrates, and is often a seasonal survival strategy to cold or desiccation.

<Figure 1 near here>

Cryptobiosis

This state of "suspended animation" has been observed for a variety of invertebrate animals and plants during extreme environmental conditions. It was first described for invertebrate animals that survived an absence of water by becoming inactive and allowing their tissues to become desiccated (anhydrobiosis e.g. rotifers). Two other forms of cryptobiosis also involve an altered state of cell water, freezing temperatures (cryobiosis e.g. a frozen insect) and high osmotic concentration (osmobiosis e.g. brine shrimp eggs in a salt lake). Another form of cryptobiosis is survival of a lack of oxygen (anoxybiosis e.g. killifish eggs sealed inside their egg capsule). The best known example of cryptobiotic animals is probably the eggs of brine shrimp (*Artemia*), which can survive extended periods of complete desiccation, high salt concentration, or anoxia; their desiccated eggs are also remarkably resistant to extremes of temperature. Various "resurrection" plants are well known examples of cryptobiotic plants, being able to recover from desiccation for extended periods. Seeds of some plants are also spectacularly resistant to desiccation, sometimes for very long periods of time (e.g. seeds more than 1000 years old of the Indian Lotus from an ancient lake bed in China).

All of these forms of cryptobiosis involve complete inactivity. Ecological advantages of cryobiosis include survival of harsh environmental conditions, and dispersal of highly resistant life stages. However, the physiological adaptations required by these animals and plants to survive extreme conditions at no detectable metabolic rate are generally complex and specialized.

Diapause and Quiescence

Diapause is an ecological strategy for the avoidance of harsh conditions that involves the cessation of development of a sub-adult life stage. It is essentially a time-delaying tactic to synchronize further stages of the life cycle with appropriate environmental conditions. Diapause is especially common in insects but is also observed in a wide variety of other invertebrate animals (e.g. brine shrimp embryos) and vertebrate animals (e.g. annual killifish embryos), as well as many plants (e.g. buds, bulbs, rhizomes and seeds). Some plant seeds require drying out before they can develop, ensuring that adverse dry seasons pass before the embryo starts to develop. Diapause is also a reproductive strategy in a variety of mammals for the delayed implantation and development of embryos (e.g. macropod marsupials, mustelids, deer).

Quiescence is a period of inactivity, similar to diapause, but is a facultative response to an immediate change in environmental conditions that is terminated simply by the resumption of more favorable environmental conditions, rather than a programmed and obligate response. It may be a response to harsh environmental conditions such as low or high temperature, or drought. Many invertebrates and plants (particually the seeds), become quiescent.

Hibernation (winter dormancy)

Hibernation is when an organism spends the winter in a state of dormancy; it is long-term multi-day torpor. Many plants survive extended periods of cold and desiccation, either as above-ground trees or shrubs, or as underground structures. Protective scales around stem tips allow buds of above-ground plants to endure winter conditions without damage. The above-ground structures of other plants die back in unfavorable conditions, leaving dormant underground bulbs, rhizomes, tubers or corms, for which the soil buffers environmental extremes. Many plants accumulate solutes in their fluids to prevent freezing during winter, while others can tolerate freezing of water in their xylem and other extracellular water pools. For ectothermic animals, hibernation is primarily a behavioral state with reduced body temperature hence activity and metabolic rate. Some use supercooling or anti-freeze solutes to avoiding freezing, or tolerate freezing of their extracellular fluids (e.g. weta crickets and wood frogs). Many endothermic mammals also hibernate (Table 1). Mammalian hibernators typically use multi-day torpor for weeks or even months (e.g. Figure 2), and attain very low T_bs (e.g. 0 to -5 C). Only one bird, the poorwill, is known to hibernate, although many other birds (and mammals) readily use single-day torpor during winter.

<Figure 2 near here>

Estivation (summer dormancy)

Estivation is summer dormancy i.e. long-term torpor during summer for survival of hot and dry periods. Many desert plants survive extended periods of high temperature and low rainfall. Some survive as desiccated seeds (5-10% water content), particularly annual species, but some survive desiccation as adults. These “resurrection” plants, such as the Rose of Jericho (*Selaginella*), can desiccate to about 5% water content during dry periods, but survive and “come back to life” after rain. Pincushion lilies similarly re-activate by regenerating from buds after rain.

