RESEARCH ARTICLE

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Body temperature distributions of active diurnal lizards in three deserts: Skewed up or skewed down?

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Abstract

1. The performance of ectotherms integrated over time depends in part on the position and shape of the distribution of body temperatures (T_b) experienced during activity. For several complementary reasons, physiological ecologists have long expected that T_b distributions during activity should have a long left tail (left-skewed), but only infrequently have they quantified the magnitude and direction of T_b skewness in nature.

2. To evaluate whether left-skewed T_b distributions are general for diurnal desert lizards, we compiled and analysed T_b (Σ = 9,023 temperatures) from our own prior studies of active desert lizards in three continents (25 species in Western Australia, 10 in the Kalahari Desert of Africa and 10 species in western North America). We gathered these data over several decades, using standardized techniques.

3. Many species showed significantly left-skewed T_b distributions, even when records were restricted to summer months. However, magnitudes of skewness were always small, such that mean T_b were never more than 1°C lower than median T_b. The significance of T_b skewness was sensitive to sample size, and power tests reinforced this sensitivity.

4. The magnitude of skewness was not obviously related to phylogeny, desert, body size or median body temperature. Moreover, a formal phylogenetic analysis is inappropriate because geography and phylogeny are confounded (i.e. are highly collinear).

5. Skewness might be limited if lizards pre-warm inside retreats before emerging in the morning, emerge only when operative temperatures are high enough to speed warming to activity T_b, or if cold lizards are especially wary and difficult to spot or catch. Telemetry studies may help evaluate these possibilities.

KEYWORDS
body temperature distribution, desert lizards, ectotherm, skewed distribution, thermal biology, thermoregulation

1 | INTRODUCTION

Body temperature affects an ectotherm's instantaneous performance (Angilletta, 2009; Dell, Pawar, & Savage, 2011; Huey & Stevenson, 1979), and consequently, the distribution of its body temperatures over time affects its integrated performance and fitness (Dowd, King, & Denny, 2015; Gilchrist, 1995; Huey & Slatkin, 1976; Sinclair et al., 2016; Vasseur et al., 2014; Waldschmidt & Tracy, 1983). Importantly, integrated performance depends not only on the position and breadth of the T_b distribution (e.g. median, variance), but also on the skewness

of that distribution, specifically because skewed T_b distributions alter the weighting of performance over time (Dowd et al., 2015; Marshall, Dong, McQuaid, & Williams, 2011; Martin & Huey, 2008; Vasseur et al., 2014).

For at least the following five reasons, lizard thermal biologists have long expected T_b distributions to be left-skewed (Figure 1) and thus have a long left tail (Cowles & Bogert, 1944; Heath, 1964; Soulé, 1963).

1. Diurnal lizards emerging from cool nocturnal retreats will initially have low T_b, but then will be able to use thermoregulatory behaviours to maintain near-optimal T_b for most of the day (Cowles & Bogert, 1944; Soulé, 1963).

2. Operative (equilibrium) temperature distributions over a day can also be left-skewed: they rise quickly in the morning but then re-main relatively stable until late afternoon (Heath, 1964; Hertz, 1992).

3. Lizards tend to active more often and have warmer T_b in summer than in cooler seasons (Huey, Pianka, & Hoffmann, 1977), and thus pooling seasonal samples will induce a left skew.

4. Because thermal performance curves are asymmetric (Dell et al., 2011; Gilchrist, 1995; Huey & Stevenson, 1979), lizards may be more likely to try to avoid high T_b than low T_b because an above-optimum T_b reduces performance disproportionately, increases risk of overheating and also elevates metabolic rates (Martin & Huey, 2008).

5. Finally, and perhaps most generally, because neural processing and walking speed increase exponentially with temperature, ther-moregulatory responses should proceed faster at higher tempera-tures, leading to left-skewed distributions (DeWitt, 1967; DeWitt & Friedman, 1979; Dillon, Rongsong, Wang, & Huey, 2012). Given that left-skewed distributions can be generated by many causes, distinguishing which of the above reasons are involved in a particular case is challenging. Conversely, if skewness is not in fact detected, figuring out why will also be challenging.

Over past decades, biologists have measured field body tempera-tures of hundreds of lizard species from all over the world (Hertz et al., 2013; Huey et al., 1977; Meiri et al., 2013; Pianka, 1986; Sinervo et al., 2010). Many have commented on skewness of T_b distributions of lizards (e.g. DeWitt & Friedman, 1979; Gvoždík, 2002; Heath, 1964; Powell & Russell, 1985; van Berkum, 1988; Werner & Whitaker, 1978) and other ectotherms (Arnold, Peterson, & Gladstone, 1995; Marshall et al., 2011; Spigarelli, Thommes, Prepejchal, & Goldstein, 1983), but no one has—to our knowledge—systematically quantified T_b skewness for diverse ectotherms.

We ourselves have measured T_b of thousands of individual liz-ards, but have never quantified or reported skewness of T_b distri-butions. However, because several papers have recently discussed the impact of T_b skewness on fitness (Dowd et al., 2015; Marshall et al., 2011; Martin & Huey, 2008; Vasseur et al., 2014), we decided to quantify skewness in our own data. We focus only on desert liz-ards and report skewness of T_b distributions for active diurnal liz-ards in North America (N = 10 species, 3,386 individuals), Australia (N = 25 species, 3,304 individuals) and southern Africa (10 species, 2,333 individuals). A total of 45 species representing eight families and 9,023 individuals from three continents are represented. We find that T_b distributions are indeed generally left-skewed (Figure 1), but note that observed skewness is small, especially when only summer T_b are analysed.

