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EVALUATING TEMPERATURE REGULATION BY FIELD-ACTIVE ECTOTHERMS: THE FALLACY OF THE INAPPROPRIATE QUESTION

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Abstract.—We describe a research protocol for evaluating temperature regulation from data on small field-active ectothermic animals, especially lizards. The protocol requires data on body temperatures (T_b) of field-active ectotherms, on available operative temperatures (T_e, "null temperatures" for nonregulating animals), and on the thermoregulatory set-point range (preferred body temperatures, T_{set}). These data are used to estimate several quantitative indexes that collectively summarize temperature regulation: the "precision" of body temperature (variance in T_b, or an equivalent metric), the "accuracy" of body temperature relative to the set-point range (the average difference between T_b and T_{set}), and the "effectiveness" of thermoregulation (the extent to which body temperatures are closer on the average to the set-point range than are operative temperatures). If additional data on the thermal dependence of performance are available, the impact of thermoregulation on performance (the extent to which performance is enhanced relative to that of nonregulating animals) can also be estimated. A sample analysis of the thermal biology of three *Anolis* lizards in Puerto Rico demonstrates the utility of the new protocol and its superiority to previous methods of evaluating temperature regulation. We also discuss several ways in which the research protocol can be extended and applied to other organisms.

Regulation and homeostasis are central paradigms of comparative and ecological physiology (Prosser 1986; Bennett 1987). Many reptiles effectively regulate body temperatures by using behavioral adjustments such as shuttling between sun and shade (Cowles and Bogert 1944). Indeed, behavioral adjustments enable some diurnal reptiles to maintain high and relatively constant body temperatures despite wide fluctuations in ambient temperature (Avery 1982; Huey 1982). Today, a voluminous literature reflects the importance of temperature to reptiles as well as the ease of taking reptile temperatures (Gans and Pough 1982). Several important aspects of temperature regulation are now reasonably well understood: the biophysics of heat exchange between reptiles and their environments (Porter et al. 1973; Tracy 1982; Stevenson 1985*a;* Bakken 1992); the behavioral (Heath 1965; Huey et al. 1977; Stevenson 1985*b;* Lillywhite 1987; Grant and Dunham 1988; Hertz 1992*a*) and physiological (Bartholomew 1982; Turner and Tracy 1986; Lillywhite 1987) adjustments used by reptiles in regulating temperature; the

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neurophysiological basis of "set-point" temperatures (Heath 1970; Barber and Crawford 1977; Firth and Turner 1982); and the physiological and ecological consequences of temperature regulation (Huey and Stevenson 1979; Christian and Tracy 1981; Heinrich 1981; Hertz et al. 1983; Stevenson et al. 1985; Lillywhite 1987; Huey et al. 1989*b;* Van Damme et al. 1989; Grant 1990).

Despite these advances, a deceptively simple but all-important question is not at all well understood: How carefully do reptiles (or other ectotherms) regulate their body temperatures? Although this question is fundamental to diverse ecological (Ruibal and Philibosian 1970; Huey and Slatkin 1976; Lister 1976; Hertz 1983; Pianka 1986; Dunson and Travis 1991) and physiological (Licht 1967; Huey 1982; Hertz et al. 1983; Lynch and Gabriel 1987) issues, a satisfactory protocol for estimating the extent and effectiveness of temperature regulation has been elusive. A primary reason is that the concept of how carefully an animal thermoregulates is itself quite vague because several distinct, though complementary, questions are embedded within it. How extensively does the animal use overt behavioral or physiological adjustments to regulate its body temperature? How variable is the animal's body temperature (the "precision" of body temperature)? How closely do body temperatures match the animal's preferred or set-point range (the "accuracy" of body temperature)? To what extent do thermoregulatory behaviors actually enhance the accuracy of body temperatures relative to those of a nonregulating control (the "effectiveness" of temperature regulation)? Thus, the simple question of how carefully an animal thermoregulates exemplifies what E. E. Williams (personal communication) has called "the fallacy of the inappropriate question." Such a question misleads research efforts by implying that a single answer is possible when, in the present case, a set of answers is required.

In this article, we develop quantitative methods for answering the above set of questions. Our methods trace primarily to three key insights that were raised in classic articles by Heath (1964, 1965, 1970), Porter et al. (1973), and Bakken and Gates (1975). First, the term *thermoregulation* necessarily implies an active regulatory process involving behavioral and/or physiological adjustments to maintain body temperature as close as possible to an independently defined "set-point range" (Heath 1970; Huey 1982; Pough and Gans 1982; Peterson 1987); thermoconformity is merely one extreme on a continuum of thermoregulatory options (Huey and Slatkin 1976; Pough and Gans 1982). Second, temperature regulation can, in part, be demonstrated by showing that the body temperatures of an animal differ significantly from those of a null model, specifically those of a hypothetical thermoconforming (i.e., nonthermoregulating) "control" (Heath 1964; DeWitt 1967; Huey et al. 1977; Stevenson 1983; Grant and Dunham 1988; Hertz 1992*a*). In particular, the thermoregulating animal's body temperatures should generally be closer to the set-point range than are those of the hypothetical thermoconformer, which results in improved performance relative to the thermoconformer. Third, the expected null distribution of body temperatures for thermoconforming controls can be obtained by randomly mapping the thermal environment. Specifically, mathematical (Porter et al. 1973; Roughgarden et al. 1981; Waldschmidt and Tracy 1983) or physical (Bakken and Gates 1975; Grant and Dunham 1988; Bakken 1992) models of heat exchange can be used to estimate the available "operative temperatures" (i.e., predicted equilibrium temperatures of nonregulating ectotherms; see below) at a variety of randomly selected sites within a habitat. This randomly sampled distribution of operative temperatures then serves as a null model for quantifying the extent of thermoregulation (Peterson 1987; Grant and Dunham 1988; Hertz 1992*a*).

Of course, a complete description and evaluation of behavioral temperature regulation would also require direct observations on the use of thermoregulatory behaviors (Heath 1964, 1965) as well as data on the animals' physiological state (Regal 1966; Stevenson 1983). Practical procedures (null models) for evaluating such behaviors have previously been developed (Huey et al. 1977; Grant and Dunham 1988; Adolph 1990; Hertz 1992*a*) and need not be repeated here.

In this article, we first describe and critique existing measures that evaluate the extent of temperature regulation; we show that each method is either conceptually or physically flawed. Next we develop a research protocol and several new indexes that provide a comprehensive, detailed, and quantitative portrait of thermoregulation by small ectotherms (see below). We then use field and laboratory data on the thermal biology of three species of *Anolis* lizards in Puerto Rico to illustrate the method's utility in comparison to more traditional methods of analysis. We emphasize, however, that the methodology is general and should be applicable to many (but not all) other types of ectotherms. Moreover, our approach can be modified for studies of regulation involving other operative environmental factors (e.g., water vapor concentration, light, pH, salinity).

