

# Natural History Miscellany

## Lizard Thermal Biology: Do Genders Differ?

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*Submitted February 19, 2007; Accepted April 13, 2007; Electronically published July 16, 2007*

*Online enhancements:* appendix tables.

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**ABSTRACT:** For more than six decades, physiological ecologists have intensively studied diverse aspects of lizard thermal biology. Nevertheless, a recent review notes that prior studies have generally ignored gender differences in body temperatures, thermal sensitivity, or other aspects of thermal biology. We concur that gender differences have been ignored and should be examined: if gender differences prove common, standard protocols for studying lizard natural history, thermal physiology, and ecology will require significant modification. To help resolve this issue, we conducted a retrospective analysis of our huge data set on the thermal biology of many desert lizards (more than 11,000 individuals from 56 species in seven major clades) from Africa, Australia, and North America. Results are unambiguous: gender differences in body temperature, air temperature, and time of activity—and thus in field thermal biology—are almost always minor. In fact, mean body temperatures of males and females differ by less than 1°C in 80.4% of species. For desert lizards, gender differences in thermal biology are the exception, not the rule. Nevertheless, gender differences should be examined when feasible because exceptions—though likely rare—could be biologically interesting.

**Keywords:** body temperature, lizards, thermal biology, sexual dimorphism.

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Ever since Cowles and Bogert (1944) highlighted the importance of body temperature ( $T_b$ ) to the natural history and ecology of reptiles, physiological ecologists have re-

corded  $T_b$  of tens of thousands of reptiles in nature as well as determined effects of  $T_b$  on physiological and ecological performance (Bennett 1987). Lizards have been the focus of most reptile studies: the relevant literature for lizards on  $T_b$  (Brattstrom 1965; Heatwole 1976; Avery 1982; Pianka 1986), thermal ecology (Tracy and Christian 1983; Dunham et al. 1989; Kearney and Porter 2004), and thermal sensitivity of physiological processes (Bennett 1980; Huey 1982; Angilletta et al. 2002) is unsurpassed for terrestrial ectotherms.

Despite this wealth of natural history information, one question has largely been ignored, namely, do males and females differ in thermal biology? In a recent review, Lailvaux (2007) draws attention to this question and cites several studies documenting gender differences in field  $T_b$ , in laboratory thermal preferences, or in thermal sensitivity of performance. He concludes that potential gender differences in thermal biology deserve greater attention.

We agree with Lailvaux (2007) that physiological ecologists should have been routinely examining gender differences (Shine et al. 1995). Anyone who has watched lizards in nature knows that males and females sometimes use different microhabitats, are active at different times, or differ in behavior (Schoener 1967; Spoecker 1967; Bauwens and Thoen 1981; Bull et al. 1991; Stamps et al. 1997; Butler et al. 2000; Kerr and Bull 2006; Ashbury and Adolph 2007). For example, in many species, males defend territories whereas females do not. Males and females sometimes differ in basking behavior as well (Huey and Webster 1975; Ashbury and Adolph 2007), and gravid females may alter thermoregulatory behavior (Beuchat 1986; Schwarzkopf and Shine 1991). Thus, males and females could easily encounter different operative thermal environments (Bakken 1992) and, if so, could have different  $T_b$  and thermal sensitivities (Shine 1999). Moreover, such differences would be relevant to models predicting ecological responses to climate change (Dunham 1993; Kearney and Porter 2004).

Whether gender differences are the rule in lizard thermal biology is, however, unresolved. If differences are common, lizard ecologists will definitely need to change the

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way they study lizards in nature and in the laboratory. The only way to resolve this issue is to conduct comprehensive surveys of diverse lizards. Fortunately, the existing database of lizard natural history is large, and some data are still accessible and can be readily mined. If gender differences in lizard thermal biology are general (see Lailvaux 2007), then differences in field  $T_b$  of males and females will be conspicuous in existing data sets.

Over the decades, we have collected more than our share of lizard body temperatures (e.g., Pianka 1970, 1986; Huey 1974; Pianka and Pianka 1976; Huey et al. 1977, 1989; Hertz 1981), and one of us has quantified the thermal sensitivity of sprint speed of numerous lizards (e.g., Hertz et al. 1983; Huey and Bennett 1987; Huey et al. 1989). Nevertheless, we seldom examined or reported gender differences. Why, even though we always recorded gender of our lizards? As best we can recall, we ignored gender in part because our focus (and that of others) at the time was on interspecific or interpopulational patterns and in part because we never noticed conspicuous gender differences in thermal biology when capturing lizards in the field.