1.1 | Why skewness matters

Here, we demonstrate why T_b skewness is ecologically meaningful. The canonical equation (Deutsch et al., 2008; Huey & Slatkin, 1976; Vasseur et al., 2014) evaluating how T_b influences cumulative per-formance (or fitness) weights the impact of T_b on instantaneous per-formance or fitness ($w(T_b)$) by the distribution of body temperatures ($p(T_b)$) experienced over an interval:

$$W \sim \int_{CT_{min}}^{CT_{max}} \left[w\left(T_b\right) . p\left(T_b\right) \right] dT_b \tag{1}$$

Because performance curves are asymmetric (Gilchrist, 1995) and because of Jensen's inequality (Ruel & Ayers, 1999), skewness in $p(T_b)$ will influence the rate summation of performance. Martin and Huey (2008) showed that left-skewed T_b distributions shift optimal temperatures (T_p), and Vasseur et al. (2014) showed that right-skewed distributions reduce integrated performance.

The performance consequences of T_b skewness are influenced by complex interactions with performance-curve asymmetry and thermal breadth, as well as the position of the T_b distribution relative to op-timal T_b (Martin & Huey, 2008; Vasseur et al., 2014). Nevertheless, a simple graphical analysis is illustrative (based in part on Vasseur et al., 2014; Sinclair et al., 2016). Figure 2a shows a thermal performance curve with an optimum at 35°C, and Figure 2b shows two sets of
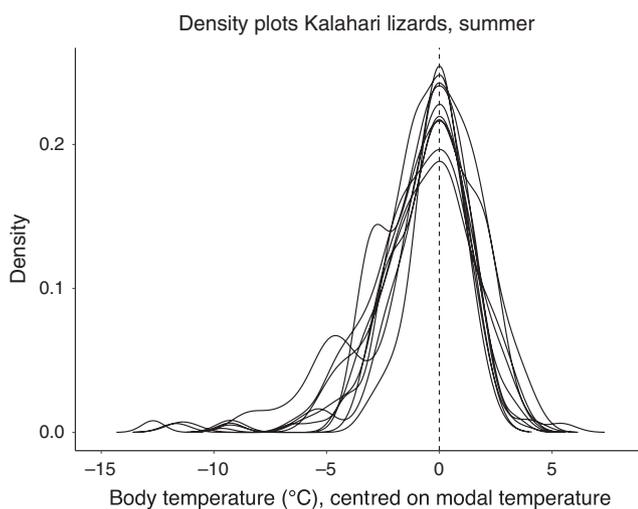

FIGURE 1 Density plots of T_b of 10 Kalahari lizard species in summer: distributions are centred on modal temperature of each species. Left skewness is visually evident for many species and significant in seven (Table S1)
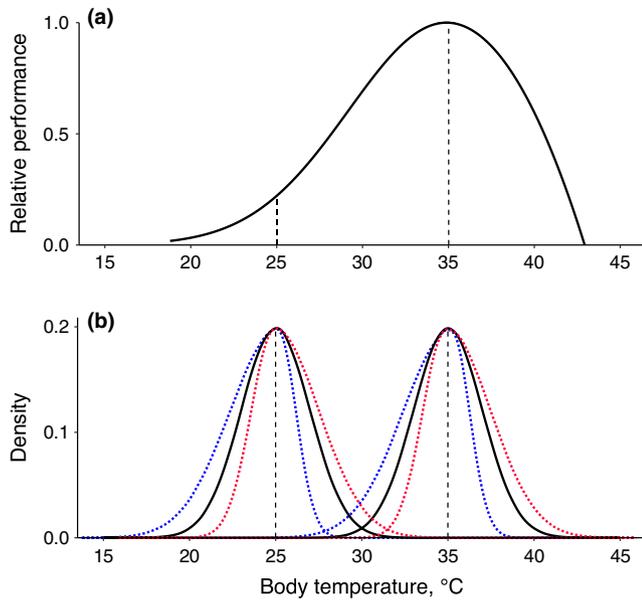
FIGURE 2 (a) Thermal performance curve. (b) Body temperature distributions (solid black curves = normal distributions, red dashed curves = right-skewed and blue dashed lines = left-skewed). Vertical dashed lines indicate modal temperatures for each distribution. Median minus mean differences are 0.27°C for left-skewed distributions and −0.24°C for right-skewed distributions. Skewness coefficients are −0.67°C and +0.49°C respectively. These compare roughly with lizard coefficients in Table S1

$p(T_b)$ distributions centred at low (25°C) or high (35°C) temperatures, respectively, and with normal (solid black), left-skewed (blue) and right-skewed (red) T_b distributions.

A left-skewed distribution at low T_b reduces average performance relative to a normal one, but enhances performance at high T_b if the thermal performance curve is narrow and highly asymmetric (Figure 2). In contrast, a right-skewed distribution increases average performance at low T_b, as more T_b are associated with relatively high performance; but reduces performance at high T_b, as many T_b will be above the optimum, where performance declines rapidly. Skewness matters.

