

Invited review

Use of operative temperature and standard operative temperature models in thermal biology

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Abstract

Operative temperature (T_e) and standard operative temperature (T_{es}) models have been used to address ecological questions about the thermal biology of ectotherms and endotherms for over 25 years. This review focuses on the accuracy and use of T_e and T_{es} models in ecological and physiological studies. The utility of T_e and T_{es} models lie in the fact that they take a multivariate problem involving inputs of air temperature, ground temperature, solar radiation, and wind speed and map them into a single thermal metric on a spatial scale appropriate for the animal. The most reliable T_e models are copper casts that mimic the morphology and absorptivity of an animal. Simplified T_e models such as cylinders and spheres have been shown to produce errors in T_e as large as 12 °C under certain conditions and should only be used after careful calibration against a live animal. The accuracy of heated T_{es} models has been addressed in much less detail than that of T_e models. When calibrated and used under conditions of low solar radiation, heated taxidermic mounts and simplified T_{es} models produce errors in net heat production on the order of 5% or less. In order to provide reliable data, all types of models must be calibrated over an ecologically realistic range of environmental conditions experienced by the animal. This advice has been largely ignored in the literature, where 61% of the of studies examined failed to properly calibrate the models prior to use. Additionally, studies using these models tend to lack experimental rigor, using only one or two models to make measurements on 1 or 2 days of the active season. When used correctly, T_e and T_{es} models can be powerful tools for integrating the thermal environment experienced by an animal into a single metric that can address questions regarding the ecology, physiology, and behavior of endotherms and ectotherms. However, until investigators make the effort to use these models in a scientifically valid manner with proper calibration and experimental design their value to thermal biologists will be limited.

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1. Introduction

Over the past 25 years, operative temperature (T_e) and standard operative temperature (T_{es}) models have been employed to study the thermal ecology, behavior, and physiology of ectotherms and endotherms (Bakken,

1992). These models provide a means to measure the thermal environment on a scale relevant to an animal's microhabitat by integrating convective and radiative heat transfer between the environment and the animal (Bakken and Gates, 1975; Bakken, 1976). When used correctly, both operative temperature and standard operative temperature models have the potential to be powerful tools for examining the relationship between an animal's thermal environment and its physiology and ecology.

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Nomenclature	
a_s	short-wave absorptance
d_e	mean deviation between field measured T_e and the animal's set point temperature ($^{\circ}\text{C}$)
h_c	convection coefficient ($\text{W m}^{-2} \text{K}^{-1}$)
u	wind speed (m s^{-1})
v_s	view factor for short-wave radiation
K_e	overall thermal conductance ($\text{W}^{\circ}\text{C}^{-1}$)
K_{em}	overall thermal conductance of taxidermic mount ($\text{W}^{\circ}\text{C}^{-1}$)
K_{es}	overall thermal conductance in a standard environment ($\text{W}^{\circ}\text{C}^{-1}$)
K_{esm}	overall thermal conductance in a standard environment of taxidermic mount ($\text{W}^{\circ}\text{C}^{-1}$)
$M-E$	net heat production; metabolic heat production minus evaporative heat loss (W)
P	heater power to maintain temperature of T_{es} taxidermic mount (W)
R	solar radiation (W m^{-2})
T_a	air temperature ($^{\circ}\text{C}$)
T_b	body temperature ($^{\circ}\text{C}$)
T_e	operative temperature ($^{\circ}\text{C}$)
T_{es}	standard operative temperature ($^{\circ}\text{C}$)
T_g	ground temperature ($^{\circ}\text{C}$)
T_r	long-wave radiative temperature ($^{\circ}\text{C}$)
ε	long-wave radiation absorptance
σ	Stefan–Boltzman constant ($5.673 \times 10^{-8} \text{W m}^{-2} \text{K}^{-4}$)

Bakken (1992) reviewed the use of T_e and T_{es} models up to 1991, including applications such as mapping the thermal environment, providing a measure of the thermal value of an animal's home range, and estimating the energetic costs of living in various thermal environments. Since then a number of construction and usage issues with both types of models have been raised (Walsberg and Wolf, 1996a, b; Laroche, 1998; Bakken et al., 1999b, 2000, 2001; Vitt and Sartorius, 1999; O'Connor, 2000; O'Connor et al., 2000; Fortin 2001; Shine and Kearney, 2001). My goals in this review are as follows: (1) to provide a brief review of the theory behind both T_e and T_{es} models, (2) to examine the reliability, accuracy, and use of these models in the literature, and ultimately (3) to suggest that in order for these models to provide useful data they must be calibrated and employed with a sound experimental design.

2. Operative temperature models

2.1. Theory

Operative temperature (T_e) is the “temperature of an inanimate object of zero heat capacity with the same size, shape, and radiative properties as the animal exposed to the same environment” (Bakken and Gates, 1975). Put another way, T_e is the body temperature of an animal if it were in thermal equilibrium with the environment in the absence of metabolic heating or evaporative cooling.

Operative temperature is measured with physical models placed in the environment or with mathematical equations describing the steady-state heat transfer between the animal and the environment. Recent

examples of studies that use various methods to measure T_e are provided in Table 1. Mathematically, T_e can be defined as

$$T_e = \frac{h_c T_a + 4\sigma\varepsilon T_r^4 + a_s v_s R}{h_c + 4\sigma\varepsilon T_r^3}. \quad (1)$$

Symbols are defined in the Nomenclature. As Eq. (1) shows, T_e integrates all the convective and long wave and short wave radiation heat exchange pathways influencing equilibrium temperature of an animal. When calculating T_e with Eq. (1), wind speed, solar radiation, T_a , and thermal radiation must be measured in the available microhabitats.

Numerous physical model representations of an animal have been used to measure field T_e (see Table 1 for recent examples). Operative temperature models are typically made of copper, due to the high heat conductance of this metal. The most sophisticated T_e models use an electroplating technique described by Bakken and Gates (1975) to produce a thin copper cast with a convection coefficient and morphological characteristics equal to that of the animal. This cast is then painted to match the animal's absorptivity (Grant and Dunham, 1988; see Table 1). To simplify the construction of T_e models, many studies have used short pieces of copper pipe painted to match the absorptivity of the animal (Peterson, 1987; Huey et al., 1989; see Table 1) or small temperature loggers to measure T_e in place of copper models (Sartorius et al., 1999; Vitt and Sartorius, 1999). For small animals such as insects, dried specimens with a thermocouple inserted in the body have been used as T_e models (Chappell, 1982; Morgan and Shelly, 1988; see Table 1).

The use of physical models allows investigators to measure T_e in many microhabitats simultaneously. These models can replace expensive equipment (multiple

Table 1
Examples of T_e models used in thermal ecology from 1991 to 2004

Model type	Animal	Reference
Copper cast models	Lizard	Hertz (1992a, b), Niewiarowski and Roosenburg (1993), Hertz et al. (1993), Bauwens et al. (1996), Walsberg and Wolf (1996a), Bashey and Dunham (1997), Lorenzon, et al. (1999)
Hollowed shell	Turtle	Penick et al. (2002)
Hollow copper cylinders	Amphibian, lizard, snake	Peterson, et al. (1993), Diáz (1994), Dorcas (1995), Belliure et al. (1996), Shine and Madsen (1996), Dorcas et al. (1997), Diáz (1997), van Marken Lichtenbelt et al. (1997), Lillywhite et al. (1998), López et al. (1998), Schäuble and Grigg (1998), Brown and Weatherhead (2000), Shine et al. (2000), Wills and Beaupre (2000), Shine and Kearney (2001), Shine et al. (2002)
Tygon tubing	Snake	Beaupre (1995a, b)
Thick-walled aluminum models	Turtle	Zimmerman et al. (1994), O'Connor (2000), O'Connor et al. (2000)
Tidbit™ or Hobo™ data loggers	Lizard	Sartorius et al. (1999), Vitt and Sartorius (1999), Klingenböck et al. (2000)
Black or gray copper ball	Bird, lizard, mammal	Weathers and Sullivan (1993), Houseal and Olson (1995), Beaver et al. (1996), Wikelski et al. (1996), Beaver and Olson (1997), Cooper (1999) Wikelski and Wrege (2000), Wikelski et al. (2000), Weathers et al. (2002)
Water filled copper model	Lizard	Grbac and Bauwens (2001)
Carcass	Insect	O'Neill and Kemp (1992), O'Neill et al. (1994), Dreisig (1995), Ashbly (1997), Bishop and Armbruster (1999), Klok and Chown (1999), Frears et al. (1999), Kingsolver (2000), Ide (2002), Merrick and Smith (2004)
Mathematical equations	Lizard	Christian and Bedford (1995, 1996), Christian and Weavers (1996), Christian et al. (1996b), Christian et al. (1997), Gloutney and Clark (1997), Christian (1998), Grigg and Seebacher (1999), Christian et al. (1999), Seebacher (1999), Seebacher et al. (1999)
T_a or T_g	Lizard	Smith and Ballinger (1994), Vitt and Avila-Pires (1998), Vitt et al. (1998), Bauwens et al. (1999), Kearney and Predavec (2000), Rock et al. (2000), Vitt et al. (2001)
Agar models	Amphibian	Navas (1996)
Unheated taxidermic mount	Mammal	Castro et al. (1992), Hayes and Shonkwiler (1996), Sharpe and Van Horne (1999), Bozinovic et al. (2000), Tieleman and Williams (2002), Stoutjesdijk (2002)

anemometers, pyrometers, radiometers, etc.) needed to measure wind speed and radiation for calculating T_e in multiple microhabitats with Eq. (1). With the use of a datalogger, the temperature of 20 or more T_e models can easily be monitored within an animal's habitat.

Operative temperature models have been used to examine the thermal environment of insects, amphibians, reptiles, birds, and mammals (see Table 1). They typically are used to test for active thermoregulation (Bakken and Gates, 1975; Bakken, 1992; Hertz et al., 1993; Wills and Beaupre, 2000); provide a method for mapping the available thermal environment on the microhabitat scale of the animal (Grant and Dunham, 1988; Hertz, 1992a,b; Bashey and Dunham, 1997; Zimmerman et al., 1994; Bauwens et al., 1996); and provide bounds of minimum and maximum T_e available in an environment.

2.2. Model accuracy

The ecological utility of physical T_e models depends on their ability to reliably estimate an animal's T_e in a given microclimate. While numerous studies have used

T_e models over the years (Table 1), surprisingly few have examined the accuracy with which they measure equilibrium T_b of a live animal (Bakken and Gates, 1975; Walsberg and Wolf, 1996a). Below I examine the literature to determine how well T_e models estimate T_e under typical wind, solar radiation, and temperature conditions found in the field.

