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Sexual Dimorphism in Namibian Endemic Herero Nama Lizards (*Namazonurus pustulatus*)

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Abstract: Sexual dimorphism in lizards is broadly attributed to intrasexual differences in morphology that affect fitness. In the lizard family Cordylidae, commonly known as girdled lizards, sexual dimorphism is common. Differences in morphological traits (e.g., body and head size) between females and males are useful for describing sexual dimorphism, and examining other traits (e.g., scar frequencies and color) is useful for understanding the selective pressures driving sexual dimorphism in cordylids. Recent morphological studies in Cordylidae reveal sexual dimorphic biases where males have larger heads, but either sex may have larger bodies. In this study, we examined body size, head dimensions, and other traits that commonly differ between sexes to identify sexually dimorphic traits and understand selective pressures in the Namibian endemic cordylid *Namazonurus pustulatus* (Herero Nama Lizard). We measured 224 field and 10 museum specimens within the known distribution of *N. pustulatus*. Our results indicate that females were larger in snout–vent length (SVL), axilla-to-groin length, and mass, but males were larger in head width and head length. Allometric growth in juvenile head dimensions was greater than that in adults. Segmented regression analyses indicated a change in growth rate of approximately 68.3–70.0 mm SVL, which we associated with sexual maturity. Adults of both sexes were larger at low elevations (1200–1700 m above sea level) than adults at high elevations (2000–2500 m above sea level), but there was no difference in head height. Epidermal glands (generation glands and femoral pores) scaled with SVL. No differences in scar frequencies were identified, but frequencies were higher than any other cordylid species recorded to date. We attributed larger female size to fecundity selection and larger male head size to sexual selection. This work establishes the first detailed biometric characteristics of the species, fills the missing literature gap of sexual dimorphism information from a species in the *Namazonurus* clade, and is the first to examine sexual dimorphism in a Namibian endemic cordylid.

Key words: Africa; Cordylidae; Elevation size gradient; Head morphology

Sexual dimorphism in lizards is broadly attributed to intrasexual differences in morphology that affect fitness (Andersson 1994). The traits that most commonly exhibit sexual dimorphism in lizards are relative head size and body size (Olsson et al. 2002), which are often ascribed to differential resource investment between sexes (Cooper and Vitt 1989). For example, despite a common diet, females often have larger bodies and males have larger heads (Tinkle et al. 1970; Vitt and Cogdon 1978). The fitness advantage to larger female bodies is more and/or larger offspring (Fitch 1970; Andersson 1994), whereas larger male head size has advantages in male–male competition and/or grasping females during copulation, translating into increased reproductive success (Cooper and Vitt 1989; Gullberg et al. 1997; Gvozdik and Van Damme 2003). Members of the lizard family Cordylidae exhibit a wide range of sexual dimorphisms, and sexually dimorphic traits have been statistically examined in eight cordylid genera (Fell 2005; Costandius and Mouton 2006; Broeckhoven and Mouton 2014). Gaps in the published literature include general morphology and sexual dimorphic studies on the cordylid genera *Ninurta* and *Namazonurus.* In this study, we examine the morphology of the Namibian endemic cordylid *Namazonurus pustulatus* (Herero Nama lizards) to identify sexually dimorphic traits and better understand selective pressures influencing its size and shape.

Cordylids are an African group of lizards comprised of 10 genera (Stanley et al. 2011), and species in the subfamily Cordylinae are protected by the Convention on International Trade in Endangered Species of Wild Fauna and Flora due to illegal trade. The family is distributed throughout southern and eastern Africa and the species are diverse in morphology, which is typically attributed to their varied lifestyles (Loveridge 1944; Branch 1998). In general, cordylid research has largely focused on morphology to better understand cordylid life history and evolution (Costandius and Mouton 2006). As a result, sexual size dimorphism data are available for 13 of the approximately 80 cordylid species (Fell 2005; summary of 10 in Costandius and Mouton 2006; Broeckhoven and Mouton 2014; Riley et al. 2021) with much variation within and among species. Females are larger in six species (*Chamaesaura anguina*, *Cordylus macropholis*, *Karusasaurus polyzonus*, *Hemicordylus capensis*, *Hemicordylus nebulosus*, and *Smaug giganteus*), males are larger in six species (*Cordylus cordylus*, *Cordylus niger*, *Namazonurus peersi*, *Ouroborus cataphractus*, *Pseudocordylus langi*, and *Pseudocordylus melanotus subviridis*), and in one species there is no difference between the sexes (*Pseudocordylus microlepidotus*). Furthermore, tail length relative to snout–vent length (SVL) is greater in adult males than that in adult females for some species but not others (Costandius and Mouton 2006). In general, male cordylids are larger in overall body size and head dimensions (Fell 2005; Costandius and Mouton 2006; Broeckhoven and Mouton 2014; Riley et al. 2021). However, allometric head growth relative to SVL varies, where heads are larger in adult males than in adult females, larger or equivalent in juveniles than in adult males, and/or larger in juveniles than in adult females (Costandius and Mouton 2006).

Cordylid bodies are under a complex functional relationship between fecundity advantage and sexual selection (Costandius and Mouton 2006). Larger body size and reduced allometric head growth in female cordylids are attributed to the Darwinian fecundity advantage hypothesis, in which natural selection favors larger body sizes that produce more and/or larger offspring (Fitch 1970; Cooper and Vitt 1989). For example, in the cordylid *K. polyzonus*, females with larger bodies produce more offspring (Flemming and VanWyk 1992). Conversely, larger male body and head size in cordylids are attributed to

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sexual selection with increased levels of male–male competition (Costandius and Mouton 2006; Broeckhoven and Mouton 2014); however, competition intensity is difficult to assess (Vitt and Cooper 1985).

