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Estimating food and water intakes by the herbivorous Moroccan *Uromastyx nigriventris* using a calibrated faecal output method and microhistological analyses

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Abstract. The Moroccan Spiny-tailed lizard *Uromastyx nigriventris* is a desert agamid species distributed from western Algeria to Morocco northeast to southwest of the Atlas range. In spite of a few studies investigating its dietary habits information regarding the daily food intake rate of this non-drinking desert species under natural conditions is lacking. Our study aimed at assessing the daily food consumption in spring and autumn calculated as dry matter intake (DMI), using calibrated faecal and nitrogenous waste outputs collected during 12 days from unfed wild-caught adult lizards originating from a desert area in southeastern Morocco. We used microhistological analyses to identify plant fragments in faecal pellets. Percentages of dry weights of individual plant species in individual diets were estimated from their fragment density, using the Sparks and Macheleck's conversion method. The obtained results indicate that these herbivorous lizards fed on a total of 18 different plant species belonging to 17 genera and nine plant families depending on the season. The total faecal and nitrogenous waste outputs were significantly correlated to the DMI of captive lizards. The combination of the two methods along with the moisture content of the plant species consumed allowed estimating the lizards' daily water intake rate (WIR). Estimated values of both DMI and WIR were compared to those predicted from body weight using allometric (or scaling) equations derived from isotopic measurements of field metabolic rate and water influx in free-ranging herbivorous lizards. The obtained results have important implications for conservation such as captive-breeding programmes and habitat restoration.

Key words. Squamata, Agamidae, Spiny-tailed lizard, faeces calibration, food consumption, water intake, frequency conversion, microhistological faecal analysis.

Introduction

Information on the dietary requirements of free-living vertebrates is an important tool in resource management. Measuring food consumption, even it is conceptually simple, it is usually difficult in the wild, though. Direct estimates of food intake for free-ranging reptiles have been made previously by establishing a laboratory relationship between food intake and the output of faecal or nitrogenous wastes, and then measuring the output of field-captured animals (Avery 1971, 1978, 1981, Andrews & Asato, 1977, Loumbourdis 1991), or from the known dietary water intake and the water content of the food (Minnich & Shoemaker 1970, Nagy 1975, Nagy & Shoemaker 1975, Congdon et al. 1982). More commonly, and probably less reliably, food consumption has been estimated by indirect methods. These included analyzing the composition and rate of production of faeces (Harris 1964), analyzing gut contents and making assumptions about stomach capacity and its rate of fill (Johnson 1966, Congdon et al. 1982); combining laboratory feeding regimes with estimates of field behaviour (Mueller 1970, Dutton et al. 1975); and combining data on field energy expenditure with estimates of assimilation efficiency and secondary production (see Avery 1971, 1978, 1981, Nagy 1975, Turner et al. 1976, Bennett & Gorman 1979). Another direct method of measuring food intake can be applied if there is a close positive correlation between food intake and the rate of Na turnover (NaTO) in the species under consideration, NaTO in turn, can be accurately measured using the turnover rate of [22]Na by following the exponential decline in the specific activity of the isotope (Buscarlet 1974). In animals whose major source of Na is dietary, food intake can be reliably estimated using [22]Na turnover if the Na content of their diet is known (Gallagher et al. 1983). However, problems may be encountered in applying this isotopic technique to

herbivores that feed on a variety of plant species, because the Na content of plants is highly variable (Allen et al. 1974).

Early indirect estimates of the food intake rates of wild animals were calculated from measuring the rates of oxygen consumption or carbon dioxide production (indirect calorimetry) under laboratory conditions. Corrections to account for the differences between metabolic rates measured in captivity and those in the field were problematic, and largely conjectural. Fortunately, the advent of the doubly labelled water method DLW (Lifson & Mcclintock 1966, Nagy & Costa 1980) has made it possible to measure carbon dioxide production in free-living, air-breathing vertebrates in their natural habitats. During the last three decades, the DLW has become the most widely used method for estimating energy and food requirements in free-living animals (Nagy et al. 1999, 2001). However, this invasive method involves capture and manipulation (e.g., administration of isotope tracers, bleeding) of wild animals. In addition, the application of isotope-measuring methods in ecophysiological vertebrate research has been limited in developing countries by the scarcity of the sophisticated and expensive equipment needed for them. Alternatively, it is possible to estimate time–energy budgets (TEB) in reptiles based on observations of activity in conjunction with body temperature data and laboratory measurements of activity and standard metabolism (see Avery 1971 for a review). Inexpensive and simpler methods were previously tested with various degrees of success in reptiles, including direct measurements of food consumption based on diet analysis (see Avery 1971 for a review). The easiest method for measuring daily food consumption is still the abovementioned calibrated faecal output (Avery 1971), however. It was successfully used in two insectivorous lizard species (*Lacerta vivipara*: Avery 1971, and *Stellagama stellio*: Loumbourdis 1991), but has not been tested yet in herbivorous reptiles.

