Herpetological Conservation and Biology 15(1):69–78.
Submitted: 30 May 2019; Accepted: 30 January 2020; Published: 30 April 2020.

# Dietary Observations of Four Southern African Agamid Lizards (Agamidae)

*Wei Cheng Tan*[1,2,3], *Anthony Herrel*[1], *and John Measey*[3,4]

[1]*Unité Mixte de Recherche 7179 Centre National de la Recherche Scientifique/ Muséum National d'Histoire Naturelle, Département Adaptations du Vivant, 55 rue Buffon, 75005, Paris Cedex 5, France*
[2]*Université de Poitiers - Laboratoire EBI Ecologie and Biologie des Interactions, Unités Mixtes de Recherche Le Centre National de la Recherche Scientifique 7267, Equipe Ecologie Evolution Symbiose, 6, rue Michel Brunet, TSA 51106, 86073 Poitiers, France*
[3]*Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa*
[4]*Corresponding author, email: jmeasey@sun.ac.za*

*Abstract*.—**Analysis of stomach contents can provide insights into foraging mode, habitat use, and dietary specialization of animals. In this paper, we make observations on the poorly known diet of four southern African agamid species, *Agama aculeata distanti* (Eastern Ground Agama), *Agama armata* (Peter's Ground Agama), *Agama atra* (Southern Rock Agama), and *Acanthocercus atricollis* (Southern Tree Agama). We examined the diet of 67 individuals by identifying and weighing prey items after stomach flushing lizards in the field. We found that these agama species fed on a broad spectrum of arthropods (11 orders). A high relative importance of ants was present for all agama species examined here, which suggests that ants are a major food source in the arid ecosystem. We found that active prey such as ants, beetles, and highly mobile flying insects like wasps and flies to be major components of the diet, indicating that these lizards are ambush predators. We also found that 43% of the stomachs contained herbaceous material and 39% contained sand particles. *Agama atra* had the most diverse dietary niche, eating fewer ants and more beetles, hemipterans, and dipterans than other species, whereas *A. armata* had a narrower dietary niche consisting mainly of ants. Lastly, although low in sample size, we found that juveniles qualitatively had a diet of functionally similar prey items, albeit with a narrower niche breadth, when compared to adults. We discuss how diet corresponds with differences in foraging behavior and habitat specialization**.

*Key Words*.—diet; index of relative importance; lizards; reptiles; southern Africa

## Introduction

Diet plays an important role in the daily life of animals as it provides a source of energy for growth, maintenance, and reproduction (Huey and Pianka 1981; Zug et al. 2001). Many animals specialize in different prey items and develop complex feeding behaviors based on their anatomy or dietary requirements (Schwenk 2000). Studying the prey eaten by an animal can provide insights into their ecological roles and the relative importance of each prey species in their diet (Losos and Greene 1988; Ortega-Rubio et al. 1995; Znari and El Mouden 1997). Studies of diet in an inter-specific context may further provide information on niche overlap and thus on how animals partition resources (Norval et al. 2012). The optimal foraging model of MacArthur and Pianka (1966) predicts that dietary specialization depends on the range and abundance of available prey, as well as the energetic gains and losses (handling and search time) associated. For example, specializing on a narrow range of food usually results in higher foraging efficiency (Britt and Bennet 2008), eliminating potential competition with generalists. In a patchy environment with few food resources, however, generalists tend to do better than specialists. Generalists have a more diverse diet and a reduced travel time between suitable patches (less search time), which makes up for their lower foraging efficiency compared to specialists. This difference has been a major interest to ecologists as the distribution pattern of organisms is largely dependent on the degree of diet specialization (MacArthur 1972).

Agamids are Old World lizards that have successfully colonized a variety of habitats ranging from hot deserts to tropical forests (Greer 1989). Some agamids even appear to favor peri-urban (rural-urban transition zones) landscapes more than natural or protected areas (Whiting et al. 2009). Surprisingly, and despite their ubiquitous nature, southern African agamids remain relatively poorly studied in terms of their ecology (but see Anibaldi 1998; Reaney and Whiting 2003; Van Berkel and Clussela-Trullas 2018). Although most agamids are generally terrestrial, some specialized saxicolous and arboreal species exist. Agamids only occasionally forage outside their home range (Whiting et al. 1999), suggesting that the microhabitats used by different species may constrain their diet.

**Figure 1.** Four agamid species from southern Africa. (A) *Agama aculeata distanti* (Eastern Ground Agama), (B) *A. atra* (Southern Rock Agama), (C) *A. armata* (Peter's Ground Agama), and (D) *Acanthocercus atricollis* (Southern Tree Agama). (Photographed by Wei Cheng Tan).

Agamas are widespread diurnal lizards that are widely distributed in Africa. Eleven agamid species are common and widespread throughout southern Africa (Bates et al. 2014). *Agama aculeata distanti* (Eastern Ground Agama; Fig. 1A) and *A. armata* (Peter's Ground Agama; Fig 1B) seem to prefer similar types of macrohabitat: open canopy and semi-arid areas (Bates et al. 2014). Although *A. a. distanti* is normally classified as a ground dwelling species (Bates et al. 2014), some *A. a. distanti* populations appear to be saxicolous, occurring in rocky woodlands. They are normally found basking on rocks, branches of bushes or termitaria (Branch 1998). Similarly, *A. atra* (Southern Rock Agama; Fig. 1C) is also a saxicolous species found on rocky outcrops and mountain plateaus. *Agama atra* has a wide distribution throughout southern Africa compared to the other agamids studied here, perhaps suggesting a more generalist lifestyle (Bates et al. 2014). *Agama armata*, however, tend to be found in open deep sand savannah and calcrete flats (Branch 1998). It has been suggested that widely foraging lizards living in open habitats specialize on feeding relatively sedentary and clumped prey such as termites (Huey and Pianka 1981). Contrary to the other species, *Acanthocercus atricollis* (Southern Tree Agama; Fig. 1D) has an arboreal lifestyle, spending much of its time on trees and logs. They consume primarily mobile, diurnal insects such as ants, beetles, and orthopterans, but also ingest occasional millipedes and centipedes (Reaney and Whiting 2002).