Generation glands are sexually dimorphic and are either absent or less abundant in females (see Mouton et al. 2010). Like femoral pores, generation glands are epidermal glands that are found on the ventral region of the thighs in cordylids (Van Wyk and Mouton 1992). All cordylids have generation glands and patches of modified scales that house glandular material, in addition to femoral pores (Van Wyk and Mouton 1992). In general, communication via femoral pore secretions is widespread among squamates (Mason 1992; García-Roa et al. 2017) and is important for intraspecific interactions (Mason and Parker 2010). As with femoral pores, generation glands may play an important role in communication and social structure in cordylids (Mouton et al. 2005; Louw et al. 2011; Mouton et al. 2014).

Our focal species, *N. pustulatus*, is a rupicolous (inhabiting or living among rocks) cordylid that belongs to a genus of five medium-sized lizard species (Stanley et al. 2011) that are restricted to semiarid landscapes in western South Africa and south-central Namibia (Reissig 2014). *Namazonurus pustulatus* is distributed throughout the central and western portions of Khomas Hochland Plateau in Namibia (Fig. 1) with a higher abundance on mountain peaks (Heaton et al. 2017). The species occurs across an elevational range of 1200–2500 m above sea level (asl) but can be further categorized to low elevation (1200–1700 m asl) and high elevation (2000–2500 m asl), where individuals were not found between low and high elevations. The maximum reported SVL is 82 mm (Peters 1862), the adult SVL range is 70–75 mm (Branch 1998), and the juvenile (presumed to be one or more years old) SVL range is 45–65 mm (Heaton 2017). The number of generation glands and wax-filled femoral pores in male *N. pustulatus* ranged between 9–20 (mode = 12–13) and 7–9 (mode = 8), respectively. Females lack generation glands but have 7–11 (mode = 8) nonwax-filled femoral pores (Heaton and Reissig 2017).

Based on previous studies of cordylid sexual dimorphism, there are contrasting relationships between fecundity and sexual selection with associated morphological patterns. The two most common patterns of sexual dimorphism in cordylids are (1) associations with sexual selection in which males have larger body size (e.g., SVL), head measurements, and a greater tail growth rate than females, accompanied with signs of male combat present in the form of increased scar frequency, and (2) associations with fecundity selection for in which females have larger body size but males have larger relative head measurements. Also, females have greater body size growth rates, but other growth rates are similar and scar frequencies are similar between sexes.

Sexual dimorphism (i.e., sex differences in morphology, growth rates, or number of generation glands relative to size) in *N. pustulatus* is largely unstudied. Our goals are to report basic morphology and identify selection patterns in *N. pustulatus* by analyzing the differences in body size, tail length, head dimensions, and scar frequencies between age classes (juvenile and adult) and sexes.

Materials and Methods

Study Site

The Khomas Hochland Plateau in central Namibia is characterized by highly dissected plains and rugged mountains. The plains are dominated by mica schists, sandstones, and granite, whereas the Auas Mountains, home to the second highest peak in Namibia (Moltkeblick, 2478 m asl), are mostly comprised of Damara origin quartzite, but also contain schist, amphibolite, marble, conglomerates, and gneiss (Miller 2008). The vegetation is dominated by Highland Shrubland Savanna (Giess 1998; Burke and Wittneben 2008). The Auas Mountain range has been identified as a national biodiversity hotspot (Irish 2002). Although locally influenced by elevation, rainfall in Namibia is more strongly driven by synoptic weather systems originating in the Atlantic and Indian Oceans; consequently, within the distribution of *N. pustulatus*, the rainfall gradient is predominantly west to east (172–481 mm annually; Kaseke et al. 2016). In contrast, regional temperatures are more strongly associated with elevation; within the distribution of *N. pustulatus*, the mean annual temperature range is 16.1–20.7°C, and it is 2.5–4.6°C warmer at lower elevations (<1700 m asl) than at higher elevations (>2000 m asl; Kaseke et al. 2016).

Data Collection

Surveys for *N. pustulatus* were conducted throughout their range from November 2014 through September 2019. Coordinates and elevation (datum = WGS84; ±3 m) were recorded for each individual. Individuals were extracted from rock crevices with every effort to maintain crevice integrity and habitat (Fig. 2A). In addition, we examined 10 specimens (SVL and head dimensions) from the existing collection at the National Museum Namibia (Appendix).

There is no information on size at sexual maturity for *N. pustulatus*, but our a priori break between juvenile and adult size class was informed by a late-stage embryo found through dissection in a female at SVL 65 mm (Heaton 2017), juvenile (SVL 55–75 mm) size in similar cordylid species (Mouton et al. 1998; Flemming and Mouton 2002; Nieuwoudt et al. 2003), and the frequency distribution of our captures (Fig. 3). Lizards were identified by sex (presence–absence of generation glands; Fig. 2F,G) and assigned to a juvenile (SVL < 65) or adult (SVL ≥ 65 mm) size class. Individuals smaller than 43 mm SVL could not be accurately sexed based on the presence or absence of femoral pores due to a lack of knowledge on size or age of pore development where 43 mm is the smallest SVL where pores were observed (this study). SVL, intact tail length (TL; tails could be identified as regenerated by a difference in color from the original tail, and regenerated tail whorls have duller spikes than original tail whorls; Fig 2D,E), and body total length (SVL + TL) of field-caught specimens were measured to the nearest 1 mm by using a straight edge ruler; SVLs of museum specimens were measured using a string and straight ruler (1 mm). We measured the distance from the axilla to groin (AG; from the flex point of the forearm to the flex point of the hindlimb), head length (HL; from snout to posterior edge of the parietals), head width (HW; across the temporal region), and head height (HH; at the midpoint of the supraoculars). We also measured the length of the humerus (upper arm: outer shoulder to outer elbow), radius–ulna (lower arm: outer knee to ankle), femur (upper leg: hip to outer knee), tibia–fibula (lower leg: outer knee to ankle), and digits (Right fourth finger and right fourth toe). Measurements were recorded to the nearest 0.1 mm with a dial caliper, and all limb and digit measurements were taken on the right side.