2 | MATERIALS AND METHODS

2.1 | Field methods

Body temperature data were collected at multiple study sites and at some incidental areas over several decades by Pianka et al. in North America (1962–1964, 1969), Western Australia (1966–68, 1978–79, 1989–92, 1995, 1998, 2003 and 2008) and the Kalahari of southern Africa (1969–70). Species authorities are accessible at http://www.reptile-database.org/db-info/taxa.html#Sau. Twelve North American study sites are arranged latitudinally extending from Idaho (42°12′ N × 115°50′ W) to Sonora, Mexico (28°23′ N × 111°32′ W). In contrast, study areas in the Southern hemisphere are all located at similar latitudes between 26°S and 28°S and extend from east to west. Ten study sites in the Great Victoria Desert of Western Australia range from 125°50′ E to 119°06′ E. Ten study areas in the Kalahari Desert

of southern Africa extend from 22°15′ 36″ E to 19°50′ 24″ E. All sites are described in Pianka (1986).

Field methods are summarized in Huey et al. (1977) and Pianka (1986), and references to the original data sources are in Pianka (1986). Lizards were captured after little or no chasing, and we used quick-reading "Schultheis" (Miller–Weber) thin-bulb thermometers to measure cloacal T_b (to nearest 0.1°C). Individual lizards were measured only once. Data were collected over all seasons in Australia and in southern Africa but only from mid-April through mid-August in North America. Males and females were pooled because gender differences in T_b and in times of activity in these lizards are minor (Huey & Pianka, 2007).

We report T_b only for diurnal species and only for individual lizards that were active (i.e. exposed above-ground) and were captured between sunrise and sunset (times calculated for each day and locality). We checked our original field notes of all individuals with $T_b < 30$°C to ascertain whether those lizards were indeed active and thus had not been captured in a retreat (e.g. under bark or down a burrow).

2.2 | Statistical methods

For Western Australia and for Kalahari sites, we pooled T_b data by species within each desert, as sites there were from restricted latitudes (c.2°). For North America, however, sites spanned almost 14° of latitude, and T_b varies inversely with latitude for *Aspidoscelis tigris* (Pianka, 1970) and also for *Uta stansburiana* and *Phrynosoma platyrhinos* (analyses not shown). Because such latitudinal variation can bias skewness, we partitioned North American sites into two latitudinal regions, arbitrarily split at 35°N. The northern section included four Great Basin sites (I, L, G and V) plus one Mojave site (P), and the southern section included three Mojave sites (M, S and T) and four Sonoran sites (W, C, A and B). (Note: Analyzing the three North American deserts separately would have resulted in insufficient sample sizes for many species.) Incidental records collected off site but with known latitudes were included.

To quantify the shape of T_b distributions, we computed standard statistics (mean, median, median absolute deviation [MAD], maximum and minimum), and the D'Agostino coefficient of skewness (D'Agostino, 1970). We determined whether the magnitude of skewness (between species within a desert region) was correlated with the basic descriptive statistics (mean, median, minimum, maximum, MAD and N T_b). For Africa and Australia, we ran separate calculations for full-year data and for summer only (e.g. December through February in the Southern Hemisphere, June through August in the Northern Hemisphere). For North America, we separated spring plus summer data from summer only data. We arbitrarily set a minimum sample size of $N = 23$ T_b for inclusion, but generally, samples were larger than that (see Table S1). A basic R script is available (see Appendix S1).

In the process of running analyses, we observed that the significance of the D'Agostino coefficient of skewness is very sensitive to sample size (see Section 4), such that species with $N < 50$ rarely displayed significant skewness (see Table S1 and power simulations in Section 4). Nevertheless, for completeness, we include data for all species with $N \geq 23$.

Because these analyses evaluate an explicit (a priori) hypothesis that T_b distributions are left-skewed, we used one-tailed tests. Values of p for skewness were corrected for multiple comparisons (false discovery rate) via the "*p.adjust*" routine (in R), which uses an adjustment proposed by Benjamini and Yekutieli (2001). However, p values in Table S1 include both original and adjusted values. p values for correlations (e.g. skewness coefficient with median, MAD, minimum or N T_b) were similarly corrected via the "*p.adjust*" (Table S2). In calculating both sets of adjustments, we treated each desert and each season separately.

2.3 | Why we did not do a phylogenetic analysis

A reviewer of a draft of this manuscript encouraged us to do a phylogenetic analysis of skewness of T_b distributions. We understand why phylogenetic analyses are important (Felsenstein, 1985; Garland, Bennett, & Rezende, 2005), and we ourselves have long advocated a phylogenetic perspective not only in applying phylogenetic analyses (e.g. Huey, 1987; Huey & Bennett, 1987; Pianka, 1995, 2001), but also in selecting species for a comparative study (Huey & Pianka, 1981). However, phylogenetic analyses are not always appropriate (Losos, 2011; Westoby, Leishman, & Lord, 1996), and we argue that this is the case here.

Consider someone interested in starting an analysis of the phylogenetic and geographic associations of skewness. If no published data are available, the researcher starts with a clean slate and can choose species to measure. Choices should be governed by phylogenetic and geographic considerations (Garland, 2001; Huey & Pianka, 1981). Ideally, the researcher will select multiple species from multiple clades and deserts, and each clade (preferably at subfamily or generic level) should occur in each desert. Such a scheme provides a complete factorial design, and a two-way ANOVA (and its phylogenetic equivalent) can assess influences of phylogeny, geography and their interaction.