The diet of only a few African agamid species has been studied (Bruton 1977; Znari and El Mouden 1997; Heideman 2002; Reaney and Whiting 2002; Ibrahim and El-Naggar 2013). These lizards have been reported to be ambush foragers (e.g. Whiting et al. 1999), feeding almost entirely on insects, including predominance of Hymenoptera, especially ants (Formicidae) and Coleoptera. To date, little or no information is available on the dietary niches of southern African agamids (Fig. 1; but see Bruton 1977; Reaney and Whiting 2002). In this study, we examined the diet of four agamid species from South Africa discussed above: *A. a. distanti, A. armata, A. atra and A. atricollis*. We determined food habits by examining their stomach contents. We sampled across species in summer to gain insights into possible differences in foraging strategies, niche overlap, and the presence of possible dietary specialists. We captured adult and juvenile lizards whenever possible to explore the presence of ontogenetic shifts in diet.

## Materials and Methods

***Study areas.***—We conducted fieldwork in three of the nine biomes of South Africa: Fynbos, Savanna, and Thicket (Fig. 2). We sampled *A. atra* primarily on Muizenberg Mountain (34º05´S, 18º26´E) in March 2008. Muizenberg is a 500 m tall mountain dominated by rich endemic fynbos vegetation and is situated on the Cape Peninsula in the Western Cape. We sampled the other agamid species throughout the austral summer of 2017 (February-March). For every species, we captured individuals over the course of several weeks. We sampled *A. atricollis* in Mtunzini (28º58´S, 31º45´E) and Eshowe (28º52´S, 31º28´E) peri-urban areas, in Kwa-

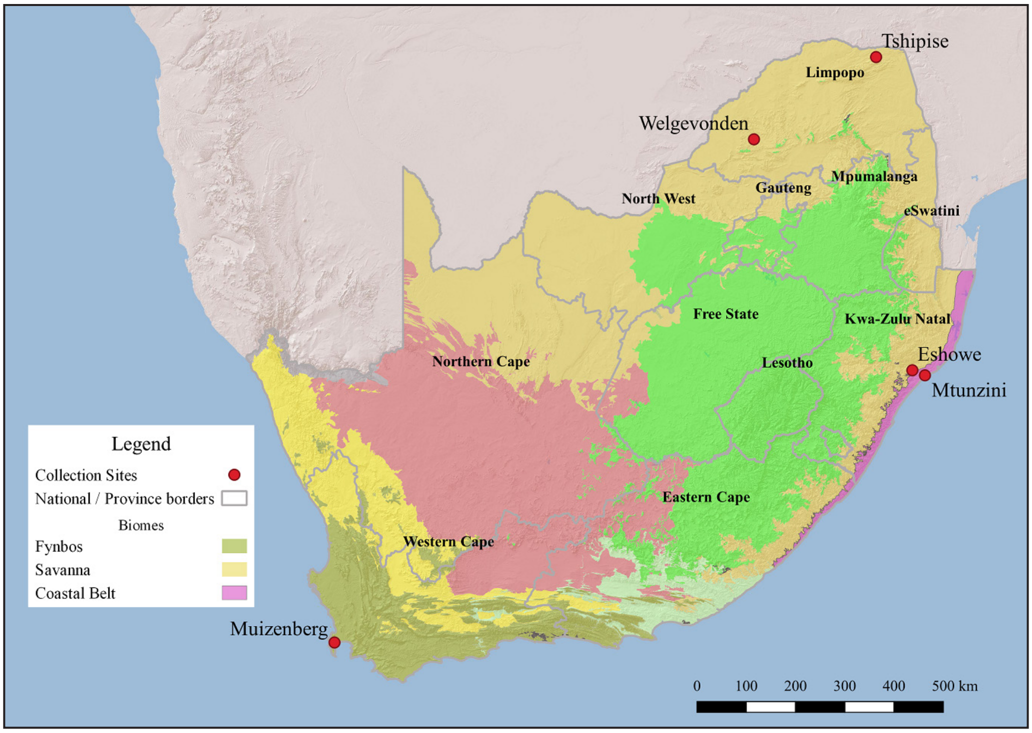


**Figure 2**. The five collection sites used in this study fell into three of nine biomes of South Africa (Coastal Belt, Fynbos, and Savanna) and three provinces (Kwa-Zulu Natal, Limpopo, and Western Cape).

Zulu Natal, where these lizards live in close proximity to humans. *Acanthocercus atricollis* has an arboreal lifestyle and lives on big trees with significant canopy cover (Reaney and Whiting 2003). We collected *A. armata* in game reserves near Tshipise (22º31´S, 30º39´E) in Limpopo. Tshipise contained flat, open, sandy acacia thornveld and occasionally dry mopane dominated woodland. We caught *Agama aculeata distanti* at the Welgevonden nature reserve, Waterberg District, also in Limpopo (24º13´S, 27º54´E). The reserve is characterized by rocky woodlands and mountain bushveld at high altitudes with minimal human activity. Note that this population of *A. a. distanti* was found predominantly on rocks.