2.2.1. Model type

Of the different model types, copper casts have been shown to provide the most accurate T_e measure (Table 2; Bakken and Gates, 1975; Walsberg and Wolf, 1996a). Walsberg and Wolf (1996a) measured the equilibrium temperature of live *Sceloporus magister*, copper casts of *S. magister*, copper cylinders, and plastic cylinders in a closed-circuit wind tunnel under one solar radiation level and a number of wind speeds. The copper casts were the most accurate predictors of the live animals equilibrium T_b . However, under the testing conditions, copper casts consistently underestimated the live lizard's T_b by 1.8–2.5 °C, depending on wind speed. Deviations between all model types and live animals were greatest at

Table 2

Comparisons of T_e models of various types, colors, sizes, and position placements

Effect	T_e deviations (°C)	T_e model types	T_e model size (l × d; mm)	T_e color	Height	Refs.
Model type	2.5–5.7°	Cylinder vs. animal ^a	121 × 22 & 112 × 16	Animals absorptivity	Ground	1.
	1.8–2.5	Cu cast ^a vs. animal ^a	96 & 68 SVL	Animals absorptivity	Ground	1.
	0.38 ± 1.25 (SD)	Tidbit vs. Cu cast ^b	30 × 40	Tidbit	Ground	2.
	0.68 ± 1.45 (SD)	Tidbit vs. Cu cast ^c	30 × 40	Tidbit	Ground	2.
	0.16 ± 2.10 (SD)	Tax. mount ^d vs. Eq. (1)		Blackbird pelt	Perch	3.
	1.19 ± 1.57 (SD)	Tax. mount ^e vs. Eq. (1)		Grassquit pelt	Perch	3.
	0.25	Cu cast ^f vs. animal ^f	9-g lizard	Animals absorptivity	Ground	4.
	0.0–6.3	Spheres vs. Tax. mount ^g	2.5, 3.5, 6.0 cm dia.		0.3 cm	5.
Color	12.5	Cylinders	64 × 16	Black vs. white	0.3 cm	4.
	4.5	Cylinders	64 × 16	Black vs. gray	0.3 cm	4.
	0.1–2.6	Cylinders	246 × 60 & 60 × 15	Jade green vs. gray	Ground	6.
Size	0.3–1.1	Casts	96 vs. 68 SVL	Animals absorptivity	Ground	1.
	0.2–1.2	Cylinders	120 × 27 vs. 118 × 16	Animals absorptivity	Ground	1.
	6	Cylinders	152.4 × 38 vs. 25.6 × 6.4	Gray	0.3 cm	4.
	4	Cylinders	64 × 16 vs. 25.6 × 6.4	Gray	0.3 cm	4.
	0.3–4.2	Cylinders	246 × 60 vs. 60 × 15	Gray and jade green	Ground	6.
Location	9.5	Cylinders	64 × 16	Gray	0.3 vs. 90 cm	4.
	6	Cylinders	64 × 16	Gray	0.3 vs. 20 cm	4.
	7.3–10.16	Cu casts ^f	12 g animal	Gray	Ground vs. 60 cm	7.
	2.9–5.5	Cu casts ^f	12 g animal	Gray	Ground vs. 1 cm	7.

^a*Sceloporus magister*, ^b*Scincella lateralis*, ^c*Sceloporus ndulatus*, ^d*Euphagus cyanocephalus*, ^e*Volatinia jacarina*, ^f*Sceloporus occidentalis*, ^g*Melopsittacus undulatus*, *Lanius ludovicianus*, *Pica nuttallia*, and *Phainopepla nitens*. References: (1) Walsberg and Wolf (1996a); (2) Vitt and Sartorius (1999); (3) Greek et al. (1989); (4) Bakken and Gates (1975); (5) Walsberg and Weathers (1986); (6) Shine and Kearney (2001); (7) Bakken (1989).

the lower wind speeds (Walsberg and Wolf, 1996a). Bakken and Gates (1975) reported smaller deviations of 0.25 °C between the equilibrium T_b of live *Sceloporus occidentalis* and T_e of a copper cast of *S. occidentalis* tested in the field.

Numerous studies have tested the accuracy of the copper casts prior to field use and found relatively good agreement between the model and a live or dead animal under the testing conditions. Copper casts of the greater earless lizard (*Cophosaurus texanus*) predicted equilibrium T_b under various wind and solar conditions to within 1 °C of a live animal (Bashey and Dunham, 1997). Under 5 heat loads, smaller deviations of 0.2 °C were observed between a tethered lacertid lizard, *Podarcis hispanica atrata*, and a copper

cast of the animal (Bauwens et al., 1996). Hertz (1992a) found that 80% of copper casts T_e measurements were within 1 °C of the equilibrium T_b of *Anolis gundlachi* and *Anolis cristatellus*. The largest deviations occurred under high solar radiation conditions and low T_a where T_e and T_b differed by more than 1 °C. Most of the studies testing copper cast accuracy suggest that these models predict operative temperature to within 1 °C. However, under certain conditions (i.e. low wind speed or high solar radiation) the models become less accurate.

In an attempt to simplify T_e model construction, investigators have used copper tubes or metal spheres to measure T_e (Table 1). These simplified models have the advantage of being easier to construct than animal casts.

The tradeoff is a potential decrease in measurement accuracy. Walsberg and Wolf (1996a) compared the T_b of *S. magister* to T_e of copper and plastic cylinders with absorptivities similar to *S. magister*. Operative temperatures of both cylinder types were as much as 6 °C lower than the corresponding T_b . Similarly, Walsberg and Weathers (1986) found that T_e measured with metal spheres deviated from taxidermic mounts by as much as 6.3 °C (Table 2). During a 5-day comparison between spherical models and taxidermic mounts, over 25% of the average hourly T_e values were 3 °C greater in the spheres than the mounts and 18% of the time the difference was greater than 4 °C. Under environmental conditions that produced low T_e values, the temperature of a black metal sphere agreed well with the equilibrium temperature of a Blackbird taxidermic mount (Bakken et al., 1985). Under higher T_e conditions, the sphere temperature was higher than the mount due to increased solar heating of the sphere. This led Bakken et al. (1985) to conclude that “simply duplicating the approximate form and color of the animal of interest is unlikely to succeed”.

Studies involving snakes have used simplified cylinder models to measure T_e (Peterson, 1987; Dorcas, 1995; Beaupre, 1995a, b; Shine and Madsen, 1996; Wills and Beaupre, 2000). Beaupre (1995b) found maximum temperature differences of approximately 1.5 °C between plastic cylinder models and equilibrium T_b of the mottled rock rattlesnake (*Crotalus lepidus*) under field conditions. Brown and Weatherhead (2000) found that cylinders accurately predicted the T_b of a dead northern water snake (*Nerodia sipedon*) under high-temperature conditions but at lower body temperatures the deviation between the dead snake and model temperature was as large as 7 °C in some cases (calculated from Fig. 1 in Brown and Weatherhead, 2000). However, it was not shown how well a dead snake represents a live snake. Wills and Beaupre (2000) found that at times, individual T_e measurements differed from T_b by as much as 4 °C. Adding to this, they found that the T_e of the cylinders did not stabilize during their calibrations under windy conditions. Peterson et al. (1993) carried out preliminary sensitivity analysis to determine how well copper cylinders would predict T_e of snakes; however, they only present the accuracy of copper cylinders to predict snake T_b as “good results” without presenting any data. Other studies using simplified snake models failed to examine the relationship between model T_e and snake equilibrium T_b (Shine and Madsen, 1996; Shine et al., 2000).

Recently, Tidbits™ temperature loggers (Onset Computer Corporation, Pocasset, MA) have been suggested to be useful, accurate, and simple T_e models (Vitt and Sartorius, 1999). Tidbits are small, cylindrical, solid epoxy temperature loggers with an internal temperature probe (diameter 30 mm; height 17 mm; mass 23 g). Comparisons of Tidbits™ T_e with copper cast T_e were carried out on the ground where heat

exchange with the ground dominates the heat transfer of small ectotherms. Under these conditions, Tidbits™ performed reasonably well with 80% of the T_e estimates deviating from copper model T_e by less than 2 °C. (Table 2; Vitt and Sartorius, 1999). Unfortunately, this study examined the potential deviations between Tidbits™ and copper models, but failed to include the response of live animals (Table 2).

There are a number of issues associated with Tidbits™ that could influence their usefulness as T_e models. Tidbits™ have a slow response time to temperature change, taking 18 min to reach 90% of a temperature excursion in moving air (Onset Computer Corporation). This limits the ability to extract instantaneous T_e measurements, especially in habitats where the thermal environment continuously fluctuates. Additionally, the possibility of thermal gradients in Tidbits™ has yet to be examined and may play a role in the T_e that is measured by the model through time.

When using any simplified model such as cylinders or Tidbits™, errors may result with arboreal animals where convection dominates heat exchange or for animals that stand on the ground with their bellies more than a few millimeters off the substrate. The placement of copper casts only 1 cm above the ground has the potential to change T_e by as much as 5.5 °C (Bakken and Gates, 1975) suggesting the importance of the animals convection coefficient. The convection coefficient is a function of shape and size and therefore, differences in the convection coefficient between simplified models and an animal may be large enough to result in significant deviations in T_e under certain conditions. In the microhabitats occupied by arboreal species the difference between realistic models and simplified models may be more prevalent because ground temperature or solar radiation will not dictate the heat exchange pathways.

2.2.2. Model color

For diurnal lizard species, basking in the sun and shuttling between various microhabitats is a major source of heat gain (VanBerkum et al., 1986; O'Connor, 1999). The absorptivity of T_e models has large effects on equilibrium temperature under high solar radiation conditions and should match as closely as possible the absorptivity of the animal. Painting a model black or gray in the hopes that the solar heat gain will match an animal will lead to inaccurate T_e estimates in partial or full sun. Cylinders that differ in absorptivity can vary in temperature by as much as 12.5 °C under high solar radiation conditions (Table 2; Bakken and Gates, 1975; Peterson et al., 1993; Shine and Kearney, 2001). Bakken and Gates (1975) showed in the extreme case that black and white cylinders of similar shape and size varied in temperature by as much as 12.5 °C during a typical sunny day. Differences as large as 4.5 °C were observed between gray and black cylinders. In contrast, Shine and

