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Ecology of Southern African Sandveld Lizards (Lacertidae, *Nucras*)

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Sandveld lizards (genus *Nucras*) are widespread in southern Africa, but are generally secretive and poorly known. We examined 385 preserved specimens from five species of *Nucras* collected over a broad time span (104 years) and a geographic area covering most of South Africa and Swaziland. We had three main objectives: to test for sexual size dimorphism, to quantify male and female reproductive cycles, and to determine diet. In addition, we examined the importance of scorpions in the diet of *Nucras* based on previous studies reporting an unusually high incidence of scorpions in the diet of Kalahari *N. tessellata*. Males of all species except *N. lalandii* had significantly larger heads than females of the same body size, although females had significantly greater snout–vent length than males in three of the five species examined. The general reproductive pattern was for females to contain vitellogenic eggs during late spring and early summer. No females simultaneously contained oviductal and vitellogenic eggs, which suggests that females produce only one clutch per season. Clutch size was unrelated to female body size in all species examined. Female follicle volume generally coincided with male testicular volume, indicating for the most part synchronized reproductive cycles between the sexes. Testis volume was generally highest during spring–early summer, with only *N. holubi* showing a second peak in autumn. We recorded 15 arthropod orders in the diet of *Nucras*. All species feed on invertebrates, primarily insects, and, to a lesser degree, spiders and centipedes. Termites, grasshoppers, and beetles both numerically and volumetrically dominated their diet. We found no evidence that scorpions form a major part of the diet of any of these five species of *Nucras*, including *N. tessellata* from biomes outside the Kalahari Desert.

UNDERSTANDING broad-scale ecological patterns of diverse living organisms is fundamental to developing life history theory (Stearns, 1976). In this regard, ecological studies of lizards have been extremely fruitful (Milstead, 1967; Huey et al., 1983; Pianka, 1986; Vitt and Pianka, 2005). For example, extensive ecological data sets combined with phylogenies of major lizard clades have facilitated our understanding of the role of early evolutionary events on the evolution of ecological traits and the associated present day structuring of lizard communities (Vitt et al., 2003; Vitt and Pianka, 2005). However, even the combined lifetime efforts of two key lizard ecologists, E. R. Pianka and L. J. Vitt, have resulted in ecological data for only about 4.25% of 'lizards' and 2.2% of squamates (Vitt and Pianka, 2007). Furthermore, these data are biased by region. We need additional ecological data from more taxa, and from taxa occupying a greater variety of habitat types in which different predator assemblages and resources occur (Vitt and Pianka, 2007) in order to elucidate and understand broad-scale ecological patterns.

One of the best-studied ecological attributes of lizards is their diet. Previous studies have focused on lizard foraging mode, preference for particular prey, and how they detect and capture prey (Vitt and Pianka, 2005; Cooper, 2007; Reilly et al., 2007). Many lizard species are generalized insectivores that consume prey of a range of sizes, while others are highly specialized. For example, *Ameiva ameiva* will eat many small prey and some large ones (reviewed in Vitt and Pianka, 2007), while *Moloch horridus* has a highly specialized diet consisting of ants only (Pianka and Pianka, 1970). Because most lizards thus far studied are generalists and eat a wide variety of prey sizes, any exceptions to this pattern are of particular interest to ecologists. Of specific interest are lizards that eat large prey and occupy a 'top predator' position in a food web.

The southern African lacertid *Nucras tessellata* is a 'top predator' (Huey et al., 2001) that consumes a high proportion of scorpions (53%), considered to be large and energetically rich prey (Pianka, 1986). *Nucras tessellata* is also an active forager that retrieves scorpions from their day-time retreats (Pianka, 1986). Current knowledge of the ecology of *Nucras* (Sandveld lizards) in general is restricted to *N. tessellata* and *N. intertexta* from the Kalahari Desert (Huey and Pianka, 1977; Pianka et al., 1979; Huey and Pianka, 1981; reviewed in Pianka, 1986). Using museum specimens, we studied the ecology of five species of the lizard genus *Nucras* with three main objectives: to test for sexual size dimorphism, to quantify male and female reproductive ecology, and to examine diet. With respect to diet, our primary aim was to determine the extent to which these species of *Nucras* eat scorpions, including *N. tessellata* from areas outside of the Kalahari Desert.

MATERIALS AND METHODS

Study system.—Lacertids of the genus *Nucras* are mainly restricted to scrubland or savannah habitats in southern Africa, with isolated species occurring in Angola (*N. scalaris*) and East Africa (*N. boulengeri*). The genus was last revised by Broadley (1972), who recognized seven species, some containing additional races. A molecular phylogeny of *Nucras* is currently in preparation (Bauer, Branch, and Burger, unpubl.), with indications that additional cryptic taxa may be subsumed within *N. tessellata* (Branch, 2006). We have assigned specimens to species as accepted in Branch (1998), but are aware that Kalahari arenicolous populations of *N. tessellata* may be specifically distinct. Previously, only *N. tessellata* and *N. intertexta* have been the subject of ecological study; both are active foragers and *N.*

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tessellata specializes largely on scorpions (reviewed in Pianka, 1986; also see Huey and Pianka, 1977; Huey et al., 1984). We present baseline ecological and morphological data from museum specimens for five of the ten currently recognized species of *Nucras* from eastern and southern Africa.

Sexual size dimorphism.—We examined 385 specimens, including *N. holubi* (77), *N. intertexta* (76), *N. lalandii* (82), *N. ornata* (84), and *N. tessellata* (66). The following morphological variables were measured to test for sexual size dimorphism: head length, width, and height to the nearest 0.01 mm using digital calipers; snout–vent length (SVL) and tail (original, complete) length, both measured to the nearest 1 mm. All data met assumptions of normality and homoscedacity. Sexual size dimorphism was tested using a one-factor ANOVA between mean values for adult males vs. females. We also tested for heterogeneity of slopes. If slopes did not differ significantly an ANCOVA was performed. Finally, we used a reduced major axis (RMA) regression (Fairbairn, 1997; Bohonak and van der Linde, 2004) to investigate whether growth patterns of characters differed significantly between the sexes.

Reproduction.—We made a mid-ventral incision to expose the gonads in order to score sex and reproductive condition. Females were considered sexually mature if the oviducts were muscular and scored as sexually active at the time of preservation if eggs or large ovarian follicles were present. We recorded the diameter of the largest vitellogenic follicle or oviductal egg to the nearest 0.01 mm using digital calipers. Males were considered sexually mature if testes were enlarged/turgid (immature males had flat, ribbon-like testes), and defined as sexually active at time of preservation if the epididymides were convoluted. Testes were measured for length and width to the nearest 0.01 mm using digital calipers. We calculated egg and testis volume using the formula for a prolate spheroid (Vitt et al., 1993):

$$\text{Volume} = 4/3\pi(\text{length}/2) * (\text{width}/2)^2.$$

Diet.—We determined diet by removing and examining stomach contents of preserved specimens. Prey items were spread out on a petri dish and identified to order. We also measured the length and width of each intact prey item to the nearest 0.01 mm using digital calipers, and calculated prey volume using the formula for a prolate spheroid (see above).