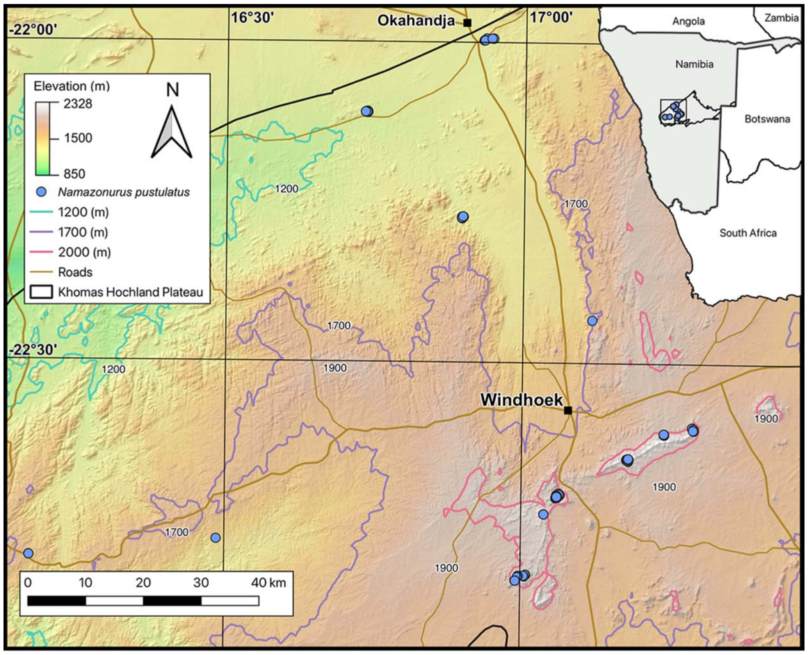

FIG. 1.—Geographic distribution of all known localities of *Namazonurus pustulatus*. Contours coincide with an elevational pattern in which individuals are found at low elevations (1200–1700 m asl) and high elevations (2000–2500 m asl).

Scars were identified as broken tail, missing toes, or visible scarring on the body or head (Fig. 2B,C,E). Mass (grams) was recorded for field-captured individuals by using a spring scale (PESOLA; 10 g and 30 g at 0.1-g and 0.5-g resolution, respectively). Femoral pores and generation glands were counted in the field and/or from high-resolution photos. Sixteen voucher specimens were deposited in the National Museum of Namibia (female = 9, male = 7; Appendix), all other captured individuals were released back to their crevice.

Data Analysis

Head and body comparisons between adult females and adult males were examined using a Wilcoxon rank sum test with Bonferroni-adjusted P values because the data were not normally distributed. Differences in adult size and the relationship between SVL and HH against elevation with sex as a factor in adult *N. pustulatus* were quantified using a generalized linear model (Nelder and Wedderburn 1972). HW, HL, and TL against elevation were not tested as the variables were correlated

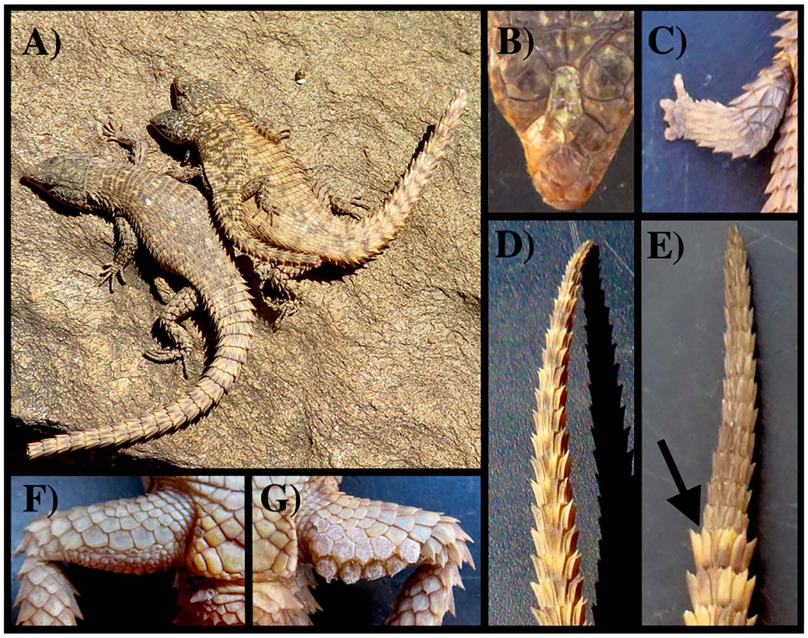

FIG. 2.—(A) *Namazonurus pustulatus* female, juvenile, and male (left to right) freshly sampled from Düsternbrook Guest Farm; (B) a head scar on a juvenile that is missing frontal, prefrontal, loreal, and pre-ocular scales; (C) picture of scarring on extremities, missing four of five digits; (D) picture of an intact tail; (E) picture of a regenerated tail, breakage indicated by the arrow, notice the whorls are less spikey and a different color from original tail; (F) female femoral region showing femoral pores but lacking generation glands; and (G) male femoral region showing generation glands and femoral pores.