Like most researchers pursuing a comparative study, we did not start from a fresh slate. The deserts and taxa for which we have T_b data were selected for reasons unrelated to skewness. Consequently, our data do not fit assumptions of a full factorial design. In North America, we have one genus each of Crotaphytidae and of Teiidae plus five genera (six species) of Phrynosomatidae. In the Kalahari, we have one genus each of Agamidae (subfamily Agaminae) and of Scincidae (subfamily Lygosominae, three species) and three genera (six species) of Lacertidae. In Western Australia, we have two genera of Agamidae (subfamily Amphibolurinae, five species), two genera of Scincidae (subfamily Lygosominae, nine species) and one genus of Varanidae.

This real-world factorial design is incomplete and has empty "treatments," as not all families or subfamilies occur in all deserts (see Figure 3). For example, Crotaphytidae, Phrynosomatidae and Teiidae are found only in our North American samples; Lacertidae are found only in African ones, and Varanidae are found only in Australian ones. We do have agamids from Africa and Australia, but agamid genera are in different subfamilies on these continents. Lygosomine skinks are in our samples from Africa and Australia, but are absent from North American ones.

Geography and phylogeny in our samples are thus not independent, as required for a full factorial ANOVA, whether ordinary or phylogenetic. Adding insult to injury, replication within some clades is limited: three families are each represented by only a single species.

Similar problems will confound many comparative studies because geography and phylogeny are generally not independent (Freckleton & Jetz, 2009; Westoby et al., 1996). [After all, field guides are usually
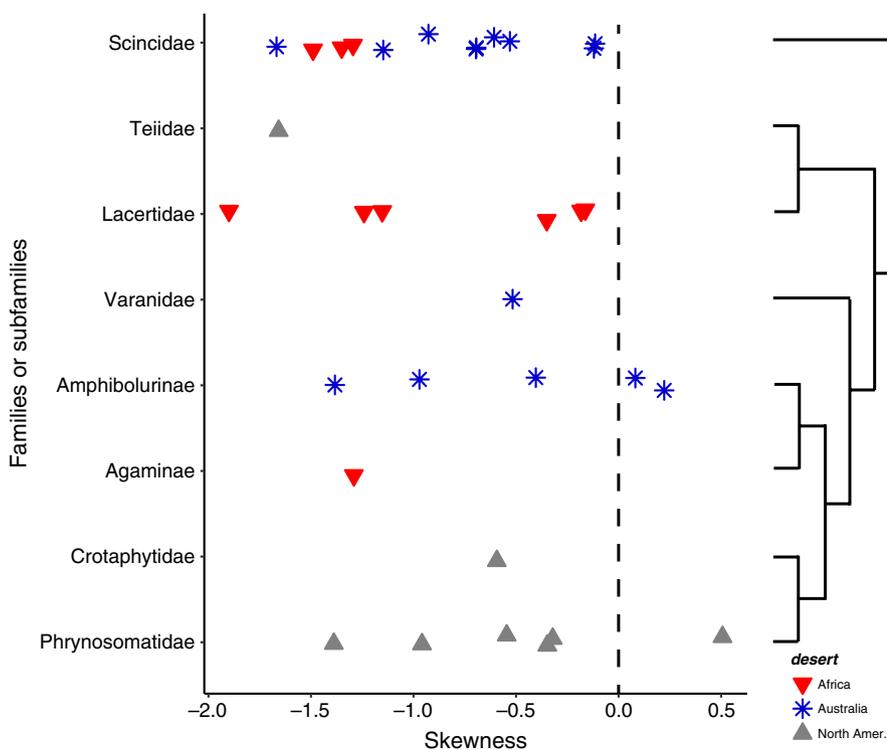

FIGURE 3 Body temperature skewness (jittered) for desert lizards, with values by family (or by subfamily for Agamidae) and by continent. Three families are represented by one species. No pattern (desert, taxon) is evident

region specific.] One general option is to raise all species in a common garden (Garland, 2001), but that is feasible only in planned studies and only for certain traits: it is inappropriate for a field study. Another would be to ignore geography and just do a phylogenetic analysis. But that would require assuming that the physical and biotic environments of different regions are identical, or that regional differences have no effects whatsoever on studied traits (Westoby et al., 1996). Neither assumption is likely to be valid. Some new techniques explore the roles of phylogeny and the spatial environment (Freckleton & Jetz, 2009), but these are not applicable to our data. For these reasons, we choose not to do a phylogenetic analysis recognizing that this induces some non-independence (Felsenstein, 1985; Garland et al., 2005).

3 | RESULTS

3.1 | Kalahari

At least 23 T_b were available for 10 species of diurnal lizards (Agamidae, Lacertidae, Scincidae) for the full year ($\sum$ = 2,333 individual T_b) and for summer only ($\sum$ = 989) (Table S1, Figures 1 and 4). If distributions are left-skewed, median T_b will be higher than mean T_b: this was the case in all 10 species over the full year and in 9 of 10 species for summer T_b. However, differences never exceeded 1°C (average difference ± SD = 0.33 ± 0.289°C year; =0.27 ± 0.245°C summer). Body temperature distributions were significantly left-skewed (original or adjusted p values) for 9 of 10 species over the full year (Table S1) and for 7 of 10 in summer (Table S1, Figure 4). For 7 of 10 species, skewness coefficient was larger for the year than for the summer, probably because T_b are lower winter than in summer and because fewer lizards are active in winter (Huey et al., 1977). The significance level of skewness was negatively but not significantly correlated with sample size (r = −.266, p = .457, see Section 4).

