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Natural History Note

Seasonality in Kgalagadi Lizards: Inferences from Legacy Data

Raymond B. Huey,[1,*] **Donald B. Miles,**[2] **and Eric R. Pianka**[3]

1. Department of Biology, University of Washington, Seattle, Washington 98195; 2. Department of Biological Sciences, Ohio University, Athens, Ohio 45701; 3. Department of Integrative Biology, University of Texas, Austin, Texas 78712

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abstract: An ecological issue can best be studied by gathering original data that are specifically targeted for that issue. But ascertaining—a priori—whether a novel issue will be worth exploring can be problematic without background data. However, an issue's potential merit can sometimes be evaluated by repurposing legacy or other data that had been gathered for unrelated purposes but that are nonetheless relevant. Our present project was initially motivated by an ecological trade-off—proposed eight decades ago—involving the depth at which desert reptiles overwintered. To address those and related issues, we repurposed our five-decades-old natural history data for 18 species of Kgalagadi lizards and then explored the seasonal ecology of these lizards, emphasizing winter. Our data were not gathered for a study of seasonal ecology but nonetheless inform diverse seasonal patterns for a major community of lizards. However, repurposed data (whether recent or legacy) present challenges and ambiguities, and we suggest targeted, next-step studies of seasonal ecology that can circumvent limitations and ambiguities.

Keywords: winter activity, body temperature, feeding, lizard, seasonality, thermal biology.

Introduction

A research agenda designed to explore a novel ecological issue often involves two steps. First, one selects an appropriate group of organisms (the Krogh principle; see Travis 2020), gathers background natural history observations, and then describes initial patterns (Bartholomew 1986; Travis 2020). Second, one uses those observations and patterns as guides for developing and executing targeted studies and experiments (Greene 2005; Travis 2020).

Implementing and funding even the first step of a novel project will be challenging if no background information is available. However, background information can sometimes be obtained by finding and analyzing existing natural history data (recent or legacy) that had been gathered for projects unrelated to the current one but may still be adequate to establish proof of concept patterns (Hawkins et al. 2015).

Here, we develop and evaluate this approach. Appropriately, our project was inspired by an eight-decades-old paper (Cowles 1941) on the winter ecology of squamates (lizards, snakes) in a Californian desert. Cowles knew that these squamates overwintered underground, but he noted that some individuals emerge, become active, and bask on warm winter days. He proposed a trade-off involving overwintering depth: namely, squamates in shallow retreats can detect a heat pulse moving down through the soil on sunny days and thus emerge and become active, but they would nonetheless incur risks of freezing on cold nights. Cowles (1941) is thus a pioneering example of trade-off thinking in ecology.

Cowles (1941) served as a springboard for exploring largely overlooked questions concerning the ecophysiology of overwintering (Huey et al. 2021*a*). For example, why do some squamates even emerge in midwinter, as this might increase risk of predation from endotherms? Are they feeding, which might reduce their risk of starvation over winter or even promote growth, or are they basking for other physiological activities, such as vitamin D synthesis, clearing toxic compounds, activating immune response, or redeploying energy stores? Such questions (as well as the who, where, when, and why of midwinter activity vs. dormancy of squamates) remain unresolved (Huey et al. 2021*a*).

The few studies examining whether midwinter squamates are feeding or fasting are usually focused on a single species (see Huey et al. 2021*a*). We realized that we could assess the winter-feeding status for a rich community of lizards in the Kgalagadi (Kalahari) semidesert of southern Africa (Pianka 1971) by repurposing our own five-decades-old dietary data (from 1969 to 1970) on these lizards. But once we began exploring these legacy data, we realized that we could use them to address additional questions about seasonal ecology. Moreover, we could apply contemporary

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[*] Corresponding author; email: hueyrb@uw.edu.

ORCIDs: Huey, http://orcid.org/0000-0002-4962-8670.

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analytical tools (Bakken 1992; Kearney and Porter 2020) that were unavailable when we were in the field.

Our natural history data are basic and include date and time of collection, body temperature (T_b), body size, sex, microhabitat, and prey volume. Importantly, these categories were selected not for a study of seasonal ecology but rather for comparative studies of community organization of desert lizards in North America and Australia (Pianka 1967, 1969). Nevertheless, even such basic data can yield insights into other topics. Importantly, because we ourselves gathered these data, we know their provenance and their limits—that is often not the case when working with published data.

Repurposing field data is hardly novel: archival data and museum specimens are routinely used in studies of faunal turnover, phenological and genetic shifts, life history dynamics, range shifts, and extinctions (Reznick et al. 1994; Hoffmann and Willi 2008; Moritz et al. 2008; Wake and Vredenburg 2008; MacLean et al. 2018; Miles 2020). However, our intent here is not merely to use legacy data to inform seasonal biology but also to highlight associated ambiguities. Our specific goals are to address open issues in seasonal ecology, show how basic data can address each issue, evaluate limitations of data and analyses, and suggest targeted methods that can be applied in follow-up studies. In addition, we suggest best practices for working with repurposed data.

General Methods

We start with a general introduction to the species, region, and field data. However, because we address several topics (which have different methodologies, analyses, and implications), we partition the main text by topic, each of which includes associated methods, results, and discussion.

The Kgalagadi semidesert supports a rich community of lizards (Pianka 1986). We have sufficient data for 10 species of diurnal lizards, including skinks (Scincidae, four species, terrestrial and semiarboreal), lacertids (Lacertidae, five species, all terrestrial), and one agamid (Agamidae, semiarboreal). We include data for two fossorial skinks (*Acontias gariepensis*, *Acontias kgalagadi*) as well as for six nocturnal geckos (Pianka 1971; Pianka and Huey 1978; Hibbitts et al. 2005). We omit species (*Chamaeleo delepis*, *Meroles squamulosa*, *Nucras intertexta*, *Mochlus sundevalli*, *Lygodactylus capensis*) that were infrequently collected.

We collected and preserved lizards between November 24, 1969, and October 15, 1970, mainly at study sites in Botswana (two sites), South West Africa (one site, now Namibia), and Republic of South Africa (seven sites; Pianka 1971, 1986). Our sites ranged from −25.7°S to −28.3°S and from 875 to 1,029 m in elevation (Pianka 1971). All studies were conducted under permits from Botswana, Northern Cape Province, South African National Parks Board, and former South West Africa.