TRADITIONAL MEASURES OF TEMPERATURE REGULATION

Variability of Body Temperature

A low variance of body temperature (T_b) has traditionally been interpreted as evidence of careful temperature regulation in small ectotherms that occupy harsh, terrestrial environments where temperatures can change rapidly (Cowles and Bogert 1944; Schmidt-Nielsen and Dawson 1964; DeWitt 1967; Bowker 1984; Lillywhite 1987; Peterson 1987; Sievert and Hutchison 1988; Hutchison and Dupré 1992). Variance of T_b is a useful (Lynch and Gabriel 1987) statistical estimate of the actual variability of T_b (i.e., the precision of T_b) that an animal experiences. Nevertheless, several reasons suggest that variance of T_b provides an incomplete portrait of thermoregulation in nature (Huey 1982). First, even a nonregulating ectotherm will experience only slight variations in T_b if it lives in a thermally homogeneous habitat (Ruibal 1961; Hertz 1974, 1981, 1992*a;* Huey and Webster 1976); conversely, an active thermoregulator may have quite variable T_b if it lives in a thermally heterogeneous habitat (Soulé 1963; Ruibal and Philibosian 1970; Huey 1974) or if its set-point range is broad. Second, variance of T_b provides no information about the accuracy of temperature regulation (i.e., whether T_b's match either preferred or physiologically optimal temperatures). Third, variance of T_b is a statistically inappropriate index (Huey 1982) for animals (e.g., lizards) that thermoregulate between upper and lower set points (Berk and Heath 1975; Barber and Crawford 1977) rather than around a single T_b.

The range of hourly mean T_b is another indicator of variability (Ruibal and

Philibosian 1970; Huey and Webster 1976; Hertz 1981, 1983; Hertz and Huey 1981) that is correlated with and suffers from some of the same problems as does the variance of T_b. This range, when compared with the range of hourly mean air temperatures (T_a), has been used to estimate thermoregulatory compensation for environmental variations (Hertz and Huey 1981; Hertz 1983). However, as noted below, T_a is an inadequate measure of complex thermal environments.

Regression Slope

The slope of the regression of T_b on T_a (often measured where the animal was first sighted) is another measure of thermoregulation (Huey and Slatkin 1976): a slope near zero suggests perfect thermoregulation, whereas a slope near one with an intercept near zero suggests thermoconformity. This method, though frequently used, is inappropriate (Huey 1982; Dreisig 1984). In particular, T_a is only one of many biophysical factors (e.g., direct solar radiation) that influence an animal's T_b (Porter et al. 1973; Bakken and Gates 1975; Tracy 1982; Stevenson 1985*a,* 1985*b*). Moreover, T_a at the microhabitat chosen by the animal is a potentially biased measure of available environmental temperatures (Tracy and Christian 1986; Bakken 1989); indeed, the animal might have selected the site because of its thermal properties.

THE GENERAL PROTOCOL

Three distinct kinds of data are necessary for a comprehensive description of temperature regulation. First, one must document the T_b's actually experienced by a representative sample of animals. Second, one must measure the null distribution of T_b's (Heath 1964; Grant and Dunham 1988) that nonthermoregulating animals could potentially experience (i.e., the distribution of operative temperatures, T_e) at the study site. (Ideally, one would measure the T_b and T_e distributions simultaneously; at a minimum they must be measured under similar environmental conditions.) Third, one must independently identify the set-point range (T_{set}), which represents the ideal "target" T_b range (Heath 1965; Licht et al. 1966) that animals achieve when circumstances do not constrain temperature selection. We assume that, as a general behavioral rule, field-active animals will maintain T_b within T_{set} whenever possible (Licht et al. 1966; Peterson 1987; Van Damme et al. 1989). (However, alternative strategies have been noted: e.g., some lizards appear to maximize activity time at a constant T_b [Christian et al. 1983] that may be lower than T_{set} in some seasons [Van Damme et al. 1989].) We outline below the basic steps required to obtain and analyze these three data sets and describe the conclusions that can be drawn at successive stages of analysis.

Activity Body Temperatures

The distribution of body temperatures can be obtained either by radiotelemetry of a small number of individuals or by random sampling of large numbers of individuals (spot sampling, "grab and jab"). The merits of these two methods have been evaluated elsewhere (McGinnis 1970; Avery 1982; Peterson 1987). Here we use data gathered with spot sampling; we assume that the observed T_b

distributions describe the T_b's experienced by each individual in a population (but see Christian et al. 1985).

Operative Temperatures

To evaluate whether ectotherms are actively thermoregulating, one also needs information on the distribution of body temperatures that nonregulating (i.e., control) animals would achieve (Heath 1964; Huey et al. 1977; Grant and Dunham 1988; Hertz 1992*a*). Operative temperature, the product of interactions between biophysical and morphological factors that influence an ectotherm's T_b, represents the equilibrium temperature of an inanimate object (i.e., one lacking physiological controls) that approximates the study animal in size, shape, and color (Bakken 1992). Hence, the random distribution of T_e in a habitat describes the "null" distribution of T_b expected in nonregulating animals (Christian and Tracy 1985; Grant and Dunham 1988; Huey 1991; Hertz 1992*a*). (The distribution of T_e should, by definition, encompass the distribution of T_b. However, because of sampling errors, it may not.) An observation that T_b's are closer to T_{set} than are T_e's would be strong but incomplete (see below) evidence that the animals thermoregulate.

The use of T_e assumes that animals are in thermal equilibrium with the environment; equilibrium will not, in fact, be the case in two general circumstances. First, large animals have large heat capacities such that variations in their T_b necessarily lag behind operative temperatures (Spotila et al. 1973; Tracy 1982; Turner and Tracy 1986). Indeed, a general theoretical model (Stevenson 1985*a*) predicts that thermal time constants for animals weighing more than 1 kg are on the order of hours. Second, the T_b of small ectotherms that move quickly among thermal patches will approach the average T_e among the patches rather than equilibrate to the T_e experienced within each patch (van Berkum et al. 1986). Although rapid movement across thermal habitats does not affect the mean T_e experienced (if one assumes no physiological control), it substantially reduces the variance of T_e unless the time constant of the animal is much less than the time spent within any patch; approaches that include the effects of thermal transients (see Tracy and Christian 1986) are appropriate under such circumstances.