In among-species comparisons for summer or for full year (Table S2), the magnitude of skewness was not significantly correlated with median T_b, median absolute deviation of T_b or sample size. However, skewness magnitude was positively correlated with minimum T_b for summer samples (p = .017) and but not for all-year samples (p = .177). Thus, Kalahari species with a low minimum T_b tended to have left-skewed T_b distributions, but only in summer.

3.2 | North America

At least 23 T_b were available for 10 species from three families (Crotaphytidae, Phrynosomatidae and Teiidae—note: none of these families is shared with our southern hemisphere lizards) for spring plus summer ($\sum$ = 3,386) and for summer only ($\sum$ = 2,445) (Table S1). Five species were represented in the north and nine in the south (Figure 5). As expected for left-skewed distributions, median T_b were higher than mean T_b for five of five species in the north and eight of nine in the south for spring plus summer, and for five of five species in north and five of six in the south for summer only; but differences were small (average difference = 0.36 ± 0.325°C north, 0.24 ± 0.305°C south for spring plus summer; 0.39 ± 0.381°C north, 0.25 ± 0.333°C south for

summer only). Distributions for spring plus summer were significantly left-skewed (adjusted p) in four of five northern species and in four of nine southern species, and in summer only were significantly left-skewed (adjusted p) in four of five northern species and in three of six southern species. In within-species comparisons, skewness coefficients in the south were greater than in the north for three of four species for spring plus summer and for two of three species in summer. The significance level of skewness was negatively but weakly correlated with sample size (r = −.457, p = .050) in spring plus summer and in summer only (r = −.506, p = .056, see Section 4).

In among-species comparisons for summer only (Table S2), skewness was not significantly correlated with median T_b, minimum T_b, median absolute deviation of T_b or sample size.

3.3 | Western Australia

At least 23 T_b ($\sum$ = 3,304) were available for 25 species of diurnal lizards, representing three families (Agamidae, Scincidae and Varanidae) for the full year and for 15 species ($\sum$ = 1,557) in summer only (Table S1, Figure 6). As expected for left-skewed distributions, median T_b were higher than mean T_b for most species (21 of 25 year, 14 of 15 summer). However, differences never exceeded 1°C (average difference = 0.25 ± 0.240°C year, =0.34 ± 0.243°C summer). Over the full year, body temperature distributions were left-skewed for 22 of 25 species and significantly left-skewed (adjusted for multiple tests) for 12 of 25 species (Table S1). For summer, 13 of 15 were left-skewed and 7 of 15 were significantly so (Table S1, Figure 6). The significance level of skewness was negatively correlated with sample size (r = −.372, p = .009, see Section 4).

In among-species comparisons with full-year and with summer samples (Table S2), the skewness coefficient was not significantly correlated with median T_b or sample sizes. However, the skewness coefficient for the full year was significantly correlated with mean absolute deviation (p = .005) and with minimum T_b (p = .012).

4 | DISCUSSION

Body temperature distributions of active diurnal lizards have long been expected to be left-skewed (see Section 1). A left-skewed distribution can result, for example, if diurnal lizards are cold when emerging from retreats but then bask and maintain high T_b during the remainder of the day. Left-skewed distributions may reflect other factors, such as the effect of temperature on neural and behavioural processing (see Section 1). Although such considerations have often been discussed, whether T_b distributions of ectotherms in nature are in fact left-skewed has not been systematically examined until now—to our knowledge.

