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Forum: rejoinder

A response to Hertz, Huey and Stevenson

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Hertz et al. (this issue) conclude their rebuttal of our review (Cumn & Alexander this issue) by criticising us of being overly negative of prior work on temperature regulation. Certainly, this was not our intention. We wanted to raise several issues of which we believe researchers should be acutely aware when conducting thermoregulatory studies. The main points of contention between Hertz et al. and ourselves revolve around the practicalities of measuring T_{b,s} used for the generation of the thermoregulatory null hypothesis, and T_{s,et}.

It is also not our intention to address each and every one of the points made by Hertz et al. in this rejoinder. We agree that the reader should use a “side-by-side” approach with the relevant manuscripts to facilitate a comprehensive comparison of the ideas. We agree that any protocol should be species-specific and we also believe that many of the differences in our views result from working on very different animals. Hertz et al. have based many of their ideas on diurnal, active and responsive lizards, whereas our current perspective is largely the result of working on secretive, inactive snakes. Many of the differences of opinion also stem from differences in the scale at which our work is conducted. Hertz et al. based their ideas on population-wide measures of free-ranging animals, while we have been working at the individual level, often in a laboratory situation. Here, we will address what we believe are the most important of the issues raised by Hertz et al. in their rebuttal.

First, we did not argue that the existence of thermophily could result in miss-measurement of T_{s,et} (although this is a possibility). Rather, we suggested that an inappropriately measured T_{s,et} could mask thermophilic responses. Thus, we contend that the reason researchers have found conflicting results for thermophily in a single species could be due to inappropriate experimental design. For example, it is possible that the “control” T_b measures (supposedly for animals not exhibiting thermophily) could have been taken while the animals were in a thermophilic state due to perceived predation risk as a result of researcher presence.

Second, Hertz et al. accuse us of being “reductionist” because we suggested that T_{s,et} is best defined by a neurological approach. We think that our suggested approach is more direct, not reductionist; Hertz et al.’s method aims to measure the same thing (the target temperature range), but in an indirect way that we believe may give misleading measures. Although we do concede that it is likely that there will be higher order behavioural integration, we believe that it is more appropriate to measure the “target temperature” at the same site that the animal is measuring that target—in the hypothalamus. This approach does not assume that neural activity perfectly predicts the behaviour of the whole animal. We are of the opinion that a measure of how well the neural activity translates to the animal choosing its T_{s,et} temperatures (through behaviour and physiological adjustment) is a measure of the animal’s intrinsic ability to thermoregulate (i.e., the ability to thermoregulate is an attribute of the organism, which is indepen-
dent of the environment). How well the thermoregulatory ability results in a match between $T_b$ and $T_{set}$ in a particular environment is a measure of the effectiveness of thermoregulation (sensu Hertz et al. 1993) in that particular environment. Thus the effectiveness of an organism’s thermoregulation will vary from one environment to the next, but thermoregulatory ability is an intrinsic attribute of the organism.

We are not persuaded by the arguments that Hertz et al. put forward in defence of the generation of their null hypothesis (the $T_b$ profile of a non-thermoregulating animal). No matter how convinced they are that their measured thermoregulatory null distribution matches the real null distribution of temperatures, they have no way of testing this match in a natural setting. A test for this match would be to measure habitat use of an animal making no thermoregulatory choices. The only conceivable way that we can think of to achieve this goal is to measure habitat use of the animal in a thermally uniform environment and realistically, this can only be achieved in a laboratory situation. A laboratory setting allows measurement of “habitat use” under uniform thermal conditions since the thermal profile can be controlled.

Hertz et al. contend that we have resuscitated a misconception in advocating the use of variability of selected $T_b$ as a measurement of precision of thermoregulation. They argue against using this measure since the variance in selected $T_b$ could arise from two sources: the organism’s thermoregulation and the variance of $T_s$ available to the organism in the environment. However, we are advocating that the measurement of precision of thermoregulation take place under laboratory conditions in a situation where the available $T_s$ cannot limit $T_b$ choice (the $T_e$ range available to the test animal should span the $CT_{Min}$ and $CT_{Max}$ of the species). Thus, under these conditions, the variance of selected $T_b$s can be attributed only to the thermoregulatory characteristics of the organism. We suggest a protocol in which multiple measures are made for

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**Figure 1.** The range of $T_b$s achieved is dependent on the level of measurement. Generally, the higher the level, the wider the range of $T_b$s. At the neurological level, the range represents the range of temperatures over which the hypothalamus shows minimal neural response (i.e., it does not illicit thermoregulatory responses). A comparison of the ranges at the neurological and organismal levels defines the intrinsic thermoregulatory ability of an organism. The increase in range between these two levels may result from imperfect transposition of neurological signals, or behavioural and physiological costs, which inhibit perfect thermoregulation. The range of achieved $T_b$s of a perfect thermoregulator would not exceed the $T_{set}$. At the organismal level, measures are made in the laboratory under conditions where the thermal environment is not limiting and ecological costs are minimised. Precision of thermoregulation is measured at this level, preventing the effects of ecological constraints such as limited thermal opportunities, or population effects such as variation in $T_{set}$, on the measure. Environmental constraints may result in the range of achieved $T_b$s at the ecological level being wider or narrower than at the organismal level. Under certain ecological circumstances, the cost/benefit nature of thermoregulation (Huey & Slatkin 1976) may result in a wider range of achieved $T_b$s. Under other circumstances, a narrow range of thermal opportunities in the environment may limit temperature selection, resulting in a narrower range of achieved $T_b$s. A comparison of the ranges of $T_b$ achieved at the organismal and ecological levels is a measure of the effectiveness of an organism’s thermoregulation in a particular environment. Since the $T_{set}$s of organisms vary according to physiological state, population-wide measures of $T_b$s are likely to be more variable than those made for individuals.
each individual (though these measures must be temporally independent—see Currin & Alexander this issue), resulting in a measure of thermoregulatory precision for each test animal, rather than a population-wide measure that conflates several sources of variability.

We would like to take Hertz et al.'s cautionary note on thermoregulatory precision a step further: for populations of free-ranging animals, precision of thermoregulation is usually measured as the variance of selected $T_b$'s collected from independent samples (e.g., $T_b$ collected by taking single $T_b$ measures from many different individuals). This protocol introduces yet another source of variance to measures of selected $T_b$: variation in $T_b$ caused by variation of $T_{set}$ between individuals, which would result in a wider variance of measured $T_b$. These sources of variation cannot be separated from each other in a field setting.

We have attempted to outline our perspectives of thermoregulation by formulating a model

(Fig. 1). Because many issues relating to the assessment of thermoregulation remain unresolved at this stage, we have used this model only to present our ideas on appropriate levels of measurement and have stopped short of providing detailed protocols for quantifying these attributes. We are currently using brown house snakes (*Lamprophis fuliginosus*) to test many of the ideas that we have put forward in this debate.

**Literature Cited**