The Kgalagadi's climate is seasonal. During our survey, minimum (air) temperatures in winter reached as low as −7.5°C, and maximum temperatures in summer reached 41.6°C (data for Twee Rivieren, −26.5°S, 20.6°E; data courtesy of South African Weather Service). Day length varied from about 10.5 h in winter to 13.8 h in summer. The winter of 1970 was slightly cooler than normal (1969–1974) and had decidedly lower rainfall (see p. 3 of the supplemental PDF, available online).

In the field we recorded date, time of activity, T_b, air temperature (T_a), microhabitat, snout-to-vent length (SVL; mm), tail length (mm), and mass (g) of captured lizards (Pianka 1986). If mass was not measured, we estimated it from species-specific regressions of log mass on log SVL (table S4; tables S1–S4 are available online). Prey were later identified, counted, and measured (volume, in mL; Pianka 1986). When we analyzed gut contents to determine whether lizards were feeding in winter, we excluded inactive lizards collected in retreats in June through September, as some might have been dormant.

We largely restrict our analyses to active lizards, which were exposed and collected aboveground. (Note that *Acontias* are fossorial, and we assumed that all individuals were active.) In winter, however, we collected individuals of two species (*Trachylepis occidentalis*, *Pachydactylus capensis*) that were seemingly dormant all winter inside retreats (underground, under bark, or in termite mounds). We determined whether these individuals were not feeding (had no food in guts), as expected.

For the phylogenetic analyses (see below and p. 14 of the supplemental PDF), we pruned an ultrametric, maximum-credible clade (MCC) tree for Kgalagadi lizards generated with treeAnnotator (Bouckaert et al. 2019) from a sample of 100 trees downloaded from VertLife (http://www.vertlife.org). We used the MCC tree for phylogenetic comparative analyses.

Seasonal Activity

Goals. Document seasonal activity patterns of each species and determine correlates of interspecific differences in relative winter activity. For example, is winter activity greater in species with low field-active T_b?

Data and analyses. Using our raw data (species, date of collection), we needed an index of relative winter activity. A between-species comparison of raw numbers of winter-active individuals of each species is unsuitable, as this will be biased if species differ in abundance. However, a within-species comparison seems more informative (but see below). For each species, we divided number of individuals collected in winter (per person-day) by the average number per person-day collected in "shoulder" seasons (autumn and spring). If the number of individuals is the same in each season, the index is 1.0. If individuals are dormant throughout winter, the index is 0.0. (Confidence intervals can be generated by bootstrapping.) L. Luiselli, B. Stille, M. Stille, W. Buttemer, and T. Madsen (unpublished manuscript) used a similar index to compare seasonal activity of Mediterranean squamates.

Results. The six species of common, nocturnal geckos were inactive all winter (Pianka and Huey 1978). The barking gecko (*Ptenopus garrulus*) was first heard near the end of winter (August 17), but other gecko species did not begin emerging until September (fig. S1; figs. S1–S4 are available online).

Ten of 12 diurnal species remained active in winter, at least on warm days (fig. 1; winter indexes in table S1). However, *Trachylepis occidentalis* (Scincidae) was inactive from May to October, and *Nucras tessellata* (Lacertidae) was inactive from May to September.

While in the field, we noticed that species normally active at high T_b (e.g., *Nucras*) appeared relatively or completely inactive in winter. An a posteriori analysis shows that the winter activity index (table S1) of a species was indeed inversely related to its mean T_b in summer (fig. 2) in both nonphylogenetic ($r = -0.713$, $P = .020$) and phylogenetic ($r = 0.8$, $P = .005$) correlation analyses. In the phylogenetic analyses, winter activity was unrelated to body mass ($P = .041$) or its interaction with T_b ($P = .68$), perhaps because interspecific variation in body size in this community is minor (Pianka 1986).

Discussion and future targeted methods. Most nocturnal geckos were dormant all winter (fig. S1), perhaps reflecting low environmental temperatures (T_e, equilibrium T_b's) at night in winter (below). In contrast, most diurnal