We compiled field T_b for 45 species of active diurnal lizards from the Kalahari Desert of southern Africa, the Great Basin, Mojave and Sonoran deserts of North America, and the Great Victoria Desert of Western Australia. Prior to computing skew statistics, we screened records to detect and eliminate records for individuals captured in
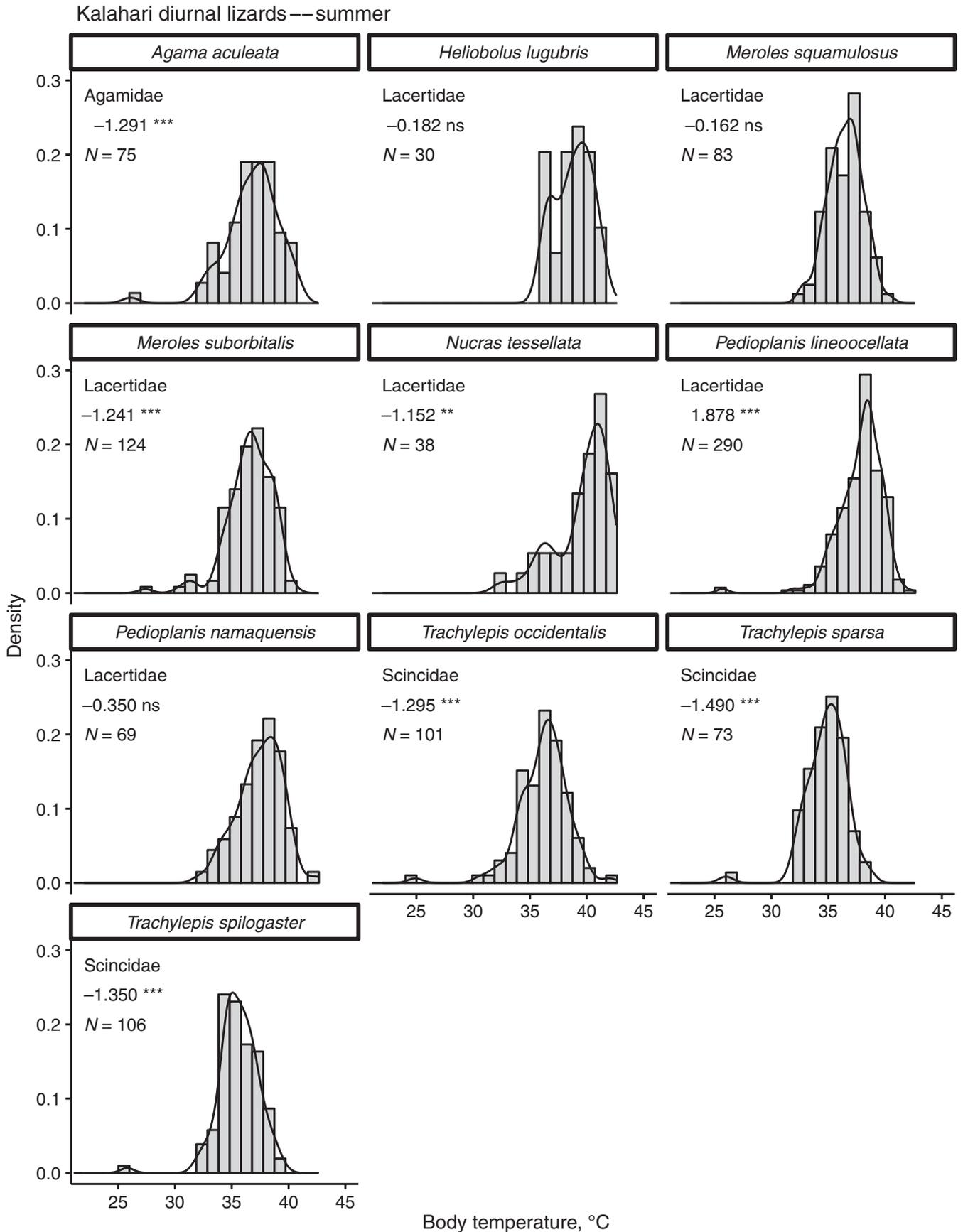
Kalahari diurnal lizards––summer

FIGURE 4 Body temperature histograms (with density curves) for Kalahari lizards in summer. Each panel gives the species name, family, D'Agostino skewness coefficient with significance levels adjusted for multiple comparisons (*p < .05, **p < .01 and ***p < .001) and sample size
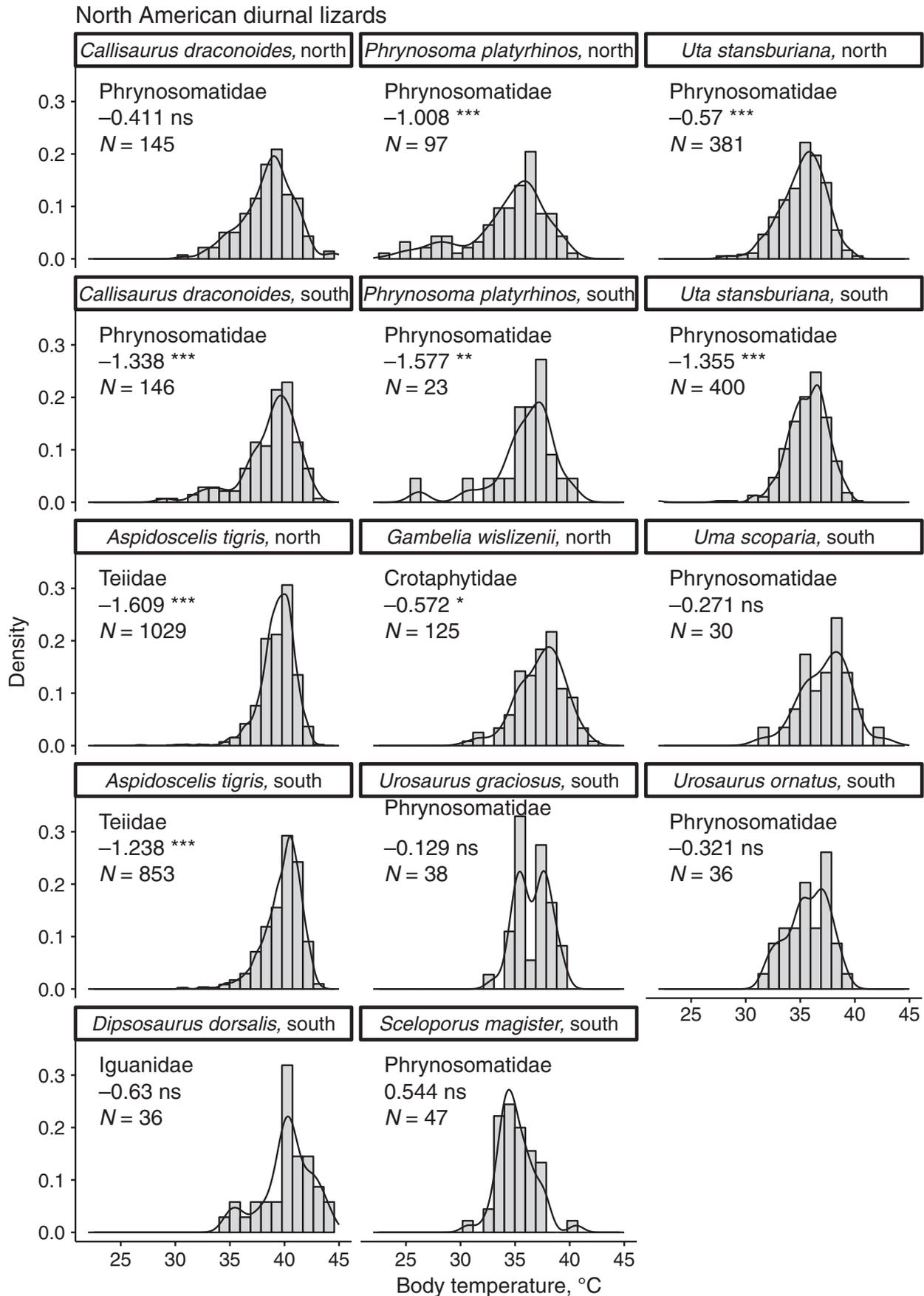
North American diurnal lizards