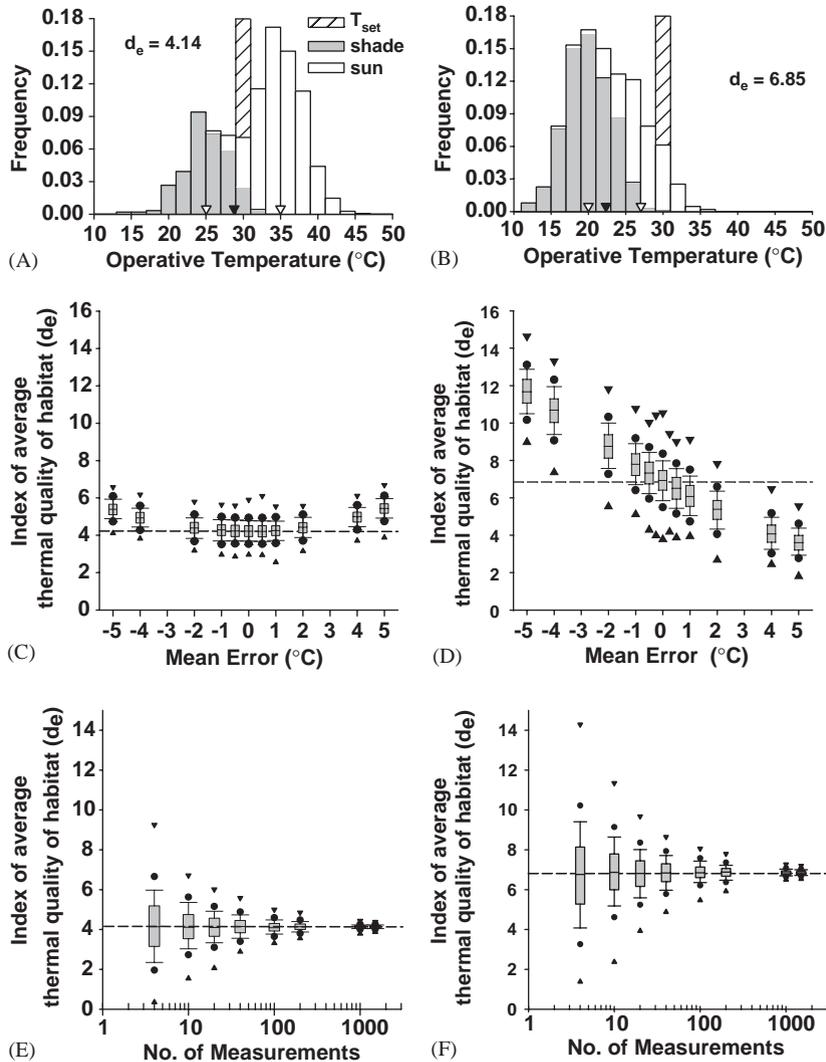


Fig. 1. A and B Simulated distributions of T_e in two hypothetical sun and shade microhabitats habitats. Set-point temperature range for the hypothetical animal is 29 to 31°C. Triangles denote the mean overall T_e (filled), the mean sun T_e (open), and mean shade T_e in the habitat (open). The index of the average thermal quality (Hertz et al., 1993) for the environment in Fig. 1A is 4.14 and for the environment in Fig. 1B is 6.85. C and D. Box plots, including maximum, 95%, 75%, median, 25%, 5%, and minimum values, for the index of the average thermal quality of the two hypothetical habitats (d_e) vs. the error in T_e measurements. Sample sizes for each simulation were 50 random measurements taken from the T_e distributions presented in A. or B. Twenty-five random values were taken from the shade distribution and 25 random values from the sunny distribution. A normally distributed random error was added to each randomly selected T_e (error $\pm 1.45^\circ\text{C}$; $\mu \pm \text{SD}$). The mean error ranged from 0 to 5°C. The SD is based on the SD of Tidbit temperatures measured by Vitt and Sartorius (1999). The figure presents the results of 1000 simulations at each error level. E and F. Box plot, including maximum, 95%, 75%, median, 25%, 5%, and minimum values for the index of the average thermal quality of the two hypothetical habitats (d_e) vs. the number of random T_e measurements made. An error was added to each randomly selected T_e as above. Half of the random T_e values were taken from the sun distribution and half were taken from the shade distribution. The figure presents the results of 1000 simulations.

Kearney (2001) examined the effect of color on the equilibrium temperature of copper cylinder models and found that differences in color (40% vs. 7.3% reflectance) had at most a 2.6°C effect on temperature under the conditions tested. However, model color was the

physical factor having the greatest influence on the length of time a model temperature was above 30°C. There was a 10% difference (0.4–0.6 h out of 4.8 h) each day in the time the temperatures of dark models were above 30°C compared with light models. Not surpris-

ingly, the greatest difference occurred at the higher temperatures when solar radiation would be highest.

Model color has a large influence on the measured T_e and the absorptivity should match the animal as closely as possible. Peterson et al. (1993, see Table 7.1) provide absorptance values for commercially available spray paints ranging from 31.4% to 98.5%. Porter (1967), Peterson et al. (1993) and Christian et al. (1996a) provide measures of reflectance or absorptance for a variety of snakes and lizards. Porter (1967) also provides values for some fish, mammals, and birds.

2.2.3. Model size

Size influences convective and radiative heat exchange of a model and thus the equilibrium temperature of T_e models (Table 2). Walsberg and Wolf (1996a) examined the effect of size on equilibrium temperature of copper casts and cylinders. Temperatures of smaller casts and cylinders were between 0 and 1 °C lower than those of larger casts and cylinders suggesting an influence of size of T_e . However, the temperatures of all sizes of copper cast and cylinder were significantly lower than the live spiny lizard, *S. magister* (Walsberg and Wolf, 1996a).

Shine and Kearney (2001) suggest that model size is one of the most important determinants of a model's thermal response. In their study, the size of the model had the largest effect on the maximum and mean temperature obtained by a cylinder. The maximum temperature achieved by small models averaged 3.7 °C above that of large models, with the extreme difference being 4.2 °C. Similarly, Bakken and Gates (1975) showed that increasing model size resulted in large T_e discrepancies between models of similar shape and color but different sizes. At ground level (0.3 cm), model size brought about temperature deviations of up to 6 °C (Table 2), with larger models producing higher T_e values. In another test, Bakken and Gates (1975) found that temperature differences between the smallest and largest models was much smaller when they were placed on the ground than when they were suspended 90 cm above the surface. Thus, demonstrating the important interaction of size, convection coefficient, and potential boundary layer.

Operative temperature models integrate all of the exchanges from the heat transfer pathways affecting an animal in a give microhabitat into a single temperature. Difficulties arise when determining the T_e of larger reptiles due to the potentially large thermal inertia of the models (Standora et al., 1982; Zimmerman et al., 1994; O'Connor, 2000; O'Connor et al., 2000). Bakken (1992) reports that animal models smaller than 30 g with a diameter less than 3 cm should have small thermal gradients. As model size increases, the potential for internal thermal gradients increases as well. Models of large animals (>0.5 kg) can be constructed with either thin walls or thick walls. In thin walled models, as size increases thermal gradients tend to development and a

single "true" value of T_e becomes difficult to determine (O'Connor, 2000; O'Connor et al., 2000). Thermal gradients in large, thin-walled desert tortoise T_e models painted black were as large as 20 °C in the dorsal to ventral direction and 18 °C in the anterior to posterior direction (O'Connor et al., 2000). In making models of large animals, a number of techniques have been employed unsuccessfully to decrease the presence of thermal gradients. These include filling the center with crumpled aluminum foil, aluminum fins, or water (Bakken, 1992; O'Connor et al., 2000). Two potential problems exist when using water filled models. First, there is a tendency for water to produce thermal layers resulting in uneven distribution of heat within the model. Second, there is the possibility of air bubbles forming in the model resulting in the dorsum of the model becoming insulated.

Typically, there is a tradeoff between wall thickness, thermal inertia, and the development of thermal gradients in large T_e models. Thick-walled models tend to have less temperature variation within the model both dorsoventrally and anterior posteriorly (O'Connor et al., 2000). Thick-walled models integrate the regional heat flows into a single T_e similar to the way an animal integrates heat flow. The cost of using thick-walled models is an increased thermal time constant resulting in a time integrated T_e , not an instantaneous T_e as provided by small models. O'Connor (2000) devised a method using a deconvolution technique to extract the instantaneous T_e from models that have long thermal time constants. For large animals, the most accurate T_e models are those with thick walls that can be subjected to the deconvolution technique to extract the true T_e for a microhabitat. These T_e values are useful when using mathematical models to predict body temperature of a large animal moving through the environment. Seebacher and Shine (2004) present another approach to dealing with T_e models with long time constants. They propose a correction factor that corrects for the time lag in temperature change due to the large body mass of the animal.

2.2.4. Acceptable error

It is apparent that the T_e models currently in use exhibit a wide range in their accuracy (Table 2). When choosing a model type to use in the field the main question to be addressed is: How much error in the estimated operative temperature is tolerable? Two simple simulations were conducted to examine the level of acceptable error in T_e models. In the first simulation, the influence of model error on measurements of the quality of available thermal habitat for a hypothetical lizard was examined (see Fig. 1 for simulation methods). The index of average thermal quality of a habitat (d_e) introduced by Hertz et al. (1993) is a measure of how the distribution of available T_e differs from the set point

temperature of an ectotherm in a habitat. This index has been used by a number of investigators (Bauwens et al., 1996; Christian and Weavers, 1996; Diáz, 1997; Schäuble and Grigg, 1998; Brown and Weatherhead, 2000).

The simulations suggest that the influence of measurement error in T_e is dependent on the T_e distribution relative to the animal's set point temperature (Fig. 1). Errors in T_e measurements are of greatest consequence when the mean of the true T_e distribution in the environment is far from the animal's set point temperature (Fig. 1C and D). In a simulation where sun and shade T_e values bound the set point temperature (Fig. 1A), measurement errors of 2 °C and lower have small effects on the distribution of randomly measured T_e and the subsequent d_e (Fig. 1C). However, when the true T_e distribution is shifted to the left (or right) relative to the set point temperature, the index d_e is much more sensitive to measurement error (Fig. 1D). In this case, a 2 °C error between the model T_e and the animal's true T_e produce unacceptable deviations in d_e . The acceptable model error depends on the relative position of the true available T_e distribution in the environment in relation to the animal's set point temperature.

A second simulation compared the distribution from 30 T_e measurements randomly sampled from the T_e distribution presented in Fig. 1A with measurement errors ranging from 0 to 5 °C (see Fig. 2 for description of simulation). The simulated random T_e distributions were compared with the true distribution using the Kolmogorov–Smirnov test. Model errors 2 °C and greater resulted in a T_e distribution that was significantly

different from the true distribution 40% or more of the time (Fig. 2). Model errors of 1 °C or less produced the most reliable results. Given the thermal dependence of many metabolic processes, a 2–4 °C difference in predicted vs. actual temperature could have a significant effect on the ecology and physiology of an organism. Regardless of how the models will be used, for most studies model errors on the order of 2 °C and higher are intolerable.

2.2.5. Calibration

To be a powerful tool for ecologist, T_e models must provide accurate and reliable T_e measurements for the animals being studied. In light of the potential deviations in a model's measured T_e from a live animal (Table 2) and the potential consequences of these errors (Figs. 1 and 2) it is important that investigators calibrate their models before use. Numerous authors have stressed the importance of calibrating and testing T_e models against live animals to ensure their accuracy (Bakken and Gates, 1975; Walsberg and Wolf, 1996a; Vitt and Sartorius, 1999). However, the investigators using T_e models have largely ignored this point. In a review of 54 studies that used T_e models over the past 12 years, only 39% (21 out of 54) of the studies carried out or even mentioned any type of calibration of the models before or after they were used. Calibration is particularly important when measuring T_e with simplified models whose shape does not match that of the animal, such as a copper bulb, copper cylinder, or Tidbits™ (Table 2). The studies that used copper casts of animals in the field were more likely to calibrate their models (6 out of 8 studies) than those using more simplified models such as cylinders, spheres, or Tidbits (15 out of 38 studies). This is unfortunate because as Walsberg and Wolf (1996a) show, T_e measured with cylinder models may be less representative of the animals true T_e than measurements made with cast models. Surprisingly, studies that used taxidermic mounts to measure T_e ($n = 8$) appear never to have calibrated their models.