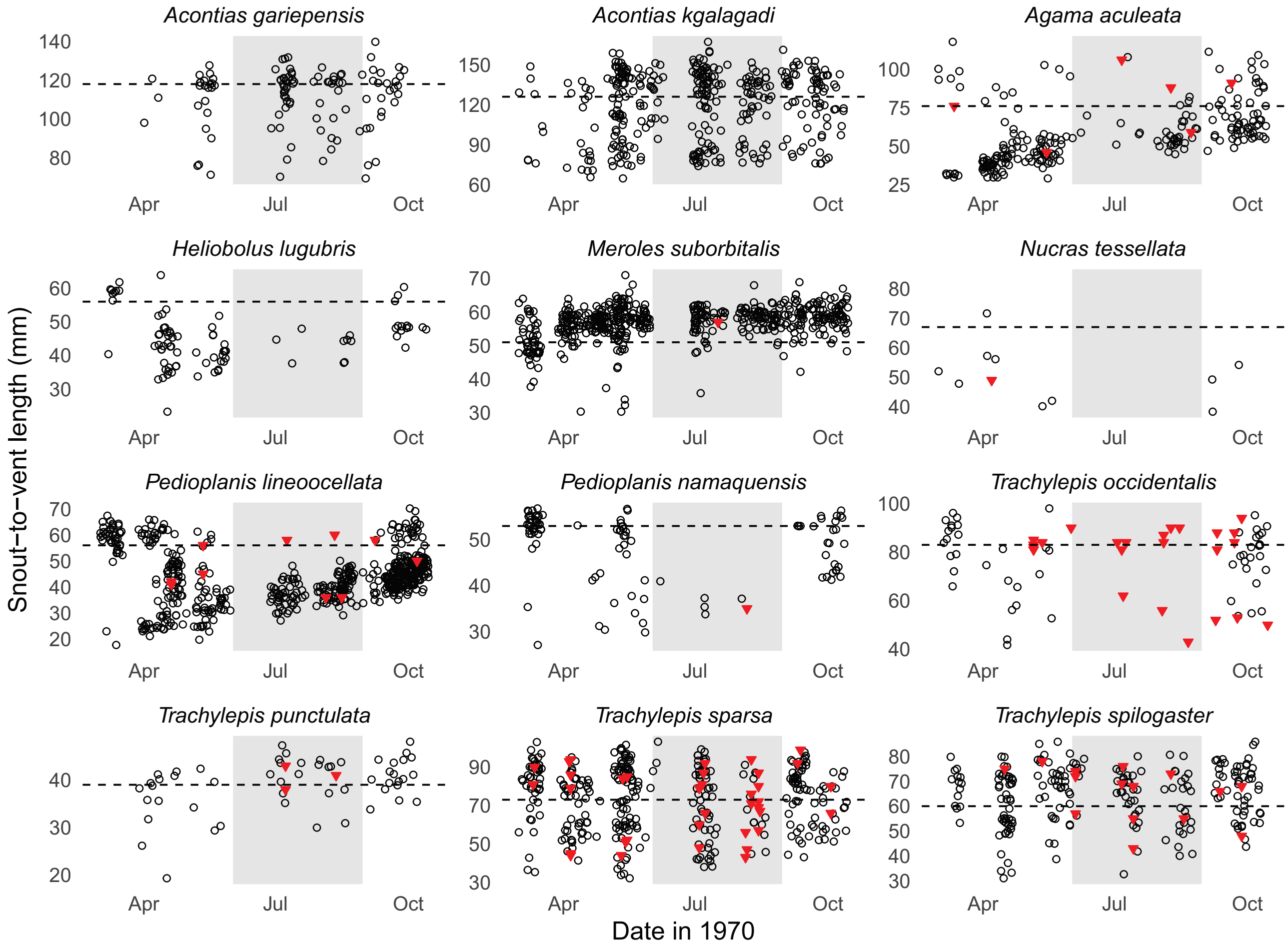

Figure 1: Size (snout-to-vent length) of individuals captured by date from March to mid-October 1970. Gray rectangles represent austral winter months. Dashed lines indicate minimum size of adult females. Circles represent active animals, and inverted triangles represent animals captured in retreats (May–October).

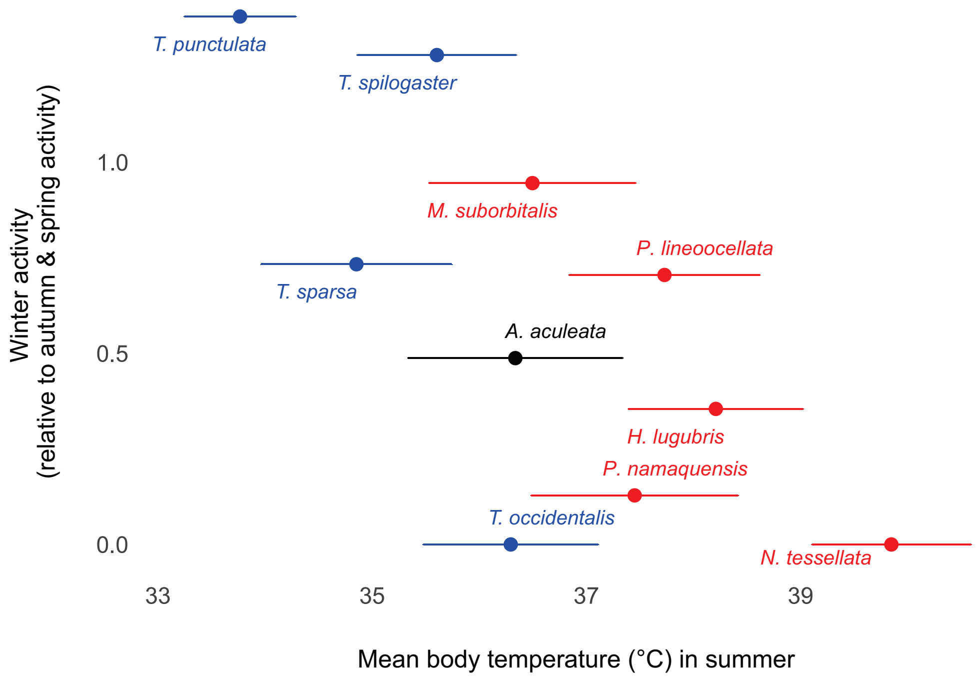

Figure 2: Activity of diurnal lizards in winter (per collecting day, scaled to activity autumn and spring; see text) is inversely related to mean body temperature (T_b) in summer. Species that are active at relatively high T_b in summer are relatively inactive in winter. Color indicates family (red for Lacertidae, blue for Scincidae, and black for Agamidae). Note that fossorial species (*Acontias* spp.) are excluded because all individuals were dug up from retreats such that their winter indexes would represent only the seasonality of our digging.

species were active in winter, but the most active species were those with relatively low T_b in summer (fig. 2). Low T_e in winter appears to restrict activity of species requiring high T_b for activity. To our knowledge, this is the first comparative evidence that differences in winter activity relate to acceptable activity temperatures.

Microhabitat associations may also be involved. Because sun angles shift seasonally, ground surfaces will be more shaded in winter than in summer, ground T_e will be low, and basking sites will be limited. In contrast, tree trunks and logs can be more exposed in winter than in summer, facilitating winter activity by arboreal species (fig. 6 in Huey et al. 1977). Terrestrial species (lacertids, *T. occidentalis*) had slightly but not significantly ($P = .304$) lower winter activity than did semiarboreal species (table S1).

Our winter index, which requires only capture numbers (per person-day) over three seasons, is crude, but the derived numbers (table S1) are consistent with capture records (table S1; fig. 1). Even so, cool-season reproduction or mortality or differential catchability by season will bias this index (see below).

Targeted studies can yield more robust activity indexes. For example, in early autumn, one could implant lizards with loggers that record movement, T_b, heart rate, and aboveground activity through spring (Davis et al. 2008; Nordberg and Cobb 2016, 2017). After retrieving the loggers in late spring, one could compute a daily and seasonal index of activity for individuals of each species and estimate dates of any seasonal mortality. If soil temperature profiles were simultaneously measured (or computed; Kearney and Porter 2020), overwinter depth could be inferred, as Cowles (1941) did long ago.

An alternative—if laborious—approach involves combining field observations of activity with a capture-mark-recapture study (Wilson and Cooke 2001). One could compute the proportion of the population of each species that was active in each season (N_{active}/N_{alive}), but one would need to adjust for catchability, reproduction, and mortality within seasons (J. Clobert, personal communication).

The apparent link between winter activity and thermal biology (fig. 2) or microhabitats (see sect. VIII in Porter et al. 1973; Huey et al. 1977) can be further explored by biophysical simulations (Sears et al. 2016; Kearney and Porter 2020). Complementary insights can be achieved by deploying models (T_e) in terrestrial and arboreal microhabitats (Bakken 1989; Hertz 1992).