FIGURE 5 Body temperature histograms (with density lines) for North American lizards (north and south populations. See legend of Figure 4 for explanation of symbols and Table S1 for mean and median T_b
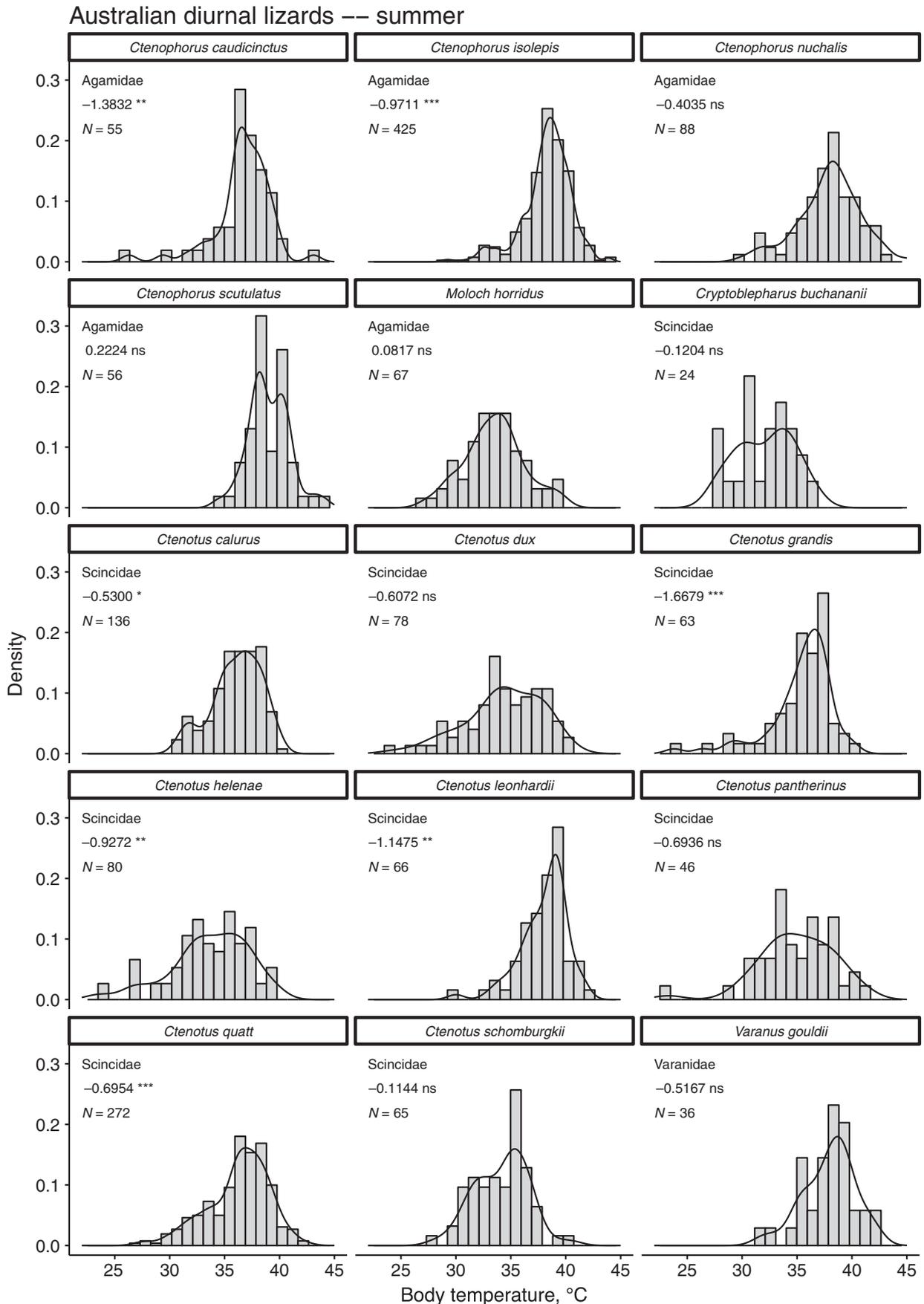
FIGURE 6 Body temperature histograms (with density lines) for Western Australian lizards in summer. See legend of Figure 4 for explanation of symbols

diurnal retreats or at night, as such records would artificially enhance left skewness. Furthermore, we checked all T_b lower than 30°C against our original field notes to determine whether these were data-entry errors.