We marked all lizards caught with a temporary nontoxic marker to avoid recapturing and remeasuring the same individual and returned them within 24 h to their exact site of capture after we measured lizards and flushed their stomachs. We considered individuals adults if they had a snout-vent length (SVL) above 100mm, while we considered lizards with a SVL below 70 mm juveniles (Appendix Table 1). We assessed lizards between these sizes individually according to secondary sexual characteristics (e.g., coloration, scale ornamentation, etc.) to determine if they were adults or juveniles.

***Stomach contents.***—We collected stomach contents of 67 individuals. We flushed stomachs within 4 h of capture of a lizard according to the protocol of Herrel et al. (2006). We held the lizard gently with one hand while opening the mouth by tapping on the sides of the jaw, which resulted in a jaw-opening threat response. We then inserted a small plastic ring into the mouth to keep the jaws open, allowing for a continuous flow of water and food out of the digestive tract. We used a syringe with a round-tipped steel needle, which we inserted gently into the stomach through the pharynx. Upon feeling a slight resistance against the pyloric end of the stomach, we pushed sufficient water into the stomach to force food out without injuring the animal. We continued the sequence while slightly moving the syringe up and down until a food bolus with fragmented matter was regurgitated. We kept the diet samples in individual vials with 70% ethanol and brought vials back to the laboratory for examination.

We identified the stomach contents to the lowest possible taxonomic level using a binocular microscope. In most cases, however, only the Order of the prey item could be identified due to the fragmented nature of the prey items. We decided to separate Formicidae prey from the other Hymenopterans as they are reported to be an important part of the diet of some agamids (Capel-Williams and Pratten 1978; Znari and Mouden 1997; Heideman 2002). We blot-dried the food items thoroughly with paper towels before measuring the mass using an electronic microbalance (AE100-S, Mettler Toledo GmBH, Zurich, Switzerland; ± 0.1 mg). Be-

**Table 1**. The composition of diet of four agamid species from southern Africa (total n = 67): *Agama aculeata distanti* (Eastern Ground Agama), *A. armata* (Peter's Ground Agama), *A. atra* (Southern Rock Agama), and *Acanthocercus atricollis* (Southern Tree Agama). Prey items are presented by Order and the corresponding evasive level (Fun.) according to Vanhooydonck et al (2011): e = evasive, i = intermediate, s = sedentary, and na = not applicable. Ants are removed from other Hymenoptera as they are reported to be a principle dietary item of agamids and have a different evasive level. Lepidoptera are larvae only. Diet is reported as occurrence (Oc), or the total number of individual lizards that contain a particular food item, and its frequency (FOO) in percentage.

| | | *A. a. distanti* (n = 23) | | *A. armata* (n = 8) | | *A. atra* (n = 15) | | *A. atricolis* (n = 21) | |
|---|---|---|---|---|---|---|---|---|---|
| Order | Fun. | Oc | FOO (%) | Oc | FOO (%) | Oc | FOO (%) | Oc | FOO (%) |
| Formicidae | i | 23 | 100 | 8 | 100 | 14 | 93.33 | 20 | 95.24 |
| Hymenoptera | e | 12 | 52.17 | 3 | 37.50 | 13 | 86.67 | 8 | 38.10 |
| Coleoptera | i | 16 | 69.57 | 4 | 0.50 | 15 | 1 | 10 | 47.62 |
| Hemiptera | i | 10 | 43.48 | 1 | 0.13 | 10 | 66.67 | 1 | 4.76 |
| Diptera | e | 5 | 21.74 | 1 | 0.13 | 10 | 66.67 | 2 | 9.52 |
| Lepidoptera | s | - | - | - | - | 3 | 20.00 | 1 | 4.76 |
| Orthoptera | e | - | - | - | - | 2 | 13.33 | 1 | 4.76 |
| Gastropoda | s | - | - | - | - | - | - | 1 | 4.76 |
| Ephemoptera | e | - | - | - | - | - | - | 1 | 4.76 |
| Isoptera | s | 1 | 4.35 | - | - | - | - | - | - |
| Diplopoda | s | - | - | - | - | 7 | 46.67 | - | - |
| Plant matter | na | 8 | 34.78 | 3 | 3.75 | 13 | 86.67 | 6 | 28.57 |
| Sand particles | na | 16 | 69.57 | 3 | 3.75 | 7 | 46.67 | - | - |

cause most prey items were crushed into fragments, we decided to include all fragments, which we sorted into different prey groups. We feel this approach provides a reasonable estimate of prey volume as prey bodies were rarely found intact.

The heads of the prey items were carefully enumerated to calculate the numeric abundance (N) of each prey category. For each prey group, we also calculated the index of relative importance (IRI) to quantify the significance of a particular prey item in the diet (Pinkas et al. 1971):

$$IRI = (\%N + \%V) \times \%Oc$$

where %N is the percentage of numeric abundance, %Oc is frequency of occurrence of a certain prey group, and %V is the proportion of mass of that prey group to total prey mass. IRI is a compound index that provides a balanced view of the diet of a lizard due to the combination of unique properties affecting individual measures (numbers, mass, and occurrence in the diet).

