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The effect of weight and prey species on gut passage time in an endemic gecko *Quedenfeldtia moerens* (Chabanaud, 1916) from Morocco

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Abstract. Gut passage time (GPT), a key factor in digestive procedure, is of pivotal importance for digestion. Several parameters may affect GPT, such as temperature, length of gastrointestinal tract and body size. Here, we examine the influence of prey weight and prey species on GPT in the endemic diurnal gecko *Quedenfeldtia moerens,* from the Anti-Atlas Mountains in central Morocco. We used two prey species, house crickets (*Acheta domesticus*, AD) and mealworms (*Tenebrio molitor,* TM). Lizards were fed with the larval stage of TM and nymphs of AD. The influence of prey weight and prey species was tested at a constant temperature. We used three weight classes of each prey species to test the influence of prey weight on GPT. Our results showed that prey species affected GPT in a distinct way: mealworms induced a longer gut passage time compared to house crickets. Moreover, GPT increased with the increasing weight of prey for both prey species. Our finding demonstrates that the effect of prey species and prey weight affect digestion and thus should be better clarified in future studies.

Keywords. GPT, prey weight, *Acheta domesticus, Tenebrio molitor*, *Quedenfeldtia moerens*, Morocco.

INTRODUCTION

Given that digestive activity regulates energy flow to animals, effective digestion is a prerequisite for survival (Karasov and Douglas, 2013). Among the many important parameters that shape the digestive repertoire of animals, the time required for food to pass through the gastrointestinal tract from consumption to defecation, known as gut passage time (GPT) stands out (Hume, 1989; Van Damme et al., 1991). GPT shapes digestive efficiency, as increasing the time food remains in the gastrointestinal tract provides more time for effective digestion (Van Damme et al., 1991; Alexander et al., 2001).

GPT may be affected by numerous factors in lizards, among which temperature is maybe the most important. Indeed, GPT is temperature-dependent and varies from few hours to several days (Christian et al., 1984; Karasov et al., 1986), decreasing with increasing temperature (Du et al., 2000; Pafilis et al., 2016, 2007; Sanabria et al., 2020). The reptilian digestive system is characterized by high plasticity and reptiles can control the time food remains in the gut (Herrel et al., 2008; Sagonas et al., 2015), by elongating the gastrointestinal tract and thus increasing GPT (Sagonas et al., 2015; Vervust et al., 2010; Pafilis et al., 2016). Furthermore, the existence of specialized digestive microstructures, such as cecal valves, may prolong the time it takes

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for food to pass through and boost GPT (Herrel et al., 2008; Sagonas et al., 2015). Furthermore, GPT may also be influenced by age (Karameta et al., 2017a) or tail autotomy aftermaths (Sagonas et al., 2021; 2017).

Here we aim to clarify whether prey characteristics have an effect on gut passage time. To this end, we assessed the impact of prey weight and prey species on the GPT of the Atlas day gecko. We expected that the increasing size of a given meal (prey weight) would consequently prolong GPT. We also predicted that different prey species would distinctly affect GPT.

MATERIALS AND METHODS

Study species

The Atlas day gecko (*Quedenfeldtia moerens*) (Chabanaud, 1916) is a small diurnal lizard, belonging to the Moroccan endemic genus *Quedenfeldtia* of the Sphaerodactylidae family. It is widely distributed in the Atlas Mountains, from 10 to 2,700 m above sea level. The study population originates from the Anti-Atlas Mountains (29°51'N, 09°01'W; 1.900 m a. s. l.). During a field survey in February 2020, we captured, by noose, 12 adult males with snout-vent length (SVL) between 40 and 48 mm (mean ± SD = 45.43 ± 1.85) and weight ranging from 2 to 3 grams (mean ± SD = 2.76 ± 0.08).

Prey species and marking technique

Captured lizards were transferred to the laboratory and housed individually in transparent plastic terraria (11 x 17 x 7 cm^3), with *ad-libitum* access to water. All lizards were maintained in natural photoperiod and acclimated, for two weeks, inside a temperature-controlled room (25 ± 1°C) (Sagonas et al., 2021; 2017). Prior to the experiment, we fed the lizards with house crickets (*Acheta domesticus,* AD) nymphs and mealworms (*Tenebrio molitor,* TM) larvae to familiarize them with the specific prey items. Both insect species originated from an in-house breeding colony.