Herbivorous lizards are known to feed selectively on plants of particular species, probably due to their nutritional properties (i.e., their contents of protein, water, fibres and sugars) (Pough 1973, Iverson 1979, 1982, Auffenberg 1982, Boersma 1982). Herbivores may also avoid consuming larger amounts of plants that contain secondary compounds to prevent toxic effects (Schall 1991). Documenting the diet and feeding behaviour of a lizard species is often the first step in developing an understanding of its ecology. Whereas investigations into diet composition have been carried out in several herbivorous reptile species around the world (Holechek et al. 1982b), daily food consumption and the relative representation of individual plant species in diets have as yet never been assessed in any herbivorous lizard species. Total food intake can be split up into the proportional intakes of different plant species, provided that the individual plant species in the diet can be identified and their relative representation can be measured. Such measurement can be made using the method of micrography (or microhistology) of converting the density of fragments present in faecal matter into relative dry weights of plant species consumed. Baumgartner & Martin (1939) first described this micrographic technique, which was later refined by Dusi (1947), Sparks & Malechek (1968), Voth & Black (1973), and Holechek et al. (1982b). Microhistological examination of faecal matter is the most popular technique employed to analyze the diets of domestic and wild herbivores. It does not interfere with the normal feeding habits of the animals and it is a feasible procedure to use when studying elusive or endangered species from which stomach contents cannot be obtained. In herbivores, it is based on the microscopic identification of the different ingested plant species from the epidermic fragments preserved in faeces or stomach contents. This technique assumes two principles: (i) the plant epidermis resists digestion processes and maintains its micro-anatomic features when excreted, and (ii) the amount of each plant epidermis present in faeces is proportional to the ingested amount of this plant.

Water intake rates (WIR) in free-ranging vertebrates can be measured by the Tritiated water (HTO) or DLW methods (Lifson & Mcclintock 1966, Nagy & Costa 1980). In herbivorous non-drinking reptiles, it can be estimated from the daily food intake, the relative dry weight of individual plants consumed and their water contents, and taking into account the metabolic water production (i.e., minimal water influx rate of unfed and inactive animals).

The Moroccan Spiny-tailed lizard, *Uromastyx nigriventris*, is one of the most remarkable reptile species in northwestern Africa (Wilms et al. 2009, Tamar et al. 2018), and liek the other *Uromastyx* species, it is listed in Appendix II of CITES. This medium-sized desert agamid lizard is non-drinking and strictly herbivorous (Dubuis et al. 1971, Bendami et al. 2018). It is a diurnal animal that will become active during the warm part of the day (Grenot 1976), spend most of its waking hours basking in the sun, and hide in burrows to escape excessive heat or when disturbed. Like many other terrestrial ectotherms, *U. nigriventris* possesses considerable behavioral and physiological thermoregulatory adaptations (Grenot & Loirat 1973, Grenot 1976). It tends to establish itself preferably in hilly and rocky areas with good shelters and accessible vegetation.

In the present study, we estimated the daily dry matter and water intake rates in the Moroccan Spiny-tailed lizard in spring and autumn 2017. For this purpose, we used, respectively, the calibrated production of faecal and nitrogenous wastes, and the relative dry-weight composition of diets from as indicated by the microhistological faecal analysis of plant species consumed and their moisture contents.

Materials and methods
Study site

Lizards and fresh samples of plant species were collected from a locality in the vicinity of Skoura (31.0604917° N, 6.5556528° W; 1,214 m a.s.l.), about 40 km northeast of Ouarzazate city (30.9255556° N, 6.9041667° W; 1,151 m a.s.l.) on the southern slope of the High Atlas range. The

annual rainfall here is 171 mm and the mean annual air temperature is 19.7°C. The ground is made up of chalky stones, pebbles, and coarse and fine sand. The vegetation is dominated by *Haloxylon scoparium* along with *Zizyphus lotus* and *Launaea arborescens* as well as various grass and forb species.

Sampling and lizard manipulation

Thirty-seven adult lizards (16 in spring and 21 in autumn 2017) were caught by hand, snares, or a net trap set at the burrow entrance (Bouskila 1983). Upon capture, they were sexed and weighed (to the nearest 0.1 g). They were then transferred to the lab, placed individually in plastic boxes (50 × 30 × 30 cm), and kept at a constant room temperature of 27 ± 1.5°C without food for 12 consecutive days, the maximal period after which no further faecal production was observed in all previously tested animals (experiments of water and food deprivation). The faecal pellets produced by the lizards were collected, and its faecal and solid excretory components (mainly urates) were separated; the uric acid was usually present as a discrete white mass at one end of each pellet.

Individual plant samples were harvested by hand (~100 g DM) in the area around the burrows where lizards were captured. They were weighed, transported to the laboratory, dried at a constant 55°C for 48 h, and then weighed again (to the nearest 0.1 g) to identify their moisture contents (ml water /g DM).