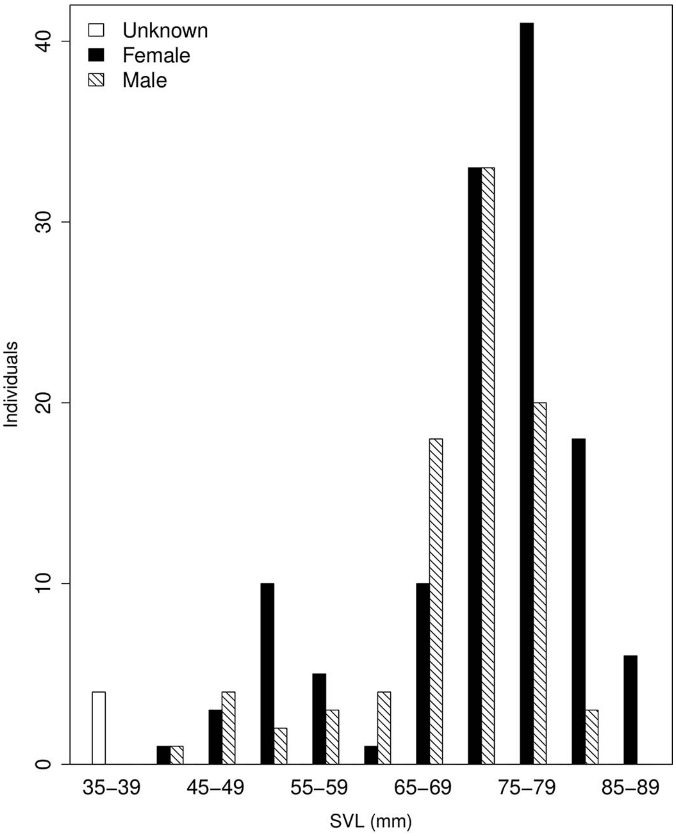

FIG. 3.—Frequency histogram of SVL distribution for field-caught *Namazonurus pustulatus*. Females reach a larger overall maximum SVL.

with SVL (HW, $t = 9.0097$, df $= 182$, $P \leq 0.01$; HL, $t = 10.857$, df $= 183$, $P < 0.01$; and TL, $t = 9.7618$, df $= 91$, $P \leq 0.01$).

The relationships between SVL versus TL and head dimensions between sexes were examined using regressions. Residuals were tested for normality using the Shapiro–Wilk test. Only the residuals for HH versus SVL were nonnormal, and transformations did not result in a normal distribution; therefore, no transformations were used. Allometric relationships were examined using regressions with the interaction of sex and age with SVL by testing for differences in the slope of AG, TL, and head dimensions.

To further explore the relationship between head dimensions and SVL, segmented regression (Muggeo 2003) analyses were conducted. Segmented regression allows for the inclusion of multiple breakpoints in a linear regression when a change in slope between two variables is detected, using a maximum likelihood approach to estimate the breakpoint. The breakpoint may indicate the size (SVL in our case) at which there is a change in growth patterns, such as growth to reproduction. The existence of breakpoints was tested for using a score test-based approach (Muggeo 2016), and a nonzero difference in the slope parameter of a segmented relationship was identified using a Davies' test, resulting in a best breakpoint (Davies 1987, 2002). A breakpoint was estimated using a segmented regression that was informed by the Davies' test results (Muggeo 2003, 2008). Finally, differences between regression slopes between size/age classes was calculated by a Z-score:

$$Z = \frac{b_1 - b_2}{\sqrt{SEb_1{}^2 + SEb_2{}^2}}$$

where b is the respective regression slopes and SEb is the standard error of that slope.

Differences in the number of missing toes and tails between the sexes (adults only, juveniles only, and combined) of field-captured individuals were tested using Pearson's chi-square test (with Yates' continuity correction for 2 × 2 tables). The correlations between field-captured adult generation glands and femoral pores with SVL were tested using Pearson's r correlation coefficient. Statistical analyses were done in R (v3.6.1; R Core Team 2019) with the *segmented* (v1.0.0; Muggeo 2003, 2008) package by using a significance level of $P \leq 0.05$.

RESULTS

Body and Head Size

Morphometric data were collected from 224 field specimens and 10 museum specimens including 113 adult females, 77 adult males, 21 juvenile females, 17 juvenile males, and 6 individuals that were too small to determine sex. The largest adult female (SVL = 87 mm; AG = 41.8 mm, and mass = 18.5 g) was larger in overall size and mass than the largest male (SVL = 82 mm, AG = 39.5 mm, and mass = 16.0 g), and on average, females were larger than males in SVL, AG, and mass (Table 1). Adults were larger at lower elevations ($R^2 = 0.35$, $t = -8.27$, $P = 0.01$) but there was no effect of elevation on HH ($R^2 = 0.00$, $t = 0.74$, $P = 0.46$).

Adults had similar body and head growth rates but grew slower than juveniles. For juveniles, the variations in HW, HL, HH, and TL were explained by variation in SVL ($R^2 = 0.79$, 0.82, 0.55, 0.90, respectively; Supplemental Table S1, available online). To a lesser degree, the variation in HW, HL, and TL size in adults was explained by variation in SVL ($R^2 = 0.30$, 0.39, 0.51, respectively) and HH was not ($R^2 = 0.05$; Supplemental Table S1). Allometric relationships of HW, HL, and HH indicated that heads of juveniles grew faster than adults (excluding juvenile HH versus adult male HH), but there was no difference in TL between juveniles and adults (Table 2; Fig. 3A,C,E, F). Finally, there were no differences in TL or head dimension growth rates between adult females and adult males (Table 2).

