Urban Ecosystems
https://doi.org/10.1007/s11252-023-01474-1

Differences between urban and natural populations of dwarf chameleons (*Bradypodion damaranum*): a case of urban warfare?

Melissa A. Petford[1,2] · Anthony Herrel[3,4,5,6] · Graham J. Alexander[2] · Krystal A. Tolley[1,7]

Accepted: 14 November 2023

Abstract

Urbanisation creates novel environments, not only through (abiotic) microhabitat alterations, but also due to changes in (biotic) inter- and intraspecific interactions. Where sheltering sites in urban habitats are limited, intra or interspecific interactions may increase, resulting in increased competition and changes in predation risk in urban areas compared to natural habitats. The Knysna Dwarf Chameleon (*Bradypodion damaranum*) occurs in both urban and natural settings, is extremely ornamented, and individuals have been observed with multiple wounds and scars. We therefore hypothesised that urban populations may have adapted to the physical features of urban habitats, and that this would be detectable through ornament size and bite force, as well as the presence of scarring. We quantified these traits from urban and natural populations from two separate localities (the towns of George and Knysna, South Africa). Our results showed that female and male *B. damaranum* from urban populations had a higher number of injuries and that urban males were more likely to be injured than males from natural habitats. Bite force was only recorded at one locality (Knysna), but both sexes in urban habitats had higher bite force when accounting for casque height as compared to those from the natural habitats. Urban chameleons also had less developed ornamentation but wider and/or higher heads compared to populations in natural habitats. Urban habitats had significantly lower tree density than natural habitats, and this may be a factor in driving the morphological differences between populations, whereby reduced ornamentation confers an advantage for remaining cryptic to predators in the open habitat but compromises the ability for signalling conspecifics with encounters escalating to physical contests.

Keywords Adaptation · Africa · Bite force · Chameleons · Convergence · Ornamentation · Reptiles · Urban populations

Introduction

Anthropogenic activities are profoundly altering ecosystem processes through environmental degradation and habitat fragmentation (Morris 2010; Ellis 2011; Hammond et al. 2020). Urbanisation has a drastic effect on the local environment, creating novel macro and microhabitats due to the construction of artificial structures, manicured and non-native vegetation and impervious substrates (Marnocha et al. 2011). Structural differences between urban and natural habitats result in unique ecological challenges and differences in selection pressures, accelerating the rate of phenotypic change in urban areas (Hendry et al. 2008). Differences in selective forces between urban and natural populations can also trigger changes in inter and intraspecific interactions leading to further changes in the direction and intensity of selection.

While abiotic alterations to habitat are a clear challenge for urban populations of animals, species occurring in urban

✉ Melissa A. Petford
melissa.petford@outlook.com

1 Kirstenbosch Research Centre, South African National Biodiversity Institute, Private Bag X7, Claremont, Cape Town 7735, South Africa

2 School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, P.O. Wits 2050, Johannesburg, South Africa

3 Département Adaptations du Vivant, UMR 7179 C.N.R.S/M.N.H.N, Bâtiment d'Anatomie Comparée, Paris, France

4 Department of Biology, Evolutionary Morphology of Vertebrates, Ghent University, Ghent, Belgium

5 Department of Biology, University of Antwerp, Wilrijk 2610, Belgium

6 Naturhistorisches Museum Bern, Bern 3005, Switzerland

7 Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, Auckland Park, Johannesburg 2006, South Africa

Published online: 23 November 2023

environments also encounter a variety of unfamiliar biotic challenges to which they must acclimatize or adapt. For example, novel predators pose a significant threat to populations of small vertebrates (Koenig et al. 2002; Bamford and Calver 2012; Seymour et al. 2020) and changes in predation risk have also been noted for some urban populations (Koenig et al. 2002). Other populations experience changes in intraspecific competition (Lacy and Martins 2003; Banks et al. 2007; Anderson and Burgin 2008; French et al. 2018; Baxter-Gilbert and Whiting 2019), and in some cases, heightened intraspecific aggression (Lacy and Martins 2003; Banks et al. 2007; Baxter-Gilbert and Whiting 2019). The latter can be particularly relevant as populations in urban areas are likely to rely on specific, but clumped and possibly scarce, resources (Winchell et al. 2018). This can lead to higher abundance of individuals per habitat patch (e.g., Baxter-Gilbert and Whiting 2019), exacerbating localised intraspecific competition. Overall, urban populations face a number of novel biotic and abiotic conditions, the complexity of which make it difficult to predict if and how the populations may respond.