Calibration of faeces production

Fifteen randomly selected adult lizards (body weight range: 217.7 to 460.2 g) were kept individually in wire cages (60 × 40 × 25 cm; length x width x height) for two weeks for intake measurements after a period of adaptation of one week. The cages were equipped with an infrared lamp (60 W) placed at one end, which provided a thermal gradient from 40°C under the heater to 25°C at the opposite end of the cage and allowed the lizards to freely select the most convenient temperature. The IR lamp was switched on for 12 h/day. We placed a food bowl in each cage; no water was provided as the lizards do not drink. Their feed consisted of lucerne (whole), lentils, and commercial food pellets for rabbits (dried vegetables, maize, and various seeds). Each lizard was fed daily with a constant quantity for 15 days. Food spilled or left over, and faeces/urates were collected completely during the day. Representative samples of offered food were placed next to the cages to measure and correct for water loss in the lizards' daily food intake. Immediately after food intake measurements, lizards were completely deprived of food, and the faeces and/or urates produced were then collected daily for the following 12 days. Representative subsamples of food offered and all faeces/urates produced were used to measure their DMs for 48 h at 55°C to constant mass.

Microhistological analyses

We quantified the individual diet composition by analyzing sub-samples of the faecal pellets collected from the wild-caught animals that were kept unfed for 12 days as described above. The food intakes of individual lizards were identified to species level from the microhistological examination of plant fragments recovered from collected fresh faeces, based on their relative representation as identifiable fragments.

A reference collection of epidermis samples of the study area plants was compiled, comprising microphotographs of slides of epidermis from different parts of fresh plants, including leaves (adaxial and abaxial faces), stems and flowers of each species. All grass and forb species in the study area were included in this reference atlas. Drawings from and digital images taken of areas of reference slides were used for the identification of plant fragments.

Epidermis of fresh plants and faecal samples were processed following Rodde's technique (Butet 1985) for microhistological analyses (for details see Bendami et al. 2018). Three microscope slides were prepared for each faecal sample according to the procedures of Sparks & Malechek (1968). This technique involves oven-drying and then grinding diet samples through a 400-μm and then a 800-μm screen to reduce all fragments to a uniform size. Five slides mounts are then prepared for each diet sample according to the procedure described by Baumgartner & Martin (1939) and Baker & Wharten (1952). After drying at 60°C, the slides are analyzed under a compound binocular microscope. Twenty locations were systematically observed on each slide. A location was considered as an area of the slide delineated by a microscope field using x 100 power magnification. Only those fragments that were recognized as epidermal tissue (other than hairs) were recorded as positive evidence for the presence of a plant species in a location on the slide. Each species present for each location was recorded. The systematic observation process described by Sparks & Malechek (1968) was used to evaluate each microscope slide. Observation began in the lower-left corner of each slide, moving bottom to top, left to right in a sweeping, back and forth motion. When three or more particles were present in the viewing area, the fragments were evaluated to determine if they contained epidermal material, prickle hairs, both, or were unidentifiable. Only areas with at least three fragments that could be identified as epidermis or hairs were evaluated further and recorded.

Frequency percentages (number of fields that the species occurred in out of 100 locations) were tabulated for each species represented in the mixture. These frequency percentages were converted to particle density per field using the table developed by Fracker & Brischle (1944) and the relative density, expressed as a percentage, of each species in the mixture was calculated. The relative density of a species was used to estimate the relative representation (dry weight) of that species in the mixture. It is calculated as the density of the fragments of items divided by the density of the fragments of all items:

$n = 100 \times Log_e \, [100/(100-i)]$ with $i = 100 \times [1-e^{-0.01 \times n}]$

where n = relative density of fragments per 100 optical fields or number of fragments per 100 optical fields likely to be a strict mathematical probability when any given percentage (i) of optical fields contain one or more fragments each e is the base of a natural logarithm.

Water intake rate

The daily water intake rate (WIR) rate is calculated as the sum of preformed water in the consumed plants and metabolic water production. The former was estimated from DMI, %DWs of plant species in an individual's diet, and their corresponding moisture contents (ml water g⁻¹ DM). Metabolic water production was estimated using the minimal value of the mass-specific water influx reported for the same species ($3.4 \, ml(kg \times d)^{-1}$) (GRENOT 1976).

Data treatment and statistical analysis

We established an allometric (or scaling) relationship between DMI (g×d⁻¹) and BM (g), as had been measured in eight free-ranging herbivorous lizards (mean BM range: 11.9–1610) using the DLW method (NAGY 2001). The obtained relationship is highly significant and described by the equation: $DMI = 0.0285 \times BWg^{0.795}$ ($F_{1,6} = 92.02$, $r^2 = 0.938$, n = 8). The equations describing this allometric relationship can be used to predict the DMI of species that have not yet been studied and to compare the obtained values with those estimated by other methods including the calibrated faecal production method. The obtained values of total water influx rate are compared with the predicted values calculated from the allometric equation (WIR, $mL \times d^{-1} = 0.38 \times BWg^{0.792}$) of NAGY & PETERSON (1988). The average values were compared using the Student's t-test. We used a two-way ANOVA analysis for the mean estimated dry matter intake (ml×d⁻¹), water intake rate (ml×d⁻¹) and their corresponding values predicted with sex, season and sex × season as factors. The statistical significance level was set at 5%. All statistics were performed with Statistica version 10.1.