Niche breadth measure for numerical and volumetric diet data were estimated using the reciprocal of Simpson's (1949) formula:

$$B = 1 \Bigg/ \sum_{i=1}^{n} p_i^{\,2},$$

where i = resource category, n = total number of categories, and p = proportion of resource category i. Values range from 1 (exclusive use of one prey type) to n (even use of all prey types). Prey categories are represented by the arthropod orders of prey items found in stomachs.

We also calculated percent utilization for each prey type numerically and volumetrically (the pi × 100 of Pianka, 1973, 1986). A regression analysis was used to determine the relationship between SVL and mean prey volume, and SVL and number of prey items consumed. We also compared prey size among species by performing an ANOVA on the number of prey items and prey volume/individual. A Bonferroni *post-hoc* test was used to determine sources of differences. Analyses were performed with SAS Enterprise Guide 3.0 (SAS Institute Inc., 2007), and all means are reported ± 1 SE. We used parametric tests when the assumptions of normality and homoscedasticity could reasonably be met.

RESULTS

Sexual size dimorphism.—Summary statistics of morphological measurements for the five species are given in Table 1, and frequency of SVL in Figure 1. Overall, sexual dimorphism in SVL and head size was variable among species and in both directions (males or females larger). Females of *Nucras holubi* and *N. lalandii* were significantly larger in SVL than males; likewise, *N. intertexta* females had significantly larger SVL, head length, and width than males. *Nucras ornata* males had significantly wider and deeper heads than females (Table 2). When the effect of body size was removed, *N. holubi* males had significantly larger heads than females (length, width, and height), *N. intertexta* males had significantly longer and deeper heads than females, *N. lalandii* males had significantly longer heads than females, *N. ornata* males had significantly wider and deeper heads than females, and *N. tessellata* males had significantly longer heads than females (Table 2). For most species, the head typically grew isometrically in relation to SVL (Table 3).

Tail length differed significantly among species ($F_{4,231}$ = 34.203, $P < 0.001$). A Bonferroni *post-hoc* test showed that *N. lalandii*, *N. ornata*, and *N. tessellata* had proportionately longer tails followed by *N. intertexta* and *N. holubi*.

Reproduction.—The smallest male and female showing evidence of sexual maturity were 59 and 61 mm (*N. holubi*), 67 and 65 mm (*N. intertexta*), 69 and 71 mm (*N. lalandii*), 57 and 59 mm (*N. ornata*), and 63 and 61 mm (*N. tessellata*), respectively (Fig. 1). Females collected during the breeding season contained clutches varying from 1–7 eggs (*N. holubi*: n = 12, mean = 4.08 ± 0.5), 4–8 eggs (*N. intertexta*: n = 12, mean = 6 ± 0.41), 4–14 eggs (*N. lalandii*: n = 2, mean = 7 ± 1), 4–13 eggs (*N. ornata*: n = 4, mean = 5.5 ± 0.87), and 3–7 eggs (*N. tessellata*: n = 6, mean = 4.67 ± 0.56). Clutch size was not related to female body size (SVL), although this is likely due to small sample sizes: *N. holubi* (r^2 = 0.039, P = 0.54), *N. intertexta* (r^2 = 0.011, P = 0.75), *N. ornata* (r^2 = 0.041, P = 0.70), *N. lalandii* (r^2 = 0.01723, P = 0.35), and *N. tessellata* (r^2 = 0.061, P = 0.59). Egg size increased significantly with SVL for *N. holubi* (r^2 = 0.189, $P < 0.05$) and *N. tessellata* (r^2 = 0.323, $P < 0.01$), but not for *N. intertexta* (r^2 = 0.051, P = 0.24), *N. lalandii* (r^2 = 0.006, P = 0.68), or *N. ornata* (r^2 = 0.031, P = 0.38). Clutch size did not differ significantly among species when controlling for body size ($F_{4,43}$ = 2.49, P = 0.06), although this marginally nonsignificant difference could be an artifact of sample size. Seasonal variation in ovarian volume of the largest follicle indicated that females were gravid during spring–summer and autumn (*N. holubi*), summer (*N. intertexta* [one individual in autumn], *N. lalandii*, *N. tessellata*), and spring–summer (*N. ornata*, Fig. 2). No evidence of double clutching was found in specimens examined.

Body size (SVL) was significantly correlated with testis volume for *N. holubi* (r_p = 0.54, $P < 0.001$, n = 51), *N.*

Table 1. Morphological Characteristics of Sexually Mature Individuals of *Nucras* spp. Means are reported ± SE; ranges are in parentheses. Only lizards with complete tails were included for tail length (*N. holubi* [m = 15, f = 36], *N. intertexta* [m = 15, f = 28], *N. lalandii* [m = 27, f = 17], *N. ornata* [m = 16, f = 32], *N. tessellata* [m = 15, f = 30]). All measurements are in millimeters.

Species/sex	Morphological traits				
	SVL	Tail length	Head length	Head width	Head height
N. holubi					
Females (n = 19)	63.95 ± 1.65 (50–77)	117.07 ± 4.94 (87–166)	12.75 ± 0.36 (9.76–15.38)	8.74 ± 0.25 (7.15–10.77)	6.76 ± 0.22 (5.43–8.72)
Males (n = 45)	59.98 ± 0.80 (49–72)	112.49 ± 2.35 (83–134)	13.05 ± 0.21 (9.78–15.71)	8.94 ± 0.14 (6.85–10.51)	6.81 ± 0.12 (5.11–8.41)
N. intertexta					
Females (n = 25)	73.32 ± 1.77 (56–91)	147.47 ± 5.46 (112–186)	13.23 ± 0.28 (11.08–15.82)	6.47 ± 0.19 (3.38–8.04)	9.04 ± 0.21 (6.88–10.91)
Males (n = 38)	63.32 ± 0.98 (49–77)	135.62 ± 3.59 (97–176)	12.54 ± 0.17 (10.28–15.09)	6.30 ± 0.14 (8.57–11.76)	8.44 ± 0.13 (6.95–10.74)
N. lalandii					
Females (n = 36)	89.11 ± 1.62 (71–107)	159.78 ± 5.20 (104–207)	14.21 ± 0.22 (11.26–16.38)	10.49 ± 0.19 (8.01–13.54)	7.80 ± 0.14 (6.07–9.17)
Males (n = 21)	80.57 ± 2.43 (47–101)	158.56 ± 6.31 (99–209)	13.68 ± 0.26 (11.34–16.26)	10.06 ± 0.21 (8.57–11.76)	7.54 ± 0.16 (6.37–9.37)
N. ornata					
Females (n = 25)	74.52 ± 2.55 (47–103)	147.50 ± 5.68 (107–207)	13.36 ± 0.43 (8.25–16.76)	10.06 ± 0.33 (7.15–13.49)	7.45 ± 0.26 (4.69–9.94)
Males (n = 48)	77.25 ± 2.11 (47–111)	159.24 ± 5.71 (104–231)	14.51 ± 0.38 (9.98–20.83)	11.20 ± 0.34 (7.26–17.12)	8.40 ± 0.24 (5.29–12.24)
N. tessellata					
Females (n = 18)	71.00 ± 1.84 (58–86)	162.73 ± 6.11 (114–196)	13.01 ± 0.26 (11.04–14.30)	9.04 ± 0.23 (7.59–10.88)	6.26 ± 0.24 (4.31–8.08)
Males (n = 37)	69.08 ± 1.07 (52–83)	165.42 ± 5.42 (98–219)	13.25 ± 0.19 (10.04–15.79)	8.72 ± 0.15 (6.01–10.39)	6.08 ± 0.11 (4.21–7.54)