Amongst invertebrates (e.g. earth worms and insects) and usually involves an inactive stage with a water-resistant covering. For example, estivating earthworms form a mucus cocoon to resist desiccation, and many insect pupae are remarkably resistant to water loss. Amongst vertebrates, fishes, amphibians and reptiles enter a similar estivation state. Fishes and amphibians often form a cocoon of dried mucus (e.g. African lungfishes) or shed epidermal layers (e.g. some desert frogs; Figure 3) to resist epidermal water loss; the cocoon covers the entire body surface except for the nostrils. Reptiles have a relatively water-impermeable epidermis and do not need to form a cocoon to reduce evaporative water loss. Estivating ectotherms typically have an intrinsic metabolic depression for energy conservation.

<Figure 3 near here>

Some mammals also estivate (Table 1). For example, desert ground squirrels enter a long-term estivation state that is physiologically similar to hibernation except for the higher T_a and T_b. Other mammals such as cactus mice and kangaroo mice use single-day torpor cycles during summer.

Thermal and energetic physiology of torpor

Torpor involves a number of physiological changes, especially related to body temperature, metabolism and water balance. These physiological changes are interrelated insofar as body temperature influences energetics, and water balance is related to both body temperature and metabolism. However, the detail of the physiological consequences of torpor differs between organisms.

Ectothermic animals and plants

For ectotherms, body temperature (T_b) is essentially equal to ambient temperature (T_a) during hibernation/aestivation. This means that any decrease in T_a during hibernation or aestivation is accompanied by a decrease in T_b, which in turn is accompanied by an exponential decline in metabolic rate (MR) as described by the Q_{10} relationship i.e

$$Q_{10} = (MR_{Tb2}/MR_{Tb1})^{10/(T_{b2} - T_{b1})} \quad \text{or} \quad MR_{Tb2} = MR_{Tb1}\, Q_{10}^{(T_{b2} - T_{b1})/10} \qquad (1)$$

where MR_{Tb2} is the metabolic rate at T_{b2} and MR_{Tb1} is MR at T_{b1}. For most physiological variables, Q_{10} is generally about 2.5. This decrease in MR results in substantial energy savings and thus a prolonged survival period in the cold.

For some ectotherms there is an unequivocal intrinsic metabolic depression during estivation that occurs without any changes in T_b (e.g. snails, fishes and amphibians).

Some plant seeds, during dormancy, are also hypo-metabolic or even ametabolic. This intrinsic metabolic depression, which is often a decrease in MR to about 20% of normal, occurs in the absence of any T_b, ionic, osmotic or any other discernable physiological perturbation. The cue for intrinsic metabolic depression would appear to be a change in environmental conditions that indicates impending potential for desiccation. Intrinsic metabolic depression is not a short-term (e.g. daily) event; it often takes about 2-4 weeks for metabolic depression to become fully developed. It is probably more important for aestivation, which has a lesser hypometabolism by lowered T_b than hibernation. The molecular or biochemical mechanisms for this intrinsic metabolic depression are not well understood; however its physiological significance is clearly extension of the hibernation/estivation period that can be survived by conserving energy.

Endothermic animals

Endothermic vertebrate animals have a fundamentally different relationship between ambient temperature (T_a) and body temperature (T_b) than ectothermic animals and plants as a consequence of thermoregulatory thermogenesis. Thermal and energetic consequences of torpor are therefore more complex for endotherms because at low T_a their MR is normally increased above basal (BMR) by metabolic thermogenesis that maintains T_b constant (normothermia). During torpor, there is a profound decrease in MR, typically to 1% or even less of normothermic MR, and a concomitant decrease in T_b often close to T_a (Figure 4). Entry into torpor appears to be a controlled physiological process, not simply an inability to thermoregulate. During torpor at moderate to high T_as, T_b declines to nearly T_a and MR declines exponentially with T_b. This is the same pattern as for ectotherms, and indicates a state of non-thermoregulation. However, if T_b decreases below a species-specific setpoint value at lowered T_a, then T_b is regulated at that setpoint by the onset of thermogenesis; this is the same as the normothermic thermoregulatory response except that the T_b setpoint is lower than for normothermia. For many single-day torpidators the torpor setpoint is about 20 ^{o}C, but it is generally much lower for hibernators (about 0-5 ^{o}C, but as low as -5 ^{o}C for arctic ground squirrels).

