

# Reptilian digestive efficiency: Past, present, and future

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## ABSTRACT

Digestion and assimilation of nutrients and energy is central to survival. At its most basic level, investigations of digestion in animals must examine digestive efficiency, or how much of a given meal (i.e., energy) or a specific nutrient an organism can acquire from its food. There are many studies examining this in reptiles, but there is large variation in methodology, and thus, in the conclusions drawn from the gathered data. The majority rely on ratio-based analyses that can jeopardize the reliability of their findings. Therefore, we reviewed the literature to identify common themes in the digestive efficiency data on reptiles. Due to the sheer number of available studies, we largely focused on lizards, but included data on all reptilian groups. As an example of what the current data can reveal, we performed a meta-analysis of digestive efficiency in lizards as a function of temperature using regression analyses. We detected a weak positive trend of soluble carbohydrate digestibility as a function of temperature, but no similar trend in broad-scale digestive efficiency, and propose that these patterns be reevaluated with non-ratio data. We conclude with calls to end conducting analyses on ratios and instead employ covariate methods, for more studies of reptilian digestive efficiency and related processes using consistent methodology, more representation of each population (e.g., many studies focus on males only), and more detailed studies examining the effects of temperature on digestion (since the current data are inconclusive).

## 1. Introduction

An animal's digestive and metabolic efficiency determine the maximum nutrients and energy it has available for its daily budget, as well as mandating the frequency and volume of feeding necessary to fuel the rest of its biological processes. Digestibility (see [glossary](#) in Appendix A) is affected by biochemical properties (i.e., food type, enzyme activity), physics (i.e., particle size, digesta flow), and mechanical constraints (i.e., gut volume and surface area) ([Bjorndal et al., 1990](#); [Iverson, 1982](#); [Durtsche, 2004](#)). If we think of digestive efficiency as the outcome of physiological reactions, it can be summarized as follows ([Penry and Jumars, 1987](#); [Karasov and Hume, 2011](#); [Karasov et al., 2011](#)):

$$\text{digestive efficiency} \propto \frac{\text{enzyme activity}}{[\text{substrate}]} \propto \frac{\text{gut volume}}{\text{digesta velocity}} \propto \text{time} \quad (1)$$

Thus, if the volume of ingested substrate is increased, the specific digestive enzyme(s) that degrade that substrate must also increase in order to maintain digestive efficiency. Similarly, faster travelling digesta (or decreased transit time or gut passage time) necessitates a longer gut

to allow for more contact with absorptive epithelia to maintain efficiency. With enough time to digest and absorb, an animal may extract nutrients from sources that are largely indigestible over shorter time-spans. Indeed, these relationships can scale from simple substrates (e.g., dipeptides containing leucine) to whole complex diets (e.g., plants and animal prey) by matching enzyme specificity (e.g., Leucyl-aminopeptidase and total digestive enzyme activity, respectively).

While nutritional performance is multifaceted and relies on interactions of appetite and voluntary feeding rates, digesta transit and retention time, and digestive and absorptive rates and capacities, we have limited the scope of this review to a single aspect of this process: how much of a nutrient or how much energy an animal can extract from its diet. While this is not the only, nor the most important, outcome of nutritional physiology, digestive efficiency is often treated as a summary of the outcome of digestion. We are using this review to synthesize the state of available information on this metric of performance in reptiles, as well as to reflect upon the methods and approaches we do and could use to investigate these topics.

As reptiles do not masticate, surface-area-to-volume ratios of food and ingesta particles are controlled primarily by the starting particle size

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of an ingested item and any piercing or smashing the reptile may accomplish. Yet reptiles can be as effective as mammals at digesting recalcitrant materials (e.g., cellulose), but with larger particle sizes (Bjorndal et al., 1990; Durtsche, 2004), suggesting that reptiles are mostly reliant on chemical digestion (i.e., digestive enzymes) as opposed to physical digestion (i.e., mastication, trituration).

Reptiles, particularly herbivorous ones, are reluctant to eat in captivity, and therefore have been challenging subjects for laboratory digestibility studies. As a result, it is common (>25% of the studies surveyed here) for feeding experiments with reptiles to rely on force-feeding (Supplemental Table 1). Bjorndal et al. (1990) identify some of the potential confounding variation generated when force-feeding reptiles for digestibility studies, including altered particle size, intake, and passage rate. For example, juvenile *Pseudemys nelsoni* (Florida Red Bellied Cooter turtles) took smaller bites than adult conspecifics, thus generating smaller particles; the young were thereby equally efficient in digesting duckweed, despite the adult's more developed and voluminous guts (Bjorndal and Bolten, 1992). However, if juveniles and adults of *P. nelsoni* were both force-fed a finely ground diet, the adults would likely have digested the material more efficiently (as has been shown in mammals, Kay and Sheine, 1979; Wondra et al., 1995), although this remains untested in turtles.

There are several measures of how efficiently an animal degrades and uses nutrients, energy, and specific components from its diet (e.g., calcium, lipids, organic matter), and the term “digestibility” is often used interchangeably with digestive efficiency. Studies on reptile digestive efficiency considering the entire diet and not a specific marker are measured as “apparent” digestive efficiency (ADE) or digestive coefficient (ADC), with “apparent” acknowledging that material other than undigested food is inherent in the feces, such as sloughed intestinal lining or enteric microbes. Apparent digestive efficiency is calculated as a ratio using the amount of a dietary component ingested and measured in feces as

$$ADE = \frac{\text{ingested} - \text{feces}}{\text{ingested}} \times 100\% \quad (2)$$

and is the most common measurement, although apparent metabolizable energy (ME) as percentage of ingested energy (MEC, also called assimilation efficiency):

$$ME = \text{energy ingested} - (\text{energy in feces} + \text{energy in urates}) \quad (3)$$

$$MEC = \frac{ME}{\text{energy ingested}} \times 100\% \quad (4)$$

is also popular (Fig. 1). These measures are periodically conflated with one another (e.g., in Licht and Jones, 1967; Ruppert, 1980; Essghaier and Johnson, 1975) despite their distinct indications. Metabolizable energy can be a more complete measure of the net energy obtained from a food as this measure excludes the post-metabolic energy lost in uric acid. As such, ME is particularly valuable for modeling energy budgets (e.g., Brewster et al., 2020), contextualizing performance of other energetically costly processes (e.g., sprint speed in Zhang and Ji, 2004), and for investigating effects of meal frequency (e.g., Moeller et al., 2015). Yet if the focus of measuring efficiency is to better understand the digestive process or what proportion of the energy in the meal can be extracted, but not the net energetics of the animal, ADE is more fitting. Estimating the energy that digestion of a meal and absorption of the nutrients provides to an animal's body enables investigation of the contribution of a single meal (e.g., van Marken Lichtenbelt, 1992), or ability to use a novel diet (e.g., Ruppert, 1980). Of the 19 studies we reviewed across 24 species of snakes and lizards that included both measures, ADE was  $7.7 \pm 3.4\%$  (mean  $\pm$  SD; range 1.2–18.0%) higher than MEC.

Thus far, we have presented the quantitative outcomes of digestion and metabolism as ratios of energy retained to energy consumed. Being flattened measures, percentages are easy to parse and easy to compare across systems. Yet even 35 years ago, Packard and Boardman (1987, 1988) pointed out the rampant misuse of ratios in physiological and ecological data. Raubenheimer (1995) specifically applied these concerns to ADE and MEC, calling for analyses of the “parent variables” (i.e., energy content of feces, urates, and consumed material) and checking for covariance. The paper details the risks of confounding due to shared error terms in the numerator and denominator of these ratios (i.e., intake values in Eqs. (2) and (4)), provides examples with randomly generated variables, and overall makes a strong case for analyzing relationships between intake and fecal contents (or energy lost to feces and urates combined) directly. Beaupre and Dunham (1995) re-analyzed their earlier published ADE and MEC data for *Sceloporous merriami* (Beaupre et al., 1993) and identified that using energy consumption as a

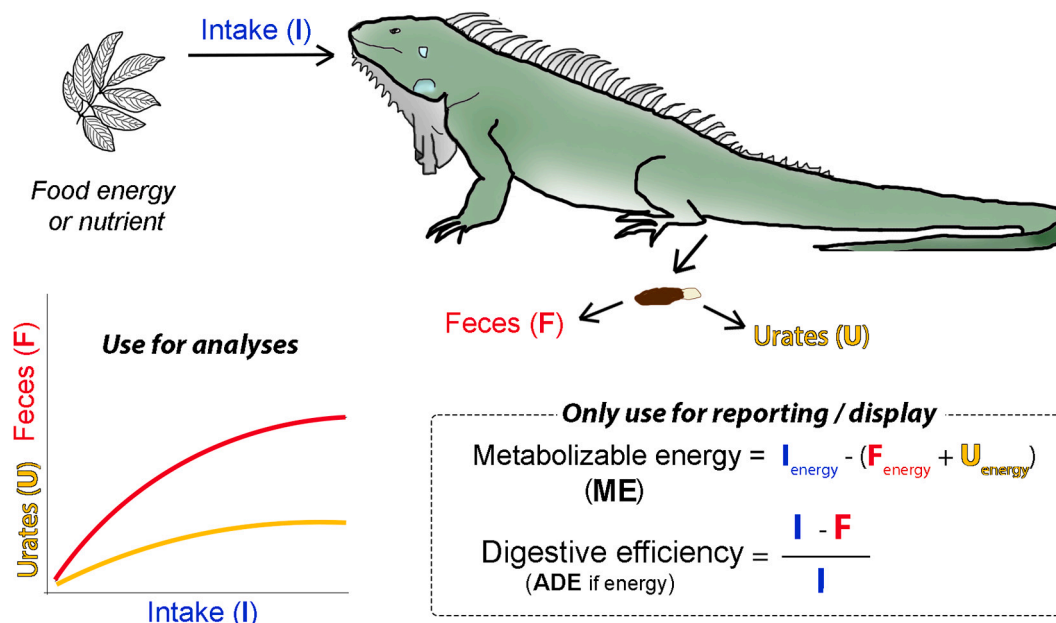


Fig. 1. Relationships among energy and nutrient terms in this review.

covariate instead of a ratio denominator decreased MEC by as much as 12 percentage points (71.6% in ratio-only analysis to 59.5% using ANCOVA). This substantial decrease in MEC revealed that a 10-day energy budget using the ratio-based estimation would overestimate the energy available to the lizard by >20%!