Winter Activity of Adults versus Juveniles

Goal. Compare winter activity of adults versus juveniles. Cowles (1941) noted most winter-active lizards at his

California desert site were juveniles (see also Ruby 1977; Gregory 1982). Does this hold for Kgalagadi lizards?

Data and analyses. Dates of collection were partitioned for adults versus juveniles, with adult status based on the minimum SVL of mature females (in supplement to Mesquita et al. 2016). A simple ratio of the number of winter-active adults to the number of winter-active juveniles of each species (Blázquez and Ortega-Rubio 1996) is unsuitable here because species differ in age-class distributions. Accordingly, for each species, we calculated separate winter activity indexes (as above) for juveniles and for adults. We then computed the ratio of these indexes by species (index juveniles/index adults). A high ratio suggests that juveniles are more active in winter than are adults.

Results. Neither adults nor juveniles of *Nucras tessellata* and *Trachylepis occidentalis* were active in winter (fig. 1). Both adults and juveniles of agamid and most scincid species were active in winter, but only juveniles of most lacertids were active in winter (fig. 1). Juveniles had a higher winter index than did adults in all but one species (table S1). (*Meroles suborbitalis* was the exception, but most individuals of this annual species [which hatched in summer] reached adulthood by winter [fig. 1; Pianka et al. 1979].) Overall, winter activity was significantly higher for juveniles among perennial species that were active in winter (Wilcoxon signed rank test, paired by species, $P = .016$).

Discussion and future targeted methods. The index comparing activity of juveniles versus adults is crude (table S1) and will be biased if some juveniles grew past the adult size threshold during winter or if seasonal mortality differed by age group. Despite these issues, the indexes consistently suggest that juveniles tend to be more active in winter than are adults (fig. 1), a pattern previously seen in Cowles (1941) and some studies on lizards elsewhere (e.g., Weintraub 1968; Ruby 1977; Gregory 1982; but see Blázquez and Ortega-Rubio 1996).

Why only (or mainly) juveniles are active in winter is unresolved. Juveniles might need to feed in winter to reduce risk of starvation (Congdon et al. 1979; L. Luiselli, B. Stille, M. Stille, W. Buttemer, and T. Madsen, unpublished manuscript) because of their relatively limited energy reserves and high mass-specific metabolic rates (Nagy 1983; L. Luiselli, B. Stille, M. Stille, W. Buttemer, and T. Madsen, unpublished manuscript). Winter feeding might also facilitate juvenile growth, leading to earlier onset of reproduction (Cole 1954; Adolph and Porter 1996). Small size might enable juveniles to heat rapidly on warm winter days (see fig. 3.4 in Porter and Tracy 1983; Kearney et al. 2020*b*). Thus, although the size (or age) dependence of overwinter activity is clear (fig. 1), its mechanistic and functional explanations require further investigation.

Targeted studies with available logger or capture-mark-recapture data would enable comparisons of proportions of all "live" adults and of all "live" juveniles that were active in winter. Biophysical simulations combined with a dynamic energy budget analysis (Porter et al. 1973; Adolph and Porter 1996; Kearney and Porter 2020) could evaluate possible reasons for juvenile activity in winter (growth, starvation resistance, thermoregulatory advantages). Whether juveniles have relatively limited energy stores at the beginning of winter can be explored retrospectively from museum specimens. Finally, whether midwinter activity is a consequence of limited energy stores could be experimentally tested by liposuction of fat bodies before the onset of winter (see Hahn and Tinkle 1965).

Seasonal Variation in Operative Temperatures and in Hours of Activity

Goal. Seasonal variation in duration and times of activity can be predicted if operative temperature data (T_e's, which are equilibrium T_b's) are available (Porter et al. 1973; Adolph and Porter 1996; Sinervo et al. 2010). We did not measure operative temperatures in 1969–1970, as the concept was not yet developed (Porter and Gates 1969; Bakken and Gates 1975). However, we can use biophysical models to hindcast both daily T_e profiles and hours of activity. In addition, we can use our field data on observed time of activity to quantify seasonal shifts in the breadth of activity times (Porter et al. 1973; Huey et al. 1977; Adolph and Porter 1993).

Methods. To hindcast maximum and minimum T_e of an exposed lizard, we used the Global Ectotherm Thermoregulation Hindcaster (http://bioforecasts.science.unimelb.edu.au/app_direct/ectotherm_ncep/) and estimated hourly T_e for a generalized 6-g lizard (parameters in the supplemental PDF) on the open ground at our Leeudril site, Kgalagadi Transfrontier Park, Botswana (−26.41°S, 20.73°E; November 1969–October 1970). To compute potential hours of activity of a thermoregulating lizard, we reran the hindcaster with a behavioral model (Kearney et al. 2021) that allowed the lizard to use shade or burrow retreats (supplemental PDF). To test the accuracy of hindcasting, we compared observed T_a from Twee Rivieren, South Africa, versus hindcasted T_a for Leeudril (10.3 km north-northeast of Twee Rivieren; TAREF in metout; see the supplemental PDF). Hindcasted maximum T_a underestimated true maximum T_a by about 2°C (fig. S2), but our estimates of times and duration of activity should still be qualitatively informative. To compare seasonal variation in observed breadth of activity times, we computed Shannon-Wiener indexes of diversity (H') for each species on the basis of the number of captured lizards in hourly bins for each season.

Results. Hindcasted maximum daily operative temperatures (T_e's) for a lacertid-like lizard on the ground surface averaged 63.2°C in summer (December–February) and 40.1°C in winter (June–August; fig. S3*A*). Potential hours of activity per day in winter were estimated to be about half those in other seasons (fig. S3*B*).

Observed hours of activity varied among seasons and are shortest in winter (fig. 3), consistent with the above biophysical hindcasts in figure S3*B*. Lizards often had bimodal activity patterns in summer but unimodal ones in winter (fig. 3; Porter et al. 1973; see also fig. 3 in Huey et al. 1977). H' values were significantly lower for winter than for summer (Wilcoxon paired [by species] signed rank test, $P = .001$).

Discussion and future targeted studies. Shifts in times of activity are a fundamental method of behavioral temperature regulation across seasons (Porter et al. 1973; Huey et al. 1977; Kenagy and Stevenson 1982; Stevenson 1985; Kearney et al. 2009), but restrictions on times of activity have severe ecological consequences (Porter et al. 1973; Adolph and Porter 1996; Sinervo et al. 2010). To the extent that T_e drives potential activity times (Porter et al. 1973; Adolph and Porter 1993), Kgalagadi lizards should have reduced activity times in winter (unimodal, centered at midday) relative to other seasons (fig. S3*B*). Our field observations are consistent with that pattern (fig. 3). As one consequence, lizards in winter should have lower prey volumes than do lizards in other seasons, especially as insect activity in winter is usually depressed (see below).