<Figure 4 near here>

Two mechanisms contribute to the marked decline in MR of endotherms during torpor. Defense of normal body temperature is relaxed and so the thermogenic increment in MR above BMR is eliminated. As a consequence, heat production is less than heat loss and T_b declines to close to T_a and so there is a there is a further decline in MR due to the Q_{10} effect. However, if T_a decreases below the torpor setpoint where T_b is again defended, then MR increases for thermogenesis. For most endotherms, the decline in MR during torpor is accounted for by the elimination of the thermogenic MR increment and the decline in T_b and MR with a typical Q_{10} (≈ 2.5).

Intrinsic metabolic depression is a third possible mechanism contributing to MR reduction during torpor. However, the contributions of the elimination of thermogenic MR increment and the decline in T_b and Q_{10} effect are so great that the contribution of intrinsic metabolic depression, should it occur in an endotherm, would be a relatively minor absolute energy saving.

Arousal from torpor is typically a physiologically-driven event requiring considerable thermogenesis by shivering (skeletal muscle thermogenesis) or metabolism of specialized brown adipose tissue (in placental mammals but not marsupials or birds). There is also increasing evidence that many species use passive rewarming (e.g. basking) to arouse, since it greatly reduces the metabolic cost of arousal. Long-term hibernation by mammals is not necessarily a continuous period of prolonged inactivity. It is periodically broken by a short period of arousal, then re-entry into hibernation (e.g. Figure 2). The reason for these periods of arousal and re-entry is not clear. There appears to be some physiological “need” to periodically arouse. It has been suggested that perhaps some accumulated metabolite needs to be eliminated by urination, which only occurs if the animal is normothermic.

The beneficial energy savings of torpor are clearly evident from the difference between the high normothermic MR and the greatly reduced torpid MR, even after accounting for the metabolic cost of arousal. For daily torpor, the energy saving depends on the length of the torpor bout and the depth of torpor; for a dunnart, the daily energy saving is about 36% for 13 hrs of torpor (see Figure 4). For hibernation, the daily energy saving is greater because metabolic rate is low for typically 24 hrs per day; for a hibernating ground squirrel, the energy saving is about 85% over 6 months.

There is a complex pattern of single-day torpor, multi-day hibernation, and multi-day aestivation amongst mammals and birds (Table 1) that partly reflects phylogeny but also body mass. Torpor is more advantageous for small than large species. Small species have a higher mass-specific metabolic rate and therefore benefit more from the energetic saving associated with torpor. The rate of entry into and arousal from torpor is strongly dependent on body mass. Small species enter torpor quicker because of their higher thermal conductance (higher surface-to-volume ratio) and they also arouse quicker because of their higher mass-specific MR and lower thermal inertia. In contrast, larger species cool and rewarm slower, so the energy savings are less, especially for daily torpor.

Cues for Dormancy

Many plants respond to the climatic cycle of their habitat. In particular, photoperiod, temperature and rainfall are important cues for the commencement, and also cessation of dormancy. Some species respond to long-term climatic cycles, while others undergo more immediate facultative responses to ambient temperature or water availability. For animals, single-day torpor can occur rapidly in response to short-term environmental changes, such as inclement weather. It generally occurs on a circadian cycle, corresponding to the normal period of activity/inactivity. Onset of hibernation or estivation, being seasonal long-term periods of dormancy, is a more prolonged and sometimes programmed response to an impending change in environmental conditions. For example, desert frogs initiate estivation if conditions become dry, by burrowing, forming a cocoon, and initiating intrinsic metabolic depression; this can take 3-4 weeks, but occurs independent of time of year. In contrast, hibernation by some mammals such as ground-squirrels is obligate and only occurs at a specific time of the year after a period of preparation (e.g. seeking out or constructing suitable hibernation sites, increased activity and feeding, deposition of energy stores ands changes in body fluid solutes). This pattern of obligate hibernation is controlled on a circannual cycle by cues that include shortening photoperiod and decreasing air temperature. Reduced water availability and high T_a are primary cues for estivation.

Ecological consequences of dormancy

The general roles of torpor, hibernation and estivation are avoidance of unfavorable short-term or long-term (seasonal) climatic conditions and conservation of energy during this period of inactivity. Seasonal dormancy also has obvious ecological benefits. It allows species to exploit ephemeral environments. Hibernation and estivation enable species to colonize habitats that would otherwise be unsuitable for growth or survival at certain times of the year due to harsh environmental conditions. Timing of active life stages or generations can be optimized. Seasonal dormancy therefore contributes to the fitness of individuals and species.