intertexta ($r_p = 0.51$, $P < 0.001$, $n = 46$), *N. lalandii* ($r_p = 0.54$, $P < 0.001$, $n = 37$), *N. ornata* ($r_p = 0.65$, $P < 0.001$, $n = 44$), and weakly for *N. tessellata* ($r_p = 0.30$, $P = 0.05$, $n = 42$). Testes were most turgid during spring–early summer, with a second peak in autumn (*N. holubi*), spring–summer (*N. intertexta*), summer (*N. lalandii*, *N. ornata* [one individual in autumn]), and in *N. tessellata* did not show a clear pattern (Fig. 3). Male and female reproductive cycles appeared to be generally synchronous.

Diet.—Of the 385 lizard stomachs examined, 167 (43%) were empty (26/77 = 34%, *N. holubi*; 28/76 = 37%, *N. intertexta*; 37/82 = 45%, *N. lalandii*; 44/84 = 52%, *N. ornata*; 32/66 = 48%, *N. tessellata*). The remaining 218 stomachs contained 1229 prey items. A wide variety of prey taxa were consumed, including termites, spiders, scorpions, insect eggs and in a few cases, lizard tails (Table 4). For all five species the largest percentage of individual prey items consumed were termites. However, the largest volume of stomach contents varied by species and constituted termites (39%, *N. holubi*), grasshoppers (15%, *N. intertexta*; 63%, *N. lalandii*; 50%, *N. ornata*), and ants (53%, *N. tessellata*). Mean number of prey items per stomach and average volume of prey per stomach were 10.61 ± 2.42 and 444.59 ± 79.46 mm^3 (*N. holubi*), 5.98 ± 2.03 and 529.66 ± 79.46 mm^3 (*N. intertexta*), 5.82 ± 1.78 and 579.40 ± 107.66 mm^3 (*N. lalandii*), 4.53 ± 1.66 and 631.52 ± 172.73 mm^3 (*N. ornata*), and 4.51 ± 1.33 and 830.86 ± 273.60 mm^3 (*N. tessellata*), respectively.

No significant relationship was found between SVL and number of prey (*N. holubi*: $r_s = 0.035$, $P = 0.19$; *N. intertexta*: $r_s = 0.03$, $P = 0.24$; *N. lalandii*: $r_s = 0.007$, $P = 0.58$; *N. ornata*: $r_s = 0.02$, $P = 0.35$; *N. tessellata*: $r_s = 0.002$, $P = 0.79$). Mean prey volume was significantly correlated with SVL for *N. intertexta* ($r_s = 0.484$, $P < 0.001$, $n = 48$) and *N. ornata* ($r_s = 0.196$, $P < 0.005$, $n = 40$), but not for *N. holubi* ($r_s = 0.005$, $P = 0.64$, $n = 51$), *N. lalandii* ($r_s = 0.06$, $P = 0.10$, $n = 45$) and *N. tessellata* ($r_s = 0.005$, $P = 0.69$, $n = 34$).

Niche breadths for prey number ranged from 1.29 (*N. holubi*)–3.40 (*N. lalandii*), indicating that many individuals of just a few prey types (termites, grasshoppers, and ants) were consumed (Table 4). For *N. holubi* and *N. intertexta*, niche breadths for prey volume were high enough to suggest that several prey categories were important, while in *N. lalandii*, *N. ornata*, and *N. tessellata* niche breadths for prey volume were low and suggest that only a few prey categories were important (Table 4).

When controlling for body size, no significant differences were found between sexes for total prey number ($F_{1,217} = 0.14$, $P = 0.71$), total prey volume ($F_{1,217} = 2.19$, $P = 0.14$), and mean prey volume/individual ($F_{1,217} = 0.24$, $P = 0.63$). Likewise, when body size was controlled for, no difference was found among species for total prey number ($F_{4,217} = 1.69$, $P = 0.15$) and total prey volume ($F_{4,217} = 0.93$, $P = 0.45$). However, mean prey volume/individual was significantly ($F_{4,217} = 8.74$, $P < 0.001$) different among species. A Bonferroni *post-hoc* test showed that *N. ornata* consumed the largest prey items, followed by *N. lalandii* and *N. tessellata*, *N. holubi*, and *N. intertexta* (Fig. 4).

DISCUSSION

Of the five species examined, females were the larger (SVL) sex in three species and males in two species, suggesting that different selective pressures are at play, depending on

