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S22-1 Heterothermia and torpor in birds: highly specialized physiological ability or just deep "nocturnal hypothermia"? — The limitations of terminology

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Abstract Advances in thermal physiology, especially of torpor and related phenomena, are complicated by wide inconsistencies in the use of terms for describing thermoregulatory states. We compare definitions given by the IUPS Thermal Commission (2001) and Swan (1974), which epitomize the variety in terminology. "Hypothermia" is the most widely disputed of the terms because in human physiology and clinical applications it describes a pathological state associated with thermoregulatory breakdown. We maintain that a term employed primarily for a pathological state should not be used; or if so, it should they be qualified by adjectives such as "regulated" or "controlled" to account for the fact that torpor is not a functionally primitive mode of thermoregulation. The terminology for the physiology of hypometabolic states such as torpor and hibernation should be directed towards one which clearly distinguishes between terms that are descriptive and those that are mechanistic. It also seems desirable to separate the terminology used for the physiology of wild animals from that commonly applied to human physiology and clinical attributes. We further stress the lack of common standards for describing even basal metabolic rate and corresponding body temperatures, especially with regard to the phase (activity, α; or rest, ρ) of the daily cycle within which measurements are taken. Here rest (ρ) phase values are recommended as the standard of reference.

Key words Terminology, Hypothermia, Heterothermia, Body temperature, Torpor

1 Introduction

We review current information on the terminology of the phenology of avian body temperatures (T_b), with emphasis on the definitions of T_b involving euthermic and heterothermic birds. The questions addressed are: what is the euthermic T_b of birds? How should deviations from this "normal" level be defined? What mechanisms underlie the patterns of heterothermia, and does terminology define them adequately? Mean euthermic T_b for birds in the rest phase (ρ phase; Aschoff and Pohl, 1970) is 38.5 ± 0.96 C (± *SD*; *n* = 202 species, 26 orders), irrespective of phylogenetic relationships and body mass (Prinzinger et al., 1991). Values below the mean resting T_b are commonly regarded as representing "hypothermia". Use of this term, nevertheless, is confusing because in the context of human physiology, as well as in some research on the physiology of wild animals, it is used to for *pathologically* depressed T_b. Torpor in birds, however, is a process clearly under permanent control of the hypothalamic regulatory systems, and does not reflect a failure of thermoregulation. So use of such terms and definitions as hypothermia is ambiguous, both descriptively and mechanistically.

Recent advances in technology, especially the development of miniature temperature transmitters and loggers, have allowed more detailed monitoring of phenology and patterns of T_b regulation in the field as well as the laboratory. Those advances raise new issues concerning the biological value of states of low T_b and metabolic rates (MR). It is now widely accepted that these states, far from simple reactions to energy shortages, are used by many species to manage energy utilization even before acute challenges occur. There is evidence, for example, that they facilitate accumulation of fat prior to migration or hibernation (McKechnie and Lovegrove, 2002). So we consider it crucial to re-evaluate currently available definitions towards developing a "common language" in thermal physiology that is unambiguous.

2 Discussion

The terminological issues in thermal physiology are summarized in the following questions:

1. Can and should terms used to describe torpor and related processes in animals be divorced from terms used to describe pathological states in humans?

2. Should the hypometabolic state in animal physiology be regarded as under constant thermoregulatory control within particular species?

3. From which phase of the daily cycle, α or ρ (Aschoff and Pohl, 1970), should values for basal metabolic rate (BMR) and corresponding body temperatures (T_b) be drawn? If the IUPS Thermal Commission definition is used as standard, normal T_b oscillations within the daily cycle

need to be taken into account and distinguished from "heterothermic" states. Against this background, is it possible to define a certain T_b boundary or threshold below which the term torpor applies?

4. Do present data permit a clear terminological differentiation between phenomena, as between torpor, "nocturnal hypothermia", etc.? Should they be regarded as steps in a physiological continuum or do they involve different physiological mechanisms requiring definition?

5. Is it possible to develop a terminology that clearly distinguishes between descriptive terms and terms implying mechanism?