We caution that hindcast T_e and hours of activity (fig. S3*A*, S3*B*) are based on National Centers for Environmental Prediction data with a ~200-km^2 grid, downscaled with hourly intervals (Kearney et al. 2020*a*). Data with a ~30-km^2 grid are currently available only back to 1979. Once finer-scale data become available, improved hindcasts should be feasible, and input parameters could be targeted for individual species. For targeted studies, T_e can be measured in real time, then input into heat transfer models (Bakken and Angilletta 2013; Sears and Angilletta 2015; Malishev et al. 2018; Kearney and Porter 2020) and compared with observational data from the field (fig. 3).

Food Volumes and Digestion Times

Goal. Determine whether winter-active individuals are feeding (reviewed in Huey et al. 2021*a*) and, if so, estimate digestion times. Because digestion may take several days in winter, prey volume may be a misleading indicator of seasonal differences in rates of gross energy gain.

Methods. Base data are total volume of prey (mL) and body mass (g) of each lizard. To adjust prey volume for a

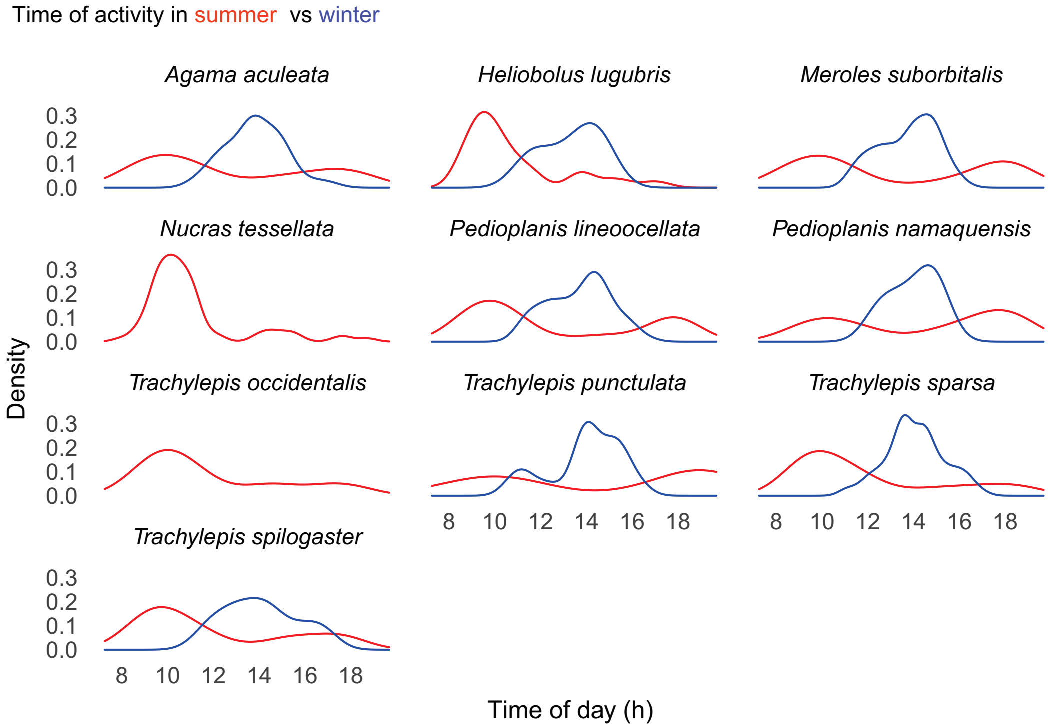

Figure 3: Density plots of time of activity of diurnal lizards (number of adults and juveniles combined) in summer (red) and in winter (blue). Lizards had bimodal activity patterns in summer but unimodal ones in winter. Note that *Trachylepis occidentalis* and *Nucras tessellata* were inactive in winter, and times of activity of fossorial species (*Acontias* spp.) are uncertain and thus excluded here.

lizard's size, we scaled food volumes by metabolic mass (mass 0.82; see Huey and Pianka 1981; Andrews and Pough 1985). We then computed the median (scaled) volume of prey per species in each month. In some analyses, we separated adults and juveniles ("maturity," as above). To compare feeding volumes in winter versus shoulder seasons (autumn and spring), we used ANOVAs (total prey volume ~ season age class). We also compared differences in prey volume between shoulder and winter seasons using a phylogenetic paired *t*-test (function phyl.pairedttest in the package phytools; Revell 2012).

To estimate gut passage time, we used the Global Ectotherm Thermoregulation Hindcaster (above) to estimate T_b (TC variable from the Hindcaster) of active (i.e., basking or foraging) lizards as well as T_b of inactive animals at multiple depths in burrows (-2.5 to -30 cm). We assumed that an inactive lizard in burrow would select a depth with a soil temperature closest to its preferred body temperature (arbitrarily set to 35°C). Next, we interwove T_b of active and inactive lizards, modified an equation for gut passage time for *Sceloporus undulatus* (Phrynosomatidae; Angilletta 2001), and then estimated gut passage times (h; see Huey et al. 2021*a*). (Note that we extrapolated predicted times when temperatures were below 20°C.) For a seasonal contrast, we randomly selected 5 days in January and again in July, assuming lizards filled their guts at 11:00, and then predicted gut passage times for these months.

Results. We expected that lizards in winter—if they were feeding at all—would have less food than in shoulder seasons because (1) winter activity periods are short (fig. 3; Adolph and Porter 1996) and (2) insect abundances in winter are low (Sánchez-Piñero and Avila 2004; Vonshak et al. 2009). Scaled food volumes varied by species and season (fig. 4), but lizards active in winter were feeding (table S2). Scaled food volume (winter-active species only) differed among species (ANOVA, $P \ll .0001$) but—surprisingly—was unrelated to season within species (i.e., winter vs. autumn and spring; $P = .197$; phylopaired *t*-test,

