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Habitat Use and Morphology of Bosc's Fringe-Toed Lizard (*Acanthodactylus boskianus*) in Central Tunisia

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Abstract.—Within-species differences in morphology can influence many aspects of an organism's ecology. We investigated the morphology and habitat use of Bosc's Fringe-Toed Lizard (*Acanthodactylus boskianus*) in sub-desert steppe habitat in central Tunisia. Our main objective was to verify the presence of sexual size dimorphism in our study population and assess whether morphological differences between males and females corresponded to differences in vegetation use while being pursued. We captured, measured, and then released 60 adults after conducting habitat-assessment trials, which consisted of pursuing an active lizard and recording the vegetation into which the lizard escaped. Concurrently, we conducted vegetation transects throughout the study site to assess vegetation availability. We recorded values for ten morphometric measures, all of which were larger for males than for females. For most measures, males and females of the same SVL had comparable values. However, a positive interaction between SVL and sex was evident, with males exhibiting increasingly larger hindlimbs and mass. Our investigation revealed selective habitat-use patterns among *A. boskianus* that were independent of sex and body size. Lizards did not use plants based on their availability, entering *Aristida pungens* (Three-awn Grass) and *Retama raetam* (White Broom) more but *Rhanterium suaveolens* (Rhanterium) and *Haloxylon schmittianum* (Saxaul) less frequently than random expectations. For the three most commonly used plants (*Astragulus armatus* (Milkvetch), Three-awn Grass, and White Broom), lizards chose to enter larger plants. This use of habitat could stem from antipredator defense or thermoregulatory concerns. Our findings differ from previous reports on the nature of sexual size dimorphism in *A. boskianus* and contribute to our understanding of the complex interplay between morphology, behavior, and local environmental conditions in shaping the ecology of *A. boskianus*.

An individual's morphology will influence both their ability to and the way in which they accomplish essential tasks (Arnold 1983; Garland and Losos 1994; Irschick 2002). The idea that the ecology of a species influences their morphology is a core concept that has led to the development of the field of ecomorphology. Differences in morphology between species can affect locomotor performance (Losos 1990) and a species' ability to navigate on different substrates (Grismer 2021), while variation in selective pressures affecting individuals within a species can influence behavior, ecology, and morphology resulting in sexual dimorphism (Garland and Losos 1994). Examining widely distributed species provides a unique opportunity to investigate the relationship between behavioral and morphological variability across populations existing in diverse ecological conditions (Madsen and Shine 1993; Shine and Wall 2005; Roitberg et al. 2020).

In sexually dimorphic species of lizards, males often have relatively larger heads whereas females have longer trunks. Sexual-selection advantages are gained by males with larger heads when subject to male-male competition, and fecundity selection benefits occur in females with longer body lengths by providing more space for eggs (Herrel et al. 1999; Olsson

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et al. 2002; Roitberg et al. 2015, 2020). Food resources used by each sex can diverge, as the larger sex can access different habitats (Buttemer and Dawson 1993; Herrel et al. 1999) or different prey items (Herrel et al. 1999; Shine and Wall 2005). Abundance of prey of different sizes also can affect whether sexual size dimorphism occurs at all (Carretero 2004), as in European Grass Snakes (*Natrix natrix*), which typically exhibit sexual size dimorphism, but not when exclusively small prey species are available (Madsen and Shine 1993).

Several species in the family Lacertidae exhibit the trend in sexual dimorphism in which the males have relatively larger heads and females have longer trunks (Nasri et al. 2015), including Bosc's Fringe-Toed Lizard, *Acanthodactylus boskianus* (Daudin 1802) (Fig. 1), which has the most extensive distribution of any congener. *Acanthodactylus boskianus* ranges widely throughout North Africa, from the Mediterranean Coast south to the Sahel, north of the Mediterranean Coast to Turkey, and east throughout the Arabian Peninsula to Iran (Salvador 1982), where this lizard occupies various habitats, including coastal plains, cultivated areas, salt marshes, oases, and wadis (Din 2006; Roobas and Feulner 2013). It generally occurs in areas near plants characteristic of arid and semi-arid environments (i.e., *Astragalus armatus*, *Vachellia* (*Acacia*) *tortilis raddiana*) (Din 2006) and exhibits geographic variation in morphology (Nasri et al. 2015) as well as in its ecological characteristics (Nouira and Blanc 2003).