We agree with the strong arguments for analyzing values from feces, urates, and consumption when considering energetics and digestibility as presented by the above sources. Ideally, studies will report slope and intercept results of variable relationships, along with the value ranges used to calculate them, such that individual efficiencies can be calculated and variable relationships may be assessed for comparisons across studies. We contend, however, that there are scenarios where ratios are relevant to digestibility. For example, some methods do not enable researchers to directly collect values for feces and consumption, or intake (e.g., the ash method). Additionally, in experiments where intake has been held constant, there is no risk of intake-based error within the study. Data collected with constant intake may even be compared to other systems using the same intake amount. However, we also acknowledge that while energy consumption has often covaried with ADE and MEC (Kitchell and Windell, 1972; Christian et al., 1984; Beaupre et al., 1993; Beaupre and Dunham, 1995; Angilletta, 2001; Brewster et al., 2020; but not so in Andrews and Asato, 1977; Qu et al., 2011) it is not the only potential variable to covary with digestibility. Body mass, feeding-rate, consumption volume, micronutrient composition, and more can be potential covariates and should be considered in models of digestion. Indeed, while we suggest digestibility ratios be reported as “flattened” data, we also suspect that utilization plots (Raubenheimer and Simpson, 1994; Beaupre and Dunham, 1995), geometric nutritional analyses (Simpson and Raubenheimer, 1993), and performance landscapes (Morimoto, 2022) are more robust tools for capturing the multidimensions that these systems contain.

Measurements of efficiency focusing on the energy contribution of food to an animal can overestimate the amount of energy available in a food item (Witz and Lawrence, 1993) while neglecting the importance of other dietary resources. Organic matter (OM) digestibility accounts for this energy overestimation by subtracting the indigestible ash from both food and feces. OM digestibility can also serve as a more generalized representation of the contributions of diet than ADE and ME. Dry matter (DM) digestibility is an even more accessible way to track change in mass of the ingested diet to feces, but it does include inorganic material. Several studies have also measured digestibility of fiber, macronutrients, and minerals, again based on the general equation:

$$\text{digestibility of } x = \frac{\text{amount of } x \text{ in diet} - \text{amount of } x \text{ in feces}}{\text{amount of } x \text{ in diet}} \quad (5)$$

where  $x$  is the substance of interest. However, as with energetic efficiencies, these other digestibilities are subject to error when analyzed as ratios.

Due to varying methods in measuring digestive efficiency or digestibility, as well as variations in diet, feeding frequency, and other pertinent methods, many studies cannot be directly compared to each other. Indeed, it is the diversity of methods, outcomes, and consequences of measuring digestive efficiency in reptiles that motivates this review. We hope to reach a common understanding of digestive efficiency for reptilian taxa, so that we might suggest ways to make findings broadly applicable to many species, and to allow for the interpretation of results in the context of changing environmental conditions (e.g., increasing temperature or aridity associated with global change). We, therefore, surveyed the literature to compile studies on digestibility from across reptilian taxa (see supplemental information for methods). Focusing on lizard studies, we evaluated and summarized the methods and findings from digestion experiments in Supplemental Table S1 (see Table 1 for a brief selection of entries). As an illustration of what conclusions we might draw from the current data, we regressed measures of digestibility against temperature (see methods in supplemental

materials for details), both including then omitting digestibility data that have not been controlled for differences in intake. We finish by making recommendations for use in studying digestibility. Because measurements of digestive performance are so important, and because global changes in climate are now widely evident, the time is right to construct a synthesis of what these disparate and disconnected studies have and have not shown, particularly with regards to the effects of temperature on digestibility.

## 2. Results and discussion

We identified 93 studies across reptile taxa from which we collected digestibility data. Fifteen studies of squamates included both ADE and MEC. The average difference was 7.8% (SD = 2.9), well within the 5–15% range of difference suggested by Bedford and Christian (2000). However, the difference between ADE and MEC was much more variable in lizards (range = 1.2–18.0%, SD = 3.1%) than in snakes (range = 3–9.9%, SD = 1.8%), likely due to greater variation in both digesta retention times between the taxa and in lizard's diets.

The proceeding portions of this manuscript are divided into reptile classes—lizards, snakes, turtles, and crocodylians. We are, unfortunately, not aware of any work on digestion in tuataras.

Lizards—Digestive efficiency has been examined more frequently in lizards than other groups of reptiles, both in terms of taxa and with respect to topics addressed. Broad topics include general description, comparing herbivory and insectivory, feeding frequency, thermal physiology, age class, and ecology. Because digestive efficiency is affected by many factors, it is often not possible to quantitatively compare these factors among or even within studies. Researchers have called for standardization of methods in these measurements (Witz and Lawrence, 1993; Beaupre et al., 1993; McKinnon and Alexander, 1999; Hoby et al., 2012), but doing so in a biologically-relevant context requires copious physiological and natural history data. Fifteen out of 44 studies we surveyed employed force-feeding; twelve used free-feeding of controlled amounts, and nineteen ad lib feedings. While Harwood (1979) found no differences in force-fed versus free-fed digestive efficiencies in the three species he studied (*Sceloporus occidentalis*, *Aspidoscelis tigris*, and *Elgaria multicarinata*), this may be dependent on factors such as experimental temperature (e.g., Waldschmidt et al., 1986), diet particle size, and amount ingested.

In general, insectivorous lizards have high digestive efficiencies (>80%; Mueller, 1970; Andrews and Asato, 1977; Harwood, 1979; Johnson and Lillywhite, 1979; Waldschmidt et al., 1986; Van Damme et al., 1991; Slade et al., 1994; Xiang et al., 1996; McKinnon and Alexander, 1999; Du et al., 2000; Chen et al., 2003; Zhang and Ji, 2004; McConnachie and Alexander, 2004; Zhang and Ji, 2004; Qu et al., 2011; Hoby et al., 2012; Miller et al., 2014; Brewster et al., 2020) and high MEC (>70%, Mueller, 1970; Avery, 1971; Andrews and Asato, 1977; Dutton and Fitzpatrick, 1975; Essgaier and Johnson, 1975; Johnson and Lillywhite, 1979; Buffenstein and Louw, 1982; Xiang et al., 1996; Du et al., 2000; Angilletta, 2001; Chen et al., 2003; McConnachie and Alexander, 2004; Zhang and Ji, 2004; Qu et al., 2011; Miller et al., 2014). We see more variation when it comes to plant eating lizards: herbivorous lizards on high quality (nutrient and energy dense) diets such as sweet potatoes or flowers can have digestive efficiencies as high as insectivorous lizards (Throckmorton, 1973; Ruppert, 1980; van Marken Lichtenbelt, 1992), yet on diets with high fiber and other structural components, digestive efficiencies may be much lower (e.g., ADE of 40% for *Iguana iguana* on a berry diet; van Marken Lichtenbelt, 1992; Christian et al., 1984; Troyer, 1984a). This increase of digestive efficiency on a high-quality diet is not limited to herbivores, but low-quality diets containing copious amounts of animal material are rarer in natural settings. To test this, McKinnon and Alexander (1999) fed artificial high- and low-quality diets (made primarily of canned dog food and supplemented with cake flour or ground wheat husks, respectively) to *Platysaurus intermedius* (a facultative omnivore). Lizards digested the

**Table 1**

Selected abbreviated entries from survey of lizard digestive performance table (Supplemental Table S1).

Species, natural diet, and paper	Feeding modality and diet	Temp. °C	ADE %	MEC %	Assessment
<i>Crotaphytus collaris</i> insectivore Brewster et al., 2020	free-fed crickets	21, 25 °C	no intake $N = 10$ $89.1 \pm 2.8\%$ $ADE = ((0.84 \times \text{intake } kJ + 2.51) / \text{intake } kJ) \times 100\%$ $N = 10$ $87.9 \pm 1.7\%$ $ADE = ((0.85 \times \text{intake } kJ + 1.45) / \text{intake } kJ) \times 100\%$ $N = 10$ $90.4 \pm 0.4\%$ $ADE = ((0.91 \times \text{intake } kJ - 0.32) / \text{intake } kJ) \times 100\%$ $N = 10$ $90.3 \pm 0.8\%$ $ADE = ((0.89 \times \text{intake } kJ + 0.66) / \text{intake } kJ) \times 100\%$ $N = 10$	no intake $N = 10$ $79.9 \pm 3.5\%$ $MEC = ((0.74 \times \text{intake } kJ + 2.95) / \text{intake } kJ) \times 100\%$ $N = 10$ $78.9 \pm 3.4\%$ $MEC = ((0.73 \times \text{intake } kJ + 2.91) / \text{intake } kJ) \times 100\%$ $N = 10$ $89.1 \pm 1.2\%$ $MEC = ((0.83 \times \text{intake } kJ + 1.04) / \text{intake } kJ) \times 100\%$ $N = 10$ $83.6 \pm 2.1\%$ $MEC = ((0.80 \times \text{intake } kJ - 1.77) / \text{intake } kJ) \times 100\%$ $N = 10$	Parent variables analyzed via ANCOVAs with intake as a covariate and no effect of body mass.
		28 °C			
		31 °C			
		34 °C			
		37 °C			
<i>Crotaphytus collaris</i> ♀ insectivore Ruppert, 1980	force-fed crickets	37 °C	$65.5 \pm 1.0\%$ $N = 2$		BDE
<i>Crotaphytus collaris</i> ♀ insectivore Ruppert, 1980		37 °C:20 °C	$56.3 \pm 1.8\%$ $N = 2$		
<i>Dipsosaurus dorsalis</i> ♀ herbivore Harlow et al., 1976	force-fed flowers	37 °C	$32.4 \pm 2.3\%$ $N = 3$		B
		37 °C:20 °C	$25.7 \pm 3.5\%$ $N = 3$		
		28 °C	0% $N = 4$		BD
		33 °C	$54.3 \pm 2.1\%^\dagger$ $N = 3$		
		37 °C	$62.8 \pm 3.8\%^\dagger$ $N = 4$		
<i>Dipsosaurus dorsalis</i> ♀ herbivore Zimmerman and Tracy, 1989, Zimmerman and Tracy, 1989	force-fed rabbit chow	41 °C	$69.5 \pm 1.2\%^\dagger$ $N = 4$		BD
		41 °C:28 °C	$57.9 \pm 0.7\%^\dagger$ $N = 3$		
		Temp. relationship equation	$ADE = 1.7435 \times \text{temperature } ^\circ\text{C} - 2.4239$		D
		33, 37, 41 °C	$59.8 \pm 3.1\%^\dagger$ $N = 16$		
<i>Phrynocephalus versicolor</i> males insectivore Qu et al., 2011	Ad lib mealworms	25 °C	$95.0 \pm 1.1\%$ $N = 17$	$90.8 \pm 3.3\%$ $N = 17$	AD
		33 °C	$90.3 \pm 1.8\%$ $N = 20$	$82.4 \pm 2.2\%$ $N = 20$	
		39 °C	$93.5 \pm 3.3\%$ $N = 22$	$88.0 \pm 5.6\%$ $N = 22$	
<i>Platysaurus intermedius</i> ♀ omnivore McKinon and Alexander, 1999	force-fed dog food/ cake flour	26, 31 °C	$87.9 \pm 5.7\%^*$ $N = 16$		D
<i>Platysaurus intermedius</i> ♀ omnivore McKinon and Alexander, 1999	force-fed dog food/ wheat husk	26, 31 °C	$51.5 \pm 5.6\%^*$ $N = 16$		D
<i>Plestiodon elegans</i> ( <i>Eumeces elegans</i> ) males insectivore Du et al., 2000	ad lib mealworms	22, 34 °C	$89.5 \pm 1.0\%^*$ $N = 23$		D
		24 °C	$92.4 \pm 1.2\%$ $N = 9$	$83.8 \pm 2.8\%^*$ $N = 94$	
		26, 28, 30, 32, 36 °C	$90.7 \pm 1.7\%^*$ $N = 62$		
<i>Xantusia riversiana</i> ( <i>Klauberina riversiana</i> ) ♀ omnivore Johnson and Lillywhite, 1979	ad lib mealworms	24 & 30–31 °C: 20–21 °C	$93.3 \pm 1.0\%$ $N = 8$	$85.1 \pm 2.0\%$ $N = 8$ $MEC = ((0.90 \times \text{intake } kJ - 1.72) / \text{intake } kJ) \times 100\%$ $R^2_{\text{feces+urates}} = 0.52$ (1.72 intercept term not significant)	D