Operative temperatures can be computed by using micrometeorological and anatomical data in solutions of complex biophysical equations (Porter et al. 1973; Roughgarden et al. 1981; Tracy 1982) or measured directly with "physical" models of an animal (i.e., T_e "thermometers"; see Bakken 1992). (The relative merits of computational versus direct measurement methods were recently reviewed in Huey 1991 and Bakken 1992.) Hollow metal or plastic models generally provide accurate estimates of operative temperatures for small ectotherms that have limited physiological capacity to control rates of heat exchange and equilibrium T_b (Bakken 1992).

The distribution of T_e can be measured at randomly selected microsites within an animal's habitat (see Hertz 1992*a*) or with various sampling and mapping procedures (see Waldschmidt and Tracy 1983; Grant and Dunham 1988). However, many habitats are thermally complex, and each microsite provides a range of potential T_e's depending on the animal's size, color, posture, and orientation

(Roughgarden et al. 1981; Bakken 1989, 1992; Huey 1991). Hence, large numbers of models may be required to sample the habitat adequately, and models must be placed in the habitat with considerable sensitivity to the organisms' natural history. Delimiting the activity times and habitat of an animal will also be difficult, especially because activity times and habitat selection are often influenced by thermoregulatory considerations (Hillman 1969; Stevenson 1985*b;* Huey 1991). Consequently, if T_e is measured only in the habitats actually used, one will be able to determine the extent of thermoregulation within that habitat, but one would miss the thermoregulatory consequences of selecting that habitat instead of others.

Set-Point Temperature Range

Central to any evaluation of temperature regulation is the identification of the target T_b's that ectotherms attempt to achieve (T_{set}). The difference between field and set-point T_b (Licht et al. 1966; Huey 1982) indicates how successfully ectotherms achieve T_b within the target range (i.e., the accuracy of body temperatures) (Sievert and Hutchison 1988). In general, set-point ranges are best estimated as "preferred" or selected body temperatures in the laboratory (Hutchison and Dupré 1992), an environment that is independent of the ecological costs (Huey and Slatkin 1976; Withers and Campbell 1985) and constraints (Porter and Gates 1969; Porter et al. 1973) that can influence temperature regulation in the field. Set-point temperatures estimated from field T_b (van Berkum et al. 1986; Rosen 1991) are inappropriate in the present context: an evaluation of temperature regulation under natural conditions requires a yardstick that is independent of field T_b.

Laboratory thermal gradients (Licht et al. 1966), shuttle boxes (Berk and Heath 1975; Reynolds and Casterlin 1979), or complex thermal arenas (Greenerg 1976) are appropriate environments for measuring T_{set} as long as laboratory conditions duplicate the illuminance of natural habitats. Thermal preferences in such settings have a solid neurophysiological basis in lizards and fishes (Barber and Crawford 1977; Firth and Turner 1982). Because some ectotherms appear to regulate between upper and lower set-point temperatures rather than around a single T_b (Berk and Heath 1975; Barber and Crawford 1977), one should ideally determine the set points directly. Alternatively, one could estimate the set-point range by measuring, for example, the central 50% (Huey 1982; see also present study) or 68% (DeWitt and Friedman 1979) of all T_b's selected in the laboratory.

Several cautionary notes are in order. A laboratory setting is, of course, artificial and may potentially cause animals to behave unnaturally. Moreover, set points themselves need not be fixed but may vary with season (Patterson and Davies 1978; Van Damme et al. 1986; Rismiller and Heldmaier 1988; Sievert and Hutchison 1989), sex and age (Patterson and Davies 1978; Van Damme et al. 1986), physiological state (Regal 1966; Barber and Crawford 1977; Huey 1982; Withers and Campbell 1985; Gibson et al. 1989), and the hydric environment (O'Connor and Tracy 1992). Therefore, reference to a single target temperature range will often be inappropriate, particularly if set-point variation is substantial.

Evaluating the Effectiveness of Temperature Regulation

Before developing a measure of the effectiveness of temperature regulation, we must first determine the degree to which field-active T_b matches T_{set} (i.e., the accuracy of T_b) irrespective of whether animals actively regulate T_b. To index the accuracy of T_b, we use the mean of the absolute value of the deviations (°C) of field-active T_b's from T_{set} (individual deviation $= d_b$). If T_b is below (above) the set-point range, d_b is the difference between the T_b and the lower (upper) bound of T_{set}. For T_b within T_{set}, d_b equals zero.

The mean d_b ($= \bar{d}_b$) is a measure of the average degree to which ectotherms experience T_b outside the set-point range. A high $\bar{d}_b$ (i.e., low accuracy) could result from a high variance of T_b (fig. 1*A*) and/or from a mean T_b that falls well outside T_{set} (fig. 1*B*). Note, however, that a low $\bar{d}_b$ (i.e., high accuracy) does not necessarily imply active temperature regulation (fig. 1*C*). Neither does a high $\bar{d}_b$ necessarily imply a lack of temperature regulation (fig. 1*B;* see also text below). Note also that $\bar{d}_b$, calculated here on a linear scale, assumes that deviations of equal magnitude above and below T_{set} are of equivalent physiological importance; when appropriate, $\bar{d}_b$ can be rescaled to correct for Q_{10} effects (see DeWitt and Friedman 1979).

Analogously, the deviations between T_e and T_{set} (d_e) indicate how closely the available T_e's in a habitat match T_{set}. Mean d_e ($= \bar{d}_e$) is thus an index of the average thermal quality of a habitat from the organism's perspective. Habitats with $\bar{d}_e$ equal to zero are thermally ideal because an animal would always have T_b within the set-point range. In contrast, habitats with high $\bar{d}_e$ (figs. 1*A* and 1*B*) are of lower thermal quality because animals would have to thermoregulate to achieve T_b's close to or within the set-point range, if one assumes that such T_b's are attainable at all.

A nonparametric alternative for $\bar{d}_b$ and $\bar{d}_e$ would involve estimating the proportions of T_b and of T_e that fall outside the set-point range (Van Damme et al. 1989). Similarly, to create a related index that measures environmental constraints on activity, one can calculate the percentage of T_e that is outside the animal's voluntary or lethal limits (Tracy and Christian 1986; Grant and Dunham 1988; Huey et al. 1989*b;* Van Damme et al. 1989).

In studies of small ectotherms, for which the heating and cooling rates of animals and models are similar, the comparison of $\bar{d}_b$ and $\bar{d}_e$ provides a simple indicator of whether the animals are actively regulating body temperatures toward the set-point range. An observation that $\bar{d}_b < \bar{d}_e$ implies that the animals behave nonrandomly with respect to the available thermal environment such that T_b's are closer to T_{set} than one would expect for null (i.e., nonthermoregulating) ectotherms. In other words, the animals are regulating T_b.