Nevertheless, there is mounting evidence for differences in the direction and intensity of inter and intraspecific interactions for some populations in urban habitats, and this can lead to a higher prevalence of injuries. Past injuries can be detectable through the presence of wounds and scars, with individuals that have more scars presumably having had a higher injury rate than those with fewer scars. For example, Australian water dragons (*Intellagama lesueurii*) from urban habitats had more wounds due to increased intraspecific aggression (Baxter-Gilbert and Whiting 2019), and increased predation was considered the cause of increased tail breakages in the tropical lizard *Anolis cristatellus* (Tyler et al. 2016). However, an elevated level of injury prevalence in urban populations could also represent a lower efficiency of predators in the urban setting – that is, injury rather than death with removal from the population could be an explanation for the suggested higher occurrence of wounded individuals in urban populations. Despite this caveat (Schoener 1979), the overall expectation is that urban populations may be at greater risk to predation and/or have more frequent aggressive encounters with conspecifics.

Dwarf chameleons of the genus *Bradypodion* are native to South Africa and southern coastal Mozambique, and approximately a third of the 20 described species occur in both urban and natural habitats. They are arboreal, inhabiting trees, bushes, shrubs or grasses, depending on the species, but are capable of occasionally crossing open ground between vegetation clumps. Many species of *Bradypodion* are conspicuous, with ornamented heads and colourful flanks, which are used for intraspecific signalling (Stuart-Fox and Whiting 2005; Stuart-Fox et al. 2006; Stuart-Fox and Moussalli 2008). In urban areas, dwarf chameleons usually inhabit parks, gardens and roadside vegetation. However, these urban patches of vegetation probably provide fewer opportunities for shelter as vegetation in urban areas is usually less dense than in natural areas (e.g., Palamuleni and Turyahikayo 2015; Stickler and Shackleton 2015; Magidi and Ahmed 2022), and in some cases may also be different in structure to natural vegetation, such as having a lack of canopy and understory complexity. Some heavily modified habitats may also be unsuitable for chameleons, totally excluding populations (Tolley and Measey 2007; Hopkins and Tolley 2011). Overall, urban areas are expected to provide much less cover than natural areas, possibly creating a situation where space is at a premium. If so, this may result in intense intraspecific competition, but also may engender a situation where conspicuous individuals may be compromised by the habitat openness, being more visible to predators.

The Knysna Dwarf Chameleon (*Bradypodion damaranum*) occurs naturally in Afrotemperate forest, is allopatric to other *Bradypodion* species and is arboreal, using vegetation ranging from the low understorey to the high canopy (Tolley and Burger 2007). However, this species is also common in suburban gardens, parks and along road verges within its geographic range (Tolley and Burger 2007). Given that urbanised areas are highly transformed, we hypothesised that chameleon populations in towns (urban) occur in less dense habitat compared to those in natural forest. Specifically, accessibility to vegetation (e.g., trees, bushes) might be comparatively limited, making shelter a scarce resource in urban areas. If so, we would expect an increase in both inter and intraspecific encounters, and that this might drive phenotypic differences between the populations.