Bosc's Fringe-Toed Lizards are diurnal and active during the warm season when foraging and reproduction occur (Goldberg 2013; Rodda 2020). These active foragers (Day et al. 1999; Seifan et al. 2009) have a variable diet consisting primarily of small invertebrates, including amphipods, beetles, ants, small grasshoppers, and termites (Roobas and Feulner 2013; Nasri et al. 2017a). They actively hunt prey in sandy terrain, with diet varying by season, habitat, and age of individuals (Nasri et al. 2017a). In Tunisia, *A. boskianus* occupies open habitats that include coastal areas as well as arid and semi-arid habitats with sandy or clay substrates (Nouira and Blanc 2003; Nasri et al. 2017a). In a population occupying a semi-arid steppe habitat similar to the present study site, males and females differed in their movement patterns when foraging, with males searching a larger area, moving for a higher proportion of their time, and spending more time in the open compared to females (Eifler et al. 2023).

Figure 1. An unsexed adult Bosc's Fringe-Toed Lizard (*Acanthodactylus boskianus*) that evaded capture in the study site south of Bouhedma National Park in central Tunisia. Photograph by Houssem Ben Othmen.

With a large geographic range and variation in habitats and diet, local conditions likely affect morphology and behavior (Garland and Losos 1994; Roitberg et al. 2020). Sexual size dimorphism has been demonstrated in three populations (Seifan et al. 2009; Nasri et al. 2015; Eifler et al. 2023). However, because the nature of sexual dimorphism can vary across populations, especially in wide-ranging species (Madsen and Shine 1993), we sought to characterize sexual size dimorphism in the study population before obtaining preliminary information on habitat use in the context of predation to test the hypothesis that any differences we detected in the morphology of males and females corresponded to behavioral differences expressed in the exploitation of habitats. We expected that males would be larger than females and have longer limbs to allow for their higher level of movement while foraging, and that their propensity to be in the open when foraging compared to females would correspond to sex-based differences in the use of sheltering plants.

Materials and Methods

We conducted surveys for *A. boskianus* from 30 May–2 June 2023 at a study site (ca. 2.8 ha) that consisted of subdesert steppe habitat in northern Africa, south of Bouhedma National Park (34.46837, 9.66599), 85 km east of Gafsa and 100 km south of Sidi Bouzid in central Tunisia (Fig. 2). The site was in a low semi-arid to sub-arid bioclimatic zone with a mean annual rainfall of ca. 150 mm (Le Houérou 1982; Ouled-Belgacem et al. 2013; Mimoun and Nouira 2015) and an average maximum temperature during the warmer months of 36 °C (Abdallah et al. 2012; Noumi 2014). The site was located on unprotected public lands, comprised open habitat with sparse semi-arid and desert vegetation dominated by the endemic subshrub *Rhanterium suaveolens* (Asteraceae = Rhanterium), as well as *Astragalus armatus* (Fabaceae = Milkvetch), *Haloxylon schmittianum* (Saxaul; Amaranthaceae = Saxaul), and *Retama raetam* (Fabaceae = White Broom). Other plants on site included *Stipagrostris pungens* (Poaceae = Three-awn Grass), *Asparagus albus* (Asparagaceae = Cat