2.1 Hypothermia

The IUPS Thermal Commission definition is too generalized and allows use of the term for pathological as well as "regulated" conditions. If it has to be used in avian physiology, we recommend qualifying it with a suitable adjective to emphasize the controlled nature of torpor and related phenomena.

Swan's definition reflects the point of view of medical doctors, where hypothermia is clearly defines the state of a pathological, non-regulated decrease in body temperature below the mean rest T_b. T_b in birds is significantly dependent on the phase of the daily cycle (Aschoff and Pohl, 1970; Prinzinger et al., 1991). In the rest (ρ) phase of the daily cycle, values fall to between 38 and 40°C, irrespective of taxon or body mass. It is also quite clear that T_b values at or above 40°C are no longer resting values (Prinzinger et al., 1991). Hence, we suggest use of the ρ phase values for reference, and also for basal metabolic rate (BMR). There is still considerable inconsistency in the definition of standards for the BMR, as, for example, in whether it should be measured in waking or sleeping animals (Reinertsen, 1996; Norberg, 1996; Dawson and O'Connor, 1996; Dawson and Whittow, 2000).

2.2 Heterothermia

This term might be considered as a useful alternative to hypothermia if that term is eliminated from definitions of non-pathological phenomena.

2.3 Torpor

The IUPS definition does not consider physiological boundaries or limits, only taking account of behavioral aspects. This implies that while an animal remains capable of responding quickly to stimuli, the state cannot be defined as torpor. Examples are larger birds such as vultures, or passerines in which T_b may hold only slightly below mean T_b range (Heath, 1968; Haftorn, 1972).

Swan's (1974) definition not only considers behavioral aspects but also takes account of the regulatory phenomena behind torpor. It separates torpor from non-regulated, pathological states as well.

2.4 Adjectival use of "regulated" and "controlled" for qualifying hypothermia

In torpor and related phenomena, both T_b and MR are obviously regulated closely. Even on entry into torpor, when decrease of T_b follows physical conditions passively and ($T_b - T_a$) is negligible, the torpid organism is capable of defending a lower critical T_b even if $T_a << T_b$, where T_a = ambient/environmental temperature. Hence, in the classical conception of torpor, can there be, by definition, such a thing as "non-regulated torpor" (Reinertsen, 1996)? There is no evidence to date that normal healthy torpidators do not defend a minimal T_b set-point or limit. Rather, hypothermia and torpor have been shown to be under constant thermoregulatory control in species investigated so far (Walker et al., 1983; Graf et al., 1989; Krüger et al., 1982; Prinzinger et al., 1991; Merola-Zwartjes and Ligon, 2000; Schleucher, 2001). We thus recommend the use of the adjectives "regulated" and "controlled" if the term "hypothermia" cannot be avoided.

2.5 Adjectival use of "facultative" for qualifying hypothermia or torpor

Use of this term is problematic because its antonym is "obligatory". These terms do not clearly differentiate regulated from pathological decrease in T_b. In fact, evidence exists that torpor can be an *obligate* feature needed to maintain energetic balance (e.g., Bucher and Chappell, 1992). The experimental need to impose food restriction (starvation) on birds to induce torpor is — at least in cases of hummingbirds and mousebirds — probably an artifact of captivity (Prinzinger et al., 1981; Prinzinger, 1982). The reason for this is that captive animals are often overweight and require a certain degree of starvation to regain normal body mass; under natural conditions, such birds are "forced" to undergo torpor every night without prior acute energy depletion. In such circumstances, it would be misleading to define this form of hypothermia as "facultative"; much more information about the frequency of torpor and related phenomena is needed before its use should be considered.

2.6 Anapyrexia

Like hypothermia, this term has unfortunately been applied in general use to a pathological state (IUPS definitions; Bicego et al., 2002; Steiner and Branco, 2002). However, if accompanied by a qualifier such as "regulated" or "controlled" and by a clear definition, it does describe a condition precisely and the circumstances under which it occurs.

3 Outlook and recommendations

1. It is necessary to agree on common standards in animal physiology, especially to reach precise definitions for such basic concepts as BMR and mean T_b. Here we recommend consistent use of (ρ) phase values as the standard of reference.