Segmented Regressions

Variation in HH was not explained by variation in SVL for adults ($R^2 = 0.05$; Fig. 4E; Supplemental Table S1), and there was no difference in TL growth rates between any age class or sex (Table 2; Fig. 4F). As a result, a segmented regression analysis was used only on HW and HL (adults and juveniles combined without identification by sex) versus SVL to determine if a breakpoint could be identified. Score tests indicated a single significant breakpoint for HW ($P < 0.01$) and HL ($P < 0.01$) and the Davies test for best breakpoint, which informed the segmented regression, was 70.0 mm and 68.5 mm, respectively. Segmented regressions identified a significant breakpoint in slopes at 16.4 mm HW (SVL = 70.0 mm, SE = 1.2 mm, $y_1 = 0.3x - 1.8$, $y_2 = 0.1x + 9.4$, $R^2 = 0.88$; Fig. 4B) and at 18.1 mm HL (SVL = 68.3 mm, SE = 1.3 mm, $y_1 = 0.2x + 3.5$, $y_2 = 0.1x + 11.6$, $R^2 = 0.89$; Fig. 4D). Z-scores indicated that the slopes before and after the break point were significantly

TABLE 1.—Morphological measurements of adult *Namazonurus pustulatus* and results of Wilcoxon rank sum tests comparing males and females. Range, $\overline{X}$, and SD are in millimeters. *P* values were adjusted with Bonferroni correction. (*) indicates median instead of $\overline{X}$. Positive % diff. values indicate that females are larger for the trait.

Morphological trait	Sex	*n*	Range	$\overline{X}$	SD	W	*P* value	% diff.
Snout–vent length	Female	111	65–87	75.9	4.9	**5953**[a]	**<0.01**	**4.4**
	Male	77	65–82	72.7	3.8			
Mass	Female	108	7.2–24.0	13.7	2.8	**4920**	**0.04**	**10.5**
	Male	72	6.9–18.5	12.4	2.2			
Tail length	Female	56	76–115	92.9	8.6	1305	0.49	4.1
	Male	37	74–110	89.2	8.7			
Body total length	Female	56	144–197	167.5	12.7	1286	0.37	3.7
	Male	36	141–190	161.6	11.3			
Axilla to groin	Female	71	29.8–52.1	37.5	4.1	**2149**	**<0.01**	**8.4**
	Male	43	27.2–39.9	34.6	3.5			
Head width	Female	109	13.2–20.0	16.7	1.0	3246	0.25	–1.8
	Male	75	14.1–19.8	17.0	1.0			
Head length	Female	109	16.6–20.6	18.7	0.8	3957	1.00	0
	Male	76	16.4–20.4	18.7	0.8			
Head height	Female	107	6.0–9.8	8.4	0.7	4242	1.00	0
	Male	76	5.8–9.9	8.4	0.8			
Humerus	Female	32	8.5–11.4	10.2	0.8	490	1.00	2.0
	Male	27	7.8–11.9	10.0	1.0			
Radius–ulna	Female	32	7.8–11.4	9.5	0.9	576	0.41	6.7
	Male	27	6.7–10.8	8.9	0.9			
Longest fore-finger	Female	32	5.2–6.7	5.9	0.4	435	1.00	0.0
	Male	26	4.8–6.8	5.9	0.5			
Femur	Female	32	11.0–15.0	13.4	1.1	511	1.00	3.1
	Male	27	11.3–14.6	13.0	1.0			
Tibia–fibula	Female	32	8.1–12.6	10.7	1.1	442	1.00	0.0
	Male	27	9.1–12.6	10.7	0.9			
Longest hind-toe	Female	32	6.0–8.4	7.2	0.7	343	1.00	–2.7
	Male	26	6.0–8.5	7.4	0.7			
Femoral pores	Female	105	7–11	8*	0.9	—	—	
	Male	74	7–11	8*	0.8			
Generation glands	Female	—	—	—	—	—	—	
	Male	74	9–23	16*	3.2			

[a] Bolded values are traits that are significantly different between males and females.

different (HW, $Z = 7.17$, $P < 0.01$; HL, $Z = 7.19$, $P < 0.01$), for which the slope before the breakpoint is steeper than the slope after the breakpoint.

Scar Frequency

Scar frequencies were similar between sex and age. There were no significant differences between sexes or size classes for missing toes (27 of 108 adult females, 22 of 74 adult males, chi-square = 0.29, df = 1, $P = 0.59$; 4 of 20 juvenile females, 1 of 14 juvenile males, chi-square = 0.30, df = 1, $P = 0.58$; adults and juveniles, chi-square = 0.03, df = 1, $P = 0.87$), broken tails (54 of 110 adult females, 39 of 75 adult males, chi-square = 0.06, df = 1, $P = 0.81$; 4 of 21 juvenile females, 5 of 17 juvenile males, chi-square = 0.13, df = 1, $P = 0.72$; adults and juveniles, chi-square = 0.15, df = 1, $P = 0.70$), or either missing toes or broken tail (72 of 127 adult females, 50 of 87 adult males, 6 of 20 juvenile females, and 5 of 14 juvenile males; adults, juveniles, and combined, chi-square < 0.01, df = 1, $P = 1.00$).

TABLE 2.—Results of *t*-tests comparing regression coefficients of head width, head length, head height, and tail length versus snout–vent length among the adult sexes and age classes of *Namazonurus pustulatus*.