In any case, we now rectify our past sins of omission. We compiled our extensive data sets on the thermal biology of desert lizards from North America, Australia, and Africa (56 species total). For males versus females of each species, we compared body temperatures, air temperatures ( $T_a$ ), and times of activity. Results of this exercise are unambiguous: males and females do not differ significantly in these measures in most species. In fact, mean  $T_b$  of males and females differ by less than 1°C in 80.4% of all species examined. For desert lizards, gender differences in field thermal biology are the exception, not the rule. Nevertheless, we still agree with Lailvaux (2007; see also Lailvaux et al. 2003): when feasible, possible gender differences should be examined.

### Material and Methods

Natural history data reported here were collected over several decades by Pianka (1986) and colleagues in deserts of western North America (nine species, 2,337 individuals), western Australia (31 species, 4,264 individuals), and southern Africa (16 species, 4,770 individuals). For the majority of species, records were obtained over their entire seasonal period of activity, although most records are from spring or summer. We considered only species ( $N = 56$ ) for which sample sizes exceeded nine individuals for each trait and each gender. (However, for completeness, data for seven additional species with smaller sample sizes are provided in the appendix in the online edition of the *American Naturalist*.) Gravid females are included (but see the fifth paragraph of “Results”). Data from different popu-

lations of a given species were pooled, except those for the North American teiid lizard *Apidoscelis tigris*. This species shows geographic variation in  $T_b$  (Pianka 1970), which could increase the probability of Type II error (see “Discussion”). So we partitioned data for four populations with large samples (see appendix) to investigate the effect of geographic pooling. However, when presenting results for all species, we included data for only the B-area population, which has the largest sample size.

Using standard precautions, we used quick-reading Schultheis thermometers to measure  $T_b$  (cloacal) of active lizards and associated (shaded) air temperatures ( $T_a$ , at chest height), and we also recorded time of activity. (Note that not all measurements were taken on each lizard.) Gender was established from external morphology or by dissection.

We computed basic descriptive statistics by gender for each species (table 1; appendix) and then compared mean  $T_b$  and mean  $T_a$  of males with those of females (two-tailed  $t$ -tests for unequal variances, with Welch-Satterthwaite approximations for degrees of freedom), as well as variances in  $T_b$  (variance ratio tests). Because we ran many tests, significant differences occasionally occurred by chance (Type I error). To control this false error rate, critical  $P$  values were often adjusted via Bonferroni-style corrections (Rice 1989; Benjamini and Hochberg 1995). Use of such corrections is, however, debated (Moran 2003; Nakagawa 2004). In any case, to give Lailvaux's (2007) hypothesis (that genders differ significantly) the maximum chance for support, we report uncorrected  $P$  values. For completeness, however, we include results following sequential Bonferroni adjustments (Benjamini and Hochberg 1995).

### Results

Descriptive statistics (body temperatures, air temperatures, and daily times of activity) for each species are collated in table 1 by continent, nested within taxa. Summary statistics for individual species are available in the appendix.

Mean  $T_b$  of males and females are strikingly similar in most species (table 1; fig. 1A). Average absolute deviation in  $T_b$  between males and females was only  $0.56^\circ \pm 0.077^\circ\text{C}$ . Moreover, absolute deviation in mean  $T_b$  was less than 1°C in 80.4% of species and was less than 0.5°C in 58.9% of species (fig. 1A; table A3). Males and females differed significantly in mean  $T_b$  in only a few species (8 of 56; table A1), even without a sequential Bonferroni correction. With that correction (Benjamini and Hochberg 1995), males and females never differed significantly.

Effect sizes (Cohen 1988), which estimate the difference in  $T_b$  between groups scaled to within-group variance, were small (Cohen's  $d \leq 0.20$ ) in 37 of 56 species (table A1). Effect sizes were large ( $d > 0.50$ ) in only 5 of 56 species.

**Table 1:** Mean absolute differences in  $T_b$  and activity times of male versus female lizards from several deserts

Taxon, desert	No. species	Body temperature (°C)		Air temperature (°C)		Time of activity (h)	
		Mean absolute deviation	SD	Mean absolute deviation	SD	Mean absolute deviation	SD
Agamidae:							
Australia	10	.75	.749	1.59	1.798	.78	.590
Kalahari	1	.13	...	1.21	...	.11	...
Gekkota:							
Australia	7	.77	.584	.66	.721	.25	.222
Kalahari + Namib	6	.23	.890	.66	.327	.23	.131
North America	1	.13	...	.58	...	.44	...
Iguania:							
North America	7	.40	.439	.66	.439	.83	.917
Lacertidae:							
Africa	6	.41	.239	.42	.323	.39	.369
Scincidae:							
Australia	11	.33	.209	.63	.58	.62	.540
Kalahari	3	.20	.181	.61	.318	.37	.304
Teiidae:							
North America	1 (4) <sup>a</sup>	.16	.094	.36	.103	.12	.067
Varanidae:							
Australia	3	1.37	.876	1.45	1.157	.49	.711
Total	56	.57	.597	.81	.937	.50	.537

<sup>a</sup> Four populations of one species.