Results
Calibration of food consumption

There are no significant differences between the sexes in daily food consumption, and we therefore pooled all individual data. The DMI (g×d⁻¹) in captive Moroccan Spiny-tailed lizards was significantly correlated to the total production of rejecta FU (faeces + urates) (g dry weight / 12 days) (Fig. 1), as described by the equation:

$FU = 0.96 \times DMI - 3.42$
($F_{1,14} = 7.60$, p = 0.016, $r^2 = 0.80$, n = 15)

This equation indicates that FU, which is proportional to the DMI, explains 80% of the variation in DMI between individuals. It is then transformed to estimate the DMI from production of FU:

$DMI = 1.05 \times FU + 3.58$

Diet composition:
percent dry matter of individual plants consumed

A regression equation that expresses the relationship between the estimated relative dry weight and the actual percentage of dry weight was developed for a combination of the five most common plant species in the natural diet. The relative dry weights (%DW) of individual plant species in the analyzed mixture are highly correlated with their corresponding numerical frequencies (%N) as assessed from our microhistological analysis; the obtained linear regression is described by the equation:

$\%DW = 1.121 \times \%N - 2.428$; $r^2 = 0,991$, $F_{1,14} = 436.3$; $p < 0.001$

Spiny-tailed lizards consumed both annual and perennial plant species. Overall, they ingested 18 different plant species belonging to 17 genera and nine families (Table 1). Diet composition varied qualitatively and quantitatively between seasons, with 12 and nine species being consumed in spring and autumn, respectively, and four species being common to both seasons.

Within each season, plant species were represented by different percentages of dry matter (DW%). The five plant species most commonly consumed (DW% > 10) were, in descending order: *Anastatica hierochuntica, Haloxylon scoparium, Asteriscus graveolens, Launaea arborescens*, and *Fagonia zilloides* in spring, and *L. arborescens, Zilla macroptera, Haloxylon scoparium, Eryngium ilicifolium*, and *Echinops spinosum* in autumn. These species constituted about 60% of the diet in each season.
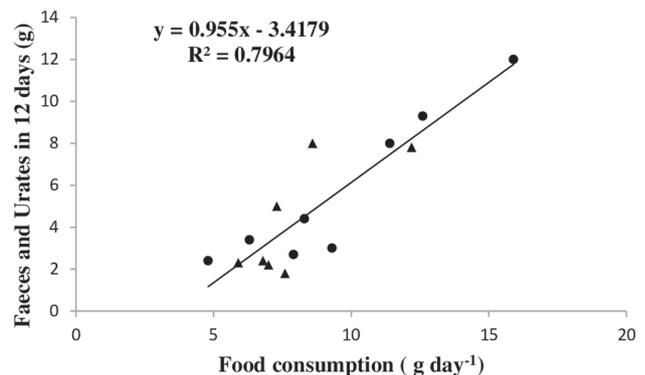

Figure 1. Relationship between food consumption in captivity and production of faeces and urates for male (circles) and female (triangles) Spiny-tailed lizards.

Table 1. Dry-weight percentages (DW% (mean ± standard deviation (range)) and occurrence frequency (OF%) of plant species consumed by the Moroccan Spiny-tailed lizard, *Uromastyx nigriventris*, in spring and autumn 2017, in southeastern Morocco. Abbreviations used for plant families: Ai, Aizoaceae; Ap, Apiaceae; As, Asteraceae; Bo, Boraginaceae; Br, Brassicaceae; Ch, Chenopodiaceae; Cu, Cucurbitaceae; Pl, Plantaginaceae; Po, Poaceae; Ra, Rhamnaceae; So, Solanaceae; Zy, Zygophyllaceae.

		Spring (n = 16)		Autumn (n = 21)	
		DW%	OF%	DW%	OF%
Anastatica hierochuntica	Br	13.51±8.70 (11.76–36.36)	68.75	–	–
Anvillea radiata	As	8.28±5.99 (3.70–20)	43.75	8.92±7.43 (3.57–29.41)	81.81
Asteriscus graveolens	As	12.90±9.46 (6.25–31.25)	31.25	–	–
Diplotaxis spp.	Br	5.79±3.89 (7.40–14.28)	18.75	–	–
Echinops spinosus	As	–	–	10.56±5.93 (4.17–23.53)	81.81
Echium plantagineum	Bo	2.49±1.18 (2.20–6.25)	25	–	–
Eruca pinnatifida	Br	9.59±7.66 (3.12–20)	37.5	–	–
Eryngium ilicifolium	Ap	6.98±6.07 (3.70–17.64)	25	11.26±4.80 (4.55–20.83)	100
Fagonia zilloides	Zy	10.51±9.18 (3.70–22.72)	56.25	–	–
Haloxylon scoparium	Ch	13.47±15.73 (4,54–53.84)	68.75	12.53±5.49 (5.56–25)	90.90
Hordeum murinum	Po	–	–	–	–
Launaea arborescens	As	12.66±16.50 (3.70–47.05)	68.75	20.19±5.79 (13.64–32)	100
Limonium sinuatum	Pl	–	–	8.08±5.25 (3.57–20)	72.72
Lycium intricatum	So	3.19±1.81 (3.10–8.33)	31.25	–	–
Peganum harmala	Zy	–	–	6.07±2.70 (3.57–10)	36.36
Stipa retorta	Po	7.10±14.18 (6.25–22.22)	62.5	–	–
Zilla macroptera	Br	–	–	17.06±7.48 (10–37.50)	90.90
Zilla spinosa	Br	–	–	7.21±3.28 (3.57–12.50)	45.45