Calibration has typically involved comparing model T_e against T_b of a dead or restrained animal in an attempt to show that T_e accurately predicts T_b . Numerous examples exist in which T_e models were calibrated and closely represent the animal's T_e (Hertz, 1992a, b). Coefficients of determination (r^2) of the relationship between T_b and T_e using copper cylinders for models tend to range between 0.87 and 0.97 (Peterson, 1987; Beaupre, 1995a, b; Diáz, 1997; Dorcas et al., 1997; Brown and Weatherhead, 2000). These coefficients are not different from values determined using copper cast models (*A. gundlachi* $r^2 = 0.97$ and *A. cristatellu* $r^2 = 0.99$, Hertz, 1992a). A number of authors provide good examples of the importance of calibrating T_e models against live animals under a range of potential solar radiation levels (Bakken et al., 1985; Beaupre,

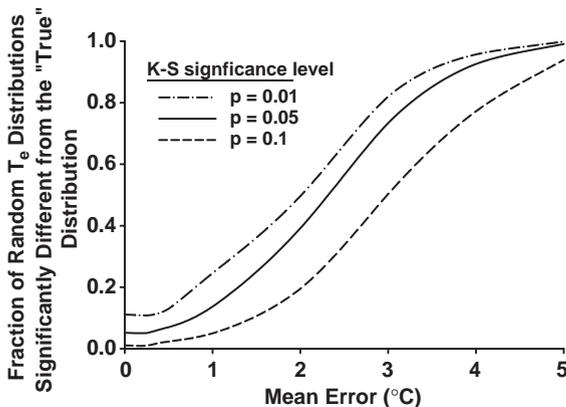


Fig. 2. Randomization analysis examining the influence of error in the measurement of T_e on the sampled distribution. Random values of T_e were taken from the distribution in Fig. 1A. Sample sizes for each distribution are 30 T_e models. A normally distributed random error ranging from 0 to 5 °C \pm 1.45 °C ($\mu \pm$ SD) was added to each T_e value selected. For each error level, 1000 random distributions were created. Each random T_e distribution was compared with the true T_e distribution using a Kolmogorov–Smirnov two sample test. Results for p values of 0.1, 0.05, and 0.01 are shown.

1995a, b; Di az, 1997). Although the relationships were strong ($r^2 = 0.89\text{--}0.98$), the slopes of the regressions of animal T_e vs. model T_e were significantly different from one. The authors corrected all field measured T_e values using the calibration regression equations. These deviations from the animal's T_e were of similar magnitude to the deviations measured by Walsberg and Wolf (1996a). Corrections in measured T_e should be made when the slope of model T_e vs. animal T_b is significantly different from 1.

Calibration of T_e models should occur over the entire range of environmental conditions expected in the microhabitat (Bakken, 1992). Many studies have calibrated models under various solar radiation loads (Di az, 1994, 1997; Beaupre, 1995a, b; Bauwens et al., 1996; Belliure et al., 1996; Grbac and Bauwens, 2001), but only one wind speed. As Bakken and Gates (1975) point out, airflow outdoors tends to be more turbulent than wind in a wind tunnel where measurements are typically made. Calibrations outdoors would be expected to provide a greater range of wind speeds and solar radiation during a multi-hour testing period. However, the drawback of calibrating outdoors is that the conditions are continuously changing and animals T_b would never come to equilibrium and would lag behind the T_e of the model. Other studies have calibrated their T_e models against dead animals placed in the field (Brown and Weatherhead, 2000) without showing that the dead animal approximates the live animal.

2.3. T_e model use in the field

Ecological studies rely heavily on appropriate experimental design when testing hypotheses (Resetarits and Bernardo, 1998). Studies on the thermal ecology of animals using T_e models should apply the same rigorous experimental design. Just as one would not accept data collected on a single individual, we should require measurements using multiple T_e models in the environment. Users of this technique must be mindful of the inherent variability in the environment available to an animal.

A significant problem with studies using T_e models is a lack of replication (Fig. 3A). In a review of 51 recent studies using T_e models in the field, the median number of models used to measure T_e in the environment was 4. A bimodal distribution was observed, with only 10 studies using 40 or more models to map the available thermal environment. In 9 studies, the number of T_e models employed was not mentioned.

Numerous studies used only one or two models of the animal in one or two "typical" microhabitats or the maximum and minimum available habitats (Peterson, 1987; Wikelski et al., 1996; Brown and Weatherhead, 2000; Klingenb ock et al., 2000). This design assumes that the investigator knows the locations in the environment that will result in the warmest and coolest

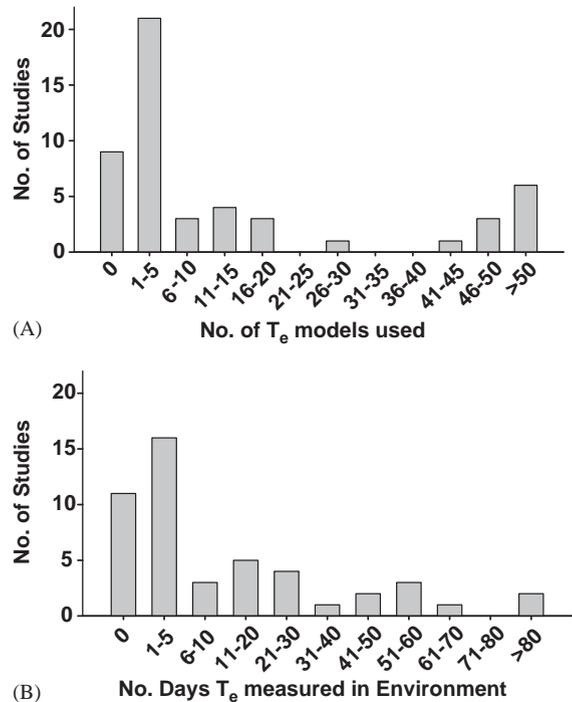


Fig. 3. (A) Frequency distribution of the number of T_e models used per study in a survey of the literature ($n = 51$). Papers where the number of models used was not provided are given as 0. (B) Frequency distribution of the number of days T_e was measured per study in a survey of the literature ($n = 48$). Papers where the number of days measured were not provided are given as 0.

body temperatures. It also makes the assumption that temperatures falling between the max and min are readily available to the animal, which might not always be the case. Another potential limit when using one or two models is the lack of information about the availability and distribution of various thermal microhabitats. Lizards typically live in diverse habitats with many microhabitat types such as logs, trees, leaf litter, and rocks (Huey et al., 1989). Large differences can exist in the thermal properties of the various microhabitats. Bauwens et al. (1996) used 44 copper lizard casts to measure T_e in four main habitat types; the center of a bush, bush edge, rock, and open microhabitats. Operative temperature ranged from 34.7 to 41.3 °C in the various habitats in the sun; and from 20.7 to 22.4 °C in the shade, providing a wide range of available T_e (Bauwens et al., 1996). In contrast, Klingenb ock et al. (2000) used 1 T_e model in the sun for a field site where habitat types of leaf litter, weeds, mossy logs, bare logs, and bare soil/rocks were categorized. Studies such as this could be improved by increasing the microhabitat coverage with T_e models to provide greater resolution of the available thermal microhabitats and microhabitat usage.

Additionally, the majority of studies have measured T_e in the environment on only 5 days or less (Fig. 3B). A quarter of the studies did not indicate the number of days T_e was measured. These experiments ignore the inherent variability in the daily weather cycle that potentially influences the ecology of animals.

A simple power analysis using the simulated T_e distributions presented in Fig. 1A and B shows the effect of sample size on estimating operative temperature in an environment (Fig. 1E and F). Large deviations in the index of average thermal quality are observed with sample sizes of 20 or less. Investigators should be encouraged to use power analysis techniques such as this to determine the number of models needed to accurately measure the environment. With the knowledge of the model error and an estimate of the thermal environment, the number of models needed to achieve a given level of accuracy can be determined.

Although experimental designs that require large numbers of T_e models (>20) are initially time consuming in terms of making the models, the detailed temperature data on the available microhabitats is well worth the extra effort. Once models are made and tested, they can easily be placed randomly in the environment and recorded using data loggers (Grant and Dunham, 1988; Peterson et al., 1993; Zimmerman et al., 1994). It is also recommended that measurements be made over a longer time period than has typically been done in the past.

2.4. Conclusion

Properly constructed and calibrated T_e models can be powerful tools that provide three main benefits. First, they map a multivariate problem involving T_a , T_g , R , and u into a single metric (T_e) that is meaningful to the animal. Second, they allow replicate measurements to be made providing a measure of the spatial variation within and among microhabitats without the need for replicating expensive equipment. Studies that use large numbers of models to map the thermal environment and provide distributions of microhabitat T_e should be encouraged. Models used by investigators to measure T_e produce errors ranging from 0 °C up to 12.5 °C depending on the characteristics of the model. Copper casts have been shown to be the most consistently accurate T_e models available. Simpler models may be useful, however they have a greater tendency to be less accurate, and their use requires they be calibrated under the conditions found in the field. Models producing errors of 2 °C or larger should be avoided. Taking the extra time to construct and calibrate the appropriate models in large numbers will pay off by providing information on the variability in available microhabitats and the T_e distribution within the habitat.

3. Standard operative (T_{es}) temperature models

3.1. Theory

Standard operative temperature (T_{es}) was devised as a measure of an animal's thermal stress in complex thermal environments (Bakken, 1976). Standard operative temperature relates heat loss from an animal in a complex thermal environment to a reference laboratory environment with a known wind speed. This loss must be balanced by heat production to maintain a stable body temperature. Two different environments in which an animal maintains the same net heat production (metabolic heat production minus evaporative heat loss; $M-E$) and body temperature (T_b) have the same T_{es} . This allows measurements of thermal stress in different environments to be compared with a single reference environment. Standard operative temperature and $M-E$ have been measured using both heated taxidermic mounts (Bakken, 1976, 1980; Bakken et al., 1981, 1983, 1999b; Buttemer, 1985; Wiersma and Piersma, 1994) and calculated from T_e (Chappell, 1981; Chappell and Bartholomew, 1981a, b; Vispo and Bakken, 1993).

Net heat production of an animal is related to T_{es} in a given environment as

$$T_{es} = T_b - (M - E)/K_{es}, \quad (2)$$

where $M-E$ is the net heat production or metabolic heat production minus evaporative cooling.

Taxidermic mounts with internal heaters can be used to measure T_{es} in the field. The power consumption of a mount maintaining T_b is used to determine T_{es} . Because of the relationship between T_{es} and heat loss, it is possible to estimate T_{es} by substituting the power (P) required by the taxidermic mount to maintain a constant T_b for $M-E$ in Eq. (2):

$$T_{es} = T_b - (P/K_{esm}). \quad (3)$$

Calibration of the power needed in various thermal environments against $M-E$ can allow a T_{es} model to estimate the minimal net heat production for animals in the thermal environment. These models provide a means to measure the metabolic cost of inhabiting an environment and can be used to calculate the minimum daily energy expenditure of endotherms.