Gender differences in  $T_b$  were uniformly small for all taxa and for all geographic areas (table 1). Absolute differences exceeded 2°C in only three species (*Colopus wahlbergi*, *Diporiphora winneckeii*, and *Varanus eremius*), which have little in common ecologically or phylogenetically (three different families represented). Sampling error and false error could well be involved, of course. For the Australian agamid *D. winneckeii*, however, the gender difference appears real (males 2.2°C colder than females). Males of this species were active 2 h earlier in the day (11.75 vs. 13.79 h) and at considerably lower  $T_a$  than were females (22.7°C vs. 28.9°C), so their lower  $T_b$  is not surprising. Most data on this species were collected during the austral spring months of August and September, and so gender differences in this species could be an artifact of partial seasonal sampling. Further field observations of *D. winneckeii* are required.

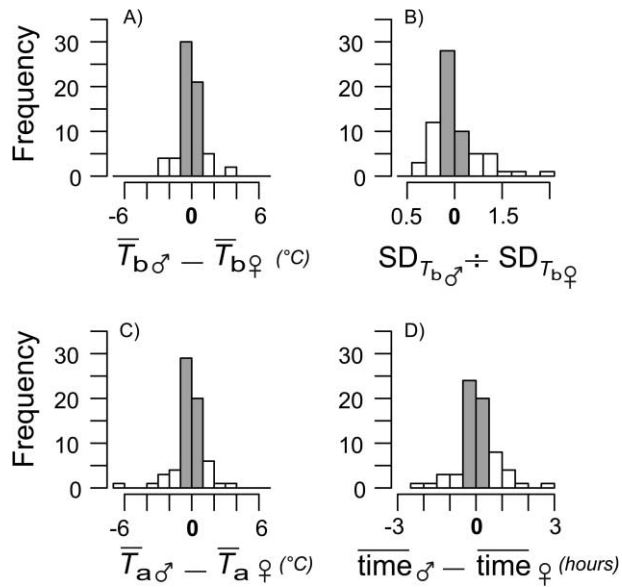
Males and females might also differ in variability in  $T_b$  (fig. 1B); if so, this might lead to disruptive selection between genders for the degree of thermal generalization of physiology (Hertz et al. 1983). However, males and females differed significantly in  $T_b$  variance in only eight species (Fisher variance ratio tests; table A1); only two species (*Pedioplanis namaquensis*, *Varanus gouldi*) remained significant after Bonferroni correction. Males and females do not differ systematically in relative magnitude of  $T_b$  variance ( $P = .415$ , paired  $t$ -test), which suggests that possible shifts in set-point temperatures of females when gravid

(Beuchat 1986; Schwarzkopf and Shine 1991) are generally minor.

Mean  $T_a$  of males and females are also strikingly similar (tables 1, A2; fig. 1C) and differed significantly in only four species (none after sequential Bonferroni correction). Average absolute deviation was only 0.90°C and was consistently small for all taxa and deserts (table 1). In fact, 75.0% of all species have an absolute deviation of less than 1°C, and 41.2% deviate less than 0.5°C. Similarly, times of activity of males and females are similar (tables 1, A3; fig. 1D): absolute median difference was only 0.50 h. Differences were significant in only seven species, and none remained significant after Bonferroni correction.

## Discussion

The literature on thermal biology of lizards is extensive, but almost all comparative studies have focused on inter-specific differences. As a result, few studies have examined within-species differences, such as those between males and females, even though genders sometimes differ conspicuously in ecology and behavior (Schoener 1967; Butler et al. 2000; Kerr and Bull 2006; Ashbury and Adolph 2007). Lailvaux and collaborators (Lailvaux et al. 2003; Lailvaux 2007) recently highlighted this gap and argued that gender differences in thermal biology should be routinely evaluated, not ignored. We agree and therefore reexamined our own extensive natural history data on desert lizards