The mean moisture content (g water/g dry matter) of vegetal matter consumed by the lizards ranged from 0.44 to 3.85, depending on the plant species and seasons. The average moisture content is 1.81 ± 0.84.

Daily dry matter intake

The mean estimated DMI (g×d^{-1}) values are significantly different from the predicted values for females and for both sexes in spring (P < 0.05), but not in autumn for females and in both seasons for males (P > 0.05 in all cases). However, the mean DMI values corrected for BM (g×kg$^{-0.795}$×d^{-1}) are not significantly different between sexes and seasons (P > 0.05 in all cases) (Table 2).

The mean estimated DMI (g×d^{-1}) and the predicted values were not significantly between seasons (F = 1.67, P > 0.05) (F = 1.66, P > 0.05), sexes (F = 0.78, P > 0.05) (F = 0.10, P > 0.05), and interactions of season x locality (F = 0.65, P > 0.05) (F = 0.71, P > 0.05), respectively.

Daily water intake rate

The mean estimated WIR (ml×d^{-1}) values are significantly higher than the predicted values for both sexes in spring (P < 0.05 in all cases), but not significantly different in au-

tumn (P > 0.05 in all cases). However, the mean WIR values corrected for BM (ml×kg$^{-0.792}$×d^{-1}) were significantly higher in spring than in autumn (P < 0.05 for each sex, P < 0.01 for sexes combined), but not between sexes in each season (P < 0.05 for both seasons) (Table 3).

The mean estimated WIR (ml×d^{-1}) and the predicted values were not significantly different between seasons (F = 1.52, P > 0.05) (F = 1.66, P > 0.05), sexes (F = 0.72, P > 0.05) (F = 0.10, P > 0.05), and interactions of season x locality (F = 0.65, P > 0.05) (F = 0.66, P > 0.05), respectively.

Discussion
Assessment of dry matter intake and the use of microhistological faecal analysis

The present study demonstrates for the first time that the use of the faecal and nitrogenous wastes output method combined with microhistological faecal analysis, and the analysis of water contents of the plants consumed provides a reliable, yet simple and inexpensive means of estimating the daily food and water requirements of herbivorous and non-drinking Moroccan Spiny-tailed lizards. Estimates of daily food and water intake values agree closely with data reported for other herbivorous lizards using alternative techniques. Direct measuring of the field metabolic rate (FMR) and then of food requirements using the DLW

Table 2. Estimated and predicted daily dry matter intake by Moroccan Spiny-tailed lizard, *Uromastyx nigriventris*, in spring and autumn, estimated by the production of faeces. Values in g ± SD. The different lower-case letters in the same column show the differences between months (p < 0.05); NS: non-significant.

Sex	Season	Initial body weight (g)	Estimated total dry matter intake		Predicted total dry matter intake g.d⁻¹
			$g.d^{-1}$	$g.kg^{-0.795}.d^{-1}$	
Males	autumn	395.86±115.98 (261.10–617.70)	3.22±1.82 (1.45–6.99)	7.24±5.12 (2.45–18.81)	2.98±0.69 (2.15–4.27)
	spring	375.65±188.11 (114.5–723.8)	3.52±1.46 (1.64–5.09)	10.74±8.29 (3.57–28.50)	2.82±1.14 (1.11–4.85)
Females	autumn	426.10±75.9 (316.91–527.8)	3.26±1.28 (1.98–5.65)	6.71±3.09 (3.31–11.78)	3.18±0.46 (2.52±3.77)
	spring	300.57±84.07 (204–357.4)	**4.57±1.02[a]** (3.42–5.37)	7.15±4.76 (2.12–11.58)	**2.40±0.55[b]** (1.77–2.77)
Total	autumn	409.97±97.17 (261.10–617.7)	3.24±1.56 (1.45–6.99)	6.98±4.15 (2.45–18.81)	3.07±0.58 (2.15–4.27)
	spring	361.57±173.69 (114.5–723.8)	**3.72±1.42[a]** (1.64–5.37)	10.06±7.76 (2.12–28.50)	**2.75±1.05[b]** (1.11–4.85)

Table 3. Estimated and predicted daily water influx rates in the Moroccan Spiny-tailed lizard, *Uromastyx nigriventris*, in spring and autumn. Values in ml ± SD. The different lower-case letters in the same row show the differences between estimated and predicted water influx rates (p < 0.05); ***p < 0.0001; **p < 0.001; *p < 0.01.