We also calculated a diet diversity index for each species. Dietary breadth (B) was computed according to Levins (1968):

$$B = 1 / \sum Pi^2$$

where P is the proportion of records of each species in prey category, *i*. The index of Levins is a simple computation that provides an indication of which species has a more specialized diet if it had a relatively low dietary niche breadth (B). In the course of the analysis, we also discovered nematodes in the stomachs of some individuals. We reported these separately as parasites. In addition, we also did not include plant matter, sand particles, or nematodes in the calculation of IRI or niche breadth. We classified all prey groups according to their evasiveness: evasive, sedentary, and intermediate based on the definitions in Vanhooydonck et al. (2007), and we used these categories to compare the prey consumed between adults and juveniles.

***Statistical analysis.***—To meet normality and homoscedasticity assumptions, we log10-transformed all continuous data before further analyses. We conducted multivariate analysis of variance (MANOVA) on the IRI of the different prey groups to compare diet between species. Following this we performed univariate ANOVAs with LSD post-hoc tests on prey IRI to determine their relative contribution among species. We performed all analyses in IBM-SPSS v24 (SPSS Inc., Chicago, Illinois, USA). For all tests, $\alpha = 0.05$.

## Results

The IRI between species differed significantly (Wilks' lambda = 0.288; $F_{36}$, 148.46 = 2.158, $P < 0.001$). There were significant differences within each prey group (Appendix Table 2). Ants (Formicidae) were present in the stomachs of all agamid species and represented the majority of their diet (> 90% occurrence; Table 1). Ants also appear to be the dominant prey by mass and

**Table 2**. Diet comparison between *Agama aculeata distanti* (Eastern Ground Agama), *A. armata* (Peter's Ground Agama), *A. atra* (Southern Rock Agama), and *Acanthocercus atricollis* (Southern Tree Agama) from southern Africa, showing the number (frequency) and total dry mass (g) of each prey taxon. The Index of Relative Importance, IRI, is displayed as mean ± standard deviation. Niche breadth, *B*, is indicated at the bottom of the table. Asterisks (*) indicate prey taxon IRI that were significantly different between agamid species ($P < 0.05$): see Appendix 2.

| | | *A. a. distanti* (n = 23) | *A. armata* (n = 8) | *A. atra* (n = 15) | *A. atricollis* (n = 21) |
|---|---|---|---|---|---|
| Formicidae | No. | 495 | 184 | 1160 | 406 |
| | Mass | 1.444 | 0.105 | 0.808 | 0.433 |
| | IRI* | 1.348 ± 0.457 | 1.503 ± 0.498 | 0.953 ± 0.560 | 1.428 ± 0.541 |
| Other Hymenoptera | No. | 28 | 3 | 43 | 20 |
| | Mass | 0.033 | 0.002 | 0.160 | 0.100 |
| | IRI | 0.041 ± 0.058 | 0.011 ± 0.016 | 0.218 ± 0.300 | 0.036 ± 0.072 |
| Coleoptera | No. | 45 | 9 | 140 | 12 |
| | Mass | 0.191 | 0.052 | 0.533 | 0.019 |
| | IRI | 0.161 ± 0.208 | 0.128 ± 0.197 | 0.362 ± 0.407 | 0.087 ± 0.230 |
| Hemiptera | No. | 13 | 1 | 23 | 1 |
| | Mass | 0.020 | < 0.001 | 0.039 | 0.002 |
| | IRI* | 0.019 ± 0.033 | 0.005 ± 0.014 | 0.036 ± 0.048 | < 0.001 |
| Diptera | No. | 9 | 2 | 16 | 2 |
| | Mass | 0.004 | < 0.001 | 0.005 | < 0.001 |
| | IRI* | 0.006 ± 0.017 | 0.002 ± 0.006 | 0.014 ± 0.024 | < 0.001 |
| Lepidoptera (larvae) | No. | - | - | 3 | 2 |
| | Mass | - | - | 0.017 | 0.006 |
| | IRI | - | - | 0.005 ± 0.012 | < 0.001 |
| Orthoptera | No. | - | - | 3 | 1 |
| | Mass | - | - | 0.591 | 0.150 |
| | IRI | - | - | 0.015 ± 0.054 | 0.002 ± 0.010 |
| Gastropoda | No. | - | - | - | 1 |
| | Mass | - | - | - | 0.002 |
| | IRI | - | - | - | < 0.001 |
| Ephemoptera | No. | - | - | - | 1 |
| | Mass | - | - | - | < 0.001 |
| | IRI | - | - | - | < 0.001 |
| Isoptera | No. | 116 | - | - | - |
| | Mass | 0.059 | - | - | - |
| | IRI | 0.003 ± 0.015 | - | - | - |
| Isopoda | No. | 1 | - | - | - |
| | Mass | 0.001 | - | - | - |
| | IRI | < 0.001 | - | - | - |
| Diplopoda | No. | - | - | 9 | - |
| | Mass | - | - | 0.089 | - |
| | IRI* | - | - | 0.032 ± 0.075 | - |
| Plant matter | Mass | 0.017 | 0.001 | 0.023 | 0.141 |
| Sand particles | Mass | 0.152 | 0.005 | 0.058 | - |
| Unidentified | Mass | 0.039 | - | 0.066 | 0.113 |
| *B (breadth)* | | 1.909 | 1.166 | 1.427 | 1.203 |

**Table 3.** Dietary composition and breadths of adult (A) and juvenile (J) *Agama aculeata distanti* (Eastern Ground Agama), *A. armata* (Peter's Ground Agama), *A. atra* (Southern Rock Agama), and *Acanthocercus atricollis* (Southern Tree Agama) from southern Africa based on Index of Relative Importance, IRI, and Levin's niche index (*B*). The IRI is displayed as mean ± standard deviation. Note, small sample sizes prevented statistical comparisons.