Dwarf chameleon populations respond to predation risk by reducing their conspicuousness and are remarkably effective at concealing themselves from avian predators (Stuart-Fox and Moussalli 2008; Stuart-Fox et al. 2008). Therefore, we expected that chameleons from urban populations would show reduced conspicuousness where the lack of cover could make them vulnerable, particularly to avian predators. However, in *Bradypodion*, intraspecific communication is achieved through display signalling (Stuart-Fox et al. 2007). Thus, reduced conspicuousness of ornamentation could represent a trade-off between display and crypsis, with less effective conspecific signalling resulting in more frequent direct intraspecific encounters (see Stuart-Fox 2006; Stuart-Fox et al. 2006). Direct encounters that are not deescalated by signalling are known to escalate into aggressive physical contests (Stuart-Fox et al. 2006). Although teasing apart the ultimate cause of many injuries is not possible, we suggest that injury frequency for urban chameleons is very likely enhanced by increased aggressive encounters with conspecifics. Furthermore, because biting forms an important component of aggressive encounters in chameleons (Stuart-Fox et al. 2006), an escalation of intraspecific encounters within urban populations could be accompanied by selection for higher bite forces. We speculate that different selection pressures linked to vegetation density could result in phenotypic changes (e.g., Kolbe and Losos 2005; Ghalambor et al. 2007; Urban et al. 2014; Baxter-Gilbert et al. 2020), either due to phenotypic plasticity through standing genetic variation (West-Eberhard 1989; Irschick and Meyers 2007; Stotz et al. 2021) or adaptation arising from *de novo* mutations (Bomblies & Peichel 2022; McDonnell and Hahs 2015). We tested these hypotheses by quantifying injuries, head morphology/ornamentation, bite force, and tree density in populations of *Bradypodion damaranum* from urban and natural habitats from two independent localities within the natural range of the species.

Methods

Bradypodion damaranum individuals were sampled during 2020–2022 from two different local municipalities – George and Knysna, South Africa (approximately 60 km apart, hereafter referred to as 'towns'), where chameleons occur in both natural and urban habitats (hereafter referred to as 'populations'; Fig. 1). Modern urbanisation began just over 200 years ago, with George established in 1811 and as of 2021 having a population of 221,637 people with a density of 43 people/km^2 (Western Cape Government 2021a).

Fig. 1 Map of the study area for George (pink; left) and Knysna (blue; right), including images for **B**) urban and **C**) natural areas

Knysna was established in 1825 with a human population of 75,918 as of 2021 but a much higher human density of 68 people/km^2 (Western Cape Government 2021b). Urban areas consist of highly anthropogenically-modified vegetation, including bare ground and lawns, exotic and indigenous trees, bushes, grasses and herbaceous plants especially along road verges. Chameleons were sampled from private property and municipal parks, covering an approximately 3-km radius in both towns. For both towns, the chameleon populations were paired with natural populations 10–12 km from the corresponding urban populations. Natural habitats consisted of large, continuous tracts of near-pristine indigenous Afrotemperate forest.

To examine whether the habitat of urban and natural populations had significantly different vegetation characteristics, we used the Global Forest Cover Change (GFCC) Tree Cover Multi-Year Global 30-m V004 (Sexton et al. 2013) to estimate tree density for both towns as a proxy for available habitat. To achieve this, we used two approaches: (1) Tree density data within the same areas where we collected *B. damaranum* were used to assess if there were differences between locations where chameleons were recorded. We spatially rarefied the geographic coordinates where chameleons were recorded by 300 m using the spThin package (Aiello-Lammens et al. 2015) in R 4.2.1 (Core Team 2022) and added a 300-m buffer around each rarefied point in QGIS 3.22.8 (QGIS 2022). We selected 300 m as a plausible home range size based on movement data from the congener, *Bradypodion pumilum* (Rebelo et al. 2022). We then randomly selected five locality points within each 300 m buffer and extracted the tree density measures from the intersecting pixel in the GFCC raster layer. (2) Tree canopy densities were estimated overall for each town to identify the broader differences between urban and natural areas. To do this, we drew polygons around each natural and urban area using satellite imagery. For larger areas, we ensured that the polygon did not extend more than 5 km away from any of the chameleon localities recorded. We randomly selected points within each polygon to extract tree density measures, accounting for size differences by ensuring that one point was generated for every 2 km². For both approaches, Mann-Whitney U-tests were used to identify whether differences in tree canopy density between urban and natural areas were significantly different per town (for George and Knysna).

To examine morphological differences between populations, adult chameleons were measured to the nearest 0.01 mm using digital callipers for the following morphological traits: snout-vent length (SVL), head width (HW), head height (HH), casque height (CH, measured from the bottom of parietal to tip of casque spur) (Fig. 2). For a subset of individuals, the right side of each head was photographed against a background grid from which additional measurements were taken using ImageJ (Schneider et al. 2012): parietal height (PH: from quadrate to the bottom of the casque spur), the length of the casque spur (CS), and the length (GL) and area of the largest gular scale (GA) (Fig. 2). These latter measurements were not taken using callipers due to the potential for measurement error (Table 1).