(continued on next page)



Table 1 (continued)

Species, natural diet, and paper	Feeding modality and diet	Temp. °C	ADE %	MEC %	Assessment
<i>Xantusia riversiana</i> ( <i>Klauberina riversiana</i> ) ♀ omnivore Johnson and Lillywhite, 1979	ad lib apple	24 & 30–31 °C: 20–21 °C	89.0 ± 1.8% N = 5  ADE = ((0.84 × intake kJ + 1.72)/ intake kJ) × 100% R <sup>2</sup> <sub>feces</sub> = 0.95	87.8 ± 1.5% N = 5  MEC = ((0.83 × intake kJ + 1.67)/ intake kJ) × 100% R <sup>2</sup> <sub>feces+urates</sub> = 0.95	<b>D</b>

Data are means ± SD. If digestibilities are not different across treatment, they have been pooled. See Supplemental Table S1 for notation key, definitions, and other notes.

more nutrient-dense diet at >1.5× efficiency over the low-quality diet.

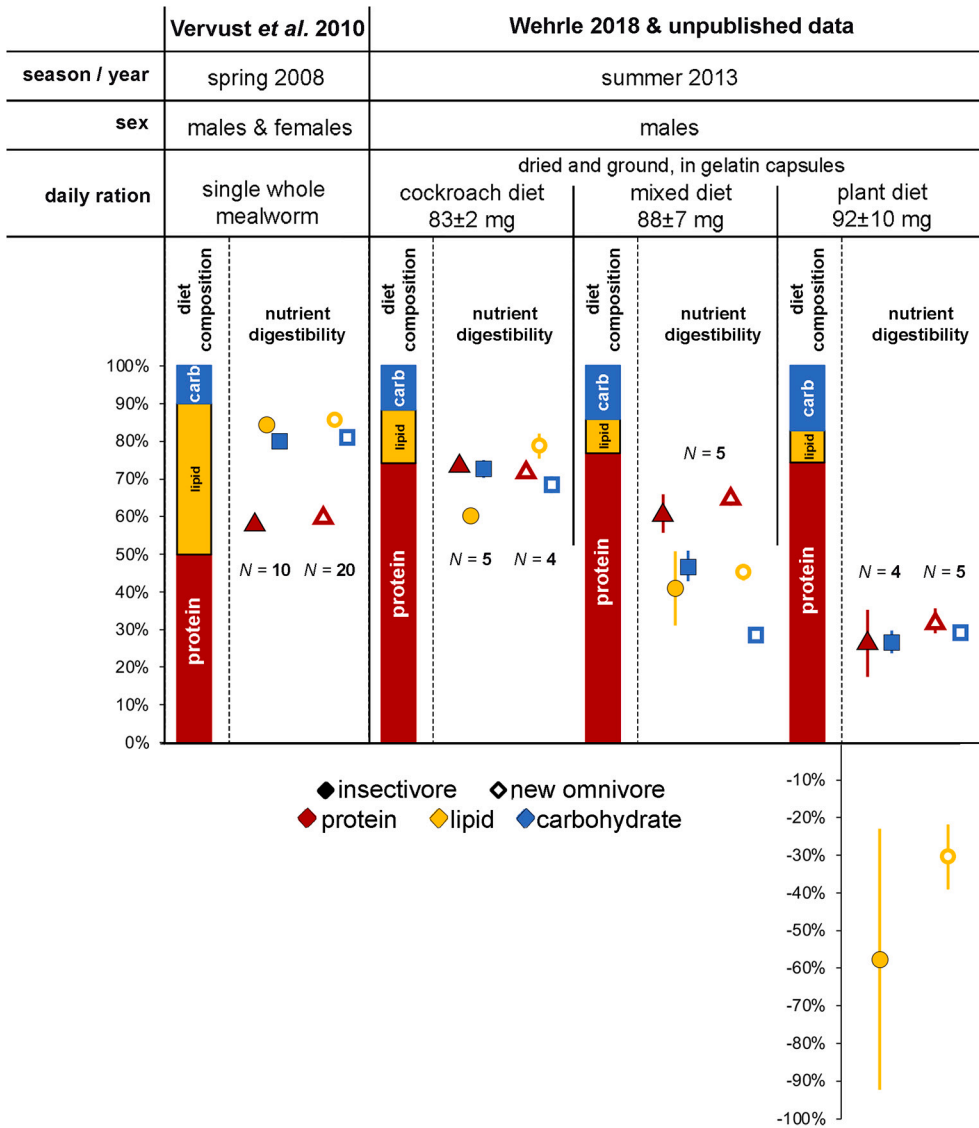
Works on lizard digestive efficiencies have mostly used ADE and ME and several papers (Skoczylas, 1978; Harwood, 1979; Johnson and Lillywhite, 1979; van Marken Lichtenbelt, 1992; Qu et al., 2011) include tables of ADE and MEC values for lizards in the contexts of diet, temperature, and taxonomic diversity. (Unfortunately, none of these tables include consumption amounts, making them of limited application. Some entries in Supplemental Table 1 of this review are similarly lacking.) A small number of lizard studies have investigated digestibility of macronutrients (Witz and Lawrence, 1993; Pafilis et al., 2007; Vervust et al., 2010) and micronutrients important to lizards such as Ca<sup>2+</sup> and P (Nagy, 1977; Durtsche, 2004; Hoby et al., 2012), estimating more detailed values of available nutrients in the meal.

Comparisons of digestibility of animal vs. plant diets are at particular risk for confounding due to differences in intake. As animal material is generally more nutrient dense than plant material, attempts to make diets energetically similar will preclude mass and volume balance across diets (and vice versa). Additionally, it can be especially challenging to get lizards to eat plants in captivity, making it necessary to use force-feeding for these studies, and thus pre-determined intake rates with little variation. ANCOVA based analyses rely on having a range of covariate values, meaning that a shift in experimental design is needed for truly understanding animal vs. plant diet digestibility comparisons. However, based on the available data, insectivorous lizards show decreased digestive performance on plant diets, but herbivorous lizards exhibit no decreases in ability to digest insects (Table 1). *Crotaphytus collaris* (insectivore) and *Sauromalus ater* (herbivore; previously *S. obesus*) were equally efficient digesting crickets, with energy assimilations ~63% (Ruppert, 1980). However, the *C. collaris* were half as efficient at assimilating dandelion flowers (32%) as the *S. ater*, which had no difference in their energy assimilation on insect or flower diets. Still, comparing these two species of very different sizes is also risky for accurate interpretation. Johnson and Lillywhite (1979) avoided the size and species comparison (Garland Jr. and Adolph, 1994) issues by working with the omnivorous *Xantusia* (formerly *Klauberina*) *riversiana*. These small-bodied insular (island dwelling) lizards had somewhat higher digestive efficiency (93%) on a mealworm diet than on an apple diet (89%), yet a lower metabolizable energy on the mealworm diet (85%) than on the apple diet (88%) (Johnson and Lillywhite, 1979). This suggests at least some performance advantage to consuming a high-quality plant food (such as fruit, as opposed to fibrous stems, for example) for an omnivorous lizard. Omnivorous *Liolaemus ruibali* digested a low fiber diet (50:50 rabbit chow/mealworms, ADE = 74%) more efficiently than a high fiber diet (90:10 rabbit chow/mealworms, ADE = 63%), but showed no differences in digestibility of fiber from the two diets (Kohl et al., 2016). Fiber digestibility has been measured in small-bodied (1.95–200 g adult mass) plant eating lizards at 21–24% (Karasov et al., 1986; Kohl et al., 2016) and in larger-bodied (>200 g) plant eating lizards at 39–76% digestive efficiency (Troyer, 1984a; Christian et al., 1984; Durtsche, 2004). This higher fiber digestibility in larger lizards is likely due to longer digesta retention in larger guts, thus allowing for greater microbial fermentation (Kohl et al., 2016). Fiber appears to play more of an indirect role in the digestibility of plants, as

greater fiber can negatively affect total digestibility with no change in fiber digestibility (Karasov and Douglas, 2013).