To test the effect of prey species on GPT, we selected AD nymphs and TM larvae. In order to evaluate the effect of prey weight on GPT, we categorize three weight classes for each prey species (in total six feeding regimes, three weight classes for TM and three for AD). For TM larvae we distinguish three classes, in ascending order of weight (mean ± SD): L1 (0.013 ± 0.0019 g), L2 (0.033 ± 0.0017 g) and L3 (0.064 ± 0.0036 g). For AD nymphs, the respective weight classes were: N1 (0.032 ± 0.0035 g), N2 (0.065 ± 0.0047 g) and N3 (0.1 ± 0.0057 g).

Gut passage time

Prior to the experiment trials, food was withheld from lizards for three days, until no feces were found in the terraria (Sagonas et al., 2017). Then, we marked the prey items before feeding them to lizards. Prey items are typically marked with small pieces of plastic (PVC) that serve as indigestible markers (Van Damme et al., 1991; Pafilis et al., 2007). To avoid possible injuries to gecko's digestive tracts because of their small body size, we marked prey species using soft thread tied around the abdominal-thorax junction of the insect prey (Fig. 1). We fed all 12 lizards with the marked prey. Terraria were inspected every hour for the appearance of the marker. After the detection of the marker, we withheld food for another three days. After this period, we repeated trials by feeding lizards with other prey species and weight classes. At the beginning of each trial, we noted the lizard code, the prey species and weight class. Gut passage time was determined as the time elapsed from the consumption of the marked prey to the defecation of fecal pellets with the marker (Van Damme et al., 1991). Each lizard was tested six times (with feeding regimes L1, L2, L3, N1, N2 and N3) and respective GPTs were recorded. Using this specific protocol, all lizards are tested identically, thus minimizing noise associated with individual particularities.

Statistical analysis

We constructed mixed-effects models in R (version 4.1.1; R Core Team 2021) using the package lme4 (v1.1-15; Bates et al., 2015) with prey species (two levels) and prey weight (continuous covariate) as fixed effect factors (including the interaction between them). To avoid pseudo-replication, we included the lizard's ID as a random effect factor. We used quantile-quantile plots and residual plots to check the models' assumptions, and we assessed the significance of both comparisons using the Anova function in the package car (Fox and Weisberg, 2019) with type II sums of squares and the chi-square test statistic.

RESULTS

The marker used in the present study was effective and the thread tied around the prey was easily visible in fecal pellets from both prey species (Fig. 1F). Before comparing the effect of prey species on GPT, feeding regime to lizards were classed on three weight classes each (Table 1). The variance explained by the random effect (lizard ID) was nearly equal to 0, which means that the major