We define the effectiveness of temperature regulation: $E = 1 - (\bar{d}_b/\bar{d}_e)$, in which E is the effectiveness of temperature regulation, and $\bar{d}_b$ and $\bar{d}_e$ are defined as above. The value of E will generally range between zero and one. When animals do not thermoregulate (i.e., they select microhabitats at random with respect to T_e), $\bar{d}_b$ and $\bar{d}_e$ will be similar (fig. 1*C*), and E will approach zero. Conversely, when animals thermoregulate carefully and successfully, $\bar{d}_b$ will be

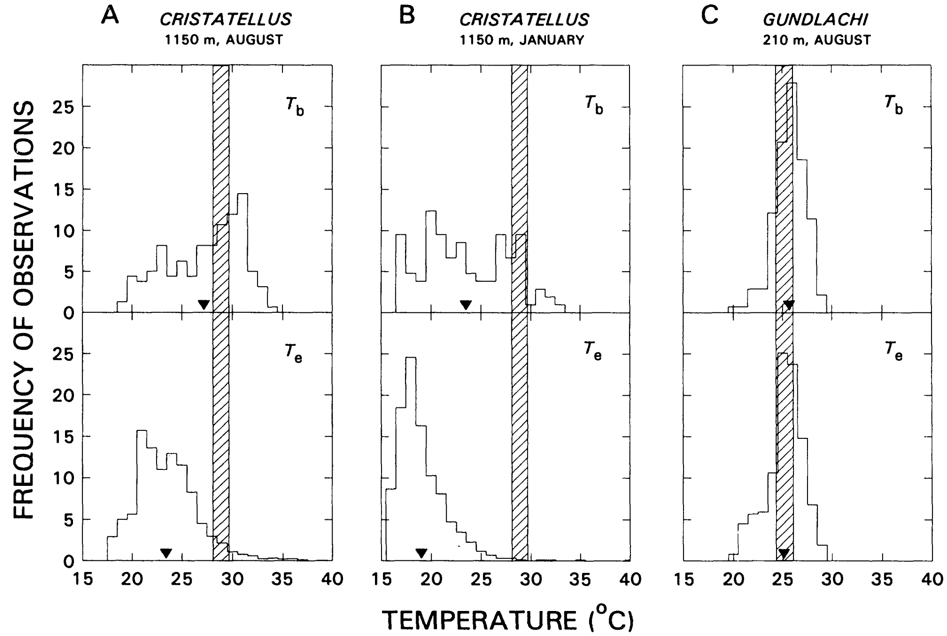

FIG. 1.—Distributions of T_b and T_e in *Anolis* lizard populations illustrating the distinction between the accuracy of T_b and the effectiveness of temperature regulation. *Cross-hatched vertical lines* indicate the T_{set} measured in the laboratory. *Arrowheads* indicate mean T_b or T_e. At high elevation in August, *cristatellus* (*A*) experiences moderately accurate T_b (T_b's cluster around T_{set}) and clearly thermoregulates (most T_b's are closer to T_{set} than T_e's are). At high elevation in January, however, *cristatellus* (*B*) experiences T_b's of low accuracy (most T_b's are well below T_{set}), even though it thermoregulates (T_b's are closer to T_{set} than T_e's are). In contrast, at low elevation in August, *gundlachi* (*C*) experiences T_b's of very high accuracy (most T_b's are close to T_{set}) although it hardly thermoregulates at all (T_b's are not much closer to T_{set} than T_e's are).

smaller than $\bar{d}_e$, and E will approach one. In an ideal thermal environment (where all T_e's are within T_{set}), $\bar{d}_e$ equals zero, E is undefined, and animals need not actively thermoregulate. Negative values of E can occur if animals actively avoid microhabitats that provide T_e within the set-point range, perhaps because predators are abundant or food is rare at such sites (Huey and Slatkin 1976; Crowder and Magnuson 1983). A given value of E may result from a variety of different $\bar{d}_b$ and $\bar{d}_e$ combinations. Consequently, a complete understanding of the pattern of thermoregulation will often require a direct examination of $\bar{d}_b$ and $\bar{d}_e$ as well as E.

Confidence intervals on E can be set by bootstrap resampling (Efron 1979) from the empirical distributions of T_b and T_e (J. Felsenstein, personal communication). For example, for a sample of 100 T_b readings and 200 T_e readings, one would compute $\bar{d}_b$ and $\bar{d}_e$ by drawing samples (with replacement) of 100 T_b and 200 T_e, respectively, then compute E as above. After repeating this process exhaustively (say, 1,000 times), one can determine the 95% confidence interval for E by the standard percentile method. Similarly, to test whether two species (or populations) differ significantly in E, one could compare many paired bootstrap estimates of E for each species. If one species has the greater E value in 95% or more of the paired comparisons, then the two species have significantly different E values.

A SAMPLE ANALYSIS

Background

Our sample analysis examines interspecific, geographical, and seasonal variation in thermoregulation by three species of the *Anolis cristatellus* group of lizards in Puerto Rico. The thermal biology of these species has been well studied (see, e.g., Rand 1964; Williams 1972; Huey 1974; Huey and Webster 1976; Gorman and Hillman 1977; Hertz et al. 1979; Hertz 1981, 1983, 1992*a*, 1992*b;* Jenssen et al. 1984). General descriptions of the thermal ecology of the species were synthesized from all of these articles, but our new analyses were based on data presented elsewhere (Huey and Webster 1976; Huey 1983; Hertz 1992*a*, 1992*b*).

Data on T_b and T_e (from populations comparable in altitude and habitat to those used in the thermal gradient studies) are taken from previous articles (Hertz 1992*a,* 1992*b*). Field studies were undertaken at three altitudes (sea-level desert: *cooki* and *cristatellus;* mesic lowland: *cristatellus* and *gundlachi;* mesic upland sites: *cristatellus* and *gundlachi*) and in two seasons (January and August). At all sites both T_b (spot sampling) and T_e were measured from 0700 to 1830 hours, the hours during which active individuals of these species were ever observed at any site. In choosing this sampling regime, we assumed that these diurnal lizards could, in theory, be active at any time during daylight hours. However, lizards in some populations are active over shorter time periods (Huey and Webster 1976; Hertz 1992*a*, 1992*b*). Consequently, our estimates of $\bar{d}_b$ and E for such populations reflect in part their restriction of activity times as a thermoregulatory behavior. Were we instead to sample T_e only when lizards were active at a given site, our estimates of $\bar{d}_b$ and E would provide information only on thermoregulation during periods of activity. (Note that the comparison of E calculated with these alternative approaches would provide information on the thermoregulatory consequences of restricting times of activity.)

Operative temperatures were measured (Hertz 1992*a,* 1992*b*) with 60 hollow, copper lizard models (each equipped with a built-in thermocouple) distributed at random on vertical substrates (randomly selected trees, heights above the ground, and compass directions) where these anoles typically perch (Rand 1964; Schoener and Schoener 1971; Jenssen et al. 1984). The temperature (T_e) of each model was generally sampled hourly over 2 d. (In some of the calculations below, we assume for simplicity that the multiple measurements on each model are statistically independent.)