| | *A. aculeata distanti* | | *A. armata* | | *A. atra* | | *A. atricollis* | |
|---|---|---|---|---|---|---|---|---|
| | A (n = 9) | J (n = 14) | A (n = 2) | J (n = 6) | A (n = 10) | J (n = 5) | A (n = 14) | J (n = 7) |
| Formicidae | 1.262 ± 0.563 | 1.402 ± 0.390 | 1.109 ± 0.410 | 1.634 ± 0.480 | 0.705 ± 0.521 | 1.451 ± 0.150 | 1.393 ± 0.624 | 1.484 ± 0.403 |
| Other Hymenoptera | 0.039 ± 0.057 | 0.043 ± 0.061 | 0.035 ± 0.009 | 0.003 ± 0.008 | 0.30 ± 0.34 | 0.059 ± 0.05 | 0.037 ± 0.087 | 0.036 ± 0.046 |
| Coleoptera | 0.171 ± 0.170 | 0.155 ± 0.236 | 0.409 ± 0.179 | 0.034 ± 0.075 | 0.484 ± 0.451 | 0.119 ± 0.110 | 0.118 ± 0.293 | 0.038 ± 0.026 |
| Hemiptera | 0.012 ± 0.014 | 0.023 ± 0.041 | - | 0.007 ± 0.017 | 0.038 ± 0.057 | 0.030 ± 0.026 | - | < 0.001 |
| Diptera | 0.010 ± 0.025 | 0.003 ± 0.009 | - | 0.003 ± 0.006 | 0.016 ± 0.030 | 0.010 ± 0.007 | - | < 0.001 |
| Lepidoptera (larvae) | - | - | - | - | 0.007 ± 0.015 | <0.001 | - | < 0.001 |
| Orthoptera | - | - | - | - | 0.022 ± 0.066 | - | - | 0.006 ± 0.016 |
| Gastropoda | - | - | - | - | - | - | - | 0.001 ± 0.003 |
| Ephemoptera | - | - | - | - | - | - | - | < 0.001 |
| Isoptera | 0.008 ± 0.024 | - | - | - | - | - | - | - |
| Isopoda | - | < 0.001 | - | - | - | - | - | - |
| Diplopoda | - | - | - | - | 0.030 ± 0.090 | 0.037 ± 0.039 | - | - |
| *B (breadth)* | 2.281 | 1.352 | 2.072 | 1.072 | 1.691 | 1.204 | 1.282 | 1.173 |

in IRI, followed by coleopterans, other hymenopterans, hemipterans, and dipterans (Table 2). *Agama atra* had a significantly lower ant IRI (0.95) than the other species, while *A. armata* had the highest ant IRI (1.5), closely followed by *A. atricollis* (IRI: 1.43) and *A. a. distanti* (IRI: 1.35), although these differences were not significant (Table 2). Moreover, Coleoptera seem to be an important part of the diet of these species, representing the second highest IRI among the other prey items. *Agama atra*, which has a low ant IRI, showed significantly higher importance of evasive prey in its diet (e.g., Hymenoptera and Diptera) compared to other agamid species (Table 2). We observed large evasive prey, such as Orthoptera, in the stomachs of two *A. atra* individuals (Table 1). Additionally, *A. atra* was the only species that was found preying on millipedes (Diplopoda). Although rare, we also found mayflies (Ephemeroptera), snails (Gastropoda), woodlice (Isopoda), and termites (Isoptera) in the stomachs of these lizards.

In addition to arthropods, all species also ingested plant matter (such as seeds, buds, and small twigs) and fine particles of sand, observed in 43% and 39% of the stomachs, respectively. Of the 67 stomachs examined, 36 (57%) also contained nematodes. They were present in all species: 12 *A. a. distanti,* three *A. armata*, 13 *A. atra,* and 21 *A. atricollis.* The dietary breadth for prey number was greatest in *A. a. distanti* (1.91) and lowest in *A. armata* (1.17; Table 2). Juveniles showed a lower dietary diversity than adults in all four species, suggesting large quantities of prey items in few categories (Table 3); however, functionally their prey types appear to be very similar to that of adults (Fig. 3). Formicidae appear to be the most important prey type in the diet of juveniles, and there was a higher ant IRI in juveniles (mean = 1.47) than in adults (mean = 1.14; Table 3).

## Discussion

Our results show that the agamids in our study are insectivorous like most other agamids (see Huey and Pianka 1981). Ants (Formicidae) were the most common and important prey items in the diet of these animals. Other major prey components included other hymenopterans such as bees and wasps, coleopterans,

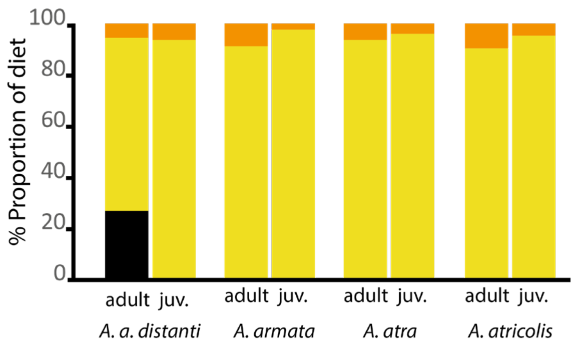


**Figure 3.** Diet as a composition of functional prey types of *Agama aculeata distanti* (Eastern Ground Agama), *A. armata* (Peter's Ground Agama), *A. atra* (Southern Rock Agama) and *Acanthocercus atricollis* (Southern Tree Agama). Functional prey types are sedentary (black), intermediate (yellow) and active (orange) prey (see Table 1 for classification) for both adults and juveniles (juv.).