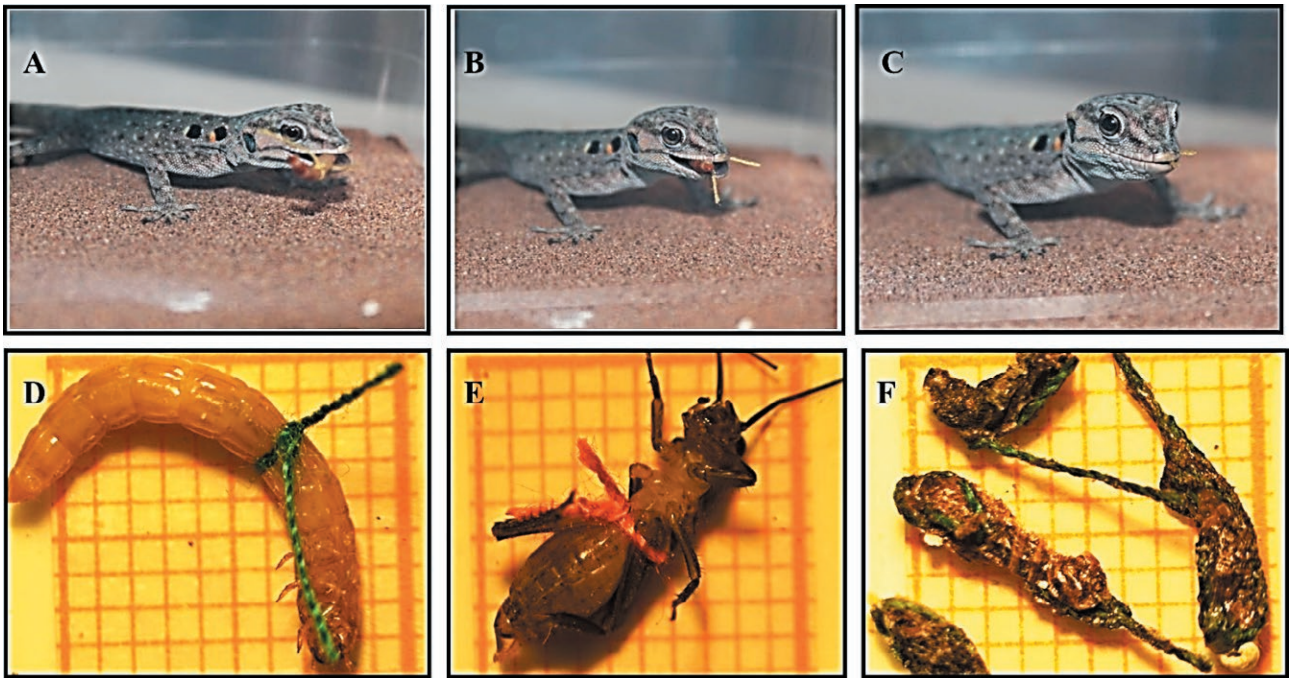

Fig. 1. (A to C): successive photos showing Atlas day gecko *Quedenfeldtia moerens* eating a marked mealworm larva. (D and E): the technique used to mark prey (here respectively mealworm larva and house cricket nymph); a thread was tied to prey as shown in photos. (F): fecal pellets where the marker (the thread tied around the prey) was clearly visible.

Table 1. Variation on gut passage time, GPT (mean ± SE), as a function of the prey species and prey weight classes in *Quedenfenldtia moerens*. (N: nymph, L: larvae. Numbers 1 to 3, designed the weight class of each prey species).

Prey species/ class	Mean weight (g)	Weight range (min-max)	GPT (hour)
Crickets/N1	0.03083	0.024 -0.039	48.20 ± 2.99
Crickets/N2	0.0656	0.054 - 0.074	51.69 ± 2.18
Crickets/N3	0.1000	0.090 - 0.100	70.96 ± 1.50
Mealworm/L1	0.0130	0.010 -0.016	51.25 ± 4.07
Mealworm/L2	0.0320	0.029-0.036	58.16 ± 1.82
Mealworm/L3	0.0650	0.059-0.072	79.14 ± 2.94

part observed in our dependent variable was linked to the fixed terms in our model. Prey weight significantly affected GPT (χ^2 = 54.97, P < 0.01). GPT was negatively correlated to prey weight (R = 0.95): the heavier the prey, the more time food remained in the digestive tract. Furthermore, prey species did affect significantly GPT (χ^2 = 56.43, P < 0.01): GPT was longer for mealworms than for crickets. Finally, the interaction between prey species and their weight was significant and positive (χ^2 = 4.49, P = 0.034). This finding indicates that feeding on heavier prey had a stronger effect on GPT for mealworms than for crickets (Fig. 2).

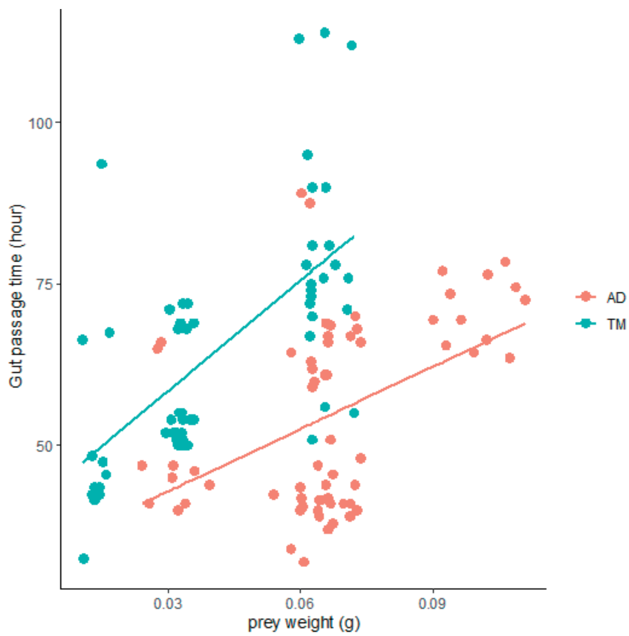

Fig. 2. Variation in the gut passage time (GPT) in hour as a function of increased weight of prey consumed by the Atlas day gecko *Quedenfeldtia moerens*, (TM) for mealworm as prey and (AD) for house cricket as prey. Solid lines represent the regression line for each prey species predicted by linear mixed model.