Generalized linear mixed models (GLMMs) were used to assess whether ornamentation and head measurements differed between populations (urban and natural) using the packages: car v3.1-2, emmeans v1.8.8, lme4 v1.1-34, nlme v1.6, Matrix v1.6-1 and MuMin 1.47-5 (Bates et al. 2015; Fox and Weisberg 2018) within R version 4.2.1 (Core Team 2022). The GLMM was run separately by sex for each independent trait as a function of body size (SVL) and population. To assess whether there was variability between sampling sites that would not be explained by the fixed factor (population), 'town' (George and Knysna) was included as a random factor with the model intercept set to 0. Both the marginal r^2 (variance explained by the fixed factor only) and conditional r^2 (variance explained by fixed + random factors) were estimated (Nakagawa and Schielzeth 2013). Comparing the difference between the marginal and the conditional r^2 values allowed for an assessment as to whether the incorporation of 'town' as a random factor explained any additional variance in the dataset. Prior to running the GLMMs, datasets were assessed for homogeneity of variance (Levene's test) and homoscedasticity (Breusch-Pagan test) using the R functions LeveneTest and ncvTest, respectively. In cases where these assumptions were violated, data were log-transformed. Equality of slopes was checked by incorporating the interaction between SVL and habitat in a GLMM, keeping town as random factor.

To quantify the occurrence of injuries (i.e., injured/not injured) and the number of injuries found on each individual, chameleons (females: $n = 101$, males: $n = 175$) were thoroughly checked for evidence of injuries, including scars, fresh wounds and broken/healed bones. All injuries were recorded photographically for future reference. The occurrence of all wounds and scars were quantified by present/absent as well as the number of scars or wounds. Many injuries were obvious conspecific bite marks, but others were amorphous and could not be attributed to either an inter or intraspecific encounter. Thus, the injuries were not partitioned into types of encounter, but were amalgamated into a single category of 'injury'. To assess whether individuals from urban or natural populations were more likely to be injured (i.e., injured/not injured), we ran a binary logistic regression with the function glmmTMB in the package glmmTMB (Brooks et al. 2017) in R. Injury status was the response variable, habitat type the predictor and town was included as a random factor. This analysis approach was used given that the response variable is dichotomous