There would also appear to be costs associated with torpor. Many species do not use or survive torpor, and species capable of torpor do not necessarily use it on a routine basis. There is a fundamental physiological advantage (at least for endotherms and even for many ectotherms) of maintaining a high and stable body temperature e.g. growth, digestion, muscle contractility, immunological defense. There is also a physiological danger of thermal death or being unable to arouse if the T_a becomes too low (e.g. freezing), or death if energy reserves become insufficient for arousal. Ecological costs of torpor could include vulnerability to predation, competition from con-specifics that do manage to successfully forage, reduced reproductive success and lower rates of essential activities such as cell division and digestion. There are also similar and additional costs of seasonal dormancy. It can delay reproduction and development, diminish post-hibernal reproduction, require that short-lived species survive for longer, and result in sex-biased populations if there is differential survival based on gender. For multi-day torpor by endotherms, there appears to be a necessity for periodic arousal, suggesting some physiological requirement for an occasional return to a high T_b (see above).

Further Reading

Dausmann, K. H., Glos, J., Ganzhorn, J. U. and Heldmaier, G. (2005). Hibernation in the tropics: lessons from a primate. *Journal of Comparative Physiology B* **175**, 147-155.

Geiser, F. (1994). Hibernation and daily torpor in marsupials: a review. *Australian Journal of Zoology* **42**, 1-16.

Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Reviews of Physiology* **66**, 239-274.

Gwinner, E. (1986). Circannual rhythms. Berlin: Springer-Verlag.

Guppy, M. G. and Withers, P. C. (1999). Metabolic depression in animals: physiological perspectives and biochemical generalizations. *Biological Reviews* **7**, 1-40.
Hochachka, P. W. and Guppy, M. (1987). Metabolic arrest and the control of biological time. Cambridge: Harvard University Press.
Keilin, D. (1959). The problem of anabiosis or latent life: history and current concept. *Proceedings of the Royal Society of London* **150**, 149-191.
Storey, K. B. (2001). Molecular mechanisms of metabolic arrest. Life in limbo. Oxford: Bios Scientific Publishers.
Tauber, M. J., Tauber, C. A. and Masaki, S. (1986). Seasonal adaptations of insects. New York: Oxford University Press.
Wang, L. C. H. (1978). Energetic and field aspects of mammalian torpor: the Richardson's ground squirrel. In Wang, L. C. H. & Hudson, J. W. (eds) Strategies in Cold. Natural Torpidity and Thermogenesis, pp 109-145. New York: Academic Press.
Withers, P. C. (1992). Comparative animal physiology. Philadelphia: Saunders College Publishing.

Tables

Table 1. Summary of torpor patterns in monotreme, marsupial and placental mammals, and birds, for single-day torpor (T), hibernation (H), or estivation (E).

Taxon	Torpor pattern
MONOTREMATA	
Tachyglossidae	H
Ornithorhynchidae	-
METATHERIA	
Didelphidae	T
Microbiotheriidae	H
Dasyuridae	T
Myrmecobiidae	T
Petauridae	T
Burramyidae	H
Acrobatidae	H
Tarsepididae	T
EUTHERIA	
Rodentia	T, H, E
Insectivora	T
Chiroptera	T, H
Carnivora	T, H?
Primates	T?, H/E
Macroscelidae	T
AVES	
Coliiformes	T
Trochiliformes	T
Strigiformes	T
Caprimulgiformes	T, H
Columbiformes	T
Coraciformes	T
Passeriformes	T

Illustrations

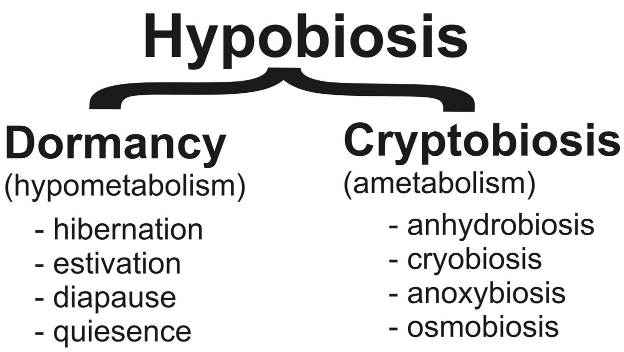

Figure 1. Schematic summer of different hypobiotic (metabolism less than normal), including hypometabolism and ametabolism. Adapted from Keilin (1959).