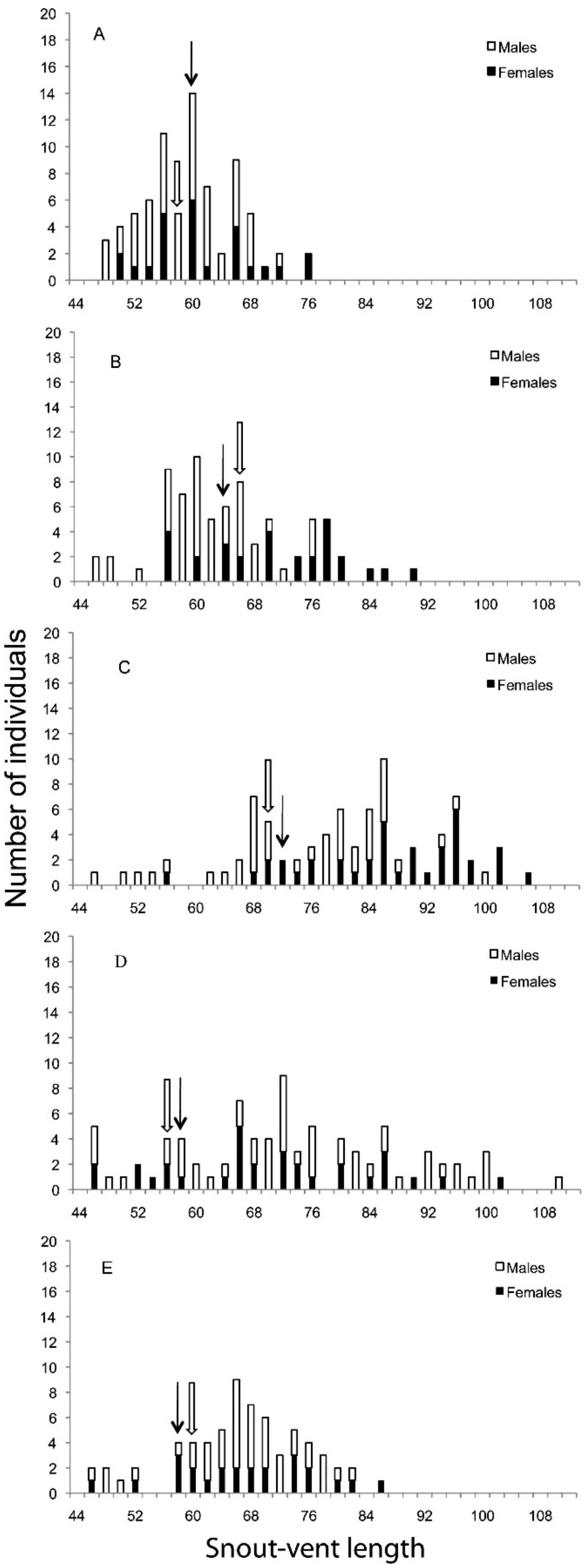

Fig. 1. Snout–vent length (mm) frequency for male and female *Nucras* spp. Solid arrows indicate minimum female size at sexual maturity; open arrows indicate minimum male size at sexual maturity. A = *N. holubi*, B = *N. intertexta*, C = *N. lalandii*, D = *N. ornata*, E = *N. tessellata*.

species. Unfortunately we did not separately measure trunk size, which appears to be under stronger selection relative to overall body size in certain female lacertids from Europe (Braña, 1996). In general, female lizards have relatively longer trunks than males as a consequence of fecundity selection favoring individuals with a capacity to carry more eggs or offspring, while males frequently have larger heads because of contest competition (Cooper and Vitt, 1989; Braña, 1996; Olsson et al., 2002), although other factors also contribute to SSD (Cox et al., 2003). When the effect of body size was removed, some aspect of head size in males of all species except *N. lalandii* was significantly larger than that of females. Although head size is typically acted on by sexual selection for contest competition (Olsson et al., 2002; Husak et al., 2009), intrasexual niche divergence can explain differences in head size as a result of sex-specific trophic ecology (Shine, 1989; Herrell et al., 1999). While there are some differences in types of prey eaten by males and females of different *Nucras* spp., prey number, total prey volume, and prey volume/individual did not differ significantly between sexes. Therefore, the most parsimonious mechanism explaining head size sexual dimorphism is male contest competition, and not trophic partitioning, but other factors could also be important (Cox et al., 2003). Sexual dimorphism in southern African lacertids is largely unstudied, although female *Pedioplanis burchelli* have larger bodies than males, but smaller heads (Nkosi et al., 2004). Among eight species of European lacertids (*Podarcis*, *Lacerta*) males have larger heads than females, but females have larger abdomens, although overall body size could be significantly greater in either sex (Braña, 1996). Abdomen length increases at a faster rate relative to SVL in females, and this is explained by fecundity selection. Conversely, larger male head size was most likely due to sexual selection with no support for intersexual dietary niche divergence. In general, lacertids appear to conform to a typical pattern seen in lizards: fecundity selection acting on female abdomen size and sexual selection acting on head size (Braña, 1996).

Females contained vitellogenic eggs during late spring and early summer. No females simultaneously contained oviductal and vitellogenic eggs, which suggests that females of all species produce only one clutch per season, although *N. holubi* and *N. intertexta* show some evidence of autumn breeding. Clutch size for all species combined ranged from 1–14 eggs, with means ranging between 4–6 (excluding *N. lalandii*). Pianka (1986) reports a mean clutch size of 3.3 ± 0.7 SD for eight *N. tessellata*, while we report a mean clutch size of 4.7 for six individuals. Clutch size and maternal body size were not significantly related, although small sample sizes for most taxa likely obscured any real relationships. Overall, male *Nucras* typically had enlarged testes during spring and summer, followed by regression in autumn and winter. In female *Nucras*, follicles were typically enlarged during spring–summer, followed by regression in late summer and continuing through winter (but see *N. holubi*, Fig. 2). Therefore, male and female reproductive cycles are largely synchronous.

Stomachs we examined from museum specimens were collected over a broad time span (104 years) and a geographic area covering most of South Africa and Swaziland. Therefore, the samples should be representative of dietary preference. *Nucras* were largely insectivorous, but also included spiders and centipedes in their diet. Their diet was numerically dominated by termites and volumetrically

Table 2. Sexual Size Dimorphism in Morphological Traits for *Nucras* spp. Results of a one-factor ANOVA between mean values for adult males vs. females, the tests for heterogeneity of slopes for *N. holubi* ($n = 64$), *N. intertexta* ($n = 63$), *N. lalandii* ($n = 57$), *N. ornata* ($n = 73$), and *N. tessellata* ($n = 55$), followed by ANCOVA if slopes did not differ significantly. Only lizards with complete tails were included for tail length (see Table 1). Sex was used as the factor in all analyses. Asterisk refers to a significant ($P < 0.05$) difference between mean values for adult males vs. females. The M/F column indicates which of the sexes has the larger trait.