Taxidermic mounts can be used to measure T_e , T_{es} , and net heat production of endotherms in various environments. Heated and unheated taxidermic mounts tend to be made from a high conductance metal such as copper using a technique similar to the hollow electroplating of T_e models (Bakken and Gates, 1975). They are constructed by electroforming a thin-walled copper shell over a cast of a skinned animal (Bakken and Gates, 1975). Heated taxidermic mounts then have heater wires placed in contact with the metal surface and a thermostat that regulates the heater power to ensure that the central model

temperature remains constant at the T_b of the animal (Bakken et al., 1981, 1983). The pelt of the animal is then placed over the cast, sewn shut, and allowed to dry. It is extremely important that the pelt or plumage is in contact with the surface of the entire cast, as air bubbles between the cast and insulation could alter the conductance of the model. In the past, the insulation layer has been cemented to the cast using adhesives such as cyanoacrylate or heat-conducting paste (Bakken, 1976; Bakken et al., 1981, 1983, 1985; Wiersma and Piersma, 1994).

There are a number of important issues to consider when constructing and using heated mounts to measure T_{es} and net heat production. As can be seen from Table 3, T_{es} models have been used with much less frequency than T_e models. This is due to the fact that they are more difficult and time consuming to construct than T_e models and the reliability of T_{es} models has been called into greater question than that of T_e models (Walsberg and Wolf, 1996b). All of the issues addressed above for operative temperature models apply to standard operative temperature models. In addition, a number of additional issues must be addressed when using heated or unheated taxidermic mounts including the effects of wind speed and weathering.

3.2. T_{es} model calibration and accuracy

Heated taxidermic mounts are calibrated by measuring net heat production for an animal over a range of air temperatures, solar radiations, and wind speeds and then measuring the power (P) required by the T_{es} model to maintain the model's internal temperature equal to the animal's T_b under identical environmental conditions (Fig. 4). Calibration should occur under controlled conditions in a wind tunnel and should span the range of environmental conditions encountered in the field. A calibration curve is determined via regression analysis as

$$M - E = b + mP, \quad (4)$$

where m and b are regression coefficients. The goal of calibration is to determine if the power usage (P) of the

model can predict $M-E$ in a linear fashion over various combinations of T_a , wind speed, and solar radiation experienced in the field as in Fig. 4. Numerous studies have shown that a model's power consumption can be calibrated to within a tolerable error of 5% of net heat production under low solar conditions (Bakken et al., 1981, 1999a, b; Buttemer, 1985). To date, very few studies have examined how T_{es} models respond to varying levels of solar radiation and their reliability under these conditions has been called into question (Walsberg and Wolf, 1996b; Larochelle, 1998; Fortin, 2001).

Calibration of models against an animal over the range of environmental conditions is time consuming and may be a limiting factor in the number of models used in previous studies. Standardization of models against a single calibrated model can decrease the time necessary to calibrate all of the models (Bakken et al., 1999b). Once a single model has been calibrated against a live animal across all environmental conditions, that model can then be used to standardize the rest of the models using a subset of environmental conditions. Calibration and standardization of all mounts is essential to ensure that the data measured by the mounts are reliable and accurate. Differences between individual taxidermic mounts occur because of variation in pelt density, pelt wear, body shape and size, leg and tail position and may, in the end, affect the ability of the mounts to work properly. Bakken et al. (1999b) found that the overall thermal conductance (K_{em}) of mounts varied by as much as 10–12%, but calibration and standardization allowed mounts to predict T_{es} to within 1 °C of each other, which is an acceptable error.

3.2.1. Wind

The effect of wind on power consumption of a model, net heat production of an animal, and T_{es} of both has been studied in depth (Bakken et al., 1981, 2001; Bakken, 1991; Fortin, et al., 2000b). Wind affects the insulation value of fur and feathers by altering convection patterns, increasing wind penetration of the pelt,

Table 3

Examples of models used to measure T_{es} or metabolic rate in thermal ecology from 1991 to 2004

Model type	Animal	Citations
Unheated taxidermic mount	Bird, mammal	Vispo and Bakken (1993), Ward and Pinshow (1995), Walsberg and Wolf (1996b), Webster and Weathers (2000)
Heated taxidermic mount	Bird, mammal	Piersma, et al. (1991), Piersma and Morrison (1994), Wiersma and Piersma (1994), Walsberg and Wolf (1996b), Thomas et al. (1998), Bakken et al. (1999b), Bakken et al. (2000), Fortin et al. (2000a,b), Fortin and Gauthier (2000)
Heated insulated Al cylinder	Bird	Bakken et al. (2001), Boysen et al. (2001)
Mathematical equations	Bird	Bakken et al. (1991), Bakken et al. (1999a)
Predictive equations	Bird, snake	Wiersma and Piersma (1994), Fortin et al. (2000a, b), Fortin and Gauthier (2000), Lawless et al. (2001)

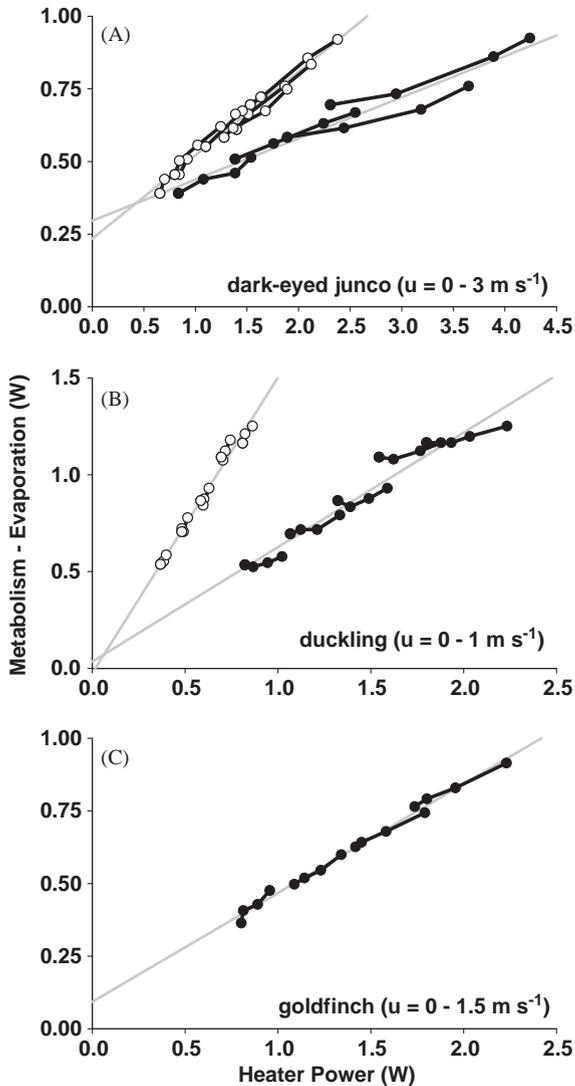


Fig. 4. (A) Calibration curves for a dark-eyed junco (*Junco hyemalis*) heated taxidermic mount (solid circles; Bakken et al., 1991) and a simple heated aluminum cylinder with synthetic fur as insulation (open circles; Bakken et al., 2001). The solid line is a best fit through all of the measurements. (B) Calibration curves for a mallard duckling (*Anas platyrhynchos*) heated taxidermic mount (solid circles; Bakken et al., 1999) and a simple heated aluminum cylinder with domestic rabbit fur as insulation (open circles; Bakken et al., 2001). (C) Calibration curve for a goldfinch (*Carduelis tristis*) heated taxidermic mount at various T_a and wind speeds (Bakken et al., 1981).

and by fiber displacement (Davis and Birkebak, 1974; Campbell et al., 1980; Bakken et al., 1981). Wind speed has a direct effect on K_e and K_{em} (Bakken, 1991; Bakken et al., 2001):

$$K_e \text{ or } K_{em} \cong a + bu^c, \quad (5)$$

where a , b , and c are regression coefficients of overall thermal conductance on wind speed (u). By substituting K_e from Eq. (5) into Eq. (2) the relationship between wind speed and T_{es} can be determined as (Bakken, 1990)

$$T_{es} = T_b - (1 + (b/a)u^c)(T_b - T_e) \quad (6)$$

The ratio b/a in Eq. (6) provides a measure of the sensitivity of K_e or K_{em} to changes in wind speed, with larger values representing increased sensitivity to wind (Bakken et al., 2001). In 18 species of passerine and non-passerine birds, Bakken (1991) found an average b/a ratio of 0.26 when $c = 0.5$. In passerines, the b/a ratio ranged from 0.14 to 0.43, while in non-passerines values ranged from 0.09 in the Ruffed Grouse to 0.73 °C in the Gambel's Quail. A similar range of b_m/a_m has been measured in heated taxidermic mounts (summarized in Bakken et al., 2001). The b_m/a_m ratio ranged from 0.35 in American Goldfinch mounts (Bakken et al., 1981) to 1.05 in the European Kestrel mounts (Masman, 1986).

Heated taxidermic mounts respond to wind differently than live animals making calibration against live animals essential (Fig. 4; Bakken et al., 1981, 1983, 1985, 1999b, 2000, 2001; Bakken, 1990, 1991; Walsberg and Wolf, 1996b). The sensitivity of both live animals and taxidermic mounts to wind speed varies considerably. Factors affecting sensitivity include the thickness of the insulation, density of the insulation, and the shape of the animal. Heated taxidermic mounts are frequently more sensitive to changes in wind than the actual animal. In the worst-case examples provided in Fig. 4(A) and (B), the predicted net heat production of a duckling and a dark-eyed junco T_{es} mount with feather plumage differed from the animal by as much as 9%. However, the majority of the values predicted by the model were less than 5% different from the live animal. A goldfinch model consistently predicted the bird's net heat production to within 5% (Fig. 4C). In order to have a linear calibration of P vs. $M-E$, a T_{es} model may have a larger b_m/a_m ratio than the real animal (Bakken et al., 2001). This requires finding insulation that provides the appropriate ratio of b_m/a_m in response to wind for the given model.

Bakken et al. (2001) found that simple cylindrical models of a dark-eyed junco and a mallard duckling with synthetic fur or domestic rabbit fur, respectively, estimated the net heat production of the animal to within 4.5% (Bakken et al., 2001) and T_{es} to within 1.5 °C (Boysen et al., 2001) under all wind conditions tested (Fig. 4A and B). The response of these simple models to changes in wind speed is dependent on the insulation material used. In a test against live juncos, artificial wool fur produced poor results at high wind speeds while a dense gray fur predicted $M-E$ to within 3%. The simple models proposed by Bakken et al. (2001) provide better responses to changes in wind speed than the heated taxidermic mounts and estimate net heat production with greater accuracy (Fig. 4A and B).

It is expected that each T_{es} model will respond differently to change in wind speed. Walsberg and Wolf (1996b) found the predicted T_{es} of multiple models diverged from each other at high wind speeds. This divergence of values stresses the importance of calibrating models prior to use. The potential for large deviations in predicted metabolic power of T_{es} models compared with those of live animals makes it necessary for all models to be calibrated. Calibration in most cases results in models providing measures of net heat production with a tolerable accuracy of 5%.