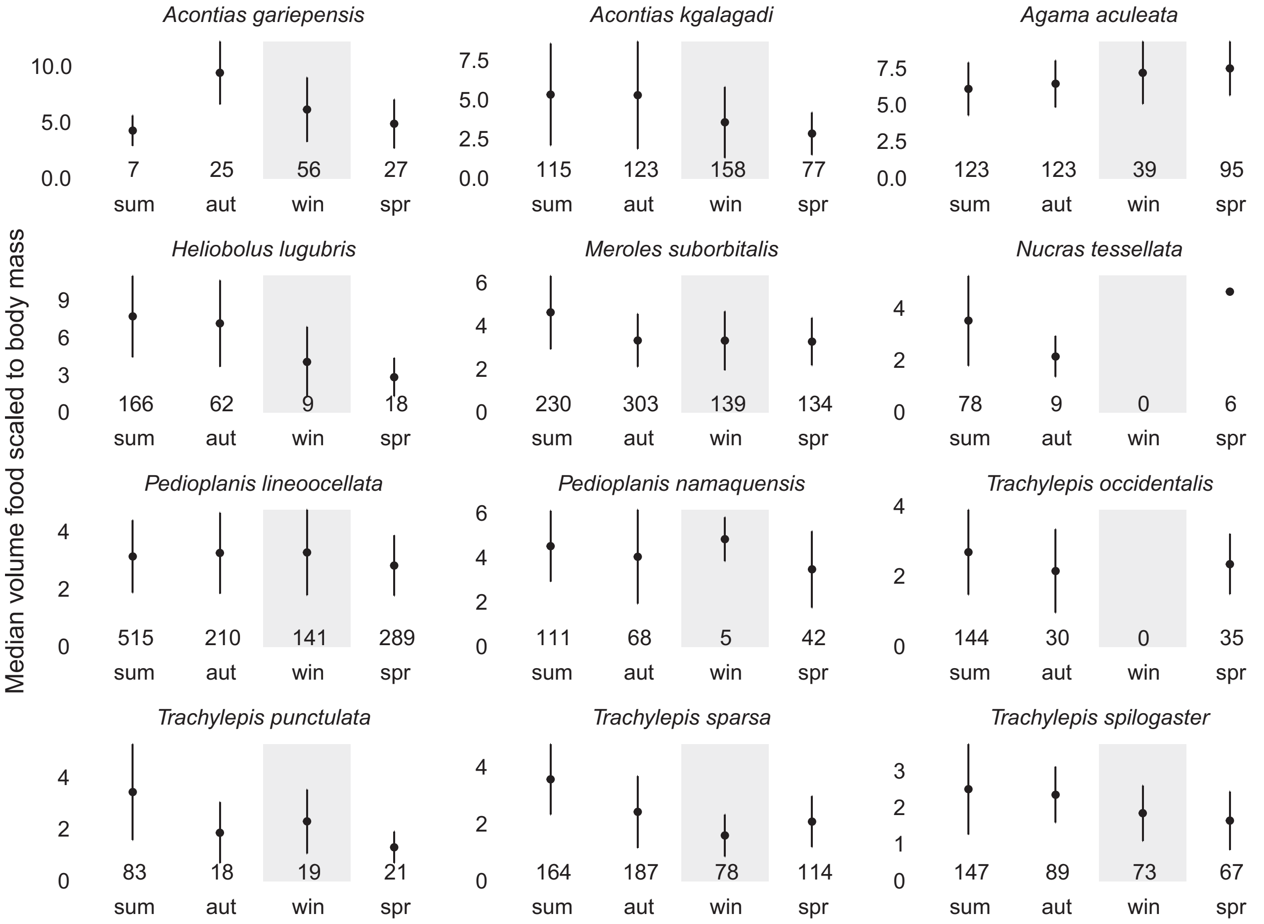

Figure 4: Monthly variation in median food volume (scaled by metabolic mass; see text) of active diurnal lizards. Error bars show median absolute deviation. Winter is depicted by a gray rectangle. Sample sizes by season are given above the *X*-axis. *Nucras tessellata* and *Trachylepis occidentalis* were inactive all winter.

$t_7 = 0.96$, $P = .37$) or to the interaction of species and season ($P = .162$). A pairwise Wilcoxon ranked sum test yielded a similar result between species and season ($P = .722$). Thus, scaled food volumes appear independent of season, at least for winter-active species.

We estimated that digestion takes about 1.3 days (1.1–1.4) in summer but 3.3 days (3.1–4.0) in winter. Thus, prey volumes in guts (fig. 4) might accumulate over several days in winter and thus could be a misleading indicator of the rate of energy gain.

Discussion and future targeted studies. The impetus for our study was to determine whether winter-active lizards were feeding (Huey et al. 2021*a*): indeed, they are (fig. 4). Prey volumes varied among seasons and species, but no consistent seasonal pattern is obvious. Food gain is thus one benefit of activity in winter in the Kgalagadi, but our data do not exclude other physiological benefits of winter activity (above).

Ideally, we would determine seasonal energy budgets (especially net energy gain; Congdon et al. 1979) not merely prey volume, which at best indexes gross energy gain. Furthermore, seasonal energy budgets of active versus inactive (and for adults vs. juveniles) will be of interest, especially for geographic patterns (e.g., cold vs. warm sites). Two general approaches are possible. First, seasonal and stage budgets can be estimated by using isotopic approaches (Nagy 1983; Nagy and Medica 1986). For example, Nagy (1983) estimated that feeding rates of *Uta stansburiana* (Nevada) were 5–15 times higher in spring than in winter and that seasonal variation in field metabolic rates was striking. Monitoring energy budgets of dormant animals will be challenging unless enclosures were used. Second, biophysical simulations coupled with dynamic energy budgets can estimate seasonal energy budgets for specific age classes or activity state (Malishev et al. 2018).

Are “Dormant” Lizards Not Feeding?

Goal. As noted above, nocturnal geckos and two diurnal species were inactive throughout winter. But were they really inactive inside retreats and thus not feeding?

Methods. Determining whether seemingly dormant individuals are feeding requires being able to retrieve dormant animals from their winter retreats. We collected individuals of three ostensibly dormant species and compared their food volumes in winter versus shoulder seasons.

Results and discussion. The ground skink (*Trachylepis occidentalis*) was not seen active (aboveground) from May 17 to September 20. However, while digging for *Acontias*, we collected 11 *T. occidentalis* in winter. Nine (81.8%) had no food, and two had trace amounts. In the other seasons, active lizards infrequently had empty guts (spring = 5.7%, $N = 35$; summer = 6.3%, $N = 143$; autumn = 33.3%, $N = 30$). Thus, this skink was not feeding during dormancy.