In a comparison between a newly (<30 generations) plant eating population of *Podarcis siculus* and its insectivorous source population, ratio analyses suggested the new omnivores were more efficient at assimilating lipids (86% vs. 83%), proteins (60% vs. 58%), and carbohydrates (81% vs. 79%) in their mealworm diet than their strictly insectivorous counterparts (Vervust et al., 2010). Digestibility data collected five years later with the same populations fed a cockroach diet (Wehrle, 2018; Wehrle et al., 2020; B. Wehrle et al., unpublished data; compared with Vervust et al. (2010) in Fig. 2) also showed higher lipid digestibility (intake-adjusted to 92% vs. 69%, 29–34 mg total lipid intake) in the new omnivores, but considerable overlap of both protein and carbohydrate digestibilities between the two populations. All three nutrient digestibilities appeared to be either unaffected or minimally affected by intake amount alone, but this may be an artifact of force-feeding all the lizards nearly equal rations. Wehrle and colleagues found much larger variation in digestibility, both between (excepting for protein digestibility) and within populations, than did Vervust et al. (2010). These more recent results by Wehrle and colleagues indicate either effects of feeding trial (e.g., cockroaches vs. mealworms [see Kitchell and Windell (1972) for a critique of mealworm use in digestive studies], use of ≤1 mm particle size instead of whole larvae), further shifts in the digestive physiology of these lizard populations than those reported by Vervust et al. (2010), seasonal or yearly variation in physiology (Wehrle, 2018; B. Wehrle et al., unpublished data), or analysis methods (i.e., dynamism from nutrient vs. mass of nutrient, as suggested by Witz and Lawrence, 1993) diverging between the two studies. Additionally in their studies, Wehrle and colleagues included feeding trials with plant and mixed (omnivore) laboratory diets, respectively composed of plant material (collected from newly omnivorous population's habitat) and bird seed, or a 1:1 ratio by dry mass of the plant and cockroach diets. Generally, they found the lizards digested the cockroach and mixed diets more efficiently than the plant diet (intake-adjusted OM digestibility of 82% and 77% vs 61%, respectively) but for the insectivorous lizard population, the carbohydrate digestibility was not different between the mixed and plant diets. Comparing these studies (Vervust et al., 2010 to Wehrle, 2018; Wehrle et al., 2020; B. Wehrle et al., unpublished data) illustrates the potential pitfalls of testing only one aspect of a multi-faceted system (i.e. insectivores and omnivores eating insects), then applying the resulting assumptions to the untested interactions (i.e. omnivores eating plants).

In addition to diversity in diets, lizards have a wide range of feeding frequencies, potentially producing up- or down-regulation of the digestive tract. In infrequent feeders, measurements of digestive efficiency and growth on more frequent feeding regimes than they would experience naturally could show decreased digestive efficiency and growth if the gut stays static and digesta moves more quickly. Alternatively, there is evidence that gut function is upregulated to disproportionately acquire a required nutrient that is deficient in the diet (Clissold et al., 2013). However, if the gut is upregulated with increased feeding, digestive efficiency and growth could increase as more nutrients are available due to increased intake. This was tested in young *Heloderma*



**Fig. 2.** Comparison of studies (Vervust et al., 2010; Wehrle, 2018, unpub. data) of the same two populations of *Podarcis siculus* from Croatia. In the two studies, wild caught lizards from the insectivorous (source; filled markers) and new omnivore (transplanted; outlined markers) populations were forced experimental diets. Fig. 1 compares diet type, amount, and composition. Diet composition for mealworms in Vervust et al. (2010) were assumed to be the same as reported in Pafilis et al., 2007. Digestibility ratios of protein, lipid, and carbohydrate are reported for each lizard population and diet. Fecal content data from Wehrle were covariate-adjusted to calculate digestibility at a common intake. Digestibility presented as means ±SD as a percent of intake.

*suspectum* (Moeller et al., 2015) that generally take 7–10 days to digest a meal. A frequent intake feeding group was fed a mouse every 7 days throughout the 56-day experiment and an infrequent intake group was fed three mice meals over 8 days, followed by 20 days of fasting. The *H. suspectum* juveniles showed no differences in growth among either feeding group. Contrary to expectations, there were no differences in MEC by feeding group excepting an increased MEC of the meal immediately preceding their 20-day fast in the infrequent intake lizards. This supports a fixed gut model, but also suggests that even 20 days between feedings may be more frequent than is ecologically relevant for this lizard. In a naturally frequent feeder, *Uta stansburiana*, four feeding groups manipulating quantity and frequency (lizards fed crickets to satiation twice per day or twice every third day, or lizards fed a single cricket once daily or every third day) showed no increase in digestive efficiency ratios among increased meal size and feeding frequency treatments (Waldschmidt et al., 1986). Indeed, in the lizards fed large meals daily, the digestive efficiencies of these meals decreased by <3% from the other feeding regimes. Consistent with a wide range of other taxa (e.g., harbor seals, Trumble et al., 2003; hippopotamuses, Clauss et al., 2007; locusts, Clissold et al., 2013), lizards may not alter their gut function enough to change digestive efficiencies from meal to meal. From the perspective of Chemical Reactor Theory, higher intake of the

same diet should lead to decreased transit time of digesta, resulting in lowered digestive efficiency (Penry and Jumars, 1987). Without a concomitant increase in gut size or in digestive enzyme activities to accommodate this increased passage rate (Eq. (1)), we should in fact expect to see lower digestibility with higher, more frequent intake. However, there is a dearth of work elucidating the effects of long-term fasting or changes in seasonal feeding on digestive efficiencies in lizards. Potential studies on this topic may explain whether mechanisms of efficient gut function are modulated with respect to feeding rate. There are examples across taxa of animals that modulate their gut length in response to diet, including birds (Martin et al., 1951; Savory and Gentle, 1976; Dykstra and Karasov, 1992; McWilliams et al., 1999), fish (Kramer and Bryant, 1995; German and Horn, 2006; Leigh et al., 2018; Herrera et al., 2022), beetles (Bounoure, 1919), and mammals (Selman et al., 2001; Starck, 2003; Stevens and Hume, 2004).

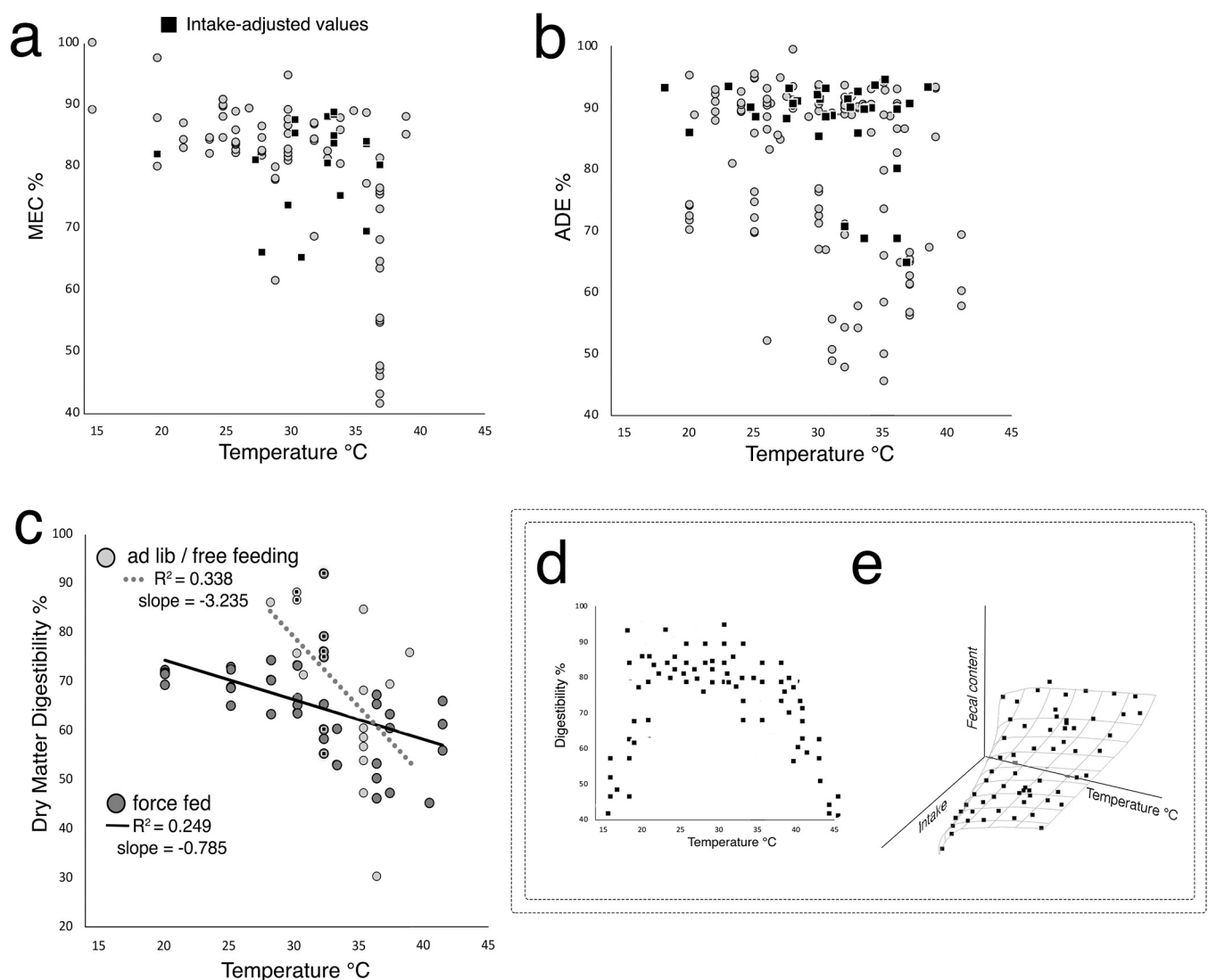
Temperature is the most studied area of lizard digestive efficiency. Although temperature generally affects lizard appetite positively (Harwood, 1979; Waldschmidt et al., 1986; Beaupre et al., 1993; Du et al., 2000; Alexander et al., 2001; Angilletta, 2001; McConnachie and Alexander, 2004; Zhang and Ji, 2004; Miller et al., 2014), there are some exceptions. Qu et al. (2011) showed a negative relationship of intake and temperature in *Phrynocephalus frontalis*, and higher appetite for

*P. versicolor* at the lowest and highest temperatures, with depressed appetite at intermediate temperatures (as is also seen in *Takydromus wolteri* by Chen et al., 2003). Others have observed no temperate effects on appetite (van Marken Lichtenbelt, 1992; Xiang et al., 1996). Increased temperature also positively impacts metabolism, gut motility, and digestive biochemistry reactions (all to be discussed later in this review), areas of great importance that aid our understanding of how lizards function, both, in their component systems and as players in an ecosystem. While thermal performance is often evaluated by measuring differences in locomotion performance (Huey and Bennett, 1987; Xiang et al., 1996; Du et al., 2000; Chen et al., 2003; Zhang and Ji, 2004), studies of thermal performance in digestion are less common, but are essential to understanding trade-offs in predation (avoiding predation and/or being successful at catching prey) and acquiring nutrients.