Some left skewness is evident in most species, as median T_b is greater than mean T_b in almost all species (Figures 1, 4–6, Table S1). However, the magnitude of difference is small and always less than 1°C for all species in all deserts and seasons.

Coefficients of skewness are generally negative for year samples in the Kalahari (10 of 10), North America (5 of 5 north, 8 of 9 south) and Australia (19 of 25). They were often significantly negative (adjusted *p* values) in the Kalahari (9 of 10) and for North America (4 of 5 north, 4 of 9 south), but less so for Western Australia (11 of 25). Overall, T_b distributions are indeed left-skewed for most species, but the magnitude of skewness (e.g. difference between median and mean) is small and not always significant.

Could the lack of significance in some species be due to small sample sizes? As noted in Section 2, we arbitrarily required a minimum sample of 23 records for a species. Even so, the significance of the skewness coefficient was negatively correlated with sample size in all deserts (though significantly so only in Australia). But if species in all deserts are combined, that correlation is highly significant (*r* = −.372, *p* = .009), suggesting that sample size may be an issue.

To evaluate the power of the D'Agostino test (D'Agostino, 1970), we used data for the Kalahari lacertid *Heliobolus lugubris*, a species with a moderate skewness coefficient (Table S1). We then randomly sampled (null model, with replacement, 1,000 samples) with different sample sizes (23, 50, 100). With samples of 23 (our minimum), skewness was significant (*p* < .05) only about 32% of the time. With samples of 50 or 100, about 64% and 92%, respectively, of cases were significant.

To explore further the influence of sample size for our species, we divided full-year data by sample size (23–50, 51–99, >99) for all 45 species (49 populations as North American populations were separated into north and south) and computed the percentage of species for which skewness coefficients were significant (adjusted *p*). For *N* = 23–49, only 2 of 13 species had significant skewness; for *N* = 50–99, 7 of 12 were significant; and for *N* > 99, 20 of 24 were significant. These exercises all demonstrate the importance of adequate sample sizes in significance testing for skewness of observed T_b distributions.

A few outliers can potentially generate significant skewness. So, using the Australian year data, we deleted the bottom 2.5% for all species and recalculated skewness. For untrimmed data, 11 of 25 species had significant skewness; and for trimmed data, 8 of 25 still had significant skewness. Thus, presumptive outliers do not appear to have a major effect for most species.

Next, we reiterate some reasons for expecting left-skewed distributions Section 1 and evaluate whether they hold in our data. Left-skewed distributions will result if seasonal data are pooled because lizards have lower T_b in winter than in warm seasons, and are less active (thus fewer T_b records) in winter (e.g. Huey et al., 1977). As expected, 7 of 10 Kalahari species show more negative skewness coefficients (of any magnitude) for the full year than in summer only; but in Australia,

only 6 of 16 species show this pattern. Thus, pooling of seasonal data does increase skewness, but not for all species and not by much.

Left-skewed distributions will result if lizards emerge early in the morning from cool over-night retreats, but soon begin basking and maintain high T_b during most of the day (Cowles & Bogert, 1944; Soulé, 1963). We made an effort to start searching early in the morning, but still might have missed early "emergers." In any case, cold individuals might be relatively wary (Rand, 1964) and difficult to spot or potentially might have pre-warmed in their burrows prior to emerging with normal activity T_b (McGinnis & Dickson, 1967). Furthermore, most of our lizards are small; and small lizards can heat quickly in deserts, such that they are cold for only a short period each day and thus difficult to sample.

Our methods, which are traditional in lizard thermal biology, involve searching for lizards and quickly taking their T_b. By this method, T_b are generally left-skewed, but less so than we ourselves expected, especially when only summer records are evaluated (Table S1). Ultimately, the ideal way to document T_b distributions is to use telemetric methods (Davis, Taylor, & DeNardo, 2008; Harlow, Purwandana, Jessop, & Phillips, 2010) that indicate not only when individuals are aboveground, but also their T_b. Such methods can eliminate potential biases due to wariness of lizards or to late emergence of biologists, but generally can monitor only a few individuals.

In conclusion, the direction and magnitude of skewness of T_b distributions should affect the performance and fitness of ectotherms, specifically because skewed T_b distributions alter the weighting of temperature-dependent performance over time (Dowd et al., 2015; Marshall et al., 2011; Martin & Huey, 2008; Vasseur et al., 2014). We find that T_b distributions of active (diurnal) lizards on three continents are generally left-skewed, as long expected (see Section 1), but are nonetheless small in magnitude. Median T_b was higher than mean T_b in 91% of cases (Table S1, average difference = 0.29° ± 0.268°), but significantly so in only 56% of cases (summer records). However, the next step should be to determine whether that skewness is still large enough to affect cumulative performance over time. Doing so will require knowing not only the distribution of field T_b, but also the thermal dependence of performance. With both datasets in hand, one could use Equation (1) (or an equivalent) to determine how much integrated performance (Martin & Huey, 2008; Vasseur et al., 2014) changes depending on whether performance is weighted by actual field T_b vs. statistically normalized T_b.

AUTHORS' CONTRIBUTIONS

R.B.H. and E.R.P. conceived the project and designed the methodology. E.R.P. and colleagues collected most of the data, except in the Kalahari, where R.B.H., E.R.P. and Larry W. Coons collected most of the data. Both authors collected, checked and analysed the data. Both authors wrote and revised the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.45g3s (Huey & Pianka, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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