Set-point temperatures were estimated from preferred body temperatures in a laboratory thermal gradient (Huey and Webster 1976); measurements were made only in summer, and our analysis assumes that T_{set} does not vary with season (but see discussions under *Set-Point Temperature Range,* above, and *Comparisons among Indexes,* below). Fifty measurements were taken for six individuals of *cooki,* six of *gundlachi,* and 18 of *cristatellus* (six from each of a desert, lowland, and upland population). We identified the temperatures bounding the interquartile range (middle 50% of the observations) for each lizard, then used the average values to represent the upper and lower limits of T_{set} (table 1).

Anolis cooki

Anolis cooki, a species with high thermal preferences and high activity T_b (tables 1 and 2), is restricted to xeric lowland habitats in southwestern Puerto Rico. Although not known to regulate its activity time, *cooki* basks both early and late in the day and avoids sunny perches at midday (Hertz 1992*b*). Previous analyses suggest that *cooki* thermoregulates rather carefully (Huey and Webster 1976; Lister 1976; Jenssen et al. 1984).

Lowland xeric habitats seem thermally suitable for *cooki.* The average deviation of T_e from T_{set} (i.e., $\bar{d}_e$) was fairly low (table 2) and was marginally higher in winter (2.4°C) than in summer (2.1°C; t-test, $P = .066$). Thus, even a nonregulating *cooki* would generally experience T_b near T_{set}. Nevertheless, a nonregulating *cooki* might also frequently risk overheating: in August, 66% of all T_e readings were above the set-point range (fig. 2). Hence, even a low-$\bar{d}_e$ environment can constrain the movements of ectotherms.

The average deviation of T_b from T_{set} (i.e., $\bar{d}_b$) was extremely low (0.8°C in January and 1.3°C in August), which indicates that *cooki* were generally active at temperatures near or within their set-point range. However, $\bar{d}_b$ was significantly higher in summer (*t*-test, $P = .009$). Because T_b's were closer to T_{set} than were T_e's, our measures of the effectiveness of thermoregulation (E) suggest that *cooki* were moderate thermoregulators (table 3). This species appeared to thermoregulate more effectively (i.e., higher E) (table 3) in winter when average T_e (table 2) was significantly lower than in summer (*t*-test, $P = .009$).

Traditional indexes of thermoregulation (table 3) provide a similar though less illuminating portrait of *cooki*'s thermal ecology in the field (see also Huey and Webster 1976; Lister 1976; Jenssen et al. 1984). The variance of T_b was low (3.8°–3.9°C), the range of hourly mean T_b was low (5.2°–5.9°C), and the slope of T_b on T_a was below one (0.73–0.84).

Anolis cristatellus

Anolis cristatellus, a species that is widespread from xeric lowlands to mesic uplands, typically occupies both open and shaded habitats on the coastal plain, but it is restricted to more open habitats at higher elevations. It has moderately high thermal preferences and activity T_b (tables 1 and 2). This eurytopic species regulates activity time at the extremes of its range: in lowland desert areas it avoids midday activity, but in montane sites it avoids activity early and late in the day. At less extreme sites it is active from sunrise to sunset. It also basks more actively at high elevation than at warmer sites. Across its diverse geographical range, and sometimes even locally, *cristatellus* varies from being a thermocon-

TABLE 1

Habitats, Bounds of Set-Point Temperature Range (°C), and Optimal Body Temperature for Sprint Speed (°C) in Three *Anolis* Lizard Species from Puerto Rico

Species and Habitat	T_{set} Bounds: Lower	T_{set} Bounds: Upper	$T_{optimal}$ for Sprinting
Anolis cooki:			
Desert	29.6 ± .4	31.6 ± .5	30.4 ± 1.8
Anolis cristatellus:			
Desert	28.6 ± 1.0	30.9 ± .3	
Lowland mesic	28.6 ± .7	30.7 ± .4	27.3 ± 1.8
Upland mesic	28.1 ± .5	29.7 ± .2	
Anolis gundlachi:			
Upland mesic	24.3 ± .7	26.1 ± .8	28.6 ± 2.5

Note.—Values listed are means ± SE. For set-point temperatures, $N = 6$ lizards per sample. For optimal sprinting temperature, $N = 4$ for *cooki*, $N = 6$ for *cristatellus*, and $N = 7$ for *gundlachi*. See text for explanations. Data on T_{set} are from Huey and Webster (1976). Data on optimal sprinting temperatures are from Huey (1983; R. B. Huey, unpublished data).

TABLE 2

Body (T_b) and Operative (T_e) Temperatures, Deviations of Body (d_b) and Operative (d_e) Temperatures from T_{set}, and Predicted Relative Sprint Speeds of Actual Lizards (P_b) and Hypothetical Nonthermoregulating Lizards (P_e) in Puerto Rico

Species, Habitat, and Season	N	$\bar{T}_b$	$\bar{T}_e$	$\bar{d}_b$	$\bar{d}_e$	$\bar{P}_b$	$\bar{P}_e$
Anolis cooki:							
Desert (5 m):							
January	58	30.8 ± .3	29.9 ± .1	.8 ± .1	2.4 ± .1	89.3	81.8
August	68	32.1 ± .2	32.8 ± .1	1.3 ± .1	2.1 ± .1	83.5	73.5
Anolis cristatellus:							
Desert (5 m):							
January	15	27.3 ± .9	29.9 ± .1	2.0 ± .8	2.3 ± .1	91.7	79.2
August	25	30.8 ± .4	32.8 ± .1	.9 ± .2	2.5 ± .1	84.6	66.0
Mesic (90 m):							
January	115	25.7 ± .4	24.2 ± .1	3.4 ± .3	4.6 ± .1	89.5	89.0
August	125	28.9 ± .2	28.2 ± .1	1.1 ± .1	1.2 ± .1	91.8	94.1
Mesic (1,150 m):							
January	105	23.5 ± .4	19.0 ± .1	5.0 ± .4	9.2 ± .1	84.2	68.9
August	159	27.2 ± .3	23.4 ± .1	2.5 ± .2	5.0 ± .1	90.1	87.5
Anolis gundlachi:							
Mesic (210 m):							
January	117	23.9 ± .2	23.9 ± .1	.9 ± .1	.9 ± .1	83.6	83.4
August	140	25.7 ± .1	25.1 ± .1	.6 ± .1	.7 ± .1	89.6	87.5
Mesic (1,130 m):							
January	72	19.4 ± .2	19.0 ± .1	4.9 ± .2	5.3 ± .1	67.7	66.3
August	138	22.2 ± .1	21.6 ± .1	2.2 ± .1	2.8 ± .1	77.9	75.9

Note.—Values listed are means ± SE. N = sample size for lizards in the field. T_e and d_e data are grand means from 12 to 24 hourly measurements on each of 60 randomly distributed models. Relative sprint speed is the percentage of the maximum speed measured for individual lizards in the laboratory. Data on T_e and T_b are from Hertz (1992*a*, 1992*b*). Data on sprint speeds are from Huey (1983; R. B. Huey, unpublished data).