3.2.2. Solar radiation

The response of T_{es} models to solar radiation has yet to be examined in detail and because of this mounts have typically been used in areas with no or low solar radiation. Walsberg and Wolf (1996b) showed that the relationship between model and animal T_{es} is nonlinear when exposed to solar radiation, making a single linear calibration impossible. Additionally, they found a 10 °C difference in T_{es} of models in the sun and out of the sun, while under the same conditions the animal's T_{es} did not differ. This has led Walsberg and Wolf (1996b) to question the utility of heat taxidermic mounts under environmental conditions with a solar component. Thus, studies that have not calibrated models under all levels of solar radiation (Piersma and Morrison, 1994; Wiersma and Piersma, 1994; Fortin and Gauthier, 2000; Fortin et al., 2000a, b) leave open the question of how mount T_{es} and power consumption vary with solar radiation when compared to the live animal. Calibration over a range of wind speeds and solar radiation loads is the only way to determine if T_{es} models actually represent net heat production for living animals under the same conditions. Further studies examining the response of T_{es} models to various levels of solar radiation are needed to determine their ultimate utility under conditions with variable solar radiation.

3.2.3. Model weathering

Animal pelts used to insulate T_{es} models are typically susceptible to weathering effects that must be taken into account when using mounts in the field over long periods. Few studies have reported the effect of weathering on K_{em} of heated taxidermic mounts (Wiersma and Piersma, 1994; Bakken et al., 1999b, 2001). Wiersma and Piersma (1994) attempted to prevent or slow weathering of their mounts plumage by spraying the mounts with a tent waterproofing. Even after spraying, K_{em} of Red Knot mounts increased by 50% from 0.063 W °C⁻¹ (range 0.058–0.074) to 0.094 W °C⁻¹ (range 0.077–0.104) over a 10 month field season. Similarly, mounts insulated with a day old Mallard duckling plumage showed progressive weathering effects over two seasons (Bakken et al., 1999b). The K_{em} increased by about 10% per season over the two seasons, with increases as large

as 30% in some models. The ratio of b/a for new, used, and field damaged American Goldfinch mounts increased from 0.35 in new mounts, 0.40 in used mounts, and 0.44 in field damage mounts (Bakken et al., 1981). Clearly weathering can impact taxidermic mount K_{em} and result in a change in the model calibration.

One way to decrease the effect of weathering is to find an artificial insulation that provides similar K_{em} values as the live animal, while standing up to the rigors of field work. Bakken et al. (2001) found that gray fur-like synthetic material of varying depths worked well as insulation of juncos (Fig. 4A). Models with this synthetic insulation exhibited no significant changes in K_{em} over a 7-week study in Indiana or a 3-week study in Churchill, Manitoba. Use of a synthetic material that does not weather and that provides changes in $K_{em}/K_{esm} = K_c/K_{es}$ are a useful alternative to the pelt of an animal and will allow for easier maintenance of T_{es} models. However, it may initially take time to match the absorbance and wind response of synthetic materials to those of the animal, but once a proper synthetic insulation is found simple models can be constructed in a shorter amount of time.

3.3. Replication and experimental design

Unlike studies using T_c mounts where up to 60 models have been used to map the thermal environment, studies using T_{es} mounts have made measurements with only one or two models placed in one or two typical locations. Because animals live in a complex thermal environment, sampling only one or two locations provides very limited information about the constraints the environment may place on an animal's ecology. A contributing factor to this limitation is the difficulty and cost in making taxidermic mounts. With the advent of simple models that perform well, investigators should be able to increase the number of T_{es} models used to sample the environment.

Bakken et al. (2000) have suggested that experiments in the laboratory must use more than one taxidermic mount per treatment. The inherent random variation between mounts plus handling and positioning errors are not accounted for when using a single mount (Bakken et al., 2000). If multiple measurements are made on a single mount within a given treatment, then each mount must be repositioned after each measurement to account for small random differences in orientation. By ignoring the difference between mount positioning, incorrect results may be obtained about morphological differences between treatments. Fortin et al. (2000b) examined the effect of age, wind speed, radiation, and body orientation on the T_{es} of Greater Snow goslings using 4 heated taxidermic mounts, one for each of 4 age classes. By making multiple measurements on the individual mounts, they increased the statistical power of their study. However, the study

could have been improved by using more than one mount for each age class, as the multiple measurements on a single mount represent pseudoreplication (Hurlbert, 1984). Walsberg and Wolf (1996b) used multiple mounts and showed that there is large variation between individual mounts. Multiple mounts provide a better measure of the random error due to positioning, construction differences between mounts, and thermal gradients that occur in each mount (Bakken et al., 2000). Use of multiple mounts in the laboratory should help to alleviate these problems.

Using multiple mounts also provides a measure of the variation in the thermal environment experienced by an organism. Even if we are examining something as simple as habitat use by birds in a tree, the use of more than one heated taxidermic mount in one typical site should be encouraged. The location of the models in the canopy and in relation to the trunk of the tree can have a profound effect on T_e , T_{es} , and ultimately the net heat production predicted by the heated mounts. In an environment such as a canopy, simple differences in orientation, wind exposure, or shade may exert large effects on T_{es} and net heat production of an endotherm. Thus, proper measurement of an environment must take position effects into consideration by using multiple models. Placing only one T_{es} mount in a “typical” location in a tree will not provide a measure of the true variation in available T_{es} and net heat production. The use of multiple T_{es} mounts will allow one to categorize the available nest and perch sites available. In ecological investigations, the most interesting aspects of a study are often the variation that is found (Zimmerman et al., 1994; O’Connor et al., 2000). We tend to think in terms of the “golden mean” of available T_e , T_{es} , or $M-E$, however, an animal will experience variation in the environment on both a spatial and temporal scale. It may be only a small portion of the environment that is thermally useful for an animal, and by focusing on one typical location, one ignores important variation in the thermal environment that may hold answers to constraints on behavior and life history. Examining this variation with more than one mount in each thermal environment will begin to provide measures of environmental variation and the possible constraints place on the energetics of organisms.

3.4. Conclusion

Continued use of T_{es} models in ecological energetic studies will benefit the field by allowing measurements on the spatial scale of the animal. Calibration of heated T_{es} mounts is imperative to ensure that measurement errors are less than 5%. Research needs to focus on how models respond to solar radiation, which will lead to an increase in the number of environmental conditions under which they can be used in the field. One of the

main limitations in the use of heated taxidermic mounts has been the difficulty and time required to construct such mounts. With the ability to construct simple heated T_{es} models that are cost efficient, easy to construct, weatherproof, and accurate, the utility of T_{es} mounts in energetic and thermal studies should increase. A single aluminum cylinder model took 1/7th the time to construct, compared with the time needed to construct a single heated taxidermic mount (Bakken et al., 2001). This will allow researchers the ability to make replicate measurements using T_{es} models in more than a few locations. Using more than one model per environment, we can gain a better understanding of how animals interact with their environment and how their energy allocation, energy expenditure, and life history are constrained by their environment and physiology. Multiple models, representing various sizes of a species can help to elucidate the effect of size and age on T_{es} and $M-E$. Examining the variation in the environment can provide useful information about the energetics and thermal biology of animals. When used correctly, standard operative temperature mounts provide the ability to predict the metabolic costs for an animal under given conditions in the field and allow for the examination of changes in posture and orientation as possible thermoregulatory strategies.

4. Limitations to T_e and T_{es} models

It is important to keep in mind the limitations of T_e and T_{es} models. Models may not incorporate the range of physiological alterations that are available to ectotherms or endotherms, such as changes in internal conduction via changes in blood flow distributions (T_e and T_{es} models) or changes in set-point T_b (T_{es} models). Both mammals and birds control the insulation value of fur and feathers by pilo- and pitoerection. To incorporate these physiological differences it may be necessary the use multiple mounts with various levels of pilo or pitoerection. Similarly, models cannot replicate the behavior of an animal. Animals have the ability to alter orientation in relation to wind and solar radiation, while a model is placed in a single position. Placing multiple models in multiple positions can help account for these orientation differences. When using only few models the confounding factor of orientation must be considered. It is important that when one uses T_e or T_{es} models they keep the limitations in mind and adjust the experimental design accordingly.

5. Perspectives

Operative and standard operative temperature models have the potential to yield valuable information on the

thermal habitats of an animal. Both types of model integrate multiple thermal inputs into a single thermal metric that is meaningful to the ecology and physiology of an animal. However, in order for these measurements to be valid, models must be used in a scientifically valid manner. First, all models must be calibrated against the body temperature or net heat production of live animals prior to their use. Given the various types of models currently in use, large variations in T_e and T_{es} can exist between uncalibrated models and live animals (Table 2). Because of the interactions between solar radiation, wind speed, and model shape, calibrations must be made within an ecologically realistic set of environmental conditions experienced by the animal in the field. In the past, a majority of investigators have failed to calibrate their models properly, severely limiting the utility of the measurements provided by the models. When calibrated properly, models provide accurate measures of T_e and T_{es} of live animals. Second, once models have been properly calibrated they must be used within the framework of a rigorous experimental design. Too many studies have used temperatures measured by only one or two models to draw conclusions about the thermal properties of available microhabitats and how it impacts the ecology of an animal. Adequate numbers of models must be used to make meaningful measurements of the inherent variability in the thermal environment. Investigators are encouraged to continue to use T_e and T_{es} models to study the thermal ecology of ectotherms and endotherms as they can produce extremely valuable data. However, these models are only valuable tools if workers calibrate and use them within a scientifically valid experimental design.