2. Reconsideration of definitions for terms in thermal physiology needs to take account of the following factors:

Behavior: Is the animal in question still capable of reacting to external stimuli; or is it lethargic, and how deep

Table 1 List of commonly used terms in thermal physiology from two sources

	IUPS Thermal Commission, 2001	Swan, 1974
Eu- (Ceno)- thermia, from eu [Gk] = well or good, and koinos [Gk] = common, shared	The condition of a temperature regulator when its core temperature is within ± 1 *SD* of the range associated with the normal post-absorptive resting condition of the species in the thermoneutral zone. Synonym: euthermy, normothermy.	A range of body temperature that is suitable, i.e., chronically viable; the zone of body temperature between the maximum … and minimal critical body temperature in non-torpidating homeotherms (in this instance synonymous with normothermia); ... The range of body temperature in which torpidation may occur.
Normothermia, from normalis [L] = average, usual	see Cenothermy-ia.	The range of body temperature of non-torpidating homeotherms between the minimal and maximal critical body temperatures; the zone of thermoneutrality in non-torpidators. Not applicable to torpidators... (see euthermia).
Hypothermia, from hypo [Gk] = less than usual, beneath	The condition of a temperature regulator when core temperature is below its range specified for the normal active state of the species. Hypothermia may be regulated (e.g. Torpor, Hibernation)...	A range of body temperature in a homeotherm which is below the minimal critical (body) temperature of a non-torpidator or below the minimal viable temperature of a torpidator or a poikilotherm; a body temperature below euthermia or normothermia, which if sufficiently prolonged, is lethal.
Heterothermia, from hetero [Gk] = other than usual, different	The pattern of temperature regulation ... in which the variation in core temperature ... exceeds that which defines homeothermy.	A vertebrate animal without a narrow range of usual temperature; an animal with a broad range of viable temperature... (.. torpidants).
Torpor, from torpere [L] = stiff, numb	A state of inactivity and reduced responsiveness to stimuli (e.g. during hibernation, hypothermia, or estivation).	... the biological state of vertebrate animals involving the onset, progression and maintenance of a diminished metabolic rate associated with a profound state of central nervous system depression resembling coma, including suppression and readjustment of thermostatic control but without complete loss of CNS monitor and control functions.
Anapyrexia*, from ana [Gk] = reverse, and pyretos [Gk] = fever	A pathological condition in which there is a regulated decrease in core temperature. Anapyrexia is distinct from hypothermia in that thermoregulatory responses indicate a defence of the anapyretic level of core temperature.	
Basal metabolic rate	Metabolic energy transformation calculated ... in an organism in a rested, awake, ... post-absorptive state, and thermoneutral zone.	

The two sources reflect divergent backgrounds and approaches among animal and human physiologists, and show that new advances in thermal physiology have only in part been considered and accomodated.

is the lethargy?

Physiology: Are the thermoregulatory systems under consideration constantly active, even during processes of passive cooling? Is there any biological evidence requiring a clear discrimination between shallow depressions of nocturnal T_b (“nocturnal hypothermia”, 2–5°C below euthermia), and “true” torpor (e.g., in the range T_b < 30°C)? And is the definition of thresholds justified? For detailed discussion, see Prinzinger et al. (1991), Barclay et al. (2001), and McKechnie and Lovegrove (2002).

Ecology: Recent studies show that captivity has a major impact on the occurrence and patterns of torpor in birds (Geiser et al., 2000; Geiser and Ferguson, 2001). The importance of hypometabolic states for birds therefore needs to be re-assessed under natural conditions.

The terminology for the physiology of hypometabolic states, such as torpor and hibernation, should be directed towards a scheme that clearly distinguishes between descriptive terms and those with a mechanistic basis, as already realized in the terms poikilotherm/homeotherm, ectotherm/endotherm, thermoconformer/thermoregulator. To avoid further confusion, it is also desirable to separate the terminology used in animal physiology from that commonly applied to human physiology, particularly in clinical circumstances.

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