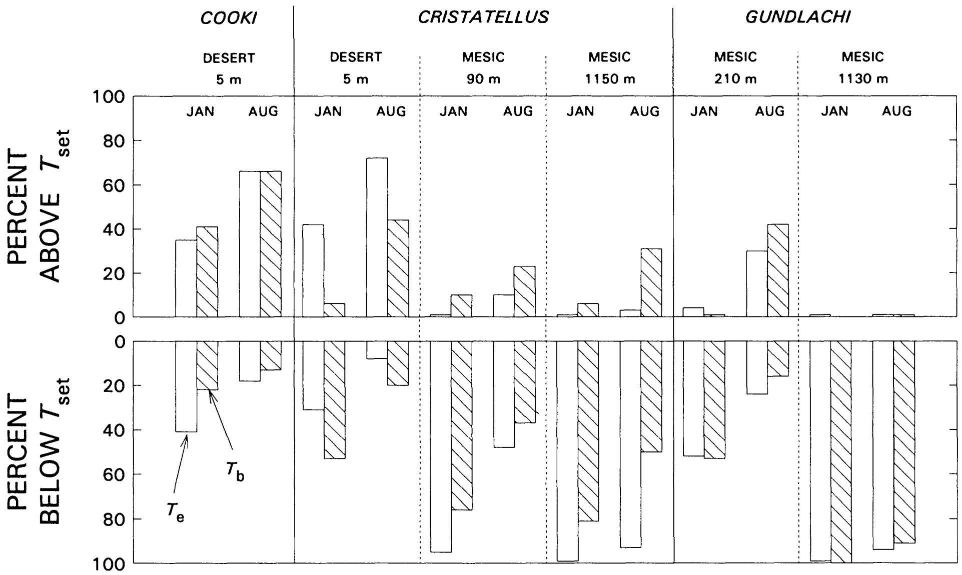

FIG. 2.—The percentage of T_e and T_b readings that fell above or below T_{set} in summer (August) and winter (January) in six *Anolis* lizard populations in Puerto Rico.

TABLE 3

SUMMARY STATISTICS DESCRIBING TEMPERATURE REGULATION IN SIX *ANOLIS* LIZARD POPULATIONS IN PUERTO RICO

SPECIES, HABITAT, AND SEASON	E	s^2	RMT_b	$T_b = mT_a + c$	
				m	c
Anolis cooki:					
Desert (5 m):					
January	.67	3.9	5.2	.73	11.4
August	.38	3.8	5.9	.84	8.1
Anolis cristatellus:					
Desert (5 m):					
January	.13	13.2	4.3	1.73	−14.1
August	.64	4.2	5.2	.86	6.6
Mesic (90 m):					
January	.26	16.6	11.4	1.33	−5.1
August	.08	5.6	7.4	1.00	1.9
Mesic (1,150 m):					
January	.46	18.8	11.0	2.41	−21.2
August	.50	14.1	10.0	1.78	−12.1
Anolis gundlachi:					
Mesic (210 m):					
January	.00	2.6	4.7	1.16	−2.2
August	.14	2.6	4.8	1.05	−.2
Mesic (1,130 m):					
January	.08	2.6	4.7	1.09	−.8
August	.21	2.8	4.9	1.28	−4.6

NOTE.—$E = 1 - (d_b/d_e)$; s^2, variance of T_b; RMT_b, range of hourly mean T_b; m and c, slope and intercept, respectively, of the regression of T_b on T_a. See text for further explanation.

former to being a thermoregulator (Huey 1974; Huey and Webster 1976; Hertz 1992*a*, 1992*b*).

We analyzed temperature data from three *cristatellus* localities (lowland desert, lowland mesic, and upland mesic). Montane habitats were less suitable (higher $\bar{d}_e$) for *cristatellus* than were lowland habitats (table 2), but $\bar{d}_e$ was influenced by a complex interaction between elevation and month (two-way ANOVA, $P < .0001$). A greater proportion of T_e readings fell outside T_{set} (fig. 2) at high elevation (> 95%) than at either the lowland mesic (58%–95%) or the desert sites (73%–80%). Not surprisingly, higher proportions of T_e readings were above T_{set} at the desert site (42% and 72% in January and August, respectively) than at the lowland mesic site (1% and 10%, respectively), which suggests that *cristatellus* (like *cooki,* above) risk overheating at the desert site.

Lizards were active at T_b closer to their set-point range (lower $\bar{d}_b$) at low elevation compared to high elevation and in August compared to January (table 2) (two-way ANOVA on $\bar{d}_b$, main effects for elevation and season, $P < .001$; interaction, $P > .05$). This species thermoregulated effectively (high E; table 3) in extreme environments. In the desert, for example, *cristatellus* thermoregulated more effectively in summer ($E = 0.64$), when the average T_e was above T_{set} (tables 1 and 2; fig. 2), than in winter ($E = 0.13$). (Interestingly, *cooki,* a species with relatively high thermal preferences, showed the opposite pattern of seasonal thermoregulation at the same desert site; see above.) At the lowland mesic site, the relative effectiveness of thermoregulation was reversed from that in the desert, but generally low ($E = 0.26$ in winter, $E = 0.08$ in summer). At high elevation, where the vast majority of T_e readings fell below T_{set} in both months (fig. 2), *cristatellus* was a moderately effective thermoregulator in both winter and summer ($E = 0.46$ and 0.50, respectively). Nevertheless, its accuracy of T_b was quite low (high $\bar{d}_b$) at high elevation, which suggests that environmental constraints can limit thermoregulatory accuracy despite considerable thermoregulatory effort.

Traditional measures of the extent of thermoregulation (table 3) provide a muddled portrait of this species' thermal ecology. Recall that a low variance of T_b is often cited as evidence of careful thermoregulation. However, variance of T_b was very high at the upland site in both months even though the lizards were clearly thermoregulating. Note also that the slopes of T_b on T_a for these *cristatellus* populations range from 0.86 to 2.41 (table 3), counter to the expectation (Huey and Slatkin 1976) that the slopes should vary only between zero and one. If opportunities to raise T_b through basking are greater at high T_a, either because of time-dependent sunlight patterns or cloud cover, the slope of the regression of T_b on T_a can be greater than one.