		ANOVA				Heterogeneity of slopes test			Intercept			
Species	Trait	*F*	df	*P*	M/F	*F*	df	*P*	*F*	df	*P*	M/F
N. holubi	SVL	5.83	1,63	0.02*	F							
N. intertexta		28.56	1,62	0.0001*	F							
N. lalandii		9.16	1,56	0.004*	F							
N. ornata		0.62	1,72	0.43								
N. tessellata		0.92	1,54	0.34								
N. holubi	Tail length	0.90	1,51	0.35		0.68	1,50	0.41	0.04	1,50	0.84	
N. intertexta		3.48	1,43	0.07		0.01	1,42	0.92	0.006	1,42	0.94	
N. lalandii		0.02	1,44	0.88		0.04	1,43	0.85	3.19	1,43	0.08	
N. ornata		1.64	1,48	0.21		0.09	1,47	0.77	1.41	1,47	0.24	
N. tessellata		0.09	1,45	0.76		0.92	1,44	0.34	1.15	1,44	0.29	
N. holubi	Head length	0.55	1,63	0.46		0.32	1,63	0.57	31.35	1,63	0.0001*	M
N. intertexta		5.15	1,62	0.03*	F	0.22	1,62	0.64	9.78	1,62	0.03*	M
N. lalandii		2.40	1,56	0.13		5.76	1,56	0.02	—	—	—	
N. ornata		3.60	1,72	0.06		1.24	1,72	0.27	3.11	1,72	0.08	
N. tessellata		0.54	1,54	0.47		0.52	1,54	0.47	4.78	1,54	0.03*	M
N. holubi	Head width	0.61	1,63	0.44		0.74	1,63	0.39	25.52	1,63	0.001*	M
N. intertexta		6.69	1,62	0.01*	F	0.17	1,62	0.68	6.30	1,62	0.01*	M
N. lalandii		2.21	1,56	0.14		1.15	1,56	0.29	0.02	1,56	0.89	
N. ornata		4.65	1,72	0.03*	M	0.12	1,72	0.73	9.20	1,72	0.003*	M
N. tessellata		1.45	1,54	0.23		0.38	1,54	0.54	0.58	1,54	0.45	
N. holubi	Head height	0.06	1,63	0.82		2.53	1,63	0.12	8.02	1,63	0.006*	M
N. intertexta		0.57	1,62	0.45		0.01	1,62	0.91	3.69	1,62	0.06	
N. lalandii		1.39	1,56	0.24		0.75	1,56	0.39	0.03	1,56	0.86	
N. ornata		6.03	1,73	0.02*	M	0.07	1,72	0.79	16.57	1,72	0.0001*	M
N. tessellata		0.64	1,54	0.43		0.88	1,54	0.35	0.02	1,54	0.88	

Table 3. Results of a Reduced Major Axis (RMA) Regression Showing the Relationship between the Growth Rate of the Head (Height, Length, Width) in Relation to SVL.

	Males			Females		
	r^2	Slope	95% CI	r^2	Slope	95% CI
N. holubi						
Head height	0.8064	1.164	1.018–1.309	0.5571	1.316	0.9381–1.694
Head length	0.8846	1.089	0.9836–1.194	0.8371	1.155	0.954–1.356
Head width	0.8969	1.051	0.955–1.147	0.7154	1.101	0.8478–1.355
N. intertexta						
Head height	0.2744	1.382	1.029–1.736	0.29	1.196	0.7982–1.594
Head length	0.7133	0.9097	0.7635–1.056	0.7907	0.7903	0.6476–0.9331
Head width	0.7017	0.9854	0.8217–1.199	0.8139	0.9152	0.7593–1.071
N. lalandii						
Head height	0.4221	0.8252	0.6272–1.023	0.546	0.986	0.7643–1.208
Head length	0.5674	0.8139	0.645–0.9829	0.7408	0.8799	0.7304–1.029
Head width	0.5095	0.8884	0.692–1.085	0.5624	0.9961	0.7762–1.216
N. ornata						
Head height	0.8806	1.08	0.9755–1.185	0.8781	1.07	0.9283–1.212
Head length	0.5765	0.8885	0.7258–1.051	0.3729	0.9061	0.6336–1.179
Head width	0.7931	1.1	0.9589–1.24	0.8907	0.9414	0.8232–1.06
N. tessellata						
Head height	0.6182	1.028	0.8249–1.231	0.6399	1.28	0.9401–1.619
Head length	0.7715	0.8502	0.7203–0.98	0.7938	0.9203	0.7355–1.105
Head width	0.5932	1.004	0.7998–1.209	0.7929	1.055	0.8429–1.268

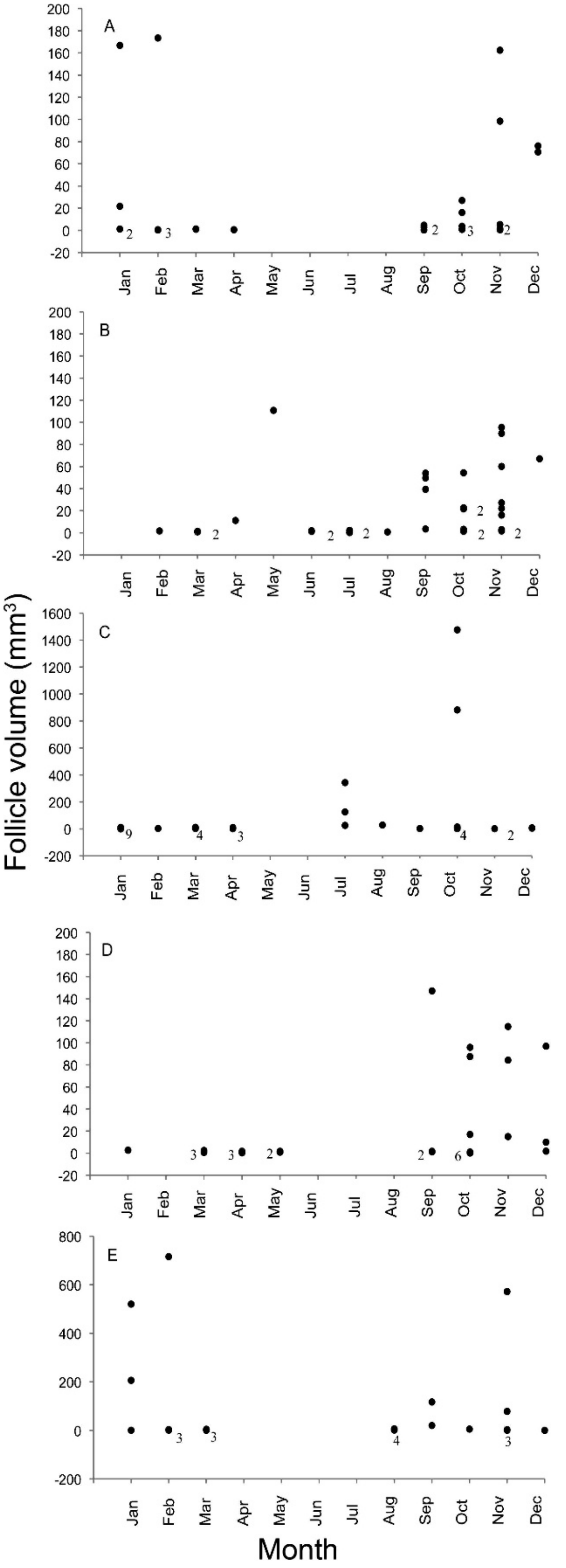

Fig. 2. Volume of largest follicle for *Nucras* spp. in relation to time of the year. Numbers adjacent to points indicate the number of overlapping values. A = *N. holubi*, B = *N. intertexta*, C = *N. lalandii*, D = *N. ornata*, E = *N. tessellata*.