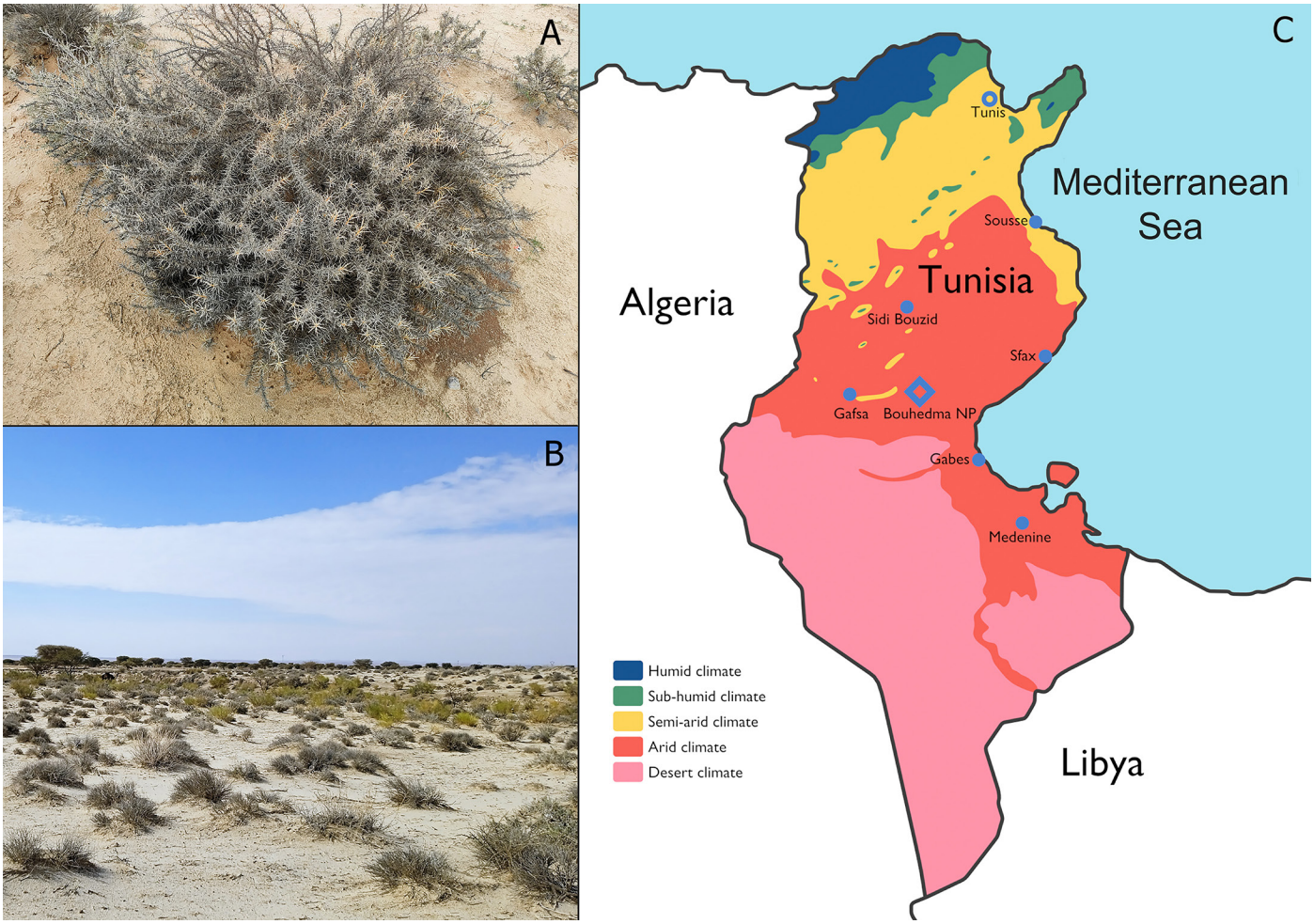

Figure 2. A Milkvetch (*Astragalus armatus*) (A), study site habitat (B), and location of Bouhedma National Park within Tunisia (C). Our study site was immediately southeast of the park. Photographs by Hamdi Ben Boubaker (A) and Wiem Nasri (B), map by Mahdi Haj Dahmen (C).