and dipterans. These observations agree with previous studies on the ecology of African agamids (Capel-Williams and Pratten 1978; Znari and Mouden 1997; Heideman 2002). Ants are small and hard prey of intermediate evasiveness (see Vanhooydonck et al. 2007). Hence, they likely provide little energetic value relative to the handling time needed to process them, as agamids crush their prey before swallowing (Herrel et al. 1996; Meyers and Herrel 2005; Schaerlaeken et al. 2008). Yet, ants are a common component of arid ecosystems and present an important feature of the diet of many lizards simply due to their abundance and ease of capture (Pianka 1986; Branch 1998).

Using quantitative measurements, *Agama atra, A. planiceps* and *A. atricollis* have been previously classified as ambush foragers (Whiting et al. 1999; Reaney and Whiting 2002). Not surprisingly, there was a high relative importance of ants and beetles (Coleopterans) in the diet of agamids in our study. This suggests that these lizards are indeed ambush predators (Pianka 1986) although our study further showed that *A. atra* also fed on prey items classified as evasive prey that typically jump or fly to escape. These prey types are thought to be captured by ambush predators possibly with very short, quick dashes from a standstill (Vanhooydonck et al. 2007), suggesting that this species may be a more specialized ambush predator.

Diet composition can vary greatly according to the prey availability in specific localities or microhabitats (Measey et al. 2011). For example, diet of agamids can change across an urban to rural gradient (Balakrishna et al. 2016) and this may account for some of the differences we found between *A. atricollis* and the other species. Our results showed a greater proportion of ants and few flying insects in the diet of *A. armata*, which is more of a ground dwelling species.

Our results indicate that the diet differs significantly among the four agamid species, but with a very similar functional grouping of prey types dominated by prey of intermediate activity with some evasive invertebrates. *Agama aculeata distanti* appeared to be the most generalist species followed by *A. atra*, based on the niche breadth index of Levin. One problem, however, with this index is that it does not take into account the mass of the prey items, which could play an important role in the energy gained from ingested prey items. When we added mass into our diet analyses (IRI calculation), *A. atra* stood out as having a more diverse and generalist diet, with ants being relatively less important compared to the other species studied here. *Agama armata*, the smallest southern African agamid (Branch 1998), preys primarily on ants and appears more specialized than the other species, although this may simply reflect the paucity of other prey in their environment. *Agama atra* and *A. atricollis* both consumed larger prey items like grasshoppers and caterpillars. Perhaps only the small to medium-sized prey items (e.g., ants and small beetles) can be consumed by smaller predators simply due to the limitations on gape or bite force (Capel-Williams and Pratten 1978). Another explanation may be that the *A. atra* population from Western Cape encounters the greatest diversity of potential prey items compared to the subtropics where *A. armata* lives. To better interpret these differences, future studies should investigate the availability and abundance of prey, in addition to diet, to understand whether agamids actively select certain prey types, avoid others, or are opportunistic predators.

Although not included in the dietary analyses, we observed that nearly half of the stomachs examined contained plant matter. Many insectivorous lizards are known to consume herbaceous material. Capel-Williams and Pratten (1978) found that plant material is an important food or water source during the dry season due to scarcity of animal food or water (Joger 1979). This feeding strategy has also been observed in *Agama impalearis* (Bribon's Agama; Znari and Mouden 1997) and *Stellagama stellio* (Starred Agama; Ibrahim and El-Naggar 2013). The high frequency of vegetation found in this study indicates that it could be an important food source for these agamids as well. We also found sand particles in the stomachs. These agamids (except *A. atricollis*) live in sandveld or rocky habitats, which likely explains the indirect ingestion of mineral particles with prey captured on sandy substrates (Capel-Williams and Pratten 1978; Ibrahim and El-Naggar 2013).

The difference in diet, but not prey functional types, between juveniles and adults could correspond to the different microhabitats occupied by juveniles and adults. For instance, ants are a major component of the diet of juveniles whereas orthopterans are an important component of the diet in adult *A. impalearis* (Capel-Williams and Pratten 1978). Juveniles may be more associated with open ground between shrubs and under rocks where ants are found, and we have observed that adults and juveniles are rarely in close proximity. This apparent specialization in juveniles, however, may also result from morphological and mechanical constraints that would prevent young (and thus smaller sized) lizards to feed only on larger prey items (Capel-Williams and Pratten 1978). Our low sample sizes prevented us from performing statistical comparisons to test for age effects and prevented us making any firm conclusions.

*Acknowledgments.*—This study was carried out under the permit for scientific collection from CapeNature (056-AAA041-00168-0056), SANParks, and Ezemvelo KZN Wildlife (OP 550/2017). This Project was financially supported by the European Commission through the program Erasmus Mundus Masters Course - International Master in Applied Ecology (EMMC-IMAE; FPA 532524-1-FR-2012-ERA MUNDUS-EMMC). WCT and JM would like to thank the DSI-NRF Centre of Excellence for Invasion Biology and National Research Foundation of South Africa incentive fund for rated researchers. This project was also supported by the National Research Foundation (NRF) of South Africa (Key International Science Capacity Fund Program) to AH. For their invaluable assistance during fieldwork in South Africa, we are indebted to members of the MeaseyLab, Gareth Coleman, Amy Panikowski, John Wilkinson, François Meyer, Jason Savage, Krystal Tolley, and Frederik Igelström for access to various sites, local knowledge of species, data collection, and generous hospitality. Additionally, we are extremely grateful for all the help by the staff and volunteers in the Welgevonden Game Reserve.