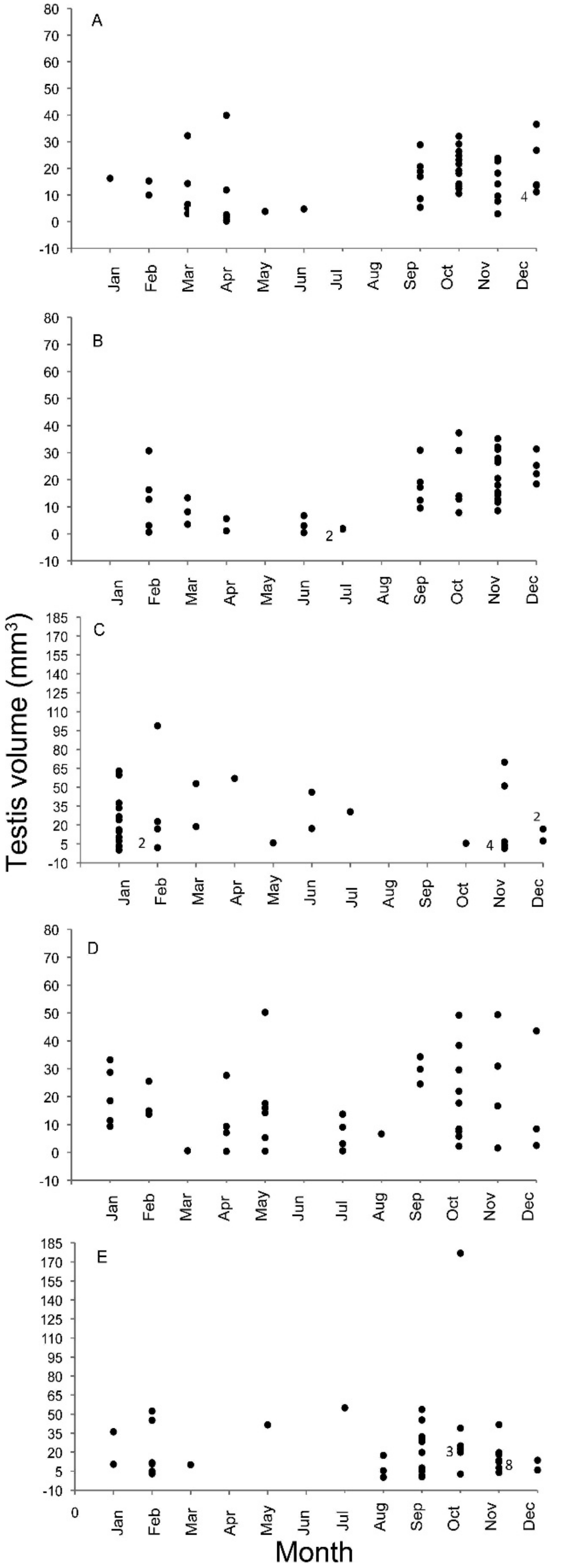

Fig. 3. Volume of largest testis for *Nucras* spp. in relation to time of the year. Numbers adjacent to points indicate the number of overlapping values. A = *N. holubi*, B = *N. intertexta*, C = *N. lalandii*, D = *N. ornata*, E = *N. tessellata*.

Table 4. Summary of Diet for *Nucras* spp. Insect taxonomy (prey categories) follows Borror et al. (1992). Frequency is the number of lizards containing a specific prey category in the respective sample. All Lepidoptera were larval. No. is the total number of individual prey items from a particular arthropod group, followed by its percentage (% No.) as a proportion of all identified arthropod prey. Vol. is the summed volume of all intact individual prey items of a particular arthropod group, while % Vol. is the proportion (expressed as a percentage) of an arthropod group in relation to total volume. Freq. (frequency) is the number of individual lizards containing prey items belonging to a particular arthropod group.

	N. holubi ($n = 51$)					*N. intertexta* ($n = 48$)					*N. lalandii* ($n = 45$)					*N. ornata* ($n = 40$)					*N. tessellata* ($n = 34$)				
Prey type	No.	% No.	Vol.	% Vol.	Freq.	No.	% No.	Vol.	% Vol.	Freq.	No.	% No.	Vol.	% Vol.	Freq.	No.	% No.	Vol.	% Vol.	Freq.	No.	% No.	Vol.	% Vol.	Freq.
Orthoptera	20	3.8	5372.7	24.6	16	14	4.9	3916.3	15.4	13	57	21.8	16496.4	63.3	36.0	28	15.7	12549.9	49.9	25	19	12.1	3862.6	13.7	18
Blattaria	6	1.1	541.4	2.5	5	6	2.1	3304.5	13.0	5						2	1.1	120.0	0.5	2					
Mantodea	1	0.2	274.5	1.3	1	1	0.3	79.7	0.3	1															
Isoptera	468	87.8	8596.7	39.3	17	195	67.9	1931.7	7.6	8	94	36.0	860.9	3.3	4.0	116	65.2	2141.1	8.5	4	95	60.5	3196.6	11.3	6
Coleoptera	12	2.3	3420.6	15.6	8	20	7.0	2911.3	11.5	15	13	5.0	4733.1	18.2	5.0	1	0.6	275.3	1.1	2	9	5.7	4623.7	16.4	5
Hemiptera	2	0.4	179.4	0.8	1	10	3.5	1116.6	4.4	3						1	0.6	103.1	0.4	1	2	1.3	158.7	0.6	2
Lepidoptera	3	0.6	546.6	2.5	3	9	3.1	2981.5	11.7	5						3	1.7	335.9	1.3	2	2	1.3	459.7	1.6	2
Neuroptera																					5	3.2	493.1	1.8	4
Diptera	3	0.6	726.4	3.3	2	3	1.0	236.4	0.9	3						3	1.7	678.0	2.7	3					
Hymenoptera	2	0.4	225.8	1.0	2	2	0.7	138.7	0.5	2						1	0.6	197.6	0.8	1					
Ants	1	0.2	49.9	0.2	1				0.0							1	0.6	73.3	0.3	1	18	11.5	14921.6	53.0	4
Insect eggs											88	33.7	376.1	1.4	4.0										
Araneae	10	1.9	420.0	1.9	8	19	6.6	1710.0	6.7	14	5	1.9	374.8	1.4	5.0	13	7.3	3855.4	15.3	10	6	3.8	360.2	1.3	5
Solifugae	1	0.2	273.4	1.2	1	1	0.3	1253.8	4.9	1															
Scorpiones	2	0.4	359.3	1.6	2	1	0.3	698.2	2.7	1	2	0.8	2740.2	10.5	2.0	2	1.1	360.1	1.4	2					
Chilopoda	1	0.2	763.9	3.5	1	5	1.7	2562.4	10.1	5	1	0.4	335.0	1.3	1.0	6	3.4	4422.8	17.6	4	1	0.6	89.4	0.3	1
Diplopoda											1	0.4	133.4	0.5	1.0	1	0.6	49.9	0.2	1					
Lizard tail	1	0.2	128.3	0.6	1	1	0.3	2582.7	10.2	1															
Total	533	100	21879	100	69	287	100	25423.8	100	77	261	100	26049.8	100	58	178	100	25162.4	100	58	157	100	28165.6	100	47
Niche breadths		1.29		4.10			2.10		9.66			3.40		2.24			2.19		3.20			2.50		2.94	