Asparagus), *Deverra scoparia* (Apiaceae), *Erica* sp. (Ericaceae), and *Marrubium deserti* (Lamiaceae). We calculated the availability of vegetation throughout the site using the line-intercept method with a tape measure, running 6 transects (100–140 m long) separated by 15 m for a total length of 800 m of plant availability data. For each transect, we identified each plant and determined the area covered by measuring the dimensions of each plant on the transect (length, width, and height). Cover of each plant species encountered was totalled from all 800 m of transects to determine percent cover.

To capture lizards for morphometric assessment, we conducted surveys of the study site throughout morning activity periods (ca. 0830–1330 h on 30 May and 1–2 Jun 2023). Thirteen researchers walked throughout the site ca. 10 m apart and searched for active lizards. To canvas the entire site, the starting point and direction of the search paths each day were randomly determined using a coin flip. When a lizard was sighted, we attempted to capture it using a lasso attached to the end of an extendable pole, identified the first plant species the lizard visited during pursuit (= pursuit habitat use), and measured that plant's dimensions (length, width, and height). In several instances, lizards were captured in the open without visiting vegetation, in which case pursuit habitat use was recorded as "open." All lizards encountered, captured, and measured were adults. We caught 60 lizards for the habitat-assessment trials, and four additional lizards for morphometric analysis. When captured, lizards were placed in individual mesh bags, brought indoors, individually marked with non-toxic paint, sexed (via probing), and measured.

We weighed each animal to the nearest 0.05 g on a digital scale, counted femoral pores (FP) on each hindleg, and measured the following using handheld digital callipers (± 0.01 mm): snout-vent length (SVL: distance from tip of the snout to the anterior edge of the cloaca), tail length (TL: distance from posterior edge of the cloaca to the tip of tail), upper forelimb length (UFL: distance from the posterior margin of the axilla to the elbow) (Thompson and Withers 1997), lower forelimb length (LFL: distance from the elbow to the wrist, as defined by a change in scale size and color) (Thompson and Withers 1997), upper hindlimb length (UHL: distance from the anterior margin of the hindlimb to the middle of the knee) (Thompson and Withers 1997), lower hindlimb

length (LHL: distance from the middle of the knee to the end of the largest scale at the ankle) (Thompson and Withers 1997), head length (HL: distance from the anterior margin of the ear to the tip of the snout), head width (HW: widest dorsal plane distance between the eyes and ears), and head height (HH: distance from the dorsal to the ventral surface at the eye orbits) (Thompson and Withers 1997). We calculated trunk length (= SVL–HL; Seifan et al. 2009). All lizards were released at the site of capture within 24 h.

We used Minitab (ver. 21.1 2021) for statistical analyses (α = 0.05 (Dytham 2011). We compared plant use to availability using a chi-square goodness of fit test and calculated Vanderploeg and Scavia's relativized electivity index (E*) (Vanderploeg and Scavia 1979) to examine possible vegetation preferences (Lechowicz 1982), with values that approached +1 indicating preference, −1 avoidance, and 0 random associations. We used Mann-Whitney tests to compare dimensions of used and available plants, general linear models to examine the possible roles of sex and lizard size in plant use, and a chi-square test to examine the association between lizard sex and plant species. For morphological analyses, we used t-tests to compare measured values of males and females. All morphometric variables were log-transformed before using general linear models to examine effects of sex, size, and their interaction. TL was only used for animals with intact tails. We used SVL as a measure of body size to compare sexes.

Results

We assessed vegetation use for 60 adult *A. boskianus* that were being pursued. The study site was primarily free of vegetation (i.e., open; 90.3%). The most common plant species was Rhanterium (45%), followed by Milkvetch (25%), Saxaul (15%), and White Broom (10%), with other plants collectively accounting for less than 5% of vegetated areas (Fig. 3A). *Acanthodactylus boskianus* pursuit habitat use was significantly different than expected based on the abundance of each plant species (χ^2 = 51.5, df = 5, P < 0.001; Fig. 3B). Lizards exhibited moderate positive electivity (i.e., preference) for Three-awn Grass (E* = 0.48) and White Broom (E* = 0.16), negative electivity (i.e., avoidance) for Saxaul and Rhanterium (E* = ⁻0.62 for both), whereas electivity for Milkvetch approached random (E* = −0.04).