## Literature Cited

Anibaldi, C., L. Luiselli, and F. Angelici. 1998. Notes on the ecology of a suburban population of rainbow lizards in coastal Kenya. African Journal of Ecology 36:199–206.

Balakrishna, S., A. Batabyal, and M. Thaker. 2016. Dining in the city: dietary shifts in Indian rock agamas across an urban-rural landscape. Journal of Herpetology 50:423–428.

Bates, M.F., W.R. Branch, A.M. Bauer, M. Burger, J. Marais, G.J. Alesander, and M.S. De Villiers. (Eds.). 2014. Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland. *Suricata* 1. South African National Biodiversity Institute, Pretoria, South Africa.

Branch, W.R. 1998. Field Gide to Snakes and Other Reptiles of Southern Africa. Ralph Curtis Books, Sanibel Island, Florida, USA.

Britt, E., and A.F. Bennet. 2008. The energetic advantages of slug specialization in garter snakes (Genus *Thamnophis*). Physiological and Biochemical Zoology 81:247–254.

Bruton, M.N. 1977. Feeding, social behaviour and temperature preferences in *Agama atra* Daudin (Reptilia, Agamidae). African Zoology 12:183–199.

Capel-Williams, G., and D. Pratten. 1978. The diet of adult and juvenile *Agama bibroni* (Reptilia: Lacertae) and a study of the jaw mechanisms in the two age groups. Journal of Zoology 185:309–318.

Greer, A.E. 1989. The Biology and Evolution of Australian Lizards. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.

Heideman, N.J.L. 2002. A comparison of the breeding and nonbreeding season diets of *Agama aculeata* and *Agama planiceps* (Reptilia: Agamidae) in Windhoek, Namibia. Journal of Herpetology 36:515–520.

Herrel, A., J. Cleuren, and F. De Vree. 1996. Kinematics of feeding in the lizard *Agama stellio*. Journal of Experimental Biology 199:1727–1742.

Herrel, A., R. Joachim, B. Vanhooydonck, and D.J. Irschick. 2006. Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. Biological Journal of the Linnean Society 89:443–454.

Huey, R.B., and E.R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.

Ibrahim, A.A., and M.H. El-Naggar. 2013. Diet and reproductive biology of the Starred Agama, *Laudakia stellio* (Linnaeus, 1758) (Squamata: Agamidae), in the northern Sinai, Egypt. Zoology in the Middle East 59:136–143.

Joger, U. 1979. Zur Ökologie und Verbreitung wenig bekannter Agamen Westafrikas (Reptilia: Sauria: Agamidae). Salamandra 15:31–52.

Levins, R. 1968. Evolution in Changing Environments: Some Theoretical Explorations (No. 2). Princeton University Press, Princeton, New Jersey, USA.

Losos, J.B., and H.W. Greene. 1988. Ecological and evolutionary implications of diet in monitor lizards. Biological Journal of the Linnean Society 35:379–407.

MacArthur, R.H. 1984. Geographical Ecology: Patterns in the Distribution of Species. Princeton University Press, Princeton, New Jersey, USA.

Macarthur, R.H., and E.R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603–609.

Measey, G.J., A.D. Rebelo, A. Herrel, B. Vanhooydonck, and K.A. Tolley 2011. Diet, morphology and performance in two chameleon morphs: do harder bites equate with harder prey? Journal of Zoology 285:247–255.

Meyers, J.J., and A. Herrel. 2005. Prey capture kinematics of ant eating lizards. Journal of Experimental Biology 208:113–127.

Norval, G., S.C. Huang, J.J. Mao, S.R. Goldberg, and K. Slater. 2012. Additional notes on the diet of *Japalura swinhonis* (Agamidae) from southwestern Taiwan, with comments about its dietary overlap with the sympatric *Anolis sagrei* (Polychrotidae). Basic and Applied Herpetology 26:87–97.

Ortega-Rubio, A., A. González-Romero, and R. Barbault. 1995. Food analysis and resource partitioning in a lizard guild of the Sonoran Desert, Mexico. Journal of Arid Environments 29:367–382.

Pianka, E.R. 1986. Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure. Princeton University Press, Princeton, New Jersey, USA.

Pinkas, L., M.S. Olpihant, and I.L.K. Iverson. 1971. Food habits of Albacore, Bluefin Tuna and Bonito in Californian waters. California Department of Fish and Game: Fish Bulletin 152:1–105.

Reaney, L.T., and M.J. Whiting. 2002. Life on a limb: ecology of the Tree Agama (*Acanthocercus a. atricollis*) in southern Africa. Journal of Zoology 257:439–448.

Reaney, L.T., and M.J. Whiting. 2003. Picking a tree: habitat use by the Tree Agama, *Acanthocercus atricollis atricollis*, in South Africa. African Zoology 38:273–278.

Schaerlaeken, V., A. Herrel, P. Aerts, and C.F. Ross. 2008. The functional significance of the lower temporal bar in *Sphenodon punctatus*. Journal of Experimental Biology 211:3908–3914.