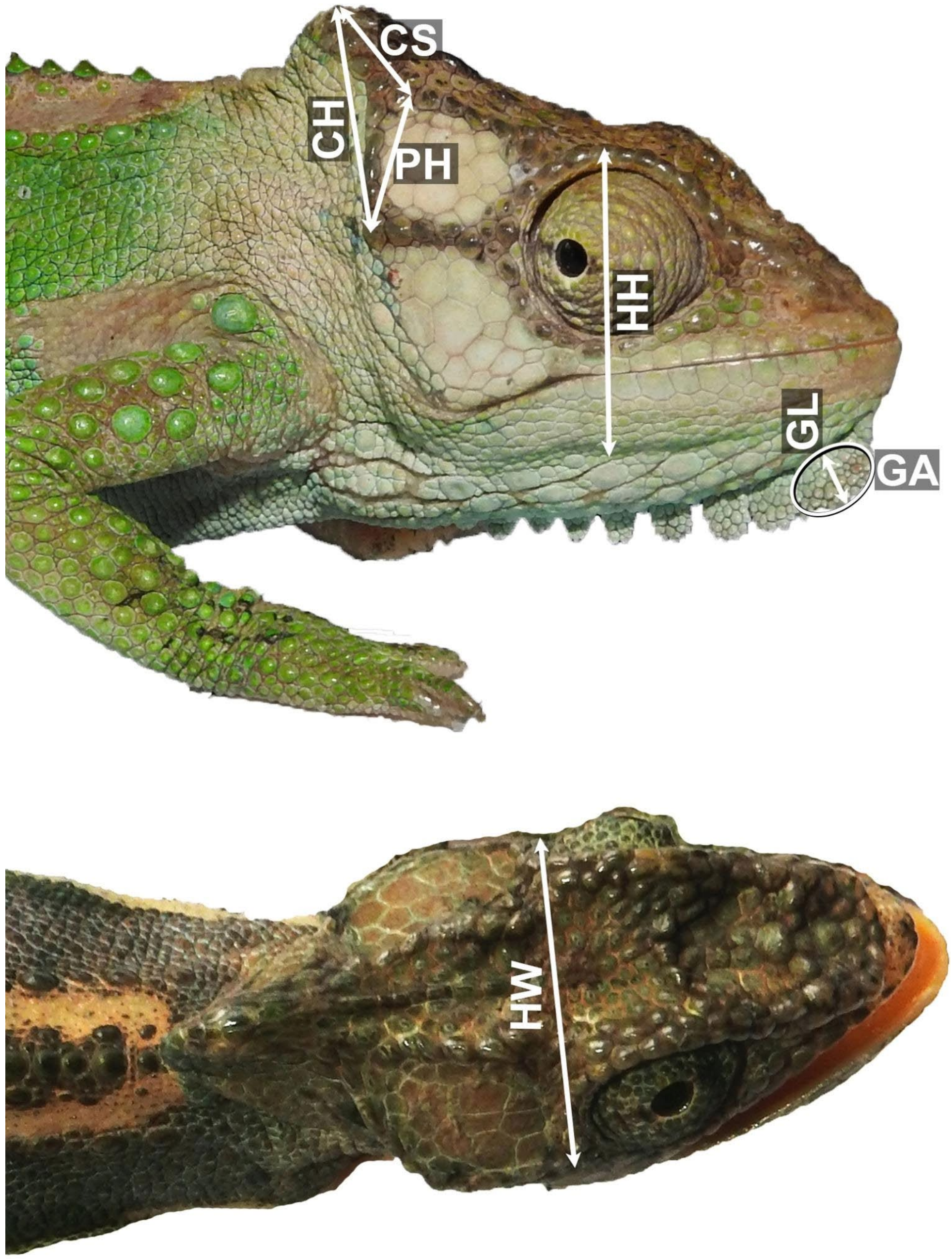

Fig. 2 Head of chameleon showing measurements. Head width (HW), head height (HH), casque height (CH), parietal height (PH), casque spur (CS), gular length and gular area (GA).

(injured/not injured). Injuries can accumulate over the lifetime of an individual and therefore it was necessary to use a covariate to account for 'age' of the individual. Because actual ages of individuals were not known, body size was used as a proxy for age by including SVL as a covariate. This allowed for differences in injury status between chameleons of different sizes ('ages') to be accounted for.

To assess differences in the number of injuries per individual between natural and urban populations, we used a zero-inflated Poisson regression model using the glmmTMB package in R. The number of injuries (count data) was set as the response variable with habitat type as the predictor and town as a random factor. We also included SVL as a covariate. Once the injury rate model had been run, we confirmed that a zero-inflation model was appropriate using the 'check zeroinflation' function of the performance package in R (Lüdecke et al. 2021). Dispersion of the model was assessed using 'check_dispersion' in the same performance package to confirm that a Poisson distribution was appropriate. All regression analyses were run separately for each sex.

To assess if chameleons from either urban or natural populations bite harder, the bite force of *B. damaranum* from Knysna (females $n = 26$; males $n = 77$) was measured using a Kistler piezoelectric force transducer (type 9203; 500 N;

Table 1 Results from the generalized linear mixed models (GLMM) comparing morphological traits for natural and urban populations of *Bradypodion damaranum* from two towns (George and Knysna) for (a) females and (b) males. F values for homogeneity of variance (variance), chi-square for homoscedasticity (homosc.), and F values for equality of slopes (slope) and the t-values for the population comparisons are given. Sample sizes for each population are in the top rows. For some traits, data were log transformed as indicated (lg). Estimated marginal means in mm (EM) are provided (Urban – U, Natural – *N*), and are back transformed for logged data. Level of significance is denoted as *** ≤0.001, ** ≤0.01, * ≤0.05 (significant values in bold), ns- not significant (degrees of freedom for GLMM are total sample size minus 2) EM values bolded to indicate the population with the largest trait value. Traits evaluated were: head width (HW), head height (HH), bottom of parietal to tip of casque spur (CH), quadrate to the bottom of the casque spur (PH), length of the casque spur (CS), length (GL) and area of the largest gular scale (GA).