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References

- Ashby, P.D., 1997. Conservation of mass-specific metabolic rate among high- and low-elevation populations of the acridid grasshopper *Xanthippus corallipes*. *Physiol. Zool.* 70, 701–711.
- Bakken, G.S., 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* 60, 337–384.
- Bakken, G.S., 1980. The use of standard operative temperature in the study of the thermal energetics of birds. *Physiol. Zool.* 53, 108–119.
- Bakken, G.S., 1989. Arboreal perch properties and the operative temperature experienced by small animals. *Ecology* 70, 922–930.
- Bakken, G.S., 1990. Estimating the effect of wind on avian metabolic-rate with standard operative temperature. *Auk* 107, 587–594.
- Bakken, G.S., 1991. Wind speed dependence of the overall thermal conductance of fur and feather insulation. *J. Thermal Biol.* 16, 121–126.
- Bakken, G.S., 1992. Measurement and application of operative and standard operative temperature in ecology. *Am. Zool.* 32, 194–216.
- Bakken, G.S., Gates, D.M., 1975. Heat-transfer analysis of animals: some implications for field ecology, physiology, and evolution. In: Gates, D.M., Schmerl, R.B. (Eds.), *Perspectives of Biophysical Ecology*. Springer, New York, pp. 255–290.
- Bakken, G.S., Buttemer, W.A., Dawson, W.R., Gates, D.M., 1981. Heated taxidermic mounts—a means of measuring the standard operative temperature affecting small animals. *Ecology* 62, 311–318.
- Bakken, G.S., Erskine, D.J., Santee, W.R., 1983. Construction and operation of heated taxidermic mounts used to measure standard operative temperature. *Ecology* 64, 1658–1662.
- Bakken, G.S., Santee, W.R., Erskine, D.J., 1985. Operative and standard operative temperature: tools for thermal energetics studies. *Am. Zool.* 25, 933–943.
- Bakken, G.S., Murphy, M.T., Erskine, D.J., 1991. The effect of wind and air temperature on metabolism and evaporative water loss rates of dark-eyed juncos, *Junco hyemalis*: a standard operative temperature scale. *Physiol. Zool.* 64, 1023–1049.
- Bakken, G.S., Reynolds, P.S., Kenow, K.P., Korschgen, C.E., Boysen, A.F., 1999a. Metabolic response to air temperature and wind in day-old mallards and a standard operative temperature scale. *Physiol. Biochem. Zool.* 72, 656–665.
- Bakken, G.S., Reynolds, P.S., Kenow, K.P., Korschgen, C.E., Boysen, A.F., 1999b. Standardization and calibration of heated mounts illustrated with day-old mallard ducklings. *Physiol. Biochem. Zool.* 72, 502–506.
- Bakken, G.S., Kenow, K.P., Korschgen, C.E., Boysen, A.F., 2000. Statistical and procedural issues in the use of heated taxidermic mounts. *J. Therm. Biol.* 25, 317–321.
- Bakken, G.S., Boysen, A.F., Korschgen, C.E., Kenow, K.P., Lima, S.L., 2001. Design and performance of a rugged standard operative temperature thermometer for avian studies. *J. Therm. Biol.* 26, 595–604.
- Bashey, F., Dunham, A.E., 1997. Elevational variation in the thermal constraints on the microhabitat preferences of the greater earless lizard *Cophosaurus texanus*. *Copeia* 1997, 725–737.
- Bauwens, D.B., Hertz, P.E., Castilla, A.M., 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 77, 1818–1830.
- Bauwens, D., Castilla, A.M., Mouton, P.F.N., 1999. Field body temperatures, activity levels and opportunities for thermoregulation in an extreme microhabitat specialist, the girdled lizard (*Cordylus macropholis*). *J. Zool. Lond.* 249, 11–18.

- Beaupre, S.J., 1995a. Comparative ecology of the mottled rock rattlesnake, *Crotalus lepidus*, in big bend national park. *Herpetologica* 51, 45–56.
- Beaupre, S.J., 1995b. Effects of geographically variable thermal environment on bioenergetics of mottled rock rattlesnakes. *Ecology* 76, 1655–1665.
- Beaver, J.M., Olson, B.E., 1997. Winter range use by cattle of different ages in southwestern Montana. *Appl. Animal Behav. Sci.* 51, 1–13.
- Beaver, J.M., Olson, B.E., Wraith, J.M., 1996. A simple index of standard operative temperature for mule deer and cattle in winter. *J. Therm. Biol.* 21, 345–352.
- Belliure, J., Carrascal, L.M., Diaz, J.A., 1996. Covariation of thermal biology and foraging mode in two Mediterranean lacertid lizards. *Ecology* 77, 1163–1173.
- Bishop, J.A., Armbruster, W.S., 1999. Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny, and ecology. *Funct. Ecol.* 13, 711–724.
- Boysen, A.F., Lima, S.L., Bakken, G.S., 2001. Does the thermal environment influence vigilance behavior in dark-eyed juncos (*Junco hyemalis*)? An approach using standard operative temperature. *J. Therm. Biol.* 26, 605–612.
- Bozinovic, F., Lagos, J.A., Vasquez, R.A., Kenagy, G.J., 2000. Time and energy use under thermoregulatory constraints in a diurnal rodent. *J. Therm. Biol.* 25, 251–256.
- Brown, G.P., Weatherhead, P.J., 2000. Thermal ecology and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. *Ecol. Monogr.* 70, 311–330.
- Buttemer, W.A., 1985. Energy relations of winter roost-site utilization by American goldfinches (*Carduelis tristis*). *Oecologia* 68, 126–132.
- Campbell, G.S., McArthur, A.J., Monteith, J.L., 1980. Wind-speed dependence of heat and mass transfer through coats and clothing. *Boundary-Layer Meteorol.* 18, 485–493.
- Castro, G., Myers, J.P., Ricklefs, R.E., 1992. Ecology and energetics of sanderlings migrating to four latitudes. *Ecology* 73, 833–844.
- Chappell, M.A., 1981. Standard operative temperature and cost of thermoregulation in the arctic ground squirrel, *Spermophilus undulatus*. *Oecologia* 49, 397–403.
- Chappell, M.A., 1982. Temperature regulation of carpenter bees (*Xylocopa californica*) foraging in the Colorado Desert of Southern-California. *Physiol. Zool.* 55, 267–280.
- Chappell, M.A., Bartholomew, G.A., 1981a. Activity and thermoregulation of the antelope ground-squirrel *Ammospermophilus leucurus* in winter and summer. *Physiol. Zool.* 54, 215–223.
- Chappell, M.A., Bartholomew, G.A., 1981b. Standard operative temperatures and thermal energetics of the antelope ground squirrel *Ammospermophilus leucurus*. *Physiol. Zool.* 54, 81–93.
- Christian, K.A., 1998. Thermoregulation by the short-horned lizard (*Phrynosoma douglassi*) at high elevation. *J. Therm. Biol.* 23, 395–399.
- Christian, K.A., Bedford, G.S., 1995. Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. *Ecology* 76, 124–132.
- Christian, K.A., Bedford, G.S., 1996. Thermoregulation by the spotted tree monitor, *Varanus scalaris*, in the seasonal tropics of Australia. *J. Therm. Biol.* 21, 67–73.
- Christian, K.A., Weavers, B.W., 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecol. Monogr.* 66, 139–157.
- Christian, K.A., Bedford, G.S., Shannahan, S.T., 1996a. Solar absorptance of some Australian lizards and its relationship to temperature. *Aust. J. Ecol.* 44, 59–67.
- Christian, K.A., Griffiths, A.D., Bedford, G.S., 1996b. Physiological ecology of frillneck lizards in a seasonal tropical environment. *Oecologia* 106, 49–56.
- Christian, K.A., Vaudinette, R.V., Pamula, Y., 1997. Energetic costs of activity by lizards in the field. *Funct. Ecol.* 11, 392–397.
- Christian, K., Bedford, G., Green, B., Griffiths, A., Newgrain, K., Schultz, T., 1999. Physiological ecology of a tropical dragon, *Lophognathus temporalis*. *Aust. J. Ecol.* 1999, 171–181.
- Cooper, S.J., 1999. The thermal and energetic significance of cavity roosting in mountain chickadees and juniper titmice. *Condor* 101, 863–866.
- Davis, L.B., Birkebak, R.C., 1974. On the transfer of energy in layers of fur. *Biophys. J.* 14, 249–268.
- Diáz, J.A., 1994. Field thermoregulatory behavior in the western Canarian lizard *Gallotia galloti*. *J. Herp.* 28, 325–333.
- Diáz, J.A., 1997. Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Funct. Ecol.* 11, 79–89.
- Dorcas, M.E., 1995. Testing the coadaptation hypothesis: the thermoregulatory behavior and thermal physiology of the rubber boa (*Charina bottae*). Ph.D. Dissertation, Idaho State University, Pocatello.
- Dorcas, M.E., Peterson, C.R., Flint, M.E.T., 1997. The thermal biology of digestion in rubber boas (*Charina bottae*): physiology, behavior, and environmental constraints. *Physiol. Zool.* 70, 292–300.
- Dreisig, H., 1995. Thermoregulation and flight activity in territorial male graylings, *Hipparchia semele* (Satyridae), and large skippers, *Ochlodes venata* (Hesperiidae). *Oecologia* 101, 169–176.
- Fortin, D., 2001. The use of heated taxidermic mounts in studies of ecological energetics. *Mammalia* 65, 195–204.
- Fortin, D., Gauthier, G., 2000. The effect of postural adjustment on the thermal environment of greater snow goose goslings. *Can. J. Zool.* 78, 817–821.
- Fortin, D., Gauthier, G., Larochelle, J., 2000a. Body temperature and resting behavior of greater snow goose goslings in the high arctic. *Condor* 102, 163–171.
- Fortin, D., Larochelle, J., Gauthier, G., 2000b. The effect of wind, radiation and body orientation on the thermal environment of greater snow goose goslings. *J. Therm. Biol.* 25, 227–238.
- Frears, S.L., Chown, S.L., Webb, P.I., 1999. Temperature dependence of feeding behaviour in the mopane worm (Lepidoptera). *J. Therm. Biol.* 24, 241–244.
- Gloutney, M.L., Clark, R.G., 1997. Nest-site selection by mallards and blue-winged teal in relation to microclimate. *Auk* 114, 381–395.
- Grant, B.W., Dunham, A.E., 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* 69, 167–176.