Lizards used three plant species (Milkvetch, White Broom, and Rhanterium) at frequencies sufficient for comparing within-species dimensions of individual plants visited or used relative to plants available at the study site. The individual plants of each species most commonly used by *A. boskianus* tended to be larger along the length axis than the mean of plants available (mean length of plants used versus mean length of plants available: Milkvetch (130 vs. 95.5 cm length, W = 737, P = 0.025), White Broom (201 vs. 88 cm, W = 313, P < 0.001), and Rhanterium (82 vs. 65 cm, W = 619, P = 0.017). The use of plant species did not differ significantly by sex (χ^2 = 2.28, df = 2, P = 0.32), nor did a relationship exist between plant size and lizard size or sex for any of the three species (GLM (SVL, sex: F (P)) Milkvetch: 0.02 (0.883), 0.34 (0.566); White Broom: 0.00 (0.965), 1.27 (0.282); Rhanterium: 0.10 (0.765), 3.01 (0.143)).

Males (n = 28) were larger than females (n = 36) for all ten linear body measurements and for the number of femoral pores (Table 1). Males also were significantly heavier than females (mean ± SE (range): 8.11 ± 0.73 g (3.40–16.15 g) vs. 5.08 ± 0.34 g (2.80–10.45 g), respectively; t = 3.77, df = 38, P = 0.001). SVL was a significant predictor of all linear body measures but not for the number of femoral pores (Table 2). Three morphometric measures (mass, UHL, and LHL) were affected significantly by sex and the interaction of SVL and sex. When SVL increased, males increased morphometrically at a faster rate than females (Table 2; Fig. 4). Notably, however, head length and trunk length were comparable for males and females of the same SVL (Table 2, Fig. 5). Only 10 of 28 males (35.7%) and 9 of 36 females (25%) had broken or

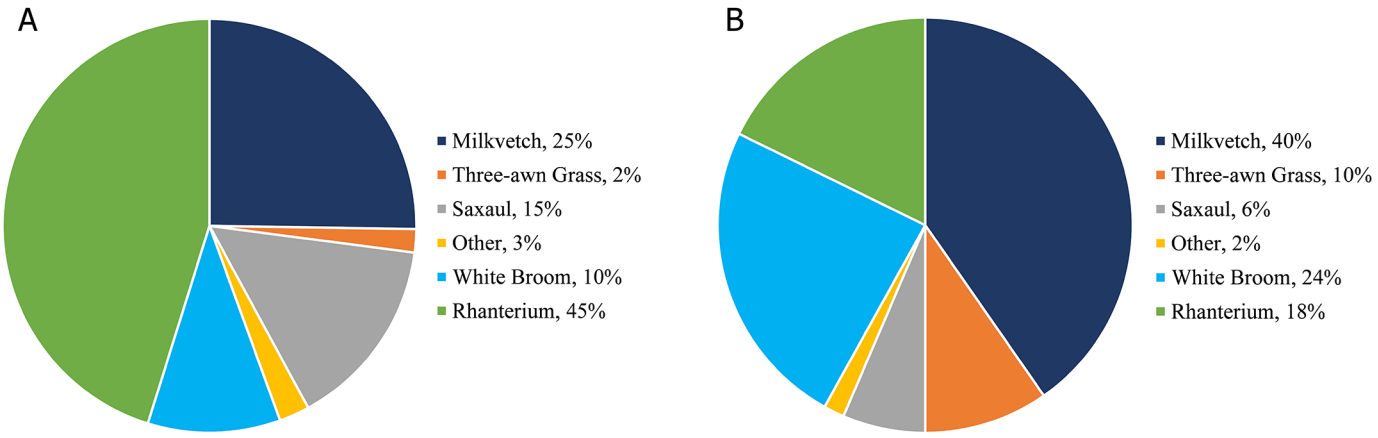

Figure 3. Plant availability as determined by vegetation transects (A) and plant use determined by the first plant to which a lizard retreated when chased (B). Plants included in "other" are *Deverra scoparia*, *Erica* sp., *Asparagus albus* (Cat Asparagus), and *Marrubium deserti*.