Anolis gundlachi

Anolis gundlachi, distributed in shaded midelevation to upland habitats, prefers and is active at relatively low T_b (tables 1 and 2). It is the archetypal nonregulator: it rarely basks and appears active throughout the day.

We analyze temperature data from two *gundlachi* localities, mesic sites at 210-m and 1,130-m elevation (Hertz 1992*a*). Although $\bar{d}_e$ was substantially smaller at the lowland site than in the uplands (table 2), it was influenced by an interaction between elevation and season (two-way ANOVA, significant interaction, $P < .001$). Indeed, the lowland site appears to represent a nearly ideal thermal environment for *gundlachi:* almost 50% of all T_e readings were within T_{set} (fig. 2); consequently, $\bar{d}_e$ was very small (<1.0°C) (table 2) in both seasons. In contrast, more than 95% of the individual T_e readings at the high-elevation site fell below T_{set} (fig. 2). Ironically, *gundlachi* is usually considered a "montane" species (Williams 1972), but it seems best suited (in terms of T_{set}) to heavily shaded, lower-elevation sites.

The mean deviation between *gundlachi*'s T_b and T_{set} ($\bar{d}_b$) was smaller at lower elevation and in August (table 2) (two-way ANOVA, significant interaction between elevation and month, $P < .0001$). Moreover, $\bar{d}_b$ was very similar to and closely tracked $\bar{d}_e$ among sites and seasons, which suggests that *gundlachi* does not thermoregulate to any great extent, even in habitats in which T_e is frequently far from T_{set}. Indeed, E was always small (0.0–0.21) for this species (table 3). The high accuracy of *gundlachi*'s T_b at low elevation is thus simply a consequence of this species' thermoconformity in a thermally permissive habitat (fig. 1*C*).

Traditional indexes (table 3) provide contradictory estimates of *gundlachi*'s thermoregulation. The slope of the regression of T_b on T_a is almost invariably near one, accurately reflecting the thermoconformity of these populations. However, *gundlachi*'s low variance of T_b (and small range of hourly mean T_b) falsely suggests careful thermoregulation.

DISCUSSION AND CONCLUSIONS

In this section we first summarize the strengths and weaknesses of various indexes of thermoregulation. We then evaluate some potential extensions of our general approach.

Comparisons among Indexes

Although variance of T_b and the range of hourly mean T_b are commonly used to measure the precision of thermoregulation, they provide no information about either the accuracy of T_b or the effectiveness of temperature regulation. Recall, for example, that *gundlachi,* which is clearly a behavioral thermoconformer and which sometimes accepts T_b far from T_{set}, usually has a low variance of T_b (table 3). Conversely, *cristatellus,* which often thermoregulates, sometimes has a high variance of T_b (table 3). Similarly, the slope of the regression of T_b on T_a also provides no information on the accuracy of T_b.

Our measures of temperature regulation are an improvement over previous indexes. Our measures use T_{set} as the standard reference to which both body temperatures and environmental temperatures are compared. The accuracy of the body temperatures actually experienced (i.e., how closely T_b's correspond to T_{set}) is estimated by $\bar{d}_b$; note, however, that this index provides no information about temperature regulation per se. The average thermal quality of a habitat (i.e., how closely the distribution of T_e corresponds to T_{set}) is estimated by $\bar{d}_e$;

this index estimates the degree to which the T_b of nonregulating individuals would differ on the average from T_{set}. Our measure of the effectiveness of thermoregulation, E, incorporates information on both the thermal quality of the habitat and the body temperatures achieved; hence, the index formally determines the degree to which thermoregulatory activity by the animals compensates for the thermal shortcomings of a particular habitat. Because E does not index the accuracy of the body temperatures per se, all three measures ($\bar{d}_b$, $\bar{d}_e$, and E) as well as information on the percentages of T_b and T_e that fall within T_{set} are necessary to describe a population's thermal ecology; no single index is adequate.

Reassuringly, independent observations (above) on the magnitude of behavioral thermoregulation invariably match estimates of E: populations that restrict times of activity and engage in conspicuous shuttling behavior exhibit high E, whereas populations that do not show such thermoregulatory behavior have low E. No other index provides comparable concordance with the behavioral patterns. Hence, when combined with complementary field observations on behavior (Heath 1964, 1965; Huey et al. 1977), these or related indexes (see below) should provide a reasonably complete portrait of behavioral thermoregulation by ectotherms.

Ideally, T_{set} should be measured in the seasons when T_e's and T_b's are obtained. In our sample analysis, the indexes that describe temperature regulation in both January and August are based on T_{set}'s measured only in summer. Nevertheless, a sensitivity analysis suggests that E (table 3) is a fairly robust measure. We recalculated E in January for the three *cristatellus* populations using hypothetical T_{set}'s in which both the lower and upper bounds were shifted downward. Neither a 1°C nor a 2°C drop in T_{set} has a dramatic impact on estimates of E for the high-elevation ($\Delta E = +0.01$ and $+0.01$, respectively) and lowland mesic ($\Delta E = -0.03$ and -0.11, respectively) populations. However, these shifts in T_{set} have more pronounced effects on estimates of E for the desert population ($\Delta E = +0.18$ and $+0.26$, respectively) where January T_b's frequently fell below the August T_{set} used in the original analysis. Larger seasonal changes in T_{set} (Sievert and Hutchison 1989) could have a dramatic impact on $\bar{d}_e$, $\bar{d}_b$, and E.

We cannot overemphasize that our general approach is merely a tool for investigating questions about the regulation of body temperature by field-active ectotherms. In the example developed above, we used the mean deviations of T_b and T_e from T_{set} and parametric statistical tests to provide a simple and easy-to-follow summary portrait of the average individual. However, mean values can be misleading because they inevitably represent a loss of information about underlying distributions and variability. For example, $\bar{d}_e$ is low for *cooki* (table 2), but, even so, 66% of individual T_e readings in summer were above T_{set} for this species. Consequently, examination of the distributions of d_b and d_e will undoubtedly provide additional insights, especially if the distributions are multimodal or highly skewed. We caution other workers to tailor the indexes to the biology of their study organisms and the specific questions or concepts being addressed. For example, if the distributions of d_b or d_e included a few extreme values, the influence of those outliers could be reduced or eliminated by using median values or the square root of the individual d values in calculations of $\bar{d}_b$ or $\bar{d}_e$. Alternatively, developing indexes that incorporate variability, and not just mean values, may often be appropriate (D. Bauwens, personal communication).