- Grbac, I., Bauwens, D., 2001. Constraints on temperature regulation in two sympatric Podarcis lizards during autumn. *Copeia* 2001, 178–186.
- Greek, T.J., Paw, K.T., Weathers, W.W., 1989. A comparison of operative temperature estimated by taxidermic mounts and meteorological data. *J. Therm. Biol.* 14, 19–26.
- Grigg, G.C., Seebacher, F., 1999. Field-test of a paradigm—hysteresis of heart-rate in thermoregulation by a free-ranging lizard (*Pogona-Barbata*). *Proc. R. Soc. Lond. Series B* 266, 1291–1297.
- Hayes, J.P., Shonkwiler, J.S., 1996. Altitudinal effects on water fluxes of deer mice: a physiological application of structural equation modeling with latent variables. *Physiol. Zool.* 69, 509–531.
- Hertz, P.E., 1992a. Temperature regulation in Puerto Rican Anolis lizards: a field test using null hypotheses. *Ecology* 73, 1405–1417.
- Hertz, P.E., 1992b. Evaluating thermal resource partitioning by sympatric *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. *Oecologia* 90, 127–136.
- Hertz, P.E., Huey, R.B., Stevenson, R.D., 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142, 796–818.
- Houseal, G.A., Olson, B.E., 1995. Cattle use of microclimates on a northern latitude winter range. *Can. J. Anim. Sci.* 75, 501–507.
- Huey, R.B., Peterson, C.R., Arnold, S.J., Porter, W.P., 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70, 931–944.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187–211.
- Ide, J.Y., 2002. Seasonal changes in the territorial behaviour of the satyrine butterfly *Lethe diana* are mediated by temperature. *J. Ethol.* 200, 71–78.
- Kearney, M., Predavec, M., 2000. Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology* 81, 2984–2996.
- Kingsolver, J.G., 2000. Feeding, growth, and the thermal environment of cabbage white caterpillars, *Pieris rapae* L. *Physiol. Biochem. Zool.* 73, 621–628.
- Klingenböck, A., Osterwalder, K., Shine, R., 2000. Habitat use and thermal biology of the “land mullet” *Egernia major*, a large scincid lizard from remnant rain forest in Southeastern Australia. *Copeia* 2000, 931–939.
- Klok, C.J., Chown, S.L., 1999. Assessing the benefits of aggregation: thermal biology and water relations of anomalous Emperor Moth caterpillars. *Funct. Ecol.* 13, 417–427.
- Larochele, J., 1998. Comments on a negative appraisal of taxidermic mounts as tools for studies of ecological energetics. *Physiol. Zool.* 71, 596–598.
- Lawless, R.M., Buttemer, W.A., Astheimer, L.B., Kerry, K.R., 2001. The influence of thermoregulatory demand on contact crèching behaviour in Adélie Penguin chicks. *J. Therm. Biol.* 26, 555–562.
- Lillywhite, H.B., Mittal, A.K., Grag, T.K., Das, I., 1998. Basking behavior, sweating and thermal ecology of the Indian tree frog, *Polypedates maculatus*. *J. Herp.* 32, 169–175.
- López, P., Salvador, A., Martín, J., 1998. Soil temperature, rock selection, and the thermal ecology of the amphibibian reptile *Blanus cinereus*. *Can. J. Zool.* 76, 673–679.
- Lorenzon, P., Clobert, J., Oppliger, A., John-Alder, H., 1999. Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). *Oecologia* 118, 423–430.
- van Marken Lichtenbelt, W.D., Vogel, J.T., Wesselingh, R.A., 1997. Energetic consequences of field body temperatures in the green iguana. *Ecology* 78, 297–307.
- Masman, D., 1986. The Annual Cycle of the Kestrel. Van denderen, Groningen, Netherlands.
- Merrick, M.J., Smith, R.J., 2004. Temperature regulation in burying beetles (*Nicrophorus* spp.: Coleoptera: Silphidae): effects of body size, morphology and environmental temperature. *J. Exp. Biol.* 207, 723–733.
- Morgan, K.R., Shelly, T.E., 1988. Body temperature regulation in desert robber flies (Diptera: Asilidae). *Ecol. Entomol.* 14, 419–428.
- Navas, C.A., 1996. Implications of microhabitat selection and patterns of activity on the thermal ecology of high elevation neotropical anurans. *Oecologia* 108, 617–626.
- Niewiarowski, P.H., Roosenburg, W., 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology* 74, 1992–2002.
- O’Connor, M.P., 1999. Physiological and ecological implications of a simple model of heating and cooling in reptiles. *J. Therm. Biol.* 24, 113–136.
- O’Connor, M.P., 2000. Extracting operative temperatures from temperatures of physical models with thermal inertia. *J. Therm. Biol.* 25, 329–343.
- O’Connor, M.P., Zimmerman, L.C., Dzialowski, E.M., Spotila, J.R., 2000. Thick-walled physical models improve estimates of operative temperatures for moderate to large-sized reptiles. *J. Therm. Biol.* 25, 293–304.
- O’Neill, K.M., Kemp, W.P., 1992. Behavioral thermoregulation in two species of robber flies occupying different grassland microhabitats. *J. Therm. Biol.* 17, 323–331.
- O’Neill, K.M., Street, D., O’Neill, R.P., 1994. Scavenging behavior of grasshoppers (Orthoptera: Acrididae): feeding and thermal responses to newly available resources. *Physiol. Chem. Ecol.* 23, 1260–1268.
- Penick, D.N., Congdon, J., Spotila, J.R., Williams, J.B., 2002. Microclimates and energetics of free-living box turtles, *Terrapene carolina*, in South Carolina. *Physiol. Biochem. Zool.* 75, 57–65.
- Peterson, C.R., 1987. Daily variation in the body temperature of free-ranging garter snakes. *Ecology* 68, 160–169.
- Peterson, C.R., Gibson, A.R., Dorcas, M.E., 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. In: Seigel, R.A., Collins, J.T. (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York, pp. 241–314.
- Piersma, T., Morrison, R.I.G., 1994. Energy expenditure and water turnover of incubating ruddy turnstones: high costs under high arctic climatic conditions. *Auk* 111, 366–376.
- Piersma, T., Drent, R., Wiersma, P., 1991. Temperate versus tropical wintering in the world’s northernmost breeder, the knot: metabolic scope and resource levels restrict subspecific options. *Acta XX Congr. Internat. Ornithol.*, 761–772.

- Porter, W.P., 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. *Ecol. Monogr.* 37, 273–296.
- Resetarits, W.J., Bernardo, J., 1998. *Experimental Ecology: Issues and Perspectives*. Oxford University Press, Oxford.
- Rock, J., Andrews, R.M., Cree, A., 2000. Effects of reproductive condition, season, and site on selected temperatures of a Viviparous Gecko. *Physiol. Biochem. Zool.* 73, 344–355.
- Sartorius, S.S., Vitt, L.J., Colli, G.R., 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. *Biol. Conserv.* 90, 91–101.
- Schäuble, C.S., Grigg, G.C., 1998. Thermal ecology of the Australian agamid *Pogona barbata*. *Oecologia* 114, 461–470.
- Seebacher, F., 1999. Behavioural postures and the rate of body temperature change in wild freshwater crocodiles, *Crocodylus johnstoni*. *Physiol. Biochem. Zool.* 72, 57–63.
- Seebacher, F., Shine, R., 2004. Evaluating thermoregulation in reptiles: the fallacy of the inappropriately applied method. *Physiol. Biochem. Zool.* 77, 688–695.
- Seebacher, F., Grigg, G.C., Beard, L.A., 1999. Crocodiles as dinosaurs: behavioural thermoregulation in very large ectotherms leads to high and stable body temperatures. *J. Exp. Biol.* 202, 77–86.
- Sharpe, P.B., Van Horne, B., 1999. Relationships between the thermal environment and activity of Piute ground squirrels (*Spermophilus mollis*). *J. Therm. Biol.* 24, 265–278.
- Shine, R., Kearney, M., 2001. Field studies of reptile thermoregulation: how well do physical models predict operative temperature? *Funct. Ecol.* 15, 282–288.
- Shine, R., Madsen, T., 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiol. Zool.* 69, 252–269.
- Shine, R., Harlow, P.S., Elphick, M.J., Olsson, M.M., Mason, R.T., 2000. Conflicts between courtship and thermoregulation: the thermal ecology of amorous male garter snakes (*Thamnophis sirtalis parietalis*, Colubridae). *Physiol. Biochem. Zool.* 73, 508–516.
- Shine, R., Sun, L., Kearney, M., Fitzgerald, M., 2002. Thermal correlates of foraging -site selection by Chinese pit-vipers (*Gloydius shedaoensis*, Viperidae). *J. Therm. Biol.* 27, 405–412.
- Smith, G.R., Ballinger, R.E., 1994. Temperature relationships in the high-altitude viviparous lizard, *Sceloporus jarrovi*. *Am. Midl. Nat.* 131, 181–189.
- Standora, E.A., Spotila, J.R., Foley, R.E., 1982. Regional endothermy in the sea turtle, *Chelonia mydas*. *J. Therm. Biol.* 7, 159–165.
- Stoutjesdijk, F., 2002. The ugly duckling: a thermal viewpoint. *J. Therm. Biol.* 27, 413–422.
- Thomas, D.W., Pacheco, M.A., Fournier, F., Fortin, D., 1998. Validation of the effect of helox on thermal conductance in homeotherms using heated models. *J. Therm. Biol.* 24, 377–380.
- Tieleman, B.I., Williams, J.B., 2002. Effects of food supplementation on behavioural decisions of hoopoe-larks in the Arabian Desert: balancing water, energy, and thermoregulation. *Anim. Behav.* 63, 519–529.
- VanBerkum, F.H., Huey, R.B., Adams, B.A., 1986. Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol. Zool.* 59, 464–472.
- Vispo, C.R., Bakken, G.S., 1993. The influence of thermal conditions on the surface activity of thirteen-lined ground squirrels. *Ecology* 74, 377–389.
- Vitt, L.J., Avila-Pires, T.C.S., 1998. Ecology of two sympatric species of neusticurus (*Sauria: Gymnophthalmidae*) in the Western Amazon of Brazil. *Copeia* 1998, 570–582.
- Vitt, L.J., Sartorius, S.S., 1999. HOBOS, tidbits, and lizard models: the utility of electronic devices in field studies of ectotherm thermoregulation. *Funct. Ecol.* 13, 670–674.
- Vitt, L.J., Avila-Pires, T.C.S., Caldwell, J.P., Oliveira, V.R.L., 1998. The impact of individual tree harvesting on the thermal environments of lizards in Amazonian river forest. *Conserv. Biol.* 12, 656–664.
- Vitt, L.J., Sartorius, S.S., Avila-Pires, T.C.S., Espósito, M.C., 2001. Life on the leaf litter: the ecology of *Anolis nitens tandai* in the Brazilian Amazon. *Copeia* 2001, 401–412.
- Walsberg, G.E., Weathers, W.W., 1986. A simple technique for estimating operative environmental temperature. *J. Therm. Biol.* 11, 67–72.
- Walsberg, G.E., Wolf, B.O., 1996a. A test of the accuracy of operative temperature thermometers for studies of small ectotherms. *J. Therm. Biol.* 21, 275–281.
- Walsberg, G.E., Wolf, B.O., 1996b. An appraisal of operative temperature mounts as tools for studies of ecological energetics. *Physiol. Zool.* 69, 658–681.
- Ward, D., Pinshow, B., 1995. Temperature regulation of the great grey shrike (*Lanius excubitor*) in the Negev Desert. 2. Field measurement of standard operative temperatures and behavior. *J. Therm. Biol.* 20, 271–279.
- Weathers, W.W., Sullivan, K.A., 1993. Seasonal patterns of time and energy allocation by birds. *Physiol. Zool.* 66, 511–536.
- Weathers, W.W., Davidson, C.L., Olson, C.R., Morton, M.L., Nur, N., Famula, T.R., 2002. Altitudinal variation in parental energy expenditure by white-crowned sparrows. *J. Exp. Biol.* 205, 2915–2924.
- Webster, M.D., Weathers, W.W., 2000. Seasonal changes in energy and water use by verdins, *Auriparus flaviceps*. *J. Exp. Biol.* 203, 3333–3344.
- Wiersma, P., Piersma, T., 1994. Effects of microhabitat, flocking, climate, and migratory goal on energy expenditure in the annual cycle of red knots. *Condor* 96, 257–279.
- Wikelski, M., Wrege, P.H., 2000. Niche expansion, body size, and survival in Galapagos marine iguanas. *Oecologia* 124, 107–115.
- Wikelski, M., Carbone, C., Trillmich, F., 1996. Lekking in marine iguanas: female grouping and male reproductive strategies. *Anim. Behav.* 52, 581–596.
- Wikelski, M., Hau, M., Wingfield, J.C., 2000. Seasonality of reproduction in a neotropical rain forest bird. *Ecology* 81, 2458–2472.
- Wills, C.A., Beaupre, S.J., 2000. An application of randomization for detecting evidence of thermoregulation in timber rattlesnakes (*Crotalus horridus*) from northwest Arkansas. *Physiol. Biochem. Zool.* 73, 325–334.
- Zimmerman, L.C., O'Connor, M.P., Bulova, S.J., Spotila, J.R., Kemp, S.J., Salice, C.J., 1994. Thermal ecology of desert tortoises in the Eastern Mojave desert: seasonal patterns of operative and body temperature and microhabitat utilization. *Herp. Monogr.* 8, 45–59.