a)	**Females**									
	Trait	Variance	Homosc.	Slope	t (sig)	EM (U)	EM (N)	r^2 (m)	r^2 (c)	r^2 (c-m)
						n = 142	*n* = 141			
	lgHW	10.380 (**)	0.29 (ns)	-0.45 (ns)	0.294 (ns)	8.95	8.93	0.795	0.810	0.015
	lgHH	12.93 (***)	1.49 (ns)	0.47 (ns)	0.004 (ns)	8.85	8.85	0.828	0.828	0.000
	CH	2.18 (ns)	1.14 (ns)	-1.14 (ns)	**-3.493 (***)**	8.30	**8.62**	0.656	0.664	0.008
						n = 36	*n* = 28			
	lgPH	5.470 (*)	0.690 (ns)	1.212 (ns)	0.155 (ns)	4.16	4.15	0.684	0.701	0.017
	lgCS	0.000 (ns)	0.043 (ns)	-0.361 (ns)	**-1.21 ***	4.06	**4.31**	0.264	0.536	0.272
	GL	8.356 (**)	0.396 (ns)	1.469 (ns)	**-3.05 ****	1.82	**1.99**	0.557	0.585	0.028
	lgGA	4.198 (*)	0.001 (ns)	1.725 (ns)	**-3.99 *****	3.4	**4.43**	0.538	0.538	0.000
b)	**MALES**									
	Trait	Variance	Homosc.	Slope	t (sig)	EM (U)	EM (N)	r^2 (m)	r^2 (c)	r^2 (c-m)
						n = 175	*n* = 192			
	lgHW	1.616 (ns)	0.568 (ns)	-2.101 (*)	**3.42 (***)**	**10.47**	10.23	0.86	0.88	0.02
	HH	6.161 (*)	0.080 (ns)	-0.449 (ns)	**4.45 (***)**	**10.19**	9.94	0.86	0.87	0.01
	CH	2.089 (ns)	2.139 (ns)	-1.757 (ns)	-1.41 (ns)	9.95	10.07	0.78	0.78	0
						n = 45	*n* = 49			
	lgPH	0.900 (ns)	4.089 (*)	-2.015 (*)	1.75 ns	5.33	5.16	0.75	0.77	0.02
	CS	0.234 (ns)	1.687 (ns)	-1.589 (ns)	**-3.58 *****	4.63	**4.98**	0.46	0.47	0.01
	lgGL	2.139 (ns)	0.914 (ns)	-0.817 (ns)	**-3.59 *****	2.11	**2.31**	0.50	0.51	0.01
	lgGA	1.519 (ns)	0.122 (ns)	0.258 (ns)	**-4.57 *****	4.81	**5.94**	0.51	0.51	0

Kistler Inc., Winterthur, Switzerland) set in a custom-built holder with two parallel plates on which the chameleons were induced to bite (following Herrel et al. 1999). The distance between the bite plates was varied relative to head size and gape of each chameleon, e.g., the plates being brought closer together for smaller chameleons. The force transducer was attached to a handheld Kistler charge amplifier which recorded forces in Newtons (N). The bite force measurements were repeated five times for each chameleon, and the maximum force recorded was used in the analyses. Data were analysed in SPSS v26 using an analysis of covariance (ANCOVA) separately for each sex using different covariates (SVL, HW, HH, CH, PH) to examine whether body size or head shape may influence bite force. Bite force measurement was conducted only at Knysna due to logistical constraints.

Results

Tree canopy density measurements from within 300 m buffers of our chameleon localities were taken for 125 random points, with 75 in George (natural = 40, urban = 35) and 50 in Knysna (natural = 20, urban = 30). For both towns, the natural habitats had significantly higher tree canopy density than urban habitats (George: U = 5.50, $p < 0.001$; Knysna: U = 1.00, $p < 0.001$; Fig. 3). The polygons created to collect tree canopy density estimates for the broader natural and urban sites varied in size for George (natural = 10.82 km², urban = 76.45 km²) and Knysna (natural = 42.68 km², urban = 49.43 km²). The random points accounted for size differences between the areas with five in George natural, 32 in George Urban, 20 in Knysna natural and 21 in Knysna urban. For both towns the natural sites had significantly higher tree canopy density than urban areas (George: U = < 0.001, $p < 0.001$; Knysna: U = 14.00, $p < 0.001$).