Sex	Season	Initial body weight (g)	Estimated water influx rate		Predicted total water influx ml.d⁻¹
			$ml.d^{-1}$	$ml.kg^{-0.792}.d^{-1}$	
Males	autumn (n = 6)	395.86±115.98 (261.10–617.70)	4.19±0.46 (3.42–4.67)	3.12±0.28 (2.66–3.40)	4.61±0.95 (3.37–6.17)
	spring (n = 13)	375.65±188.11 (114.5–723.8)	**7.11±2.39a** (4.37–12.17)	4.72±1.25** (3.01–7.29)	4.08±1.65b (2.56–4)
Females	autumn (n = 4)	426.10±75.9 (316.91–527.8)	3.65±0.38 (3.28–3.56)	2.80±0.23 (2.57–3.12)	4.94±0.56 (4.34±5.44)
	spring (n = 3)	300.57±84.07 (204–357.4)	**7.67±1.45 (6.40–9.25)a**	5.04±0.76** (4.37–5.86)	**3.47±0.79 (2.29–6.99)b**
Total	autumn (n = 10)	409.97±97.17 (261.10–617.7)	3.98±0.50 (3.28–4.67)	2.99±0.30 (2.57–3.40)	4.74±0.80 (3.37–6.17)
	spring (n = 16)	361.57±173.69 (114.5–723.8)	**7.22±2.21 (4.37–12.17)a**	4.78±1.16*** (3.01–7.29)	**3.96±1.52 (2.29–6.99)b**

method were carried out in various free-ranging species including herbivorous lizards (see Nagy et al. 1999, 2001) (Table 4). On the other hand, direct estimations of food intakes using calibrated faecal output were tested only in two insectivorous lizard species (Avery 1971, Loumbourdis & Hailey 1991). This simple method is based on the assumption that the proportion of faecal residues to the weight of food consumed is identical in lizards fed in the laboratory and lizards feeding on a wide range of food items in the wild. As it has not been possible to test the validity of this assumption, and as suggested by Avery (1971), any introduced error is likely to be small. However, the faecal output method has a disadvantage, as the animals to be tested must be removed from the wild for several days for each sampling and then be released.

The estimated values of DMI in Moroccan Spiny-tailed lizards were similar to those predicted by the allometric equation based on DLW data for free-ranging herbivorous lizards (see Materials and methods), except for females in spring which was when they had a higher estimated food intake. This is probably due to increased energy requirements for reproduction (i.e., egg production). The calibrated faecal production method can therefore be used for estimating food and energy requirements in free-living Moroccan Spiny-tailed lizards and probably other herbivorous reptiles, namely tortoises. Foley et al. (1992) estimated the DMI in *U. aegyptia* (10.3 ± 0.7 g×(kg×d⁻¹)) from the daily water influx as measured by the Tritiated Water method and the known moisture contents of the plant species identified in stomach contents. These authors suggest treating cautiously their estimate of food intake by this lizard species, since it is based on just few observations of water turnover and it was possible that water content of plants was very variable. The same authors proposed evaluating the impor-

Table 4. Body mass corrected by daily dry matter intake (g×d⁻¹), measured by different methods in various lizards. Methods used: DLW, doubly labelled water; CFP, calibration faeces production; DGM, direct gravimetric measurement (see text).

Species	Method	Body mass (g)	DMID (g×kg$^{-0.795}$×d⁻¹))	Reference
Gallotia atlantica	DLW	11.9	**5.90**	Nagy et al. (1999)
Gallotia galloti	DLW	25.6	8.46	
Gallotia stehleni	DLW	47.3	8.95	
Dipsosaurus dorsalis	DLW	52.5	**6.75**	
Angolosaurus skoogi	DLW	57.4	2.88	
Sauromalus obesus	DLW	167	**6.51**	
Iguana iguana	DLW	860	**6.78**	
Amblyrhynchus cristatus	DLW	1610	**6.25**	
Uromastyx aegyptius	TW	2310	5.31	Folley et al. (1992)
Uromastyx nigriventris	CFP			This study
Autumn		410	**6.98**	
Spring		361.6	10.06	
Uromastyx philbyi	DGM			Zari (1998)
Male		142.8	3.90	
Non-gravid female		105.2	2.94	
Gravid female		165.5	1.71	

tance of short-chain fatty acids (SCFA) (byproducts of microbial fermentation in the hindgut and a reliable measurement of its rate) in the daily energy budget. In the case of *U. aegyptia*, and at a temperature of 40°C, SCFA in-vitro production represents about 47% (68.7 ± 15.3 kJ×(kg×d)⁻¹) of the daily digestible energy intake, which was estimated to be 147 ± 9 kJ×(kg×d)⁻¹. The microbial fermentation thus highly contributes to the energy intake of *U. aegyptia* and allows the animals to continually acquire metabolic energy while avoiding lengthy foraging and reducing the consequential risk of predation (Bouskila 1986).