The nocturnal gecko *Chondrodactylus bibronii* was not seen active from May 24 to September 25, 1970. During that period, we collected 15 individuals from retreats (mainly under bark, logs). Only one had food volume greater than 0.1 mL, whereas 43 of 71 collected in April had food volumes great than 0.1 mL. This gecko is generally not feeding during dormancy.

The nocturnal gecko *Pachydactylus capensis* was not seen active from May 24 to September 21, 1970. During that period, we collected 21 individuals, 18 of which were collected inside termite mounds (seven and six individuals were inside just two mounds). All but four had some food, and prey volumes were similar to those in the shoulder months (April, May, September, October; Wilcoxon test, $P = .8637$; median volume in winter = 0.0598, median absolute deviation (mad) = 0.0704, $N = 20$; median volume in shoulder months = 0.0734, mad = 0.0593, $N = 37$). Apparently, these geckos—even though not active and exposed aboveground—were feeding inside termite mounds (prey included spiders, ants, beetles, termites). Interestingly, 17 of 18 *P. capensis* from inside termite mounds had food, whereas none of the three captured from other retreats had food. Termite mounds thus provide shelter, buffered temperatures (Cowles 1928), and even food (Vitt et al. 2008). “Dormant” may be an inappropriate adjective for these geckos, as their winter surface inactivity does not necessarily imply either dormancy or fasting.

Are Lizards Growing in Winter?

Goal. Determine whether lizards that are active in winter are growing. Given that some diurnal lizards are feeding over winter (above), they might be growing.

Methods and results. Our raw data are SVL and date of collection. Winter growth would be suggested (but see below) if SVL of captured lizards (especially juveniles) increased from late autumn to early spring. SVL of individual lizards over time (March through mid-October 1970) are plotted in figure 1. SVL of juveniles increased significantly for *Agama aculeata*, *Heliobolus lugubris*, and *Pedioplanis lineoocellata* and decreased significantly for *Pedioplanis namaquensis* (see below) but did not change significantly in other species (table S3).

Discussion and future targeted studies. Significant increases in body size of juveniles over winter suggests growth (fig. 1), but other patterns are possible. A size increase could also reflect selection favoring large size. Also, if some individuals grew past the adult size threshold during winter, they would be excluded in our analyses, reducing the coefficient for growth of juveniles.

Juveniles of *A. aculeata*, *P. lineoocellata*, and possibly *H. lugubris* appear to be growing in winter (fig. 1; table S3). Were only selection involved, the variance in SVL should decrease during winter, and the upper limit of SVL should be stable. Neither pattern is visually obvious for *A. aculeata*, *P. lineoocellata*, or *H. lugubris*, suggesting growth and not selection. Furthermore, we ran quantile regressions (0.2, 0.5, 0.8) for these species (fig. S4). Quantile regression lines are not heterogeneous (except marginally for *P. lineoocellata*; see legend of fig. S4), suggesting that the juveniles of these species were growing. Of course, selection favoring large size might also be occurring.

The significant negative correlation for *P. namaquensis* is likely an artifact. Quantile regressions for *P. namaquensis* are statistically homogeneous ($P = .423$) but negative (fig. S4; table S3). Note that some individuals in May were nearly adult size (fig. S4), whereas others were still small. If the large juveniles grew past the adult size threshold by early spring, they would have been excluded from the spring records (we excluded adult-size lizards), potentially causing a negative upper quantile and negative overall correlation. The size bimodality of juveniles in late autumn (figs. 1, S4) may reflect offspring from two clutches, which is supported by reproductive data in this species (Goldberg 2006).

We conclude that single-capture data can detect evidence of growth but should be accompanied by a quantile analysis. Follow-up studies should use capture-mark-recapture studies to directly partition the influence of growth versus selection. Wilson and Cooke (2001) used a capture-mark-recapture study and found no evidence of directional or stabilizing selection over winter on body mass of *Uta stansburiana* (multiple sites in the western United States) and no evidence of selection favoring body condition (i.e., residual of mass on SVL). They did not report whether the lizards were growing over winter. Analyzing single-capture data, Nagy (1983) found that juvenile *U. stansburiana* appeared to grow over winter in Nevada, but he did not use his capture-recapture data to follow individuals or evaluate selection.

General Discussion—Seasonal Ecophysiology

In cold environments lizard activity can be greatly restricted—or even absent—for many months (Porter et al. 1973; Gregory 1982). In fact, some populations can be dormant for more months than they are active (Etheridge et al. 1983). The physiology of cold tolerance in reptiles has been studied extensively (Storey and Storey 1988; Costanzo et al. 1995; Storey 2006; Berman et al. 2016), but the ecological trade-offs of dormancy versus midwinter activity have received little attention (Huey et al. 2021*a*), even though this topic was first raised eight decades ago (Cowles 1941).

Observations and speculations in Cowles (1941) were a springboard for us to ask multiple questions about seasonal biology, especially in regard to winter. We soon discovered that relevant studies that address those questions were scarce and generally focused on a single species, not on communities (Huey et al. 2021*a*). We soon realized that we could determine whether winter-active lizards were foraging by accessing our own legacy natural history data (collected one-half century ago) for a large community of lizards. In the process of answering that issue, we realized that our base data could address other questions in winter ecophysiology. The inferential methods we used are indirect, but the observed patterns seem sufficiently robust to serve as critical background information for follow-up studies (see the introduction).

Suggestive patterns did emerge. Nocturnal geckos were largely inactive all winter, presumably because operative temperatures at night are just too cold in winter (black points, fig. S3*A*). Most diurnal species were active in winter, but those species most active in winter were ones active at relatively low T_b's in summer (fig. 2). Juveniles were consistently more active than adults in winter, for reasons that remain uncertain but may involve ratios of surface to body volume. Hours of activity of diurnal species are greatly reduced in winter, no doubt because of low T_e's in that season (fig. 3*A*, 3*B*). Even so, active species were feeding but may require several days to digest prey. We collected individuals of three species in their winter retreats: two (a skink overwintering underground, a gecko under bark or logs) were not feeding, but one (gecko overwintering in termite mounds) had fed. Juveniles of three diurnal species appeared to have grown over winter, and our quantile analysis provided no evidence of directional selection favoring large size over winter.