Morphological trait	Comparison	*t*	df	*P* value
Head width	Adult female vs. adult male	0.40	219	0.69
	Adult female vs. juvenile	4.09	219	<0.01
	Adult male vs. juvenile	2.80	219	0.01
	Adult vs. juvenile	5.13	221	<0.01
Head length	Adult female vs. adult male	0.85	219	0.40
	Adult female vs. juvenile	5.58	219	<0.01
	Adult male vs. juvenile	3.59	219	<0.01
	Adult vs. juvenile	6.41	221	<0.01
Head height	Adult female vs. adult male	1.07	218	0.29
	Adult female vs. juvenile	2.78	218	0.01
	Adult male vs. juvenile	1.15	218	0.25
	Adult vs. juvenile	2.82	220	0.01
Tail length	Adult female vs. adult male	1.04	120	0.30
	Adult female vs. juvenile	0.160	120	0.88
	Adult male vs. juvenile	–0.98	120	0.33
	Adult vs. juvenile	–0.34	122	0.73

Epidermal Glands

In adult males, the number of generation glands and femoral pores were correlated with SVL (generation glands, $n = 72$, Pearson's $r = 0.33$, $P < 0.01$; femoral pores, $n = 72$, Pearson's $r = 0.33$, $P < 0.01$). In adult females, the number of femoral pores were correlated with SVL ($n = 103$, Pearson's $r = 0.29$, $P < 0.01$).

DISCUSSION

Body Size

We provide quantitative evidence that *Namazonurus pustulatus* is a sexually dimorphic species. Adult females were the larger sex, having a higher maximum and average SVL, AG, and mass than adult males. The magnitude of the size difference increased with increasing body size, suggesting that fecundity selection acts on female *N. pustulatus*, as implicated in other

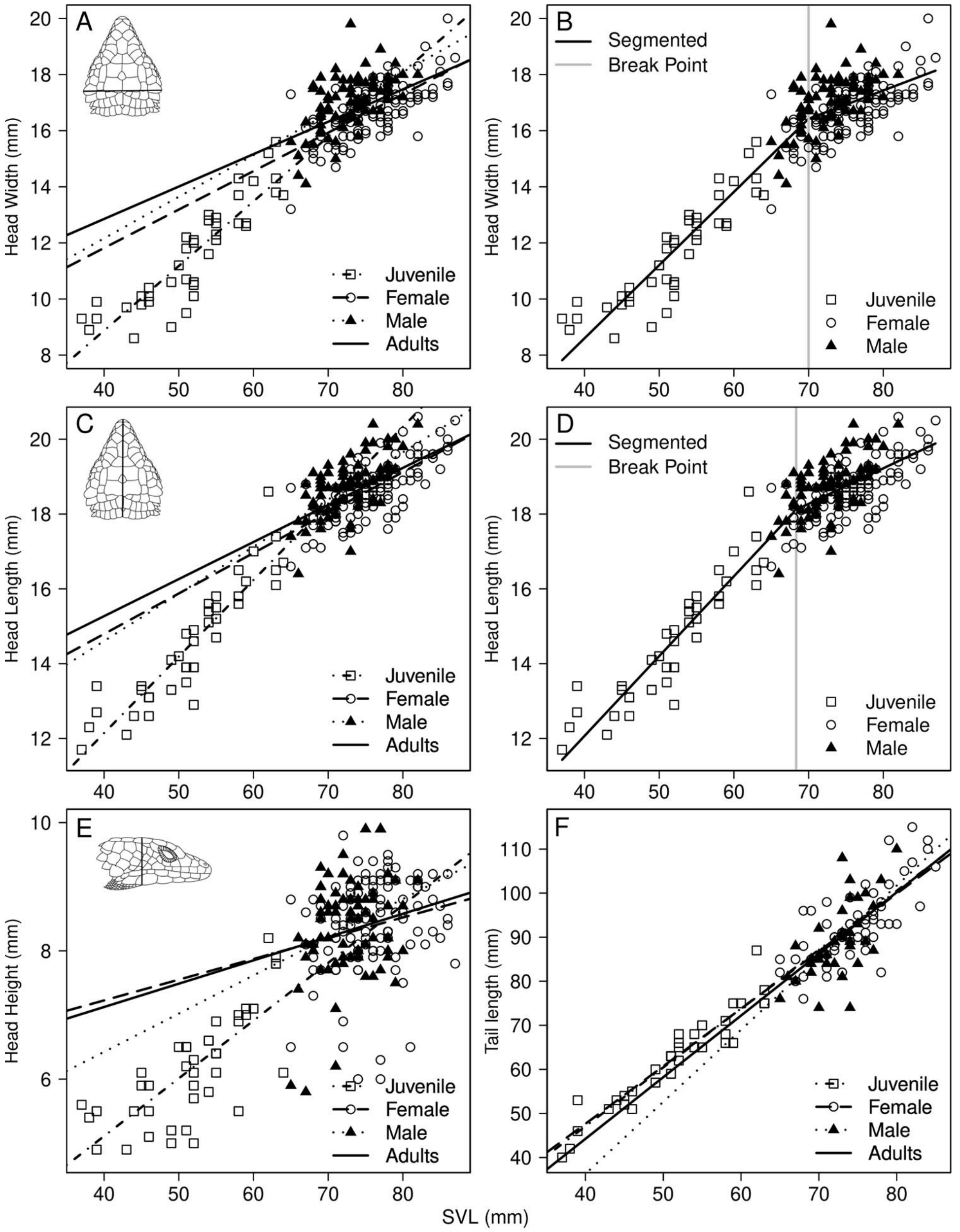

Fig. 4.—Regressions of (A) head width, (C) head length, (E) head height, and (F) tail length against SVL for adult female, adult male, juveniles, and adult sexes combined of *Namazonurus pustulatus*. Segmented regressions of (B) head width and (D) head length against SVL for all individuals.

reptiles, such as snakes and turtles (Shine 2000; Fairbairn et al. 2007; Ceballos et al. 2013; Jimenez-Arcos et al. 2016) and cordylids (Van Wyk and Mouton 1998; Costandius and Mouton 2006).