Table 1. Summary of morphometric measurements (mm) and femoral pore counts (FP) for all animals (mean ± SE (range)), with t-test results for comparisons between the sexes. All P-values were significant. We also include the sexual dimorphism index (SDI) for each morphometric character (Lovich and Gibbons 1992). Character abbreviations are in the text.

Character	SDI	Males	Females	T (df)	P
SVL	–0.135	65.61 ± 1.75 (49.00–80.00)	57.81 ± 1.23 (49.00–76.00)	3.64 (50)	0.001
Trunk	–0.136	50.09 ± 1.37 (36.54–61.29)	44.10 ± 0.97 (37.19–59.14)	3.58 (50)	0.001
Tail	–0.151	136.72 ± 4.85 (107.00–171.00)	118.78 ± 2.22 (97.00–148.00)	3.36 (24)	0.003
UFL	–0.121	6.02 ± 0.23 (4.38–8.64)	5.37 ± 0.16 (3.52–8.52)	2.31 (50)	0.025
LFL	–0.131	7.42 ± 0.17 (5.95–8.89)	6.56 ± 0.14 (5.05–8.79)	3.95 (56)	< 0.0001
UHL	–0.181	10.88 ± 0.35 (7.90–13.81)	9.21 ± 0.18 (7.40–12.55)	4.27(40)	< 0.0001
LHL	–0.139	12.38 ± 0.36 (9.77–16.12)	10.87 ± 0.19 (8.90–13.47)	3.71 (41)	0.001
HL	–0.131	15.51 ± 0.40 (12.27–19.93)	13.71 ± 0.28 (11.54–17.26)	3.68 (51)	0.001
HH	–0.179	8.18 ± 0.41 (5.85–17.10)	6.94 ± 0.16 (5.74–9.83)	2.82 (35)	0.008
HW	–0.160	10.67 ± 0.35 (7.04–14.25)	9.20 ± 0.24 (6.50–13.54)	3.47 (49)	0.001
FP	—	45.82 ± 0.52 (39–51)	44.28 ± 0.55 (39–53)	2.03 (61)	0.046

Table 2. GLM results by the predictor variables SVL, sex, and SVL x sex (F (P)). All variables were log-transformed prior to analyses. Significant P-values are in **bold type**.

Morphometric Character	SVL	Sex	SVL x Sex
Tail length (TL)	66.92 (**< 0.0005**)	1.96 (0.169)	2.17 (0.148)
Upper forelimb (UFL)	79.18 (**< 0.0005**)	0.11 (0.746)	0.09 (0.762)
Lower forelimb (LFL)	193.13 (**< 0.0005**)	0.57 (0.453)	0.50 (0.481)
Upper hindlimb (UHL)	206.26 (**< 0.0005**)	6.87 (**0.011**)	7.30 (**0.009**)
Lower hindlimb (LHL)	154.50 (**< 0.0005**)	7.07 (**0.010**)	7.30 (**0.090**)
Head length (HL)	712.13 (**< 0.0005**)	0.00 (1.00)	0.00 (0.981)
Head height (HH)	44.03 (**< 0.0005**)	0.16 (0.688)	0.19 (0.661)
Head width (HW)	181.97 (**< 0.0005**)	1.00 (0.321)	1.04 (0.312)
Mass	878.78 (**< 0.0005**)	5.38 (**0.024**)	5.58 (**0.021**)
Trunk	8622.36 (**< 0.0005**)	0.00 (0.955)	0.00 (0.973)

regenerated tails. The difference in the tail-breakage rates of males and females was not significant (Fisher's exact test: P = 0.41). Combined, 19 of 64 lizards on the study site experienced tail loss (regrown or broken, 29%), which was not significantly different from reports for other populations (26 of 68 lizards with tail loss (38%), Seifan et al. 2009; Fisher's exact test: P = 0.36).