Our analyses touch only the surface of overwinter ecophysiology (Congdon et al. 1979; Nagy 1983; Wilson and Cooke 2001; Zani 2008; Williams et al. 2014; Huey et al. 2021*a*). Whether the costs and benefit of activity versus dormancy vary geographically and phylogenetically is unexamined. Similarly, although winter-active lizards in the Kgalagadi were foraging, our data do not indicate whether activity and basking might be driven by other physiological benefits that are unrelated to energetics (see the introduction; Lee 2010). For example, does midwinter basking promote vitamin D synthesis (Ferguson et al. 2013)? But if so, do the derived benefits outweigh elevated risks of predation? And if nonenergetic factors are involved with winter activity, what are the physiological consequences for high-latitude species, which may be dormant for many months and never bask? Targeted field and laboratory studies are required here (Denlinger and Lee 2010; Zani et al. 2012).

Cowles (1941) was published eight decades ago, but many open questions in ecophysiology remain to be answered, especially in regard to the impact of climate shifts (Zani 2008; Bradshaw and Holzapfel 2009; Williams et al. 2014). Opportunities for integrated field and laboratory studies are many.

Repurposed Data in Contemporary Biology

Because we ourselves collected the data that we analyze here, we know their provenance and limitations. This will not be the case when analyzing published data (recent or old) gathered by others. Indeed, a reviewer specifically asked us to recommend best practices for repurposing or reanalyzing data gathered by others. On the basis of our own experience during this project, we recommend several actions. First, attempt to contact the workers who collected the data and ask them to review your analyses and interpretations. Learn how they gathered and recorded trait data. Unfortunately, contact will not always be possible, especially for very old data. Second, try to obtain and study the original field notes, as these may contain critical information not recorded in spreadsheets or published papers. In our own field notes, for example, we recorded whether each collected animal was active or was retrieved from a retreat, but we never recorded that in our original spreadsheets. Consequently, if someone looked only at dates of capture, they would have incorrectly concluded that some Kgalagadi geckos were active in winter (see fig. S1). Third, be skeptical of data in spreadsheets (see Broman and Woo 2018). Data entry errors happen (note that our original data were keypunched in 1970 on 80-column computer cards by E. R. Pianka when he was 30). We caught a case in which body and air temperatures were reversed for a subset of our data. Fourth, when present-day workers deposit data in repositories, they should thoroughly document their data (provide metadata and data dictionary; Broman and Woo 2018) and field protocols and indicate whether and where the original field notes are stored. Such efforts will help reduce future errors and misinterpretations.

We have argued that natural history data—whether recent or from one-half century ago—can still have value, even in a biological world dominated by developmental and molecular biology. We offer two justifications.

First, many contemporary questions in ecophysiology require ecophysiological answers, not developmental or molecular ones. Consider, for example, the fitness consequences of midwinter activity versus dormancy or of climate change. Molecular studies may illuminate mechanistic issues underlying these consequences, but these basic questions are fundamentally ecological and require field studies. Natural history data may guide future field studies.

Second, many ecological and evolutionary issues that require molecular answers likely emerged from field biologists asking natural history questions. Consider character displacement in the bills of Darwin's finches. Darwin himself proposed the principle of ecological character displacement, and intensive field studies by Peter and Rosemary Grant provided solid field evidence of ecological character displacement in bill size of ground finches on Daphne Major (Grant and Grant 2006). Their finding eventually inspired genomic studies, which determined that rapid evolution of bill size had been facilitated by a major genomic locus that evolved early in the diversification of Darwin's finches (Lamichhaney et al. 2016). Very likely, genomic studies can inspire field studies, such that molecular and ecological studies can be complementary.

Most legacy data will be descriptive and gathered for reasons unrelated to a contemporary issue. Nonetheless, legacy data preserve a snapshot of ecology in time that is impossible—or at least difficult—to impute retrospectively (fig. 3). Moreover, descriptive patterns can be misleading indicators of process (Dayton 1973), but descriptive patterns can indicate whether additional studies may be worthwhile and can guide the choice of targeted methodologies. As others have emphasized, legacy natural history data are "a gift that keeps on giving" (Bartholomew 1986; Futuyma 1998; but see Arnold 2003; Dayton 2003; Greene 2005).

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Statement of Authorship

R.B.H. conceptualized the study. R.B.H., E.R.P., and others collected the field data. E.R.P. obtained dietary and reproductive data, coded all data, and obtained all funding. D.B.M. performed the phylogenetic analyses. R.B.H. validated data, ran analyses, created the figures, and wrote the original draft. R.B.H., E.R.P., and D.B.M. reviewed and edited the manuscript.

Data and Code Availability

Data underlying all figures and tables have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.573n5tb6g; Huey et al. 2021*b*). R code is included in the supplemental PDF.[1]

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[1] Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

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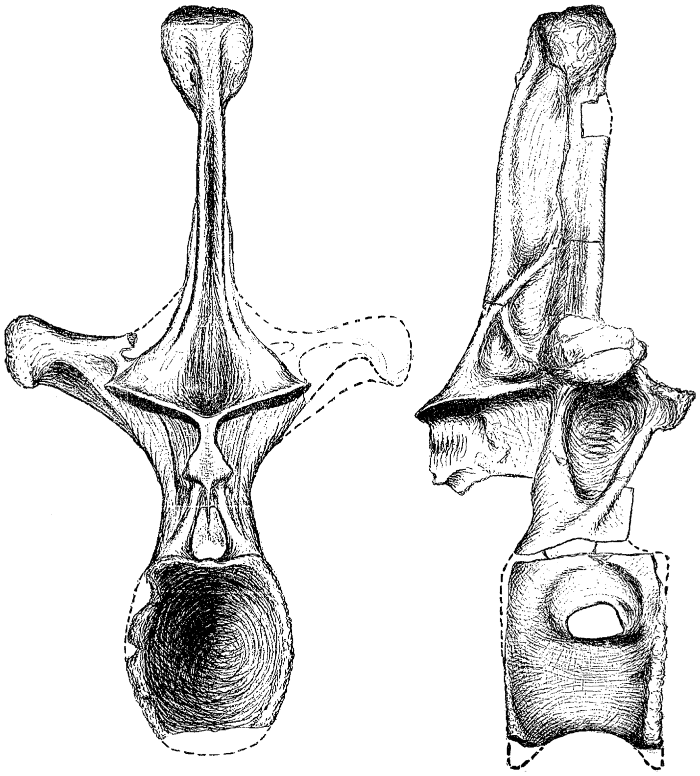

“The species of *Camarasaurus* and *Amphicœlias* [figured], which attained to the most gigantic proportions, are remarkable for the light construction of the vertebræ anterior to the tail.” From “On the Saurians Recently Discovered in the Dakota Beds of Colorado” by E. D. Cope (*The American Naturalist*, 1878, 12:71–85).