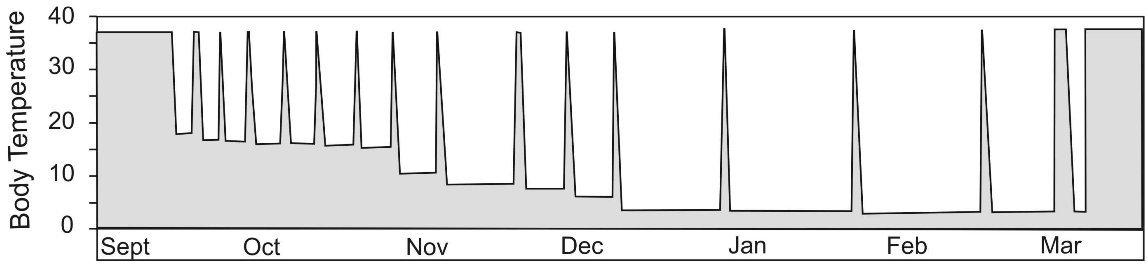

Figure 2. Pattern of body temperature during a seasonal hibernation cycle for a groundsquirrel. Modified from Wang (1978).

Figure 3. Aestivating frog (*Cyclorana cultripes*) in cocoon of shed skin. Photograph by G. Thompson and P. Withers.

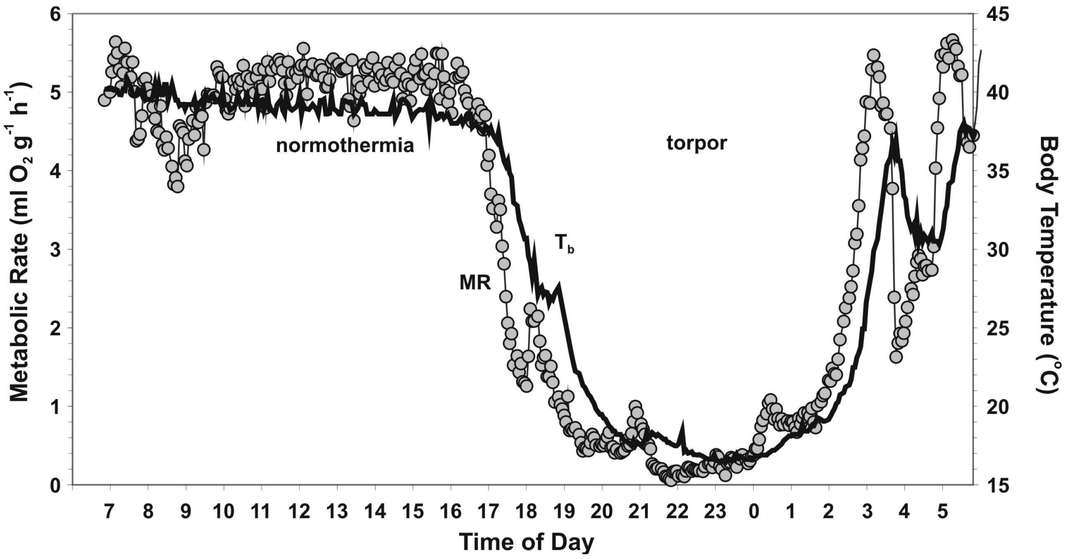

Figure 4. A daily torpor cycle in a typical single-day torpor mammal, the dunnart *Sminthopsis macroura*, showing the decline in T_b and MR during entry into torpor, a short period of sustained torpor, and then the increase in T_b and MR during arousal from torpor. Data from F. Geiser.

Permissions

Figure 1. Not required - adapted from Keilin (1959).

Figure 2. Not required - adapted from from Wang (1978).

Figure 3. Not required - photograph by P. Withers and G. Thompson.

Figure 4. Permission granted by F Geiser for use of data to redraw figure (see email).

Cross-references

Endotherms, Poikilotherms, Homeotherms, Freezing and Thawing, Animal Physiology, Environment, Physiological Ecology, Plant Physiology,