These findings are consistent with those of seven other cordylid species in which females were larger and their size was ascribed to fecundity selection (Fell 2005; Costandius and Mouton 2006; Broeckhoven and Mouton 2014) and was also related to temperature (Mouton and Van Wyk 1993; Mouton et al. 1999; Mouton et al. 2000; Costandius and Mouton 2006). Mouton and Van Wyk (1993) suggested that when resources are limited, such as at cooler temperatures at higher elevations, females allocate more energy to the growth of reproductively significant characters. *Namazonurus pustulatus* is considered a high-elevation species and is found at the peak of Moltkeblick (2,478 m asl; –22.6506°S, 17.1803°E; datum = WGS84) in the Auas Mountains, and cooler temperatures may result in more limited resources. However, female-biased size dimorphism is present in species that are not limited to high elevations and cooler temperatures (Costandius and Mouton 2006).

Female-biased dimorphism in body size has also been attributed to a terrestrial lifestyle, whereas male-biased dimorphisms in body and head size have been attributed to a rupicolous lifestyle. Mouton et al. (2000) suggested that females are the larger sex in the terrestrial species *C. macropholis* because, in general, selection favors small body diameter due to habitat constraints, but longer bodies can hold more or larger embryos. *Chamaesaura anguina*, a terrestrial snake-like cordylid, also has larger females, and there is a positive correlation between female SVL and clutch size (du Toit et al. 2003). Male-biased dimorphisms in the rupicolous species *O. cataphractus* are attributed to male competition in response to space limitation whereby a larger body and a larger head size have fitness advantages (Mouton et al. 1999). However, sexual dimorphism cordylid studies are contradictory because some rupicolous species have female-biased size dimorphism (Costandius and Mouton 2006; Broeckhoven and Mouton 2014). As a rupicolous species, *N. pustulatus* females being larger is also counter to the terrestrial female body-size link. With the apparent conflicting relationships between fecundity selection with either temperature or lifestyle, it is likely that multiple biological and ecological factors influence sexual dimorphism in *N. pustulatus*.

There have been no studies on resource availability for *N. pustulatus*, but it likely varies along environmental gradients (i.e., temperature and precipitation) and may contribute to overall body size. In our study population, regional temperatures are 2.5–4.6°C warmer at lower elevations than at higher elevations, but annual precipitation increases from the west to east across Namibia (172–481 mm annually; Kaseke et al. 2016). We observed a strong correlation between SVL, TL, HL, and HW versus elevation; adult females and males were larger at low elevations (1200–1700 m asl) than those at high elevations (2000–2500 m asl) but showed increased population density at higher elevations (Heaton et al. 2017). Reduced size at high elevations could be due to fewer resources, which is observed in lizards and snakes (Case 1979; Wikelski et al 1997; Amarello et al. 2010). More information on resource availability is required to see if resources are a factor in overall size for *N. pustulatus*.

The female-biased size dimorphism could be due to a delay in maturation whereby females attain a large body size before sexual maturity (Tinkle et al. 1970). Delayed maturation is common in viviparous lizards and is often accompanied with long gestation periods, large offspring, and fewer births per year (Tinkle et al. 1970). *Namazonurus pustulatus* is a viviparous lizard, and gestation data on follicle and embryo development, as well as parturition, indicate a long (6–8 mo) gestation period and large neonate SVL relative to adults (50–53%, female versus male respectively; Heaton 2017). These patterns are also reported in the *Ouroborus–Karusasaurus–Namazonurus–Hemicordylus–Cordylus* clade but contrast to those in the *Ninurta–Chamaesaura–Pseudocordylus* clade and *Smaug* clade, which have larger clutches of smaller offspring (Mouton et al. 2012). *Namazonurus pustulatus* likely gives birth to a small clutch of offspring ($n = 1–2$) once a year (Heaton 2017), but females may not reproduce every year, as observed in other cordylids (Van Wyk 1991). Delayed maturation may play a large role in the body size of *N. pustulatus* females, but no sexual maturity information is available on the species apart from estimates based on size (Branch 1998; this study, below).

Head Dimensions

Male *N. pustulatus* has larger HW and HL than females. Larger male head size is attributed to sexual selection in which increased male head size could have fitness advantages in male competition or mating (Cooper and Vitt 1989; Gullberg et al. 1997; Gvozdik and Van Damme 2003). These findings are consistent with those of other cordylids in which male head dimensions are larger and are ascribed to male competition and sexual selection (Costandius and Mouton 2006; Mouton 2011; Broeckhoven and Mouton 2014). In the congener *N. peersi*, adult males have slightly larger HW than adult females (male $n = 64$, female $n = 59$), but no differences are identified in other head dimensions (Fell 2005; Mouton 2011). Male *N. pustulatus* with larger HW and HL may have an increased advantage for mating. Specifically, HW and HL are positively associated with bite-force in cordylids (Broeckhoven and Mouton 2014), which is commonly associated with reptile mating behaviors (Herrel et al. 2001; Husak et al. 2006; Lappin et al. 2006; McLean and Stuart-Fox 2015).

The lack of a difference in HH between male and female *N. pustulatus* could indicate other selective pressures influencing head shape, such as their rock-crevice niche. For instance, head morphology in the lizard family Gymnophthalmidae (microteiids), comprising several fossorial and niche-restricted species, is a consequence of microhabitat rather than sexual dimorphism or diet (Barros et al. 2011). In cordylids, HH is constrained by habitat for rupicolous species (Losos et al. 2002).