While some studies found an increase in digestive efficiency with increasing temperature (Harlow et al., 1976; Harwood, 1979; Ruppert, 1980; Waldschmidt et al., 1986; Angilletta, 2001), more found no

relationship between temperature and digestive efficiency (Ruppert, 1980; Troyer, 1987; Zimmerman and Tracy, 1989; Van Damme et al., 1991; Beaupre et al., 1993; Xiang et al., 1996; McKinnon and Alexander, 1999; Chen et al., 2003; Zhang and Ji, 2004; McConnachie and Alexander, 2004; Miller et al., 2014; or significant differences, but not biologically relevant in Du et al., 2000). McKinnon and Alexander (1999) hypothesized high-quality experimental diets could dampen the signal of digestive efficiency changes in response to temperature. Yet, their results showed that lizards fed low-and high-quality diets kept constant digestive efficiencies at different temperatures. When digestive efficiency was constant across temperatures, researchers generally found that transit time decreased and appetite went up as temperature increased (see Xiang et al., 1996; Chen et al., 2003; Qu et al., 2011 for exceptions), likely changing the true digestibility with the increase in consumption.

Indeed, while decreased transit time can contribute to a decreased digestive efficiency, enzyme activity and other digestive mechanisms



**Fig. 3.** Regressions of digestibility (zeroes excluded) vs. average daytime temperature from all lizard digestibility studies that included records of temperature during feeding period. Each point is the average of digestibility for a species-treatment combination from a single study. Fig. 3a and b use all MEC and ADE data, respectively and show no relationship of digestibility to temperature. Fig. 3c displays relationships between DM digestibility and temperature for ad lib and free-fed lizards (light markers, dotted regression line; slope =  $-3.235$ ,  $R^2 = 0.338$ ,  $P < 0.03$ ,  $F_{1,12} = 6.13$ ) and force-fed lizards only (dark markers, solid regression line; slope =  $-0.7854$ ,  $R^2 = 0.249$ ,  $P < 0.001$ ,  $F_{1,39} = 14.27$ ). On all three plots, black squares denote covariate-adjusted data points using 37KJ / 1.8 g intake and 5 g lizard body mass as common values. Fig. 3d and e represent theoretical visualizations: 3d of digestibility vs. temperature using only intake-adjusted data; 3e using a geometric plot intake vs. fecal contents with respect to temperature.

also increase with temperature, with all factors potentially balancing out to hold digestive performance steady (see Eq. (1)). However, *Tachylepis margaritifera* has faster transit times at low temperatures, but still shows no differences in overall digestive efficiency with respect to temperature (Miller et al., 2014). This may be to prevent food from rotting in the digestive tract. Miller et al. (2014) propose that *T. margaritifera* increases digestive enzyme concentrations in their digestive tract at low temperatures, but this has not been tested. Across most studies, temperatures presumably below or above the lizards' thermal tolerances elicited decreased digestive efficiencies, or halted digestion (Table 1; Supplemental Table S1). It is thus of great importance to consider the temperatures that the lizards experience, and their preferred range, to ensure any results of changing or static digestive efficiency given proper context.

Our analyses of 50 studies largely produced a similar lack of relationship between digestibility and temperature. Generally, at lower temperatures, digestive processes take longer and move more slowly, using less energy per unit time. But lower temperatures also draw out the time that energy is expended on digestion, often resulting in a consistent increase in metabolic rate post-feeding (Specific Dynamic Action or SDA—see SNAKE section), regardless of temperature (Secor, 2009). Linear regressions of MEC and ADE with temperature show no relationship (Fig. 3a,b). Indeed, this was the case with most of our comparisons; but in a flat landscape, even small changes stand out. As temperatures increase, DM digestibility decreases (Fig. 3c)—minimally in force-fed lizards (slope =  $-0.7854$ ,  $R^2 = 0.249$ ,  $P < 0.001$ ,  $F_{1,39} = 14.27$ ), and with greater effect in lizards allowed to feed voluntarily (slope =  $-3.235$ ,  $R^2 = 0.338$ ,  $P < 0.03$ ,  $F_{1,12} = 6.13$ ). Voluntary intake is very sensitive to temperature changes, with lower voluntary feeding rates at lower temperatures (Buffenstein and Louw, 1982; Waldschmidt et al., 1986; Waldschmidt et al., 1987; Angilletta, 2001; Du et al., 2000; Qu et al., 2011). Few of these data (25% of DM digestibility data points, and 12 of the 50 digestibility studies overall) are adjusted for intake, likely leading to studies using ad lib or free-feeding to be most affected by artifacts of positive relationships of heating and intake. However, should this pattern persist with intake-adjusted data (see Fig. 3d,e for examples), it may indicate that decreased transit time from increased intake outpaces the increased performance of digestive and absorptive mechanisms. On the other hand, restricting lizards from feeding according to their appetites by applying force-feeding may inhibit their ability to reach maximum digestive efficiency. We may even expect SDA to be decrease with force feeding as digesta transit time may be artificially shortened.

Another factor that may confound our understanding of the relationship between temperature and DM digestibility is that this measure is overrepresented in studies of plant-eating lizards. Dry matter digestibility is an easily-accessible measure of digestive performance, especially when working with low-energy density feces. As it is especially challenging to get lizards to eat plants in the lab, it is also more likely that researchers would not be able to conduct experiments using voluntary intake. However, DM digestibility can be measured with higher-energy-density-diets without preventing the sample from being used in other analyses. To allow for greater comparability across digestibility studies, especially those testing temperature effects, it may be useful to include DM along with more sophisticated digestibility measures.

We found no relationship between temperature and macronutrient digestibility from the data spanning this meta-analysis, yet there are mechanisms for dietary components to differ in digestibility with temperature. In a study of the digestive energetics of *Agama atra*, proteins and lipids oxidized faster and produced a greater energetic yield as temperature increased (Plasman et al., 2019). With that increase in nutrient metabolism, however, came an increase in the cost of digestion (SDA). Proteins require more energy to metabolize than soluble carbohydrates, and both proteins and lipids take considerably longer to digest. Macronutrient digestibility is little represented in the lizard literature—

protein digestibility was only measured in nine (20%) of the lizard studies we surveyed, and carbohydrate digestibility in six. Five of those studies are on lacertids, primarily of the genus *Podarcis*, and all five used force-feeding.

McKinnon and Alexander (1999) further hypothesized that the relationship of temperature to digestive efficiency is species-specific. Without controlling for methods across trials such as intake, feeding modality, and even how much of the reptile's thermal breadth is represented in the experiment, it is difficult to assess if an effect on efficiency would be due to temperature. Reported patterns in the literature do not appear to have relationships with phylogeny nor whether a species' range extends into the temperate zone (Supplemental Fig. 1), but this lack of pattern may be an artifact of intake or any number of other uncontrolled variables mentioned above. For taxa in which temperature patterns were reported, ADE either increased or decreased as lizards got hotter, or reached the maximum at intermediate temperatures, presumably close to the thermal optima for other traits. It appears notable, then, that the two *Phrynocephalus* species deviated from patterns seen in other clades, demonstrating an apparently bimodal pattern: higher digestive efficiency outside its preferred temperature range, and lowest digestive efficiency at an intermediate temperature within its preferred temperature range (Qu et al., 2011). Similarly, from macronutrient data reported by Pafilis et al. (2007), we calculated that a single *Podarcis* species, *P. peloponnesiacus*, appears to have the lowest ADE, ME, and DM digestibility at the intermediate of the three temperatures at which that study measured nutrient digestibility. All three temperatures were within or below *P. peloponnesiacus*'s preferred thermal range.

There are not enough data across lizard taxa to assess if these relationships, or absence thereof, between temperature and digestive efficiency are due to evolutionary history. In comparing studies using voluntary intake (i.e., free-feeding and ad lib) vs. force-feeding, we found that temperature effects on ADE are more likely to appear with force-feeding ( $\chi^2 = 6.95$ ,  $N = 33$ ,  $P = 0.008$ ). Indeed, force-feeding can generate confounding challenges through artificial particle size, feeding frequency, and meal size. Zimmerman and Tracy (1989) replication of the Harlow et al. (1976) experiment found a slight trend ( $P = 0.08$ ) towards increasing digestive efficiency with increased temperatures in *Dipsosaurus dorsalis* where Harlow and colleagues had found a clear and steeper positive effect. Zimmerman and Tracy argued that Harlow and colleagues had confounded their results by overfeeding their lizards by as much as 330%.

As implied earlier when discussing macronutrient digestibility and temperature, meta-analyses of digestive efficiency and temperature may be further confounded by confining studies to using multiple closely related species, thereby potentially inflating the representation of similarities in sister taxa (although the same may be true of diet or environment). In their study of five closely related lacertid lizards force-fed mealworms, Pafilis et al. (2007) found that lipid and carbohydrate digestion increased with temperature, but protein digestion decreased with increasing temperature. At warmer temperatures, ratio-based protein digestion showed a larger decrease ( $\sim 30\%$ ) in the three mainland lizards versus the comparatively small ( $\sim 5\%$ ) decrease in the two insular species studied. Since the insular species were not each other's closest relatives, these findings support insularity as a driver of change in digestive physiology. Thus, if relationships between temperature and overall digestive efficiency converge with respect to ecology, differences in protein digestion may be a mechanism of interest.

The Temperature Constraint Hypothesis (TCH) developed in fishes (Gaines and Lubchenco, 1982; Floeter et al., 2005) proposes that there are few herbivorous fishes at high latitudes because of decreased digestive efficiency at low temperatures. The TCH assumes that digestive rate decreases more sharply than metabolic rates at lower temperatures (Floeter et al., 2005), and thus, an ectotherm consuming a low-quality diet may not be able to absorb enough nutrients to meet their metabolic demands when temperatures dip too low (see also Tracy et al., 2005). This hypothesis is supported in the systems showing decreased



digestive efficiency with decreased temperature. However, most of the studies we surveyed showed either no effect of temperature on digestibility (as have recent studies in fishes; Johnson et al., 2017; Johnson et al., 2020) or a different relationship than the TCH posits, thus making this hypothesis potentially less applicable for herbivorous lizards. In a sample of 75 species of *Iolioides* lizard, for example, herbivory is negatively correlated with temperature (Espinoza et al., 2004; Pincheira-Donoso, 2021)! It is very reasonable, and indeed, likely, that other physiological and behavioral factors such as feeding rate, enzyme activity, and transit time decrease and increase with cooling such that digestibility stays static or behaves non-linearly across the range of a reptile's thermal tolerances. *Sceloporus undulatus*, for example, decreased their intake much faster than their energy loss to feces and urates with decreased temperatures (Angilletta, 2001). Accordingly, their transit time increased sharply with the drop in temperature, leaving them with less ingested material to process over a longer-times. This resulted in the highest ADE and ME at an intermediate temperature, a pattern or trend also seen in several other species (Harwood, 1979; Xiang et al., 1996; Du et al., 2000; Brewster et al., 2020).