Discussion

Habitat Use.—Lizards were selective in their use of habitat while being pursued, but no relationship was evident between lizard sex or size and either plant species or size. An earlier study in southeastern Turkey indicated that habitat with Milkvetch was often used by *A. boskianus* (Üzüm et al. 2014). We found *A. boskianus* using Milkvetch randomly, but using Three-awn Grass and White Broom more than and Saxaul and Rhanterium less than predicted based on availability. Their behavior on our study site, as well as in other locations, supports the generalization that selectivity in choice of vegetation by *A. boskianus* is independent of sex.

Among the three most common plant species on our site, lizards tended to use plants of each species that were larger than the mean plant size available, perhaps reflecting antipredator concerns or thermoregulatory behavior. Other populations of adult *A. boskianus* remained close to vegetation that could serve as refuges and run under cover when threatened (Nasri et al. 2017b). In mostly open habitats, larger vegetation with dense canopies could provide better protection, especially from visually-oriented predators. Additionally, larger plants could provide more shade or more stable thermal

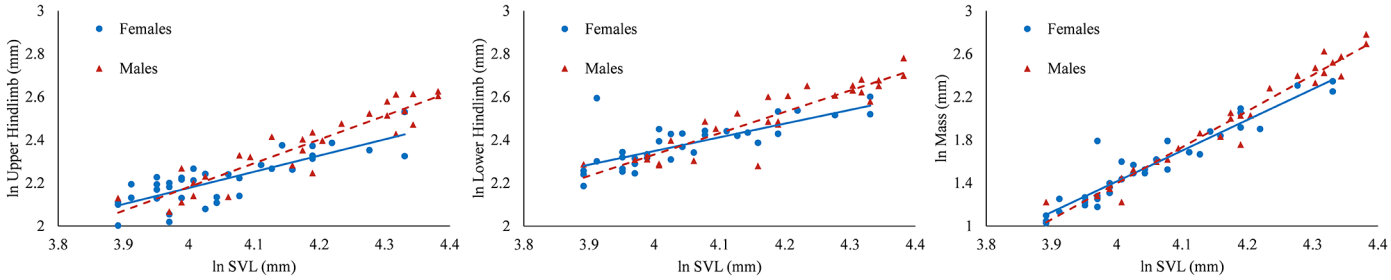

Figure 4. Relationships from general linear models between upper hindlimb length and the interaction between snout-vent length and sex (P = 0.003) (left), lower hindlimb length and the interaction between snout-vent length and sex (P = 0.004) (center), and mass and the interaction between snout-vent length and sex (P = 0.021) (right).