DISCUSSION

Digestion, a crucial function for nutrient absorption, rules energy acquisition (Karasov et al., 2011). There are many parameters affecting the digestive performance in lizards and, as mentioned above, gut passage time (GPT) is one of them (Pafilis et al., 2016; Sagonas et al., 2017; Karameta et al., 2017b). The latter may be affected by many intrinsic and extrinsic factors such as temperature, length of the gastrointestinal tract, body size and age (Van Damme et al., 1991, Du et al., 2000; Pafilis et al., 2016; 2007; Sanabria et al., 2020). In this study we found that GPT is also influenced by prey weight and prey species.

Gut passage time is a general indicator of the digestive process that measures the time that food remains in the gastrointestinal tract, a period which is decisive for digestive efficiency (Pafilis et al., 2007). Interestingly, though the impact of prey species and prey weight is known to influence overall digestion (Johnson and Lillywhite, 1979; Starck and Beese, 2001), the (presumable) impact of the aforementioned prey features on GPT has not been investigated. In this study, we selected two species typically used in captive lizard breeding (*Tenebrio molitor* and *Acheta domestica*) that have been analyzed in previous studies, thus allowing a comparative framework (Pafilis et al., 2016; Sanabria et al., 2020; Miller et al., 2013).

According to our results, GPT was significantly longer after the consumption of *T. molitor* than of *A. domestica* (Table 1). This finding could be attributed to the different energy content and chemical composition of the two prey species. Indeed, previous studies focusing on the nutritional composition of invertebrate prey found that TM larvae contained more than double metabolizable energy (2056 Kcal/Kg) than AD nymphs (949 Kcal/Kg) (Finke, 2002; 2015). Additionally, TM larvae have been reported to be richer in fat and proteins (134 g/Kg and 187 g/Kg, respectively) than AD nymphs (33 g/Kg and 154 g/Kg, respectively). In contrast, AD nymphs had higher water content than TM larvae (77.1% vs 61.9%). Furthermore, lizards fed with mealworms ingested significantly more energy, had significantly higher food conversion efficiencies, higher daily gains in mass, and greater total growth in mass than lizards fed on crickets (Rich and Talent, 2008). It seems that the nutrient and energy rich TM meals require more time compared to AD to get effectively absorbed. The observed difference in GPT between the two prey species could be explained by an adaptive strategy of the focal gecko to nutrient and energy rich prey. TM larvae contain more energy than AD nymphs, so lizards increase GPT to maximize the gain of this energy.

Prey weight also had an impact on GPT. Higher prey weights resulted in increased GPT in both cases of the two tested prey species. There was a linear correlation between the prey weight classed and GPT, with L1 and N1 (the lighter weight classes) resulting in lower GPTs and L3 and N3 (the heavier weight classes) inducing higher GPTs (Fig. 2). This should come as no surprise. Animals need more time to digest larger meals (Karasov and Del Rio, 2007) and thus the increase of prey weight dictates a considerable prolongation of GPT. The extra time provided by the longer GPTs offer gastric enzymes more time to act on ingested food and thus absorb more nutrients and energy (Alexander et al., 2001).

The GPT values found here are comparable with those reported in previous studies. Mean GPT for AD varies between 48.2 and 70.96 hours, while the respective values for TM are somewhat higher (51.25-79.14 hours). GPT may vary with the family: in lacertids, GPT receives values between 36-85 hours (Zhang and Ji, 2004; Vervust et al., 2010; Sagonas et al., 2015; Pafilis et al., 2016), in cordylids between 20-32 hours (McConnachie and Alexander, 2004), in skinks between 45-74 hours (Du et al., 2000) and in agamids between 67-86 hours (Karameta et al. 2017a). Those differences should be attributed to different body sizes and also distinct phylogenetic histories. More studies on sphaerodactylids will enrich the respective literature and give the opportunity for a comparative approach in saurian digestion.

Temperature greatly affects digestion and GPT represents no exception (Van Damme et al., 1991; Pafilis et al., 2007). Gut passage time decreases with increasing temperature (Du et al., 2000; Pafilis et al., 2007). Our experiment took place exclusively in 25°C, hence we cannot assess the impact of temperature on digestion under different feeding regimes (prey species and weight). In a future study we plan to assess this very important aspect of digestion process.

To conclude, this study shows that prey species and weight affected gut passage time in *Q. moerens*. More studies on digestive efficiency, including other variables such as temperature and apparent digestive performance would be valuable. Moreover, a comparative study between lizards from different populations will shed more light on the ecology of this Moroccan endemic diurnal gecko.

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