Still, these works on reptiles generally do not include temperatures nearly as low as those experienced by higher-latitude fishes as many reptiles will not or cannot feed at these temperatures. We recommend more empirical studies of digestibility over different temperatures across lizards to elucidate the proximal and ultimate mechanisms behind temperature-digestibility relationships, particularly in herbivores. We encourage researchers to choose temperatures that span the animal's thermal tolerances to capture the entirety of these patterns, but that include sufficient resolution to identify critical temperature points (as is represented in Harlow et al., 1976; Harwood, 1979; Waldschmidt et al., 1986; Van Damme et al., 1991; Xiang et al., 1996; Du et al., 2000; Angilletta, 2001; Chen et al., 2003; McConnachie and Alexander, 2004; Zhang et al., 2004; Brewster et al., 2020).

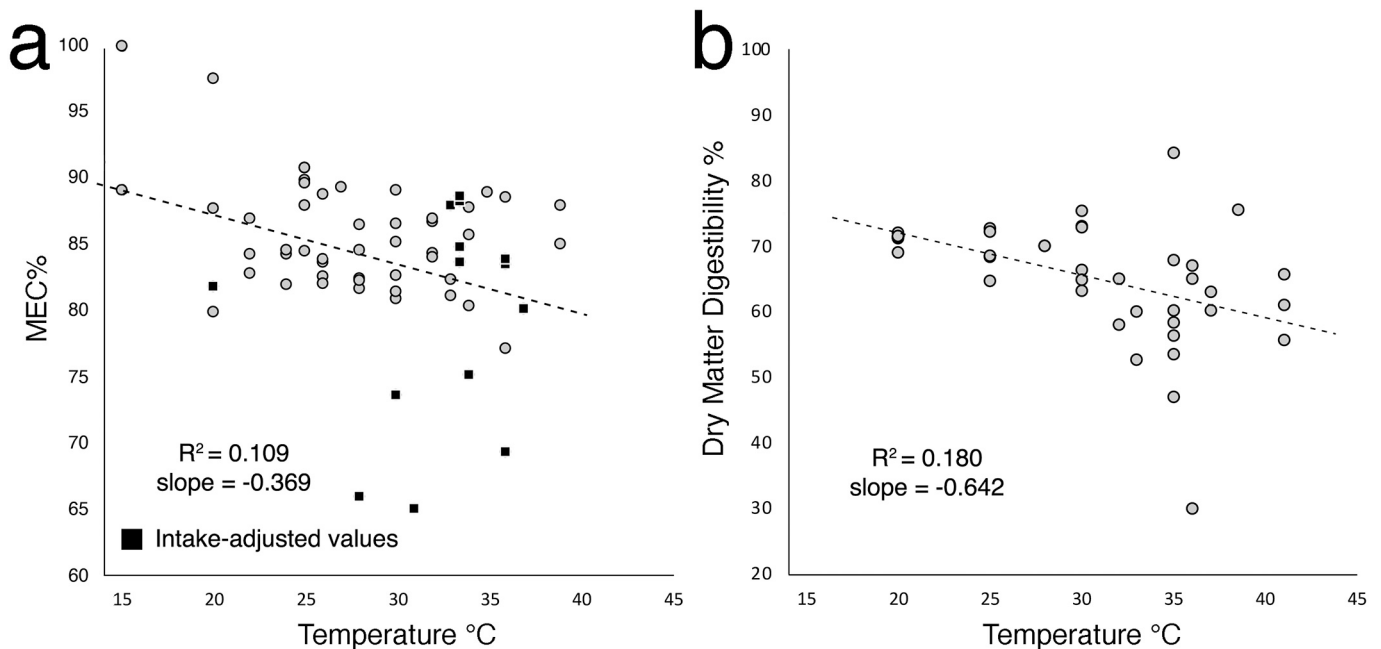
In using temperature data from studies not driven by thermal questions, our meta-analyses overrepresent temperatures that are close to predetermined species optima. To remove this artifact, we performed linear regressions of digestibility measures against temperature restricted to studies that included at least two temperature treatments per lizard species-treatment combination. This decreased our sample

pool to 21 studies, not all of which included each digestibility measure. As such, we considered ADE (19 studies, 21 species), MEC (11 studies, 12 species), and DM digestibility (4 studies, 8 species). Both MEC and DM digestibility showed negative relationships between digestibility and temperature (Fig. 4a,b; MEC slope =  $-0.369$ ,  $R^2 = 0.109$ ,  $P < 0.008$ ,  $F_{1,61} = 7.55$ ; DM slope =  $-0.642$ ,  $R^2 = 0.180$ ,  $P < 0.008$ ,  $F_{1,36} = 7.91$ ). That MEC shows some sensitivity to temperature while ADE does not implicates nitrogen metabolism. Beaupre et al. (1993) investigated this pattern, too, examining whether voluntary intake increases at higher temperatures and decreases at lower, and thus more feces are produced at higher temperatures. If the lizard is in a positive energy balance, the protein catabolism rate should remain proportionally similar. Thus, the proportion of energy consumed that is lost to urates does not change with temperature, even as urate production increases. The feces:urates ratio should track with temperature, leading to an increased MEC at low temperatures. Indeed, none of the thermal studies measuring MEC employ force-feeding, supporting this explanation.

To our knowledge, ontogenetic effects on digestive efficiency have only been studied in the context of plant eating. *Iguana iguana* are completely herbivorous from hatching. In the wild, hatchling, sub-adult, and adult iguanas preferentially consume different age classes of leaves (Troyer, 1984b). Though age classes of leaves have differing nutritional characteristics (e.g., young leaves have less fibrous components and more protein), hatchling, sub-adult, and adult iguanas display no differences in digestive efficiency across lizard age classes. Troyer (1984b) also proposes a model by which the hatchling iguanas meet their high relative energy requirements while having the same digestive efficiencies as adult iguanas:

$$\frac{\text{digestive efficiency} \times \text{protein intake}}{\text{transit time} \times \text{fiber intake}} = \frac{\text{energetic intake}}{\text{digestion time}} \quad (6)$$

Thus, a hatchling iguana that has a comparable digestive efficiency to adults and lower digesta transit times can select a diet that favors increased protein intake (even if that increases fiber) to match their increased protein requirements for high growth rates (see Troyer, 1984b, Table 8 for quantitative calculations). Additionally, these young iguanas may also be selecting diet types that decrease their exposure to toxic plant metabolites.



**Fig. 4.** Regressions of MEC (4a) and DM digestibility (4b) vs. average daytime temperature from studies that included multiple temperature treatments per lizard species. Each point is the average of digestibility for a species-treatment combination from a single study. Fig. 4a slope =  $-0.369$ ,  $R^2 = 0.109$ ,  $P < 0.008$ ,  $F_{1,62} = 7.55$ . Fig. 4b slope =  $-0.642$ , adj.  $R^2 = 0.180$ ,  $P < 0.008$ ,  $F_{1,36} = 7.91$ . No data in 4b have been adjusted for intake.

Although *Ctenosauria acanthura* (formerly *C. pectinata*) adults are primarily herbivorous, *C. acanthura* juveniles eat mostly insects. When fed pure diets of flowers, leaves, fruit, or insects that make up their natural diet, Durtsche (2004) reported that juveniles were 25% more efficient than adults at digesting insects, particularly insect protein, and that the juveniles were also generally better at digesting fruit than were the adults. Durtsche (2004) proposes this is due to the smaller particle size of their meals. Yet without considering the potential effects of intake amount (as discussed above), it is very difficult to compare adult and juvenile diets quantitatively. Still, *Croton suberosus* leaves, which posed no challenge to the adults compared to other leaves, killed 80% of the juveniles that fed on it. Adult *C. acanthura* may be able to digest the leaves toxic to juveniles due to biochemical physiology, gut microbes (e.g., Kohl et al., 2016), and/or a dilution of the leaves' effects due to the adults' larger size. Adult males and females also showed differences in their  $\text{Ca}^{2+}$  and P digestion, likely due to reproductive allocation needs, but also potentially due to intake, or behavior (e.g., social interactions affecting basking as suggested by Liwanag et al., 2018).

Insularity (island dwelling) appears to be correlated with higher digestive efficiencies in general. Protein digestion was highest in insular lacertid lizards compared to closely related mainland species (Pafilis et al., 2007). Indeed, the insular lizards were more closely related to the mainland species than to each other, suggesting that this higher digestion is an island effect. In feeding trials comparing *Lacerta trilineata* from two insular and two mainland populations, the island populations had higher overall digestive efficiencies, as well as higher digestive efficiencies of lipids, sugars, and proteins, effects that were not due to food transit time and thus were likely due to gut structure or biochemistry (Sagonas et al., 2015).

Snakes—Digestive efficiency and metabolizable energy in snakes has been succinctly reviewed in the introduction of Alexander et al. (2012), including a summary of efficiencies from 21 snake species (Table 2 in Alexander et al., 2012). As snakes are a monophyletic group nested within lizards, it is logical that their digestive efficiencies would follow similar patterns compared to other lizards. However, snakes, as an ecological group, are considerably constrained and can differ from lizards due to greater likelihoods of the following: venom, swallowing prey whole and consuming large meals, low feeding frequency, and vertebrate-based diets (Greene, 1997; Colston et al., 2010). Most studies on snakes' digestion have used diets of mice or rats in their investigations, which generally reveals digestive efficiency ratios for snakes that are comparable to those of insectivorous lizards (as there are no herbivorous snakes), ranging from 83 to 98% (Greenwald and Kanter, 1979; Bedford and Christian, 2000; Sievert et al., 2005; Chu et al., 2009; Beaupre and Zaidan III, 2012), but as low as 73% in *Trimeresurus stejnegeri* (Chu et al., 2009). Ratio-based MEC of mouse and rat diets were generally 3–8% lower than ratio-based ADE (Bedford and Christian, 2000) ranging 75–97% in normal lab conditions (Vinegar et al., 1970; Greenwald and Kanter, 1979; Bedford and Christian, 2000; McCue, 2007; Tsai et al., 2008; Chu et al., 2009; LaBonte et al., 2011; Alexander et al., 2012; Beaupre and Zaidan III, 2012; Bonnet et al., 2013). Bedford and Christian (2000) point out that snakes that are sit-and-wait predators feed infrequently, so it is necessary for them to be highly efficient digesting their meals to meet their energy requirements.