In free-ranging herbivorous lizards, DMI scaled to BM$^{0.795}$. This is relatively close to the allometric relationships reported for semi-captive herbivorous tortoises (BM$^{0.76}$) (Franz et al. 2011) and for all herbivorous reptiles (BM$^{0.717}$), including eight lizard species and one tortoise (the Desert tortoise *Gopherus agassizii*) (Nagy 2001). However, for a given body mass, DMI values predicted for free-ranging tortoises are 35 to 40% as high as those in semi-captive tortoises. In this regard, Zari (1998) measured DMI and energy requirements in captive *U. philbyi* during spring in males, and gravid and non-gravid females, but the obtained values corrected for BW revealed to be two to three times lower than those measured in other free-ranging herbivorous desert lizard species, including values estimated for *U. nigriventris* by the calibrated faecal output method. As was previously explained by Nagy (2001) for wild animals kept in captivity, such as in zoos, small outdoor enclosures or indoor cages or pens, the predicted food intake rates might be higher than the actual food requirements. Possible reasons for this are that free-ranging animals must invest relatively more energy into their foraging for scattered foods, escaping or fighting predators and parasites, coping with more extreme climatic conditions, and being involved in social activities; and the foodstuffs offered to captive animals are usually of higher quality (more metabolisable energy per gram of matter). This means consuming less biomass, which reduces the food requirements, i.e., reducing the metabolic cost of food processing due to its improved digestibility.

Microscopic examination of faecal matter is the most commonly employed method for analyzing the food habits of herbivorous vertebrates including reptiles. However, this technique has several limitations. Microscopic examination of faecal matter from herbivores suggested a higher total content of grasses and a lower total content of forbs in the diet for both trials than other methods, such as oesophageal fistulation, stomach content analysis, and forage utilization. Problems with the microhistological analysis of plant epidermis have arisen from comparing forage since several small-size forbs were not found in faeces in grazing trials (Korthage 1974, Vavra et al. 1978, McInnis et al. 1983). This may be explained in part by different degrees of digestibility. Certain species of forbs are probably digested in their entirety, leaving no residues in the faeces (Slater & Jones 1971, Johnson & Pearson 1981). In addition, some plant fragments can be present but are so transparent that their cellular structures are not readily discernible. The accuracy of faecal analysis could probably be enhanced by working out the digestibility coefficients of various plant species at different phenological stages.

The use of microhistological faecal analysis for analyzing the diet composition in herbivorous vertebrates has some limitations that may introduce biases to assessments. One of its major disadvantages is that the micro-anatomic characteristics of epidermis are not always preserved due to the epidermis being more or less altered while passing through digestive tract and digested to different ex-

Table 5. Daily water influx rate (in ml. $d^{-1} \times kg^{-0.792} \times d^{-1}$) of different herbivorous desert lizard species including those of *Uromastyx*.

Species	Body weight (g)	N	Conditions	Water influx rate		Reference
				$ml \times d^{-1}$	$ml \times kg^{-0.792} \times d^{-1}$	
Uromastyx aegyptia	2310	3	spring	57.98	29.87	Foley et al. (1992)
Uromastyx acanthinurus (currently *U. nigriventris*)	385	42	semi-natural, autumn, moist food	6.39	14.42	Lemire et al. (1979)
	377	19	semi-natural, autumn, dry food	2.86	6.19	
	392	13	semi-natural, autumn, fasting	2.08	4.37	
	360	10	semi-natural, autumn, underground	1.48	3.32	
	474	31	semi-natural, autumn, moist food	5.55	10.02	
	481	13	semi-natural, autumn, dry food	2.26	4.04	
	377	9	semi-natural, autumn, underground	1.32	2.86	
Uromastyx nigriventris	409.97	10	autumn	3.98	8.06	This study
	361.57	16	spring	7.22	16.16	
Angolosaurus skoogi	57.4	10	summer, natural	0.74	7.11	Nagy et al. (1991)
Dipsosaurus dorsalis	47	80	summer	0.85	9.57	Minnich & Shoemaker (1972)
	50	130	summer, natural vegetation	1.5	16.09	Minnich & Shoemaker (1970)
	50	210	summer, irrigated vegetation	2.4	25.74	
	3.5	68	hatchlings, spring	0.11	1.56	Mautz & Nagy (1987)
	50.3	71	adults, spring	0.80	1.38	
	98.1	130	adults, summer	2.32	2.36	
Sauromalus obesus	150	220	mid-spring	5.43	24.40	Nagy (1972)
	140	100	late spring	2.39	11.34	
	120	6	autumn, aestivating	0.12	0.64	
	100	3	winter, hibernating	0.05	0.31	
	92.8	31	force-fed spring diet, no water	1.68	1.78	Nagy (1972)
Sauromalus hispidus	970	35	mid-spring	3.40	3.48	Smits (1985)
	900	69	late-spring	6.30	0.33	
	860	78	mid-summer	6.88	7.75	
	840	73	late-summer	6.30	7.23	