For the morphological comparisons, chameleons from the urban habitat had significantly smaller ornamentation traits (casque height, casque spur, gular length and gular area) than the natural populations, for both sexes (Table 1). In contrast, the urban populations of males had significantly larger head width and height (Table 1). Comparison of the marginal and conditional r^2 values for these traits shows that the variance can be attributed to population (i.e., urban/natural). The inclusion of town in the model did not capture additional variance, suggesting that sampling site/town has little to no effect, and that the trait differences are due to habitat (i.e., natural and urban populations). The exception to this was for the casque spur in females, whereby approximately half the variance was due to town/site. To explore this further, a *post hoc* general linear model (SVL covariate) was run separately for each town with population as the fixed factor. This showed that the females from the natural population in Knysna has significantly larger casques spurs than the urban population ($F_{(1,65)} = 7.74$, $p < 0.01$; Estimated marginal means: Urban 4.45 mm, Natural 7.74 mm). The estimated marginal mean show that the George females are also larger for this trait (3.67 mm Urban, 3.78 mm Natural), but the difference was not significant ($F = 0.63_{(1,66)}$, $p =$ ns).

Binary logistic regressions showed a significant difference in injury status (i.e., injured/not injured) between urban or natural populations when using town as a random factor and SVL as a covariate (Table 2), with males from urban habitats more likely to be injured (88.1% injured) compared to those from natural habitats (72.5% injured). There was no significant difference for injury status in females. The Poisson regressions showed that *B. damaranum* from urban populations did have significantly more injuries than those from natural habitats for both sexes when using town as a random factor and SVL as a covariate (Table 2; Fig. 4). The dataset met model assumptions of being zero-inflated and not over-dispersed.

When casque height (CH) or parietal height (PH) were included as covariates, bite forces were significantly different (CH – females: $F_{(1,16)} = 7.09$, $p \leq 0.05$; males: $F_{(1,57)} = 6.52$, $p \leq 0.01$ and PH – females: $F_{(1,17)} = 8.40$, $p \leq 0.01$; males: $F_{(1,57)} = 10.57$, $p \leq 0.01$), with chameleons from urban populations biting harder than those from natural populations for both sexes (Fig. 5). Bite forces were not significantly different between the Knysna natural and urban populations with SVL as the covariate (females: $F_{(1,25)} = 2.05$, $p =$ ns; males: $F_{(1,76)} = 0.13$, $p =$ ns), or with head width as the covariate (females: $F_{(1,17)} = 0.64$, $p =$ ns; males: $F_{(1,57)} = 0.81$, $p =$ ns).

Discussion

Urban populations of *Bradypodion damaranum* had significantly more injuries compared to populations from natural areas, with males also being more likely to be injured. As expected, the urban populations had less developed ornamentation for both sexes, and the incorporation of town as a random factor showed that the variance was not due to site/town and that urban populations from both towns have converged on the same phenotype. Additionally, the urban populations had wider and higher heads, and higher bite force when accounting for casque height, compared to those from the natural populations. Finally, tree cover was significantly less dense in the urban habitats than in the natural habitats, and thus shelter might be a scarce resource for urban chameleons. Therefore, our hypothesis that lack of cover/shelter and with a trade-off for more frequent intraspecific (or possibly also intraspecific) aggressive encounters, as measured by injury, resulting in selection for