Hair played a large role in decreasing digestibility, even with such low overall energetic losses to feces and urates. When mice with hair removed were fed to seven species of Australian pythons (*Antaresia childreni*, *A. stimsoni*, *Morelia spilota variegata*, *Morelia s. spilota*, *Aspidites melanocephalus*, *Liasis fuscus*, and *L. olivaceus*), metabolizable energy jumped up by ~10%, reaching a 99.8% ADE ratio (Bedford and Christian, 2000). LaBonte et al. (2011) attribute their findings of much higher metabolizable energy for *Crotalus oreganus helleri* (compared to other studies of similar venomous snakes; McCue, 2007; Chu et al., 2009) to their use of younger, less hairy mice as prey items. For *Hemachatus haemachatus*, frogs were much more digestible than intact mice, but comparable to mice with hair removed (Alexander et al., 2012).

Adaptation to specialized diets can also play a role in metabolizable energy. In an interesting example, individuals of *Thamnophis elegans* from a generalist fish-eating population and a specialist slug-eating population were fed their natural diets or were switched to the other population's diet (i.e., fish eaters fed slugs and vice versa) in the laboratory. No differences in digestive efficiency were detected among the populations when consuming fish, yet the snakes from the slug-eating population digested slugs significantly better than snakes from the fish-eating population (Britt et al., 2006). Thus, some unknown alterations of gut structure or function allowed the slug-eating population to better use their molluscan diet.

Two studies tested the effect of meal size on assimilability. Meals of 10 or 20% of the snakes' body mass did not produce any differences in digestibility ratio (Bedford and Christian, 2000; Tsai et al., 2008). Metabolic rate increased linearly with these increasing meal sizes, leading to a constant proportion of the energetic intake to the cost of digestion. However, a meal of ~30% of the snakes' body mass increased MEC by 6% in *Trimeresurus stejnegeri stejnegeri*, likely due to a nearly doubled gastric-retention time with consumption of such a large meal (Tsai et al., 2008). (It's unclear if these findings are vulnerable to being artifacts of ratio-based analyses as Tsai et al. (2008) used ANCOVAs with appropriate covariates in their study, but did not clearly state that these analyses were used for their ME comparisons.) Snakes, particularly pythons, have been used to model the metabolic costs of digestion and assimilation in the context of feeding frequency and meal size. Metabolic rates increase with larger meals (McCue, 2006). For example, *Python bivittatus* (published as *P. molurus*) have been measured to increase their metabolic rates 43-fold over their resting metabolic rate after consuming a meal of 100% the snake's body mass (Secor and Diamond, 1997). However, a maximum 5- to 8-fold metabolic rate increase has been more commonly observed across studies (Wang and Rindom, 2021). This postprandial metabolic increase is known as Specific Dynamic Action (SDA), Heat Increment of Feeding (HIF), Thermic Effect of Food (TEF), and Dietary Induced Thermogenesis (DIT) (see Secor and Diamond, 2000; Secor, 2001; Tsai et al., 2008); however this topic is vast and cannot be done justice within the scope of the current review. It is extensively reviewed in Andrade et al. (2005), McCue (2006), Secor (2009), and Wang and Rindom (2021). It is worth noting, however, that since SDA is often expressed as a ratio to snake body mass and meal size, it is susceptible to the same ratio-based analysis errors as are common for digestibility (Beaupre, 2005).

Researchers have postulated that venom contributes to snakes' digestion of their prey. An early study (Thomas and Pough, 1979) using five species of non-venomous Colubrids claimed to find increased digestion of venom-dosed mice vs. control mice that the snakes had been forced to regurgitate after 24 h. Their assessment of digestion, however, was based on qualitative scoring of the regurgitated mouse's appearance and inferred rate of digestion based on whether the ingested mouse could be recovered. Two later studies of venomous snakes found no differences in MEC or ADE of prey dosed with venom versus unmanipulated prey (McCue, 2007; Chu et al., 2009). Further investigations comparing prey envenomated with adult and juvenile venom yielded no differences in energy assimilation of the meal (LaBonte et al., 2011). Thus, venom likely does not aid digestion in venomous snakes.

Like in lizards, snakes generally show no differences in digestive efficiency or metabolizable energy at different temperatures (Greenwald and Kanter, 1979; Bedford and Christian, 2000; Tsai et al., 2008; Alexander et al., 2012; Beaupre and Zaidan III, 2012). However, when snakes were too cold (20 °C and below, depending on species) digestion is likely to halt all together (Henderson, 1970; Tsai et al., 2008) and regurgitation is common (Bonnet et al., 2013). When allowed to thermoregulate, digesting *Pantherophis guttata* preferred warmer temperatures than did fasting snakes (Sievert et al., 2005), though the temperatures they picked varied seasonally (Greenwald and Kanter, 1979). Since digestive efficiency does not increase with warmer temperatures, yet metabolism (and thus metabolic costs) does, considering digestibility alone would

lead to hypotheses that to conserve energy, snakes would choose a low temperature at which digestion is still possible. This does not appear to be supported (Greenwald and Kanter, 1979; Sievert et al., 2005), suggesting that optimizations other than digestive efficiency are of greater importance to snakes' nutritional budgets. For example, intake and digesta processing rates increase with temperature (reviewed in Dan-drifosse, 1974; Skoczylas, 1978; Stevens and Hume, 2004), decreasing transit time. Decreased transit time can allow the snake less costly locomotion and defense, as well as the potential to feed again sooner. Still, increased metabolic expenditure of foraging, prey capture, and digestion may add to the increased metabolic burden of a warmer snake. Assessing the metabolic balance of these variables is a necessary and contextual undertaking to evaluate a snake's nutritional ecology (Sievert et al., 2005; Alexander et al., 2012; Beaupre and Zaidan III, 2012), deserving of a review of its own.

**Turtles**—Work on the digestive efficiency of turtles primarily focuses on plant eating clades (see Bjorndal, 1987, Table 2 for a summary of digestive efficiency and digestibility of fiber, OM, and nitrogen in six turtle species). Strict reptilian herbivores have lower plant digestibility than mammalian ruminants (see Franz et al., 2011 for a review of this comparison), but can be functionally as effective at digesting plant material as sheep (Bjorndal, 1979; Zimmerman and Tracy, 1989; Bjorndal, 1997; Franz et al., 2011) due to increased intakes and transit times in turtles. Depending on specific diet items and ecological conditions, both herbivorous and omnivorous turtles digest ~65–85% of the OM in leaf-based diets (Bjorndal, 1979; Bjorndal, 1980; Bjorndal, 1987; Bjorndal et al., 1990; Bjorndal and Bolten, 1993; Hailey, 1997; Bouchard and Bjorndal, 2006a, 2006b; Amorocho and Reina, 2008; Franz et al., 2011).

Omnivorous turtles such as *Trachemys scripta* have served as a model for investigations of non-additive effects of mixed plant/ animal diets (Bouchard and Bjorndal, 2006a; Bouchard et al., 2010). While turtles are more efficient bite-for-bite at digesting animal material (85–97% OM digestibility; e.g., Bjorndal, 1991; Bouchard and Bjorndal, 2006b; Amorocho and Reina, 2008), they often accommodate plant diets by greatly increasing intake (Bjorndal and Bolten, 1993). The mixture of dietary items with different transit times (e.g., fibrous plants, animal material) can negatively or positively affect digestive efficiency though increasing or decreasing the time the digesta is exposed to endogenous enzymes or enteric microbes, depending on proportions of each item (Bouchard and Bjorndal, 2006a; Bouchard et al., 2010). Mixtures of dietary items can also remodel the gut microbiome, rendering a greater or lesser role in digestion, and changing the chemical environment of the gut (e.g., addition of insect larvae making more nitrogen available for microbial growth). Experiments using pure diets of duckweed or shrimp, or diets of different proportions of duckweed and shrimp showed no effect on transit time or measures of fiber fermentations. However, digestibility of a 67% duckweed: 33% shrimp diet exhibited a marked decrease, and the digestibility of a 14% duckweed:86% shrimp diet an increase in digestibility in comparison to expected digestibilities (Bouchard and Bjorndal, 2006a). These ratio-specific findings suggest each nutrient or factor can experience additive positive or negative effects in different ecological conditions. Often omnivores choose to eat more low fiber plant material (Hailey, 1997; Stone and Moll, 2006; Wilson and Lawler, 2008; McMaster and Downs, 2008; Hazard et al., 2010) such as fruits or flowers as their primary energy sources, and supplement with more fibrous plant material (e.g., leaves) as protein sources (Bjorndal and Bolten, 1993). This strategy can lead to increased digestive efficiencies compared to a higher fiber diet.

Young turtles are better than adults at digesting animal material and have equal efficiencies on plant diets (Bjorndal and Bolten, 1992; Bouchard and Bjorndal, 2006b). Often young ingest more food and have smaller food particle size due to a smaller bite, yet they also have the tradeoff of a smaller, shorter gut overall, meaning decreased gut surface area, volume, and digesta transit time. Increased fiber consumption correlates with general decreased digestibility of any diet (Karasov and

Martínez del Río, 2007), thus leading to decreases in growth rate (Hatt et al., 2005). A lower growth rate may be less advantageous for hatchlings, but is also correlated with increased fitness in the long term, possibly deriving greater benefit for adult turtles (Hatt et al., 2005).

As many turtle species are experiencing considerable population declines (Lovich et al., 2018), hatchling headstart programs are a popular conservation tool. Thus, understanding the specific nutritional physiology of young turtles and reproductive adults is integral to contributing to their survival. *Chelonia mydas* (Green Sea Turtles) can more efficiently digest commercial diets than their wild diets (Wood and Wood, 1981; Hadjichristophorou and Grove, 1983; Kanghae et al., 2014). Mineral supplementation can increase digestibility further—added calcium increased digestibility of calcium and magnesium for two tortoises (*Testudo hermanni*, *Geochelone nigra*) on a captive diet, with no ill effects of over-supplementation (Liesegang et al., 2001; Liesegang et al., 2007). A third tortoise, *Gopherus agassizii*, also increased calcium digestibility as their dietary calcium increased (Hazard et al., 2010), in contrast to the opposite relationship of decreased calcium digestibility with increased dietary calcium observed in many mammals (Robbins, 1993).