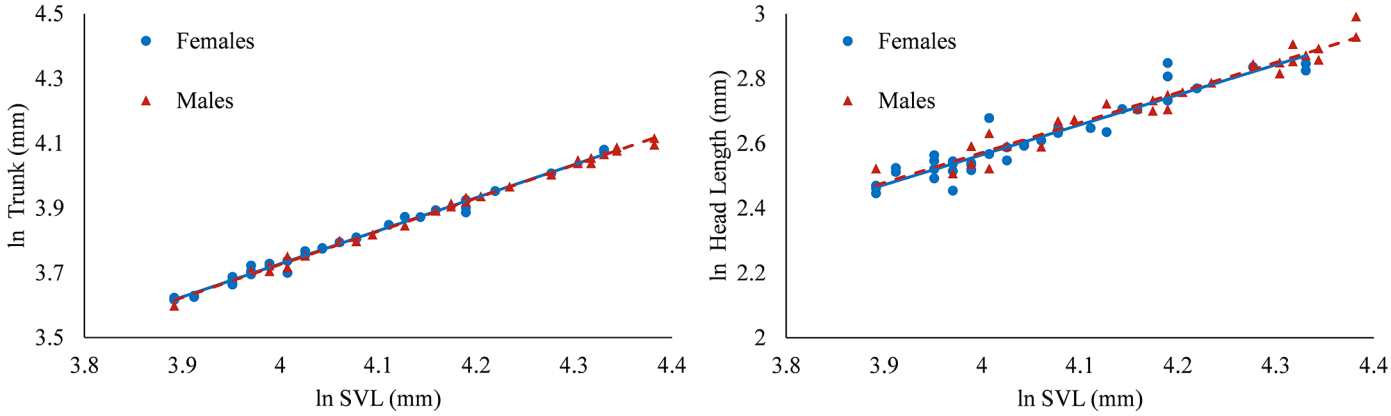

Figure 5. Relationships from general linear models between head length and snout-vent length, neither sex (P = 1.000) nor the interaction between sex and snout-vent length were significant (P = 0.981) (left), and between trunk length and snout-vent length, neither sex (P = 0.955) nor the interaction between sex and snout-vent length were significant (P = 0.973) (right).

conditions for thermoregulation (Roobas and Feulner 2013). Further study is necessary to distinguish the relative importance of predatory versus thermoregulatory factors affecting vegetation use by *A. boskianus*. Additionally, because our study was limited to a specific antipredator context, future studies could examine whether daily habitat use differs among males and females or ontogenetically.

Morphology.—Males in our population had slightly more femoral pores than females, a trend that has been documented for other populations of *A. boskianus* (Seifan et al. 2009; Nasri et al. 2015). The consistency in femoral pore differences between the sexes across populations indicates that the trait could be related more to social behavior than movement or foraging-related performance. Further investigation into the use of femoral pores in *A. boskianus* is merited.

Males were significantly larger than females for all our recorded morphological measurements, indicating a general male-larger sexual size dimorphism with males reaching longer SVLs. SVL significantly predicted all of the variables we measured, with the sexes being similar in shape (i.e., with comparable values for a given SVL) for most measurements. However, this study population exhibited an interaction between sex and SVL that predicted significant sex-based shape differences in both mass and hindlimb length (Tables 1 & 2). As males grow, they become increasingly heavier and longer-limbed than females of comparable sizes (i.e., different slopes; Fig. 4), which contrasts with other populations of *A. boskianus*, in which no interaction between SVL and sex was evident for hindlimbs and both head length and hindlimb length were larger for males of a given SVL (Seifan et al. 2009). Different sex-based patterns in morphology between populations can arise if spatial variation in habitat use promotes geographic variation in morphology in the species (Muñoz and Losos 2018; Lattanzio et al. 2020). The presence of sexual dimorphism in some but not in other populations could arise if individuals in different populations adapt to local environmental conditions (= local adaptation; Lenormand 2002) in different ways (Garland and Losos 1994; Roitberg et al. 2020). In addition, detecting within-species variation in sexual size dimorphism can be influenced by the statistical methodologies applied and sample characteristics measured by different studies. For example, we used the definition of trunk length from Seifan et al. (2009) and found sex differences (Table 1), whereas Nasri

et al. (2015) used a different measure of trunk length and found no sex differences. The differences in results could be due to differences in measurements and statistical tests used by various studies, which influence how patterns are detected and interpreted (Liebhold and Gurevitch 2002).

Hindlimb-length values have been reported to be larger and increasing with SVL for males (Seifan et al. 2009), but we found that hindlimb measurements differed in slope for the sexes, with hindlimbs becoming progressively larger for males (Table 2, Fig. 4). In a separate study on movement ecology of *A. boskianus* at a different site in Tunisia, males moved much more frequently over much larger areas and spent less time near vegetation compared to females (Eifler et al. 2023). The relatively longer limbs of male *A. boskianus* compared to females (present study) might enhance their ability to forage effectively and respond to predators while searching large areas (Carretero 2004). In addition, variation in the kinds of prey available as well as their nutritional content and how they are handled by predators on different sites (based on prey carapace hardness) could account for variation in ecology or morphology in the same species (Herrel et al. 1999; Carretero 2004). Further studies that directly compare the ecomorphology of *A. boskianus* in different populations are merited.

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