Estimating the Physiological Impact of Temperature Regulation

Our approach can be extended to elucidate the impact of temperature regulation (or the lack thereof) on physiological performance. To do so, one must measure the thermal sensitivity of ecologically meaningful whole-animal activities (Huey and Stevenson 1979), then compare the predicted relative (0%–100% of maximal) performance of real animals to that of hypothetical nonthermoregulating animals. Thermal sensitivity is typically measured in the laboratory (see, e.g., Bennett 1980) but could in principle be measured in the field. The thermal sensitivity of sprint speed is frequently used in this context (Hertz et al. 1983; Huey 1983; Stevenson et al. 1985; Tracy and Christian 1986; O'Connor and Tracy 1992), but other performance traits can be used (see Stevenson et al. 1985; Huey et al. 1989*b;* Van Damme et al. 1991). In any case, such thermal performance data require cautious interpretation because performance "curves" can be influenced by acclimation, physiological state, and ecological factors (reviewed in Huey 1991). Moreover, the relative performance of one performance activity may not always be a reliable indicator of relative fitness (Huey and Slatkin 1976; Crowder and Magnuson 1983; Grant and Dunham 1990; Van Damme et al. 1991; but see Jayne and Bennett 1990).

We use data on the thermal sensitivity of sprint speed for the three *Anolis* species examined above to describe the impact of temperature regulation on their performance in the field. Data on sprinting in *cristatellus* were taken from Huey (1983); comparable unpublished data are available for *gundlachi* and *cooki*. Performance curves describing the thermal sensitivity of sprint speed were estimated using a minimum convex polygon algorithm (van Berkum 1986). From these curves we interpolate relative spring speed (percentage of maximum speed) at the T_b's and T_e's relevant to our analysis.

Temperature regulation by *cooki* appears to improve sprint performance only slightly (less than a 10% improvement in maximum speed) relative to that of hypothetical nonthermoregulating lizards (table 2). Furthermore, season has little impact on the predicted performance of either thermoregulating or nonthermoregulating lizards.

The relative sprint performance of *cristatellus* (P_b in table 2) was surprisingly independent of altitude and season: predicted mean speeds were generally 85% of maximum speed or greater (but see below). In contrast, predicted relative speeds of nonregulating lizards (P_e in table 2) varied greatly with altitude and season. Consequently, thermoregulation sometimes substantially improved sprint performance, especially in extreme environments. For example, in the desert in summer, real lizards, even though they were hot relative to the optimum temperature for sprinting (tables 1 and 2), could have run much faster (85% of maximum) than null lizards (66% of maximum), which would have been even hotter (mean T_e in table 1). At high elevation in winter, real lizards, though cold (table 1), ran faster than would null lizards (84% versus 69% of maximum speed), which would have been even colder.

Not surprisingly, *gundlachi* had predicted performances that were nearly identical to those expected in null lizards. Lowland *gundlachi* should have been able to run on the average at 84%–90% (winter and summer, respectively) of maximal levels; null lizards would run at comparable levels (83%–88%). At high elevation, however, real lizards and null lizards were substantially colder than conspecifics at low elevation (table 1), and their performance levels were correspondingly reduced (68%–78% for real lizards, 66%–76% for null lizards). These performance levels are well below those typical of diurnal lizards (Hertz et al. 1983; Huey et al. 1989*a*); however, Van Damme et al. (1989, 1990) also recorded impaired sprint performance in high-altitude populations of *Podarcis tiliguerta* and *Lacerta vivipara*. Thus, thermal conformity by *gundlachi* appears to be disadvantageous for maximizing sprint performance, especially at high elevation.

Other Possible Extensions

Our general approach can be tailored to address a variety of additional questions. For example, in the sample analysis, we combined data across full days. However, Dreisig (1984), Peterson (1987), Grant and Dunham (1988), and others have argued that the time dependence of the thermal environment and temperature regulation should not be ignored; dynamic diel shifts in thermoregulatory demands and activity may be missed. We agree, and our approach could be easily adapted to study hour-by-hour, weekly, or seasonal patterns. One could also, for example, restrict the analysis to those hours or days when preferred T_b could be achieved (i.e., when T_e overlapped T_{set}).

Similarly, we studied thermoregulation and thermal environments by lumping microhabitats within each locality. This is appropriate for a study of localitywide patterns. However, the analysis could easily be restricted to specific microhabitats (e.g., logs in the open) or even to the territories of specific individuals, which would foster insights on microhabitat- or individual-specific patterns (Huey et al. 1977, 1989*b;* Christian and Tracy 1985; Grant and Dunham 1988; Adolph 1990).

Our approach was derived with *Anolis* lizards, animals that normally live in relatively equable environments, in mind. For animals living in more extreme environments, where the risk of either overheating or not achieving suitable T_b can be high, the thermal environment may more appropriately be viewed as a constraint on where and when animals can be active (Porter and Gates 1969; Porter et al. 1973; Stevenson 1983; Peterson 1987; Grant and Dunham 1988, 1990; Huey et al. 1989*b*). During most of the day, for example, virtually the entire ground surface at a desert locality is well above the lethal temperature of canyon lizards (*Sceloporus merriami*), which greatly restricts the lizards' movement and activity (Grant and Dunham 1988). Accordingly, an index based on a measure of how the thermal environment constrains animals (e.g., lethal temperatures rather than T_{set}) may be more suitable for studies of animals that occupy such extreme environments (Grant and Dunham 1988).

Our approach may not be directly applicable to some insects, however, especially flying and endothermal ones. Although such insects are small, they can exert strong physiological control over T_b. In addition, set-point temperatures of such insects can vary dramatically from rest to flight and can even differ among body segments (Heinrich 1992). Other insects are able to modify local T_e by constructing webs (Joos et al. 1988). Accordingly, more complex models, sampling schemes, and indexes may be necessary to analyze thermoregulation in these organisms.

Finally, our measures of average habitat quality ($\bar{d}_e$) ignore the costs incurred to regulate temperature, and such costs potentially affect set-point temperatures and the extent of temperature regulation (Hertz 1974; Huey 1974; Huey and Slatkin 1976; Withers and Campbell 1985). Similarly, relative sprint speed (or any other performance trait) is an overly simplistic metric for evaluating the performance consequences of thermoregulation (Huey 1983; Stevenson et al. 1985; Tracy and Christian 1986). Although performance may sometimes influence fitness (Christian and Tracy 1981; Bennett and Huey 1990; Jayne and Bennett 1990), any mapping of fitness on performance is complex and depends on the environment as well as on physiology (Huey and Slatkin 1976; Huey 1982, 1991; Crowder and Magnuson 1983; Dunham et al. 1989). In addition, different physiological systems can have different thermal sensitivities (Huey 1982; Stevenson et al. 1985; Van Damme et al. 1991). Consequently, we again caution that the indexes developed here—or unrelated indexes—must be applied with careful sensitivity to the natural history of the organism in question.

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