**Figure 1:** Thermal biology of male versus female desert lizards. Histograms of differences in mean body temperature  $T_b$  (A), SD  $T_b$  of males/SD  $T_b$  of females (B), differences in mean air temperature  $T_a$  (C), and differences in mean time of activity (D).  $N = 56$  species in each panel. Shaded bars indicate species for which mean differences in  $T_b$  or  $T_a$  were less than  $1^\circ\text{C}$  (A, C), for which the ratio of SDs ranged between 0.85 and 1.15 (B), or for which mean differences in time of activity were less than 1 h (D).

from three continents. Specifically, we compared body temperatures, air temperatures, and daily times of activity of males versus females of 56 species (11,371 individuals) representing seven major clades from the deserts of Africa, Australia, and North America. Sample sizes are generally large for each gender and provide adequate power (see below) to detect significant differences between males and females ( $\Sigma T_b = 8,956$ , average  $N$  per species = 79 for males, 73 for females). Thus, our analyses should help establish—at least for desert lizards—whether gender differences in these thermal traits are major or not.

The observed pattern is striking: males and females have remarkably similar body temperatures (means, variances), air temperatures, and times of activity (fig. 1). In only a few species do males and females have differences in  $T_b$  or  $T_a$  exceeding  $2.0^\circ\text{C}$  (fig. 1A, 1B) or differences of time of activity exceeding 1 h (fig. 1C). Thus, male and female desert lizards have similar thermal biologies, at least with respect to the three metrics addressed here.

The apparent rarity of significant gender differences in field thermal biology in desert lizards (table 1; fig. 1) might, however, be an artifact of inadequate statistical power (Type II error). To evaluate the adequacy of our sample sizes, we ran a power test to find the minimum group size

appropriate to detect a  $2.0^\circ\text{C}$  difference in mean  $T_b$ . With power set at 80% and with a standard deviation of 2.82 (median value for all samples), minimum sample sizes are 21 individuals of each sex. Our samples equal or exceed that limit in 80.4% of species. If we delete species with fewer than 42 individuals, significant gender differences are still relatively uncommon (e.g., only 7 of 52 cases).

Another way to evaluate a potential power confound is to examine the correlation between sample size and  $P$  value. If power is limiting, then  $P$  values should decrease with sample size. This is not the case ( $r_s = -0.085$ ,  $P = .5232$ ).

If thermal biology of a species varies geographically, our lumping of data from multiple populations will inflate variances and thus cause Type II errors. One species, the North American teiid *Apidoscelis tigris*, shows geographic variation in  $T_b$  (Pianka 1970). However, mean male and mean female  $T_b$  differ by a maximum of only  $0.27^\circ\text{C}$  in four populations of this species (table A1); thus, pooling of geographic samples seems unlikely to be masking gender differences in our data.

In conclusion, Lailvaux and colleagues (Lailvaux et al. 2003; Lailvaux 2007) have recently challenged physiological ecologists to examine gender differences in thermal biology of reptiles. Their rationale is inarguable, and in response we compiled natural history data for desert lizards that we have accumulated over several decades. We find little evidence that male and female lizards differ substantively in  $T_b$ , in  $T_a$ , or in time of activity. Because our sample sizes are large and include many species from several different clades on three continents, gender differences in field thermal biology of desert lizards are the exception, not the rule. Whether this pattern holds for lizards in other habitats remains to be determined. Lizard species are also diverse in closed tropical forests, but we expect that gender differences will prove to be minor there. At least below the canopy, thermal heterogeneity is limited in space and time (Hertz 1992), thus providing few opportunities for thermal differentiation.

#### Acknowledgments

We thank S. Lailvaux and colleagues for calling attention to this issue and thus inspiring us to reexamine our data. We thank A. Bennett, H. John-Alder, and S. Lailvaux for comments on the manuscript. Numerous friends have helped us collect these data over the years: they have been acknowledged in many previous articles, but we do so again. Field research was supported by the University of Texas and by grants and fellowships from the National Science Foundation (NSF), the National Geographic Society, the Guggenheim Foundation, and the Fulbright

Foundation to E.R.P. Write-up was supported by NSF grant IOB-0416843 to R.B.H.