tents (Stewart 1967). For instance, the relative representation of forbs is generally underestimated, whereas that of grasses (Poaceae) and browse (shrub and tree leaf litter) tends to be overestimated. ElMouden et al. (2006) found a percentage of as low as 7% of fragments that could not be identified in faecal samples of the Moorish tortoise from west-central Morocco. The other inconvenience is that this method is very laborious and time-consuming. Nevertheless, this method, which is widely used to investigate the dietary habits of herbivores including reptiles, has also some advantages: i) ease of sampling, and ii) its being particularly useful for endangered species, as it is non-disruptive and does not require handling, collecting or killing individuals (Chapuis & Lefeuvre 1980, Holechek et al. 1982, Hanley et al. 1985). Therefore, given the threatened status of the Spiny-tailed lizards, this method has been considered being the most appropriate and inexpensive for investigating its dietary habits (Bendami et al. 2018).

Micrographic faecal analysis has been used for more than 60 years to investigate the diets of herbivores. Considerable amounts of literature have been accumulated con-

cerning its actual potential for quantification by means of measuring the actual dry-weight percentages of each plant ingested (Stewart 1967, Sparks & Malechek 1968, Zyznar & Urniss 1969, Free et al. 1970, Dunnet et al. 1973, Westoby et al. 1976, Fitzgerald & Waddington 1979, Barker 1986). The accuracy of faecal analysis has also been tested in respect to other techniques such as oesophageal fistula, ruminal analysis, utilization, and bite counts (Martin 1955, Tood & Hansen 1973, Anthony & Smith 1974, Dearden et al. 1975, Vavra et al. 1978, Kessler et al. 1981, Gill et al. 1983, Bullock 1985). Westoby et al. (1976) pointed out the risks of underestimating the importance of species that are present only in small amounts and how errors tend to increase when working with desert vegetation. Many authors have employed this technique satisfactorily (e.g., Dusi 1949, Hercus 1960, Storr 1961, Kiley 1966, Stewart 1967, Hansen 1975, Hughes 1975, Hansen & Clark 1977, Korfhage et al. 1980, Chapuis 1981, Hosey 1981, Butet 1985, Bhadresa 1986), which provides a suitable degree of relative reliability (conforming with actual amounts of ingested plant species) when correction factors

are used (Adams et al. 1962, Sparks & Malechek 1968, Dearden et al. 1975, Kessler et al. 1981, Holechek et al. 1982) or if frequencies are left out and species are ranked according to their abundance (Vavra et al. 1978). Faecal analysis is considered particularly useful in comparative studies (Chapuis & Lefevre 1980, Butet 1985).

Estimation of daily water intake rate

The estimated WIR corrected for BW (ml×kg$^{-0.792}$×d^{-1}) in *U. nigriventris* in autumn (8.06) is within the range of values (2.86-14.42) obtained for the same species under semi-natural conditions in western Algeria (Lemire et al. 1979). The corresponding value in spring (16.16) was twice that in autumn, but lower than those reported for *U. aegyptia* and *Sauromalus obesus* (29.87 and 24.40, respectively) (Table 5). WIR in the former species was more than three times the value predicted as per the allometric equation of Nagy (1982), i.e., 25 *vs.* 7.6 ml×(kg×d)$^{-1}$. The higher values in spring may be related to a higher aboveground activity and greater food abundance of and water content in the consumed plant species. In this regard, Lemire et al. (1982) established a correlation between the variation in WIR and the activity levels of individuals: for example, in September 1977, in *Uromastyx* excavating burrows and undertaking frequent excursions per day, WIR was 46.5 ml×kg$^{-0.792}$×d^{-1}. On the other hand, at low aboveground activity, the lizards were able to reduce their water loss through evaporation and avoid potentially hazardous imbalances that would ensue from the ingestion of plants with insufficient water contents. The rate of water turnover was very low under these conditions (WIR = 8.67 ml×kg$^{-0.792}$×d^{-1}, May 1978 (Lemire et al. 1980), and this rate corresponds closely to that measured in semi-captive lizards (Lemire et al. 1979).

We conclude that, when combined with microhistological analysis for identifying the %DWs of plants species in diets and moisture contents of these plants, the faecal and nitrogenous wastes output method can be successfully used as an easier and inexpensive alternative for estimating daily food and water requirements in free-living herbivorous non-drinking reptiles. Such indirect estimates can be compared with the predicted values using the published allometric equations derived from direct measurements of FMR and WIR in free-ranging lizards obtained by the DLW method. The calibrated faecal output method along with microhistological analysis can be also very useful in estimating the intake of different nutrients (minerals, proteins, carbohydrates, lipids, carotenoids etc.) based on the nutrient contents of consumed plant species and their parts.

Overall, the utility of such information ranges from practical applications to theoretical evaluation of the role of vertebrate consumers in ecosystem models. Estimates of food, energy and water requirements of the herbivorous and non-drinking Moroccan Spiny-tailed lizard may be of a great interest for the management, restoration and conservation of their natural habitats. It might be also useful in captive breeding programs, especially for the formulation of nutritional and dietary regimes for both growing and adult animals.

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