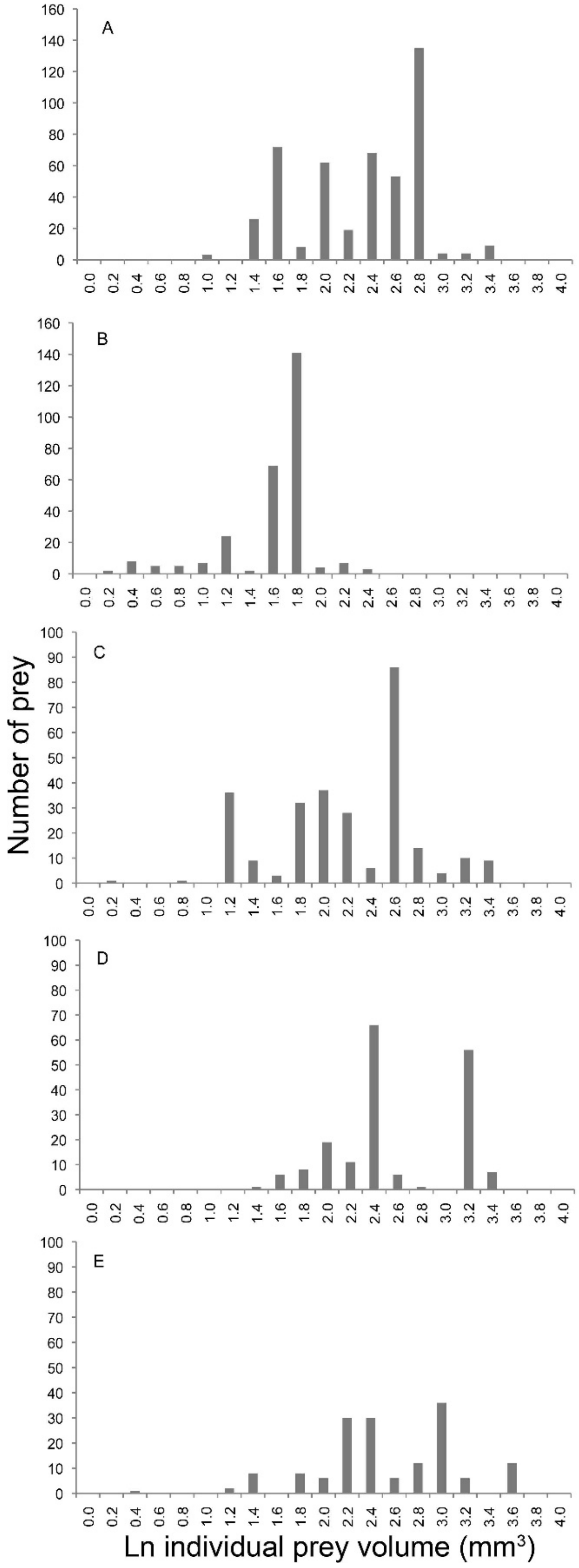

Fig. 4. Distribution of individual prey sizes (volume) consumed by *Nucras* spp. A = *N. holubi*, B = *N. intertexta*, C = *N. lalandii*, D = *N. ornata*, E = *N. tessellata*.

dominated by termites, grasshoppers, and beetles. All five species had similarly high proportions of termites and orthopterans in their diet, suggesting that although they eat a wide variety of prey, they are quick to take advantage of high quality prey items. Typically, widely foraging lacertids eat relatively slow-moving prey such as termites or inactive prey such as scorpions (Huey and Pianka, 1981). Termites are an important dietary component for many South African lizards (Pianka, 1986; Bauer et al., 1990; Shuttleworth et al., 2008), including other *Nucras* (Branch, 1998) and desert dwelling lizards (Huey and Pianka, 1981). However, termites are patchily distributed both spatially and temporally in arid areas of southern Africa (Lepage and Darlington, 2000; Traniello and Leuthold, 2000). Because all *Nucras* are likely to be active foragers (Cooper and Whiting, 1999), they may gain substantial nourishment from excavating subterranean termites or by encountering termite foraging parties or swarms. Termites, when present, were in high numbers (up to 70) in the gut, suggesting that lizards binge-feed on termites when they are available.

More than half the lizards examined (57%) were in a positive energy balance (i.e., stomachs contained food). In a global review of the proportion of lizards containing gut contents, Huey et al. (2001) found that of 101 diurnal lizard species, only 10.5 ± 9.6% had empty stomachs, and when only wide-foraging lizards were included, this number increased slightly to 15.1 ± 1.3% (n = 53 spp.). Therefore, the *Nucras* we examined had a lower frequency of individuals in positive energy balance, although the possibility that collectors kept individuals alive for sufficient time for their stomach contents to be digested, can not be discounted. Interestingly, Pianka (1986) reports that the scorpion specialist *N. tesselata* from the Kalahari Desert had a frequency of 16.1% of individuals with empty stomachs. In our limited sample of *N. tesselata* (n = 34), only one individual (2.9%) had an empty stomach.

Nucras, like other lacertids, are diurnal foragers (Pianka et al., 1979; Pianka, 1986). Many prey items found would need to be retrieved from beneath surface objects or sand because they are not diurnally surface active (hidden prey). Such prey include antlions, centipedes, scorpions, and even some spiders. Lizards would likely have to use vomerolfaction rather than visual searching, to find them, and Cooper (1990) has suggested that teiids and lacertids use chemical cues to identify and locate non-moving or hidden prey. However, in the case of *N. tesselata* from the Kalahari, it is possible that they locate scorpion burrows visually before entering them to retrieve the scorpion (R. Huey, pers. comm.). All of the species in our study consumed spiders and centipedes; however, *N. ornata* appeared to rely quite heavily on these as one of its main food sources (33% by volume). Millipedes (Diplopoda) were found in the gut of a single *N. lalandii* and a single *N. ornata*. Millipedes are known to produce toxins from repugnatory glands (Vitt, 1992) and are thus avoided by most lizards (Vitt and Cooper, 1986; Wapstra and Swain, 1996). Active foragers can detect released toxins and avoid them (see Evans, 1961); however, as only two lizards consumed one millipede each, they may have done so accidentally or these millipedes might be less toxic.