### Literature Cited

- Angilletta, M. J., Jr., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27:249–268.
- Ashbury, D. A., and S. C. Adolph. 2007. Behavioral plasticity in an ecological generalist: microhabitat use by western fence lizards. *Evolutionary Ecology Research* 9:801–815.
- Avery, R. A. 1982. Field studies of body temperatures and thermoregulation. Pages 93–166 in C. Gans and F. H. Pough, eds. *Biology of the Reptilia*. Vol. 12. Physiological ecology. Academic Press, London.
- Bakken, G. S. 1992. Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist* 32:194–216.
- Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology* 50:733–743.
- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B* 57:289–300.
- Bennett, A. F. 1980. The thermal dependence of lizard behaviour. *Animal Behaviour* 26:455–462.
- . 1987. The accomplishments of ecological physiology. Pages 1–8 in M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey, eds. *New directions in ecological physiology*. Cambridge University Press, New York.
- Beuchat, C. A. 1986. Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia* 1986:971–979.
- Brattstrom, B. H. 1965. Body temperature of reptiles. *American Midland Naturalist* 73:376–422.
- Bull, C. M., A. McNally, and G. Dubas. 1991. Asynchronous seasonal activity of male and female sleepy lizards, *Tiliqua rugosa*. *Journal of Herpetology* 25:436–441.
- Butler, M. A., T. W. Schoener, and J. B. Losos. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* 54:259–272.
- Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*. Earlbaum, Hillsdale, NJ.
- Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* 83:261–296.
- Dunham, A. E. 1993. Population responses to environmental change: physiologically structured models, operative environments, and population dynamics. Pages 95–119 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, eds. *Biotic interactions and global change*. Sinauer, Sunderland, MA.
- Dunham, A. E., B. W. Grant, and K. L. Overall. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiological Zoology* 62:335–355.
- Heatwole, H. 1976. *Reptile ecology*. University of Queensland Press, St. Lucia.
- Hertz, P. E. 1981. Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): field thermal biology and physiological ecology. *Journal of Zoology (London)* 195:25–37.
- . 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology* 73:1405–1417.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* 37:1075–1084.
- Huey, R. B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184:1001–1003.
- . 1982. Temperature, physiology, and the ecology of reptiles, Pages 25–91 in C. Gans and F. H. Pough, eds. *Biology of the Reptilia*. Vol. 12. Physiological ecology. Academic Press, London.
- Huey, R. B., and A. F. Bennett. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098–1115.
- Huey, R. B., and T. P. Webster. 1975. Thermal biology of a solitary lizard: *Anolis marmoratus* of Guadeloupe, Lesser Antilles. *Ecology* 56:445–452.
- Huey, R. B., E. R. Pianka, and J. Hoffmann. 1977. Seasonal variation in thermoregulatory behavior and body temperatures of diurnal Kalahari lizards. *Ecology* 58:1066–1075.
- Huey, R. B., P. H. Niewiarowski, J. Kaufmann, and J. C. Herron. 1989. Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? *Physiological Zoology* 62:488–504.
- Kearney, M., and W. P. Porter. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119–3131.
- Kerr, G. D., and C. M. Bull. 2006. Movement patterns in the monogamous sleepy lizard (*Tiliqua rugosa*): effects of gender, drought, time of year and time of day. *Journal of Zoology (London)* 269:137–147.
- Lailvaux, S. P. 2007. Interactive effects of sex and temperature on locomotion in reptiles. *Integrative and Comparative Biology* (forthcoming), doi:10.1093/icb/icm011.
- Lailvaux, S. P., G. J. Alexander, and M. J. Whiting. 2003. Sex-based differences and similarities in locomotor performance, thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. *Physiological and Biochemical Zoology* 76:511–521.
- Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405.
- Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology* 15:1044–1045.
- Pianka, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51:703–720.
- . 1986. *Ecology and natural history of desert lizards: analyses of the ecological niche and community structure*. Princeton University Press, Princeton, NJ.
- Pianka, E. R., and H. D. Pianka. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia* 1976:125–142.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155:474–477.
- Schwarzkopf, L., and R. Shine. 1991. Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: why do gravid females bask more? *Oecologia (Berlin)* 88:562–569.

- Shine, R. 1999. Why is sex determined by nest temperature in many reptiles? *Trends in Ecology & Evolution* 14:186–189.
- Shine, R., M. J. Elphick, and P. S. Harlow. 1995. Sisters like it hot. *Nature* 378:451–452.
- Spoecker, P. D. 1967. Movements and seasonal activity cycles of the lizard *Uta stansburiana stejnegeri*. *American Midland Naturalist* 77:484–494.
- Stamps, J. A., J. B. Losos, and R. M. Andrews. 1997. A comparative study of population density and sexual size dimorphism in lizards. *American Naturalist* 149:64–97.
- Tracy, C. R., and K. A. Christian. 1983. Ecological relations among space, time and thermal niche axes. *Ecology* 67:609–615.

Natural History Editor: Henry M. Wilbur