Disruption of a turtle's native habitat and diet can lead to decreased micronutrient availability. For instance, Hazard et al. (2010) calculated that adult *Gopherus agassizii* feeding on a diet of invasive plants might only obtain 40% of the calcium they could acquire from a native plant diet. Expanding upon this calculation, *G. agassizii* eating an invasive diet may only be able to produce four eggs per year instead of a possible 10 eggs on a native plant diet (Hazard et al., 2010). These studies highlight the importance of micronutrient interactions in understanding turtle nutritional physiology as a whole.

**Crocodylians**—Most studies on crocodylian digestive efficiency are in the context of crocodylians in aquaculture. For example, Garnett (1988) investigated *Crocodylus porosus*' digestive efficiencies on multiple meat diets, finding no discernable differences in effects of those diets on the digestive efficiency in protein, fat, nor energy assimilation. Reigh and Williams (2013) investigated *Alligator mississippiensis* digestive performance with protein found in commercial alligator diets. They supplemented standard diets with 30% and 45% of either fish meal or high- or low-protein plant products, finding the alligators had different energy, protein, and amino acid assimilation on the different diets (as estimated via a tracer ingredient). Yet, despite these differences, the alligators still had very high digestibility of each of these constituents, including >90% availability of amino acids, regardless of diet. In this clade, the effects of dietary fat on protein digestibility, however, has shown both an inhibitory effect (Garnett, 1988) and a positive relationship (Coulson et al., 1987; Staton et al., 1990a). Staton et al. (1990a) attributed the positive effect of fat on protein digestion to an overall increase in transit time. While crocodylians have lower digestibility of dietary fats than they do proteins (Garnett, 1988), they store high proportions of the fat they do digest (Garnett, 1988; Reigh and Williams, 2013).

Prior to Staton et al. (1990a), it was thought that alligators could not digest plant material. Staton et al. (1990b, 1992) went on to show that alligators could in fact achieve high digestive efficiencies of diets containing corn, especially if the corn had been cooked and processed. The addition of small amounts of low-soluble carbohydrates did not decrease the alligators' ability to extract maximum nutrients from their diet. A 2022 review of plant-based nutrition in crocodylians (Hileveski et al., 2022) provides a thorough overview of evidence that crocodylians can and do eat plants—both in natural settings and in aquaculture. Indeed, supplementing *Caiman latirostris* diets with 20–45% soybean meal increased nutrient digestibility overall, although over 45% soybean meal in the diet contributed to a decrease in digestibility and animal growth (Hilevski and Siroski, 2021).

Across crocodylians, species and even different age classes appear to use varying digestive strategies based on temperature and other ecological factors. Of note is the hypothesis in Davenport et al. (1992)



that the lack of gastroliths is a major contributor to their observations that *Caiman crocodilus* eats less, takes longer to digest, and has lower protein, energy, and dry mass digestive efficiency than the gastrolith using *Crocodylus porosus*, suggesting that physical processes have a role *C. porosus*' digestion. Overall, Crocodylians are probably the second-least studied group of the herpetofauna. We, therefore, call for more studies of digestive efficiency within this group.

### 3. Conclusions

Reptiles' digestive success with the diets available to them is a key determinant of their overall success in their environments. As many of the examples surveyed in this review show, reptiles generally are very efficient at extracting energy from their food and so may have the ability to accommodate dietary challenges in the short-term when energy availability is the most important determinant of fitness. However, our understanding of how well reptiles meet their other nutritional needs (e.g., protein balance, vitamins, minerals) is still rather rudimentary in most contexts. Thus, we make the following recommendations:

- 1) Analyze digestibility as the energy or nutrient output (feces) covaried with its intake. As called for and well-justified by earlier works (Beaupre and Dunham, 1995; Raubenheimer, 1995), the analysis of ratios has the potential for significantly confounding results. When applicable, collect data and meta-data for other potential covariates (e.g., body mass, dietary fiber content, age) and test for their influences on the "parent variables."
- 2) More digestibility studies including analyses of macronutrients. Such data will allow for better integration of investigations of diet with other aspects of physiology. Even including measures of DM digestibility will allow for greater use of datasets across practitioners (especially combined with ADE or ME), as this is something that can be measured outside of a laboratory setting and may facilitate improved modeling of energetics across systems.
- 3) Collect data on voluntary intake, transit time, and body temperature. While not all these measures are possible for each system, their inclusion makes for much a more robust interpretation of the entire digestive process.
- 4) Studies of nutrient acquisition and use across the range of population experiences. The fitness of a population is more than just daily survival. As illustrated in Table 1 and Supplemental Table S1, consideration of sex is missing from many studies. Often if sex is specified, it is in that females have been excluded from the study due to potential reproductive effects (e.g., Harwood, 1979; Van Damme et al., 1991; Wehrle et al., 2020). Unfortunately, in considering males the default for observing digestive parameters, we may be missing important effects, reproductively-related or otherwise. (Although, males also contribute to reproduction, as well as reproduction is surely important to fitness!) Indeed, when feeding *Iguana iguana* a diet of flowers, Durtsche (2004) reported considerable differences in protein and mineral digestibility by sex. Additionally, given the presence of stark sex differences in gut structure and function in populations of *Podarcis siculus*—with differing natural diets, but no accompanying sex differences in stomach contents or tissue isotopic signatures—the question of whether these mechanistic differences translate to aspects of digestive performance remain unanswered (Wehrle, 2018; B. Wehrle et al., unpublished data).

In addition to reporting sex, measuring digestibility in controlled ways across populations (e.g., Beaupre et al., 1993; Angilletta, 2001) and ages (e.g., Essghaier and Johnson, 1975; Bouchard and Bjorndal, 2006b) will aid in the construction of more precise models for use in physiology, ecology, and conservation.

- 5) More studies explicitly testing the effects of temperature on digestion. Although forays have been made into this topic regarding lizards, greater taxonomic representation is needed, with special focus on environments projected to experience much greater fluctuations

in temperature than historically observed. The status of the Temperature Constraint Hypothesis remains unresolved in reptiles and due to the conflicting findings across temperature studies and digestibility measures, a much larger data set is necessary to identify the context(s) in which temperature does or does not affect digestive performance. Ideally, experiments of temperature-digestion interaction would span thermal pejus limits, if those have already been assessed for other characters (e.g., sprint speed), and include fine enough temperature coverage to detect performance decreases that occur at temperatures intermediate to the lowest and highest temperatures used in the study (e.g., the patterns measured by both Qu et al., 2011; Chen et al., 2003). Indeed, such experiments would be a constructive in testing the Multiple Optima Hypothesis (Huey, 1982; Van Damme et al., 1991; Twiname et al., 2020). It is also key that digestibility studies without intentional temperature manipulation should measure and report temperature data, including that from heat-lamps, so that their findings may be better contextualized. Roughly 20–30% of the studies we surveyed did not characterize temperature in ways that we could compare across systems. Modern temperature loggers are becoming more affordable and available in assorted styles, making collection of robust temperature data ever more accessible.

- 6) While the most pressing issues affecting the quality of digestibility data for reptiles are primarily need for standardization of methodology, analysis, and reporting, future endeavors will eventually need to address phylogenetic and ecological bias. In this review we identified a rich literature on digestive performance in lizards, but with haphazard representation of clades. In addition to unbalanced coverage, different experimental methods both within and among experimental systems make for difficult broader comparisons.

Snakes generally exhibited high digestive efficiencies overall, but different feeding strategies and non-mammalian diets are under-represented in the literature. As turtles are particularly vulnerable to decline, and are the focus of many conservation efforts, we recommend that future studies incorporate more ecological variables such as temperature and fluctuating habitat conditions to best ensure that digestive tools are functioning as expected in challenging and changing environments. We identified a particular dearth of digestibility information on crocodylians (particularly outside of farming contexts) and tuataras. Tuataras, being both evolutionarily unique and resident in colder environments than many reptiles, would be an especially interesting addition to our understanding of reptile digestion as a whole.

### Data accessibility

All data used within the manuscript, figures, and supplemental material are summarized in Supplemental Table S1.

### Author contributions

BAW and DPG contributed to all facets of this project and the writing of the manuscript.

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### CRediT authorship contribution statement

**Beck A. Wehrle:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Donovan P. German:** Conceptualization, Methodology, Resources, Supervision, Writing – review & editing.



## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The data used in the analyses are all contained in the supplemental table included with the manuscript.

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## Appendix A. Supplementary data

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## Glossary

Although definitions refer to fractions, all digestibility variables are presented as percent in this review.

**Apparent:** denotes that material in feces is not just wastage from digesta but also includes sloughed enterocytes and microbes, making true digestibility somewhat higher than it is measured.

**Digestibility or Digestive Efficiency:** general term for the fraction of a substance available from ingested food and not lost to feces.

**ADE:** Apparent Digestive Efficiency, also called **Apparent Digestive Coefficient (ADC)**, proportion of energy available from the diet that is not lost to feces.

**ME:** Metabolizable Energy, the energy available from the diet that is not lost to feces and urates combined. This measure is intended to approximate the net energy the animal assimilates, the energy content of the meal minus the sum of the energy lost in feces plus the energy it takes to metabolize the food. **Metabolizable Energy Coefficient (MEC)** or **Apparent Assimilation Efficiency (AAE)** are the terms for ME with as a proportion of ingested energy.

**DM digestibility:** Dry matter digestibility, based on the masses of both ingesta and feces that have had all water removed.

**OM digestibility:** Organic Matter digestibility, based on the dry mass loss of ingesta and feces

after each have been combusted into ash. The carbon combusts, removing all organic compounds and leaving the indigestible fraction, producing a more accurate measure of how much of the food that theoretically could be absorbed is absorbed.:

**NDF:** Neutral Detergent Fiber, hemicellulose, cellulose, lignin:

**ADF:** Acid Detergent Fiber, cellulose, lignin:

**Digestible fiber:** fibrous plant material such as hemicellulose that can be digested by gut microbes. Often calculated as NDF-ADF.:

**Feces:** the excreted waste of ingested material that has not been absorbed through the gut wall, plus sloughed enterocytes and microbes:

**Digesta:** ingested material that is in the process of being digested in the alimentary canal but has not yet left it. Can be found in any portion of the digestive tract in varying states of breakdown, until it leaves the body.:

**Urates:** nitrogenous wastes that are primarily the product of protein catabolism, as collected via the renal system. In most reptiles this consists of a densely packed, chalky pellet or paste of uric acid.:

**Intake:** the type of material, quantity, or rate that an animal ingests, either voluntarily (i.e., feeding in the wild, experimental conditions allowing for ad libitum or free feeding on a set amount) or involuntarily (i.e., force-feeding):