Nucras tessellata from the Kalahari Desert represent a paradox among lacertids because they consume relatively low numbers of termites (4.6% by volume) but high numbers of scorpions (53% by volume; Pianka et al., 1979;

Huey and Pianka, 1981) in a termite-rich landscape where other lacertids eat large quantities of termites (Pianka, 1986). In contrast, we found no scorpions in the 34 *N. tessellata* we examined from outside the Kalahari, and they contained a relatively higher volume of termites (11.4%). There are several possible explanations for this finding. First, *N. tessellata* from the Kalahari may be specifically distinct from other populations of currently recognized *N. tessellata* (Bauer, Branch, and Burger, unpubl.); therefore, dietary differences may be an artifact of phylogeny. Second, *N. tessellata* from outside the Kalahari occur in very different habitats that are sometimes less sandy and more rocky. This habitat may make scorpion capture more difficult. Third, *N. tessellata* from the Kalahari are active at high temperatures and begin activity later in the morning than other lacertids (Huey and Pianka, 1977; Pianka et al., 1979), under conditions that may preclude termite activity or when termites are further underground. Therefore, they may simply not eat termites because the prevailing thermal conditions make termites less accessible. While these theories are somewhat speculative, they are testable. We need field studies of *Nucras* to assess the relative influence of phylogeny and environment on ecology and life history. In particular, understanding how Kalahari *N. tessellata* have become such dietary specialists compared to closely related congeners will contribute to our understanding of the evolution of feeding specialization in lizards.

MATERIAL EXAMINED

TMP specimen numbers: 94, 96, 562, 563, 567, 683, 1144, 1385, 1389, 1390, 1505, 1764, 2217, 2501, 2537, 3169, 3170, 3171, 3426, 3675, 3723, 4431, 4433, 4434, 4435, 4502, 4522, 4526, 4539, 9220, 11055, 11068, 11133, 11181, 11187, 11188, 11334, 11628, 12289, 12290, 12352, 12376, 12812, 15676, 15705, 15707, 15951, 18030, 18056, 18179, 19377, 20129, 21130, 22180, 27161, 27166, 27840, 27841, 28791, 28820, 29997, 30184, 30434, 33292, 33420, 33539, 33540, 33541, 33632, 34024, 34052, 34140, 35292, 35404, 35497, 35693, 35734, 36045, 36133, 36282, 36393, 36621, 36694, 37211, 37212, 37213, 37214, 37218, 37219, 37220, 37716, 37717, 37718, 37844, 37845, 37846, 37847, 37898, 39102, 39500, 39920, 42459, 42460, 42461, 43259, 43285, 43288, 43289, 43291, 43292, 43293, 43304, 43306, 43307, 43308, 43308, 43309, 43310, 43311, 43393, 43407, 43411a, 43412, 43428, 43446, 43450, 43474, 43476, 43515, 43518, 43559, 43560, 43561, 43562, 43576, 43669, 43671, 43769, 47458, 47580, 49504, 50111, 50325, 51562, 51563, 51564, 51565, 51568, 52450, 52451, 53294, 53909, 53910, 53922, 54768, 55223, 55301, 55554, 55714, 55752, 55761, 55773, 55909, 55913, 56041, 56100, 57525, 62994, 63006, 63986, 66485, 66499, 66766, 66865, 66970, 67345, 67945, 68838, 68839, 68840, 68848, 69068, 70049, 70631, 70942, 70943, 70947, 71071, 72340, 72342, 72343, 72344, 72348, 72350, 72351, 72352, 72353, 72354, 72356, 72359, 72658, 72659, 72661, 72663, 72666, 72667, 72669, 72673, 72674, 72675, 72676, 72677, 72678, 72679, 72684, 72686, 72687, 72689, 72690, 72691, 72693, 72694, 72695, 72696, 72698, 72699, 72708, 76868, 76869, 76870, 76871, 76872, 76873, 76874, 76877, 76878, 76879, 76880, 76881, 76882, 76883, 76884, 76885, 77797, 77802, 77811, 77812, 77828, 77830, 77834, 77836, 77837, 77838, 77839, 77840, 77841, 77842, 77843, 77844, 77845, 77846, 77849, 77850, 77851, 77853, 77854, 77857, 77858, 77859, 77860, 77862, 77863, 77865, 77867, 77867, 77868, 77869, 77870, 77871, 77873, 77875, 77876, 77877, 77879, 77880, 77881, 77882, 77886, 77887, 77888, 77889, 77890, 77891, 77892, 77894, 77900, 78316, 78317, 78318, 78322, 78324, 78325, 78326, 78327, 78330, 78331, 78332, 78338, 78669, 78670, 78671, 78705, 78706, 78708, 79455, 80027, 80036, 80070, 83011, 83016, 83370, 83563, 83564, 83566, 83662, 83831, 84030, 84729, 84861, 84983, 85378, 85426.

PEM specimen numbers: 569, 1914, 1939, 2378, 2693, 2985, 3043, 3044, 3053, 4099, 4101, 4132, 4135, 4142, 4147, 4220, 4294, 4857, 4980, 5027, 5067, 5079, 5791, 5906, 7064, 7070, 7102, 7155, 7156, 7207, 7247, 7278, 7386, 7590, 7629, 7681, 7899, 8055, 8056, 8147, 8164, 8168, 8400, 8421, 8438, 8439, 8440, 8450, 8478, 8483, 8719, 9707, 10425, 10426, 10427, 10428, 10429, 10430, 10431, 10432, 10433, 10438, 10439, 10440, 10441, 10442, 10454, 10455, 10456, 10457, 10458, 10459, 10460, 10461, 10462, 10463, 10464, 10465, 10466, 10467, 10468, 10469, 10470, 10471, 10472, 10473, 10474, 10475, 10476, 10477, 10478, 10479, 10480, 10481, 10482, 10483, 10484, 10679, 10680, 11111, 12161, 12162, 12410, 13259, 13344, 13355, 13357, 13358, 13373, 13507, 13762, 15990, 15991, 15992, 15993, 15994, 15995, 15996, 15997, 15998, 15999, 16000, 16001, 16002, 16003, 16004, 16005, 16006, 16007, 16008, 16009, 16010, 16011, 16012, 16013, 16014, 16015, 16016, 16017, 16018, 16019, 16020, 16021, 16022, 16023, 16024, 16025, 16026, 16027, 16028, 16029, 16030, 16031, 16032, 16033, 16034, 16035, 16036, 16037, 16038, 16039, 16040, 16041, 16042, 16043, 16044, 16492, 16493, 16495, 16496, 16497, 16498, 16499, 16500, 16503, 16504, 16506, 16872, 16873, 16874.

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