Schwenk, K. 2000. Feeding in lepidosaurs. Pp. 175–291 *In* Feeding: Form, Function and Evolution in Tetrapod Vertebrates. Schwenk, K. (Eds.). Academic Press, San Diego, California, USA.

Van Berkel, J.B., and S. Clusella-Trullas. 2018. Behavioral thermoregulation is highly repeatable and unaffected by digestive status in *Agama atra*. Integrative Zoology 13:482–493.

Vanhooydonck, B., A. Herrel, and R. Van Damme. 2007. Interactions between habitat use, behavior, and the trophic niche of lacertid lizards. Pp. 427–449 *In* Lizard Ecology: The Evolutionary Consequences of Foraging Mode. Reilly, S.M., L.D. McBrayer, and D.B. Miles (Eds.). Cambridge University Press, New York, New York, USA.

Whiting, M.J., P. le FN Mouton, J.H. Van Wyk, and W.E. Cooper. 1999. Movement-and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa. Amphibia-Reptilia 20:391–399.

Whiting, M.J., K. Chetty, W. Twine, and P. Carazo. 2009. Impact of human disturbance and beliefs on the Tree Agama *Acanthocercus atricollis atricollis* in a South African communal settlement. Oryx 43:586–590.

Znari, M., and E. El Mouden. 1997. Seasonal changes in the diet of adult and juvenile *Agama impalearis* (Lacertilia: Agamidae) in the central Jbilet Mountains, Morocco. Journal of Arid Environments 37:403–412.

Zug, G.R., L.J. Vitt, and J.P. Caldwell. 2001. Herpetology. An Introductory Biology of Amphibians and Reptiles. 2nd Edition. Academic Press, San Diego, California, USA.

**Appendix Table 1**. Mean and range values of snout vent length (SVL in mm) and mass (in g) for adults and juveniles of *Agama aculeata distanti* (Eastern Ground Agama), *A. armata* (Peter's Ground Agama), *A. atra* (Southern Rock Agama) and *Acanthocercus atricollis* (Southern Tree Agama).

| | *A. a. distanti* | | *A. armata* | | *A. atra* | | *A. atricollis* | |
|---|---|---|---|---|---|---|---|---|
| | adult | juvenile | adult | juvenile | adult | juvenile | adult | juvenile |
| SVL mean | 78.8 | 40.5 | 71.6 | 32.6 | 83.1 | 55.4 | 119.2 | 61.9 |
| SVL range | 71.8–85.9 | 30.2–48.2 | 70.8–72.3 | 28.0–39.6 | 71.2–95.0 | 35.4–69.4 | 100.82–139.45 | 40.54–93.63 |
| Mass mean | 18.8 | 2.5 | 15.5 | 1.7 | 20.2 | 8.9 | 65.8 | 16.4 |
| Mass range | 16.0–24.0 | 1.0–5.0 | 14.0–17.0 | 1.0–3.0 | 12.1–28.1 | 4.8–11.3 | 40.0–112.0 | 2.5–30.0 |

**Appendix Table 2**. Results of the ANOVAs performed on the prey Index of Relative Importance (IRI) comparing *Agama aculeata distanti* (Eastern Ground Agama), *A. armata* (Peter's Ground Agama), *A. atra* (Southern Rock Agama) and *Acanthocercus atricollis* (Southern Tree Agama). Asterisks (*) indicate prey taxa that were significantly different between species of agamids. The degrees of freedom for all prey taxon is 3 and 61.

| IRI | F | P |
|---|---|---|
| Formicidae | 0.200 | 0.022* |
| Other Hymenoptera | 0.566 | 0.345 |
| Coleoptera | 0.106 | 0.832 |
| Hemiptera | 2.537 | < 0.001* |
| Diptera | 3.374 | < 0.001* |
| Diplopoda | 2.134 | < 0.001* |
| Lepidoptera | 0.433 | 0.114 |
| Orthoptera | 0.103 | 0.345 |
| Gastropoda | 0.050 | 0.532 |
| Ephemoptera | 0.110 | 0.532 |
| Isoptera | 0.597 | 0.619 |
| Isopoda | 0.597 | 0.619 |

**Wei Cheng (Nicholas) Tan** is a Masters graduate from the Université de Poitiers, France, and Universidade de Coimbra, Portugal. He received his B.Sc. with a major in zoology at the Australian National University, Canberra, Australia. Wei Cheng is interested in the evolution of phenotypic diversity and the mechanisms that drive biodiversity. He is currently a Ph.D. Candidate at the Alexander Koenig Research Museum, Bonn, Germany, where he is conducting further research in herpetology. Wei Cheng is passionate about conservation of reptiles and enjoys studying them in the field. (Photographed by Jason Savage).

**Anthony Herrel** is a Research Director at the Centre National de la Recherche Scientifique working at the Natural History Museum in Paris, France. His research interests encompass the evolution of form and function. He is specifically interested in both the drivers of phenotypic diversity and the constraints that hamper phenotypic diversification. Anthony works at one of the oldest and largest natural history museums in Europe where he is lucky enough to be able to study the anatomy and function of a diversity of vertebrate species. He has a keen interest in herpetology and loves doing field work to study organisms in their natural environment. (Photographed by Colin Donihue).

**John Measey** is a Chief Researcher in Invasion Biology at the Department of Science and Innovation-National Research Foundation, Centre of Excellence for Invasion Biology at Stellenbosch University, South Africa. His research interests encompass all things herpetological, with a special focus on invasions. John lives and works in the unique and diverse fynbos biome of South Africa where many species are impacted by invasive species. (Photographed by Thalassa Matthews).