Overall, selective pressures on head size and SVL are complex, and the fit of our regression models of head size against SVL is comparatively weak compared to other studies of sexual dimorphism in cordylids (Cordes et al. 1995; Van Wyk and Mouton 1998; Mouton et al. 1999, 2000, 2005; Costandius and Mouton 2006; Broeckhoven and Mouton 2014). These results are consistent with other rupicolous reptiles that have conflicting selective pressures on head dimensions where males have larger heads for male competition, but the HH is restricted by microhabitat or niche constraints (Losos et al. 2002; Lappin et al. 2006). We also identified no differences in head growth rates in *N. pustulatus*. This finding is similar to that in *Hemicordylus capensis* in which adult males have larger heads, but head growth rates between sexes were the same (Van Wyk and Mouton 1998). Conflicting selective pressures cannot optimize all functions simultaneously leading to trade-offs in morphology (Herrel et al. 2007, 2009), and in *N. pustulatus*, adult females and adult males have equivalent absolute HH, indicating that there might be an optimal head size that balances habitat (rock crevices) and sexual selection pressures in cordylids (Cooper and Vitt 1989).

Sexual Maturity

Our study did not directly seek to determine age at sexual maturity, but the results show a clear change in growth rates that is indicative of sexual maturity in reptiles (Halliday and Verrell 1988; Bjorndal et al. 2013). Our regression analyses indicate significant differences between the slopes of HW and HL versus SVL between adults and juveniles. Furthermore, segmented regressions indicate a change in the rate of head growth relative to SVL at 70.0 mm for HW and 68.3 mm for HL. These analyses suggest a point of differential resource allocation from body growth to reproduction (Cooper and Vitt 1989) in the range of 68.3 – 70.0 mm. The estimated breakpoint is just below that in a report by Branch (1998) on an adult SVL size of 70 – 75 mm. The shift in resource allocation is further supported by the difference in allometric head growth relative to SVL in juveniles versus adults and is also observed in other cordylids (Cordes et al. 1995; Mouton et al. 1999, 2005; Costandius and Mouton 2006). However, some individuals are capable of reproducing before 70 mm, which was demonstrated by a late-stage embryo in a smaller female (SMR 2677, SVL = 65 mm; Heaton 2017), but there could be reproductive size variation among populations. This information means that although we can identify when there is a change in growth rates, we may not be able to statistically determine the breakpoint of differential growth until after sexual maturity has been reached.

Scar Frequencies

The total scar frequency of *N. pustulatus* is not significantly different between the sexes when comparing adults, juveniles, or the two combined. The total scar frequency of 62% (110 of 179) in *N. pustulatus* is much higher than that in any other cordylid species recorded to date (Cordes et al. 1995; Mouton et al. 1999, 2000; Costandius and Mouton 2006). In general, high frequencies of tail loss are associated with higher predator pressures (Arnold 1988; Fox et al. 1994; Pafilis et al. 2008; Bateman and Fleming 2009), whereas toe loss is associated with intraspecific competition (Vitt et al. 1974; Schoener and Schoener 1980; Vitt and Cooper 1985). Tail loss is greater than toe loss in *N. pustulatus*, suggesting that predation pressures are greater than intraspecific competition.

Epidermal Glands

Generation glands are sexually dimorphic in *N. pustulatus* and are present in males and absent in females. Within *Namazonurus*, femoral pores ($n = 8$–30) and generation glands ($n = 10$–32) were present in males of all species, but generation glands were absent in females (Mouton et al. 2010). For male *N. pustulatus*, the number of femoral pores ($n = 7$–11, median = 8) and generation glands ($n = 9$–23, median = 16) were lower than most *Namazonurus* spp., but closest to their nearest relative (Stanley et al. 2011), *Namazonurus campbelli* (femoral pores = 8, generation glands = 10; Fitzsimons 1938). The number of generation glands and femoral pores in *N. pustulatus* increased with increasing SVL, which is congruent with other cordylids (Mouton et al. 2010; Mouton 2011). However, generation gland development before sexual maturity is uncommon in cordylids (Mouton et al. 2010), and only a few species have generation glands at birth (Mouton et al. 1998). We found eight generation glands on an individual as small as 43 mm SVL (SMR 10731), indicating its sex as male, but not on any smaller individuals ($n = 4$, SVL = 37–39). We did not dissect any embryos, neonates, or small individuals that could not be sexed by the presence of generation glands (SVL $<$ 43 mm), which may reveal if generation glands are present at birth. Whether for communication or another undetermined function, the presence of generation glands on nonreproductive males suggests that *N. pustulatus* has an increased need for the early development of generation glands in comparison to cordylid species that develop generation glands later in life.

Conclusion

We found that *N. pustulatus* is sexually dimorphic, which is a novel result for this species. Larger female size is attributed to fecundity selection, in which larger females have a fitness advantage. Larger male HW and HL is attributed to sexual selection. Selection pressures on head dimensions in *N. pustulatus* are likely operating across multiple scales, as follows: HW and HL may provide competitive advantages, whereas HH may be constrained by the lizard's rocky niche habitat. The scar frequencies are higher than in any previously recorded cordylid species, and more occurrences of tail loss over toe loss may indicate increased overall predation pressures. Epidermal glands scale with body size for both sexes, which is consistent with other cordylids. These results provide additional information for understanding patterns of sexual dimorphism in cordylid lizards, and this study is the first to examine sexual dimorphism in a species endemic to Namibia.

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Supplemental Material

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Appendix

Museum specimens measured for this study were from the National Museum of Namibia (NMN), State Museum Reptile (SMR) collection, as follows: 1789, 1790, 2677, 5388, 5389, 5390, 7058, 1791a, 1791b, and 1791c. The following individuals were additionally accessioned to the NMN: SMR 10643–10647, 10666–10668, 10690, 10705, 17030, 10731, 10740, and 10745–10747.