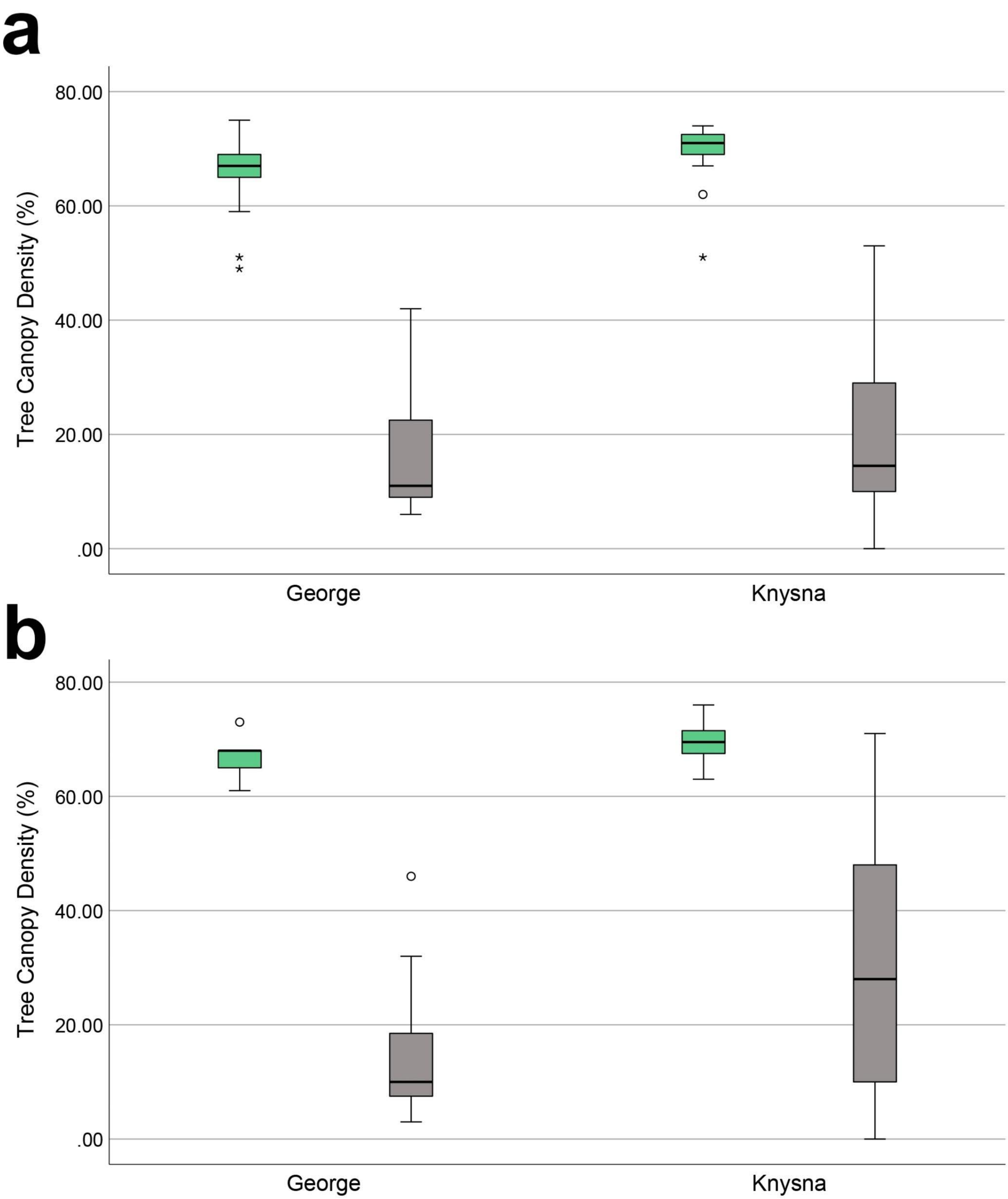

Fig. 3 Tree canopy density values from random points in natural (green) and urban (grey) habitats using **(a)** 300 m buffers of our chameleon localities and **(b)** polygons across each study area for *B. damaranum*

Table 2 Results from regression models for natural and urban populations of *Bradypodion damaranum* from two towns (George and Knysna), with sample sizes given in parentheses (urban/natural). Injured (i.e., injured/not injured) models used binary logistic regression while number of injuries models used Poisson regression. Snout-vent-length (SVL) was used as a covariate in all regressions and town was used as a random factor. Significant *p*-values are shown in bold

Model	Sex	Factor	Estimate	Std Error	z-value	*p*-value
Injured	Females (52/49)	Population	0.603	0.585	1.031	0.390
		SVL	0.045	0.033	1.381	0.167
	Males (84/91)	Population	1.060	0.435	2.440	**0.015**
		SVL	0.018	0.019	0.902	0.367
Number of Injuries	Females (52/49)	Population	0.560	0.174	3.227	**0.001**
		SVL	0.007	0.008	0.840	0.401
	Males (84/91)	Population	0.324	0.118	2.734	**0.006**
		SVL	0.012	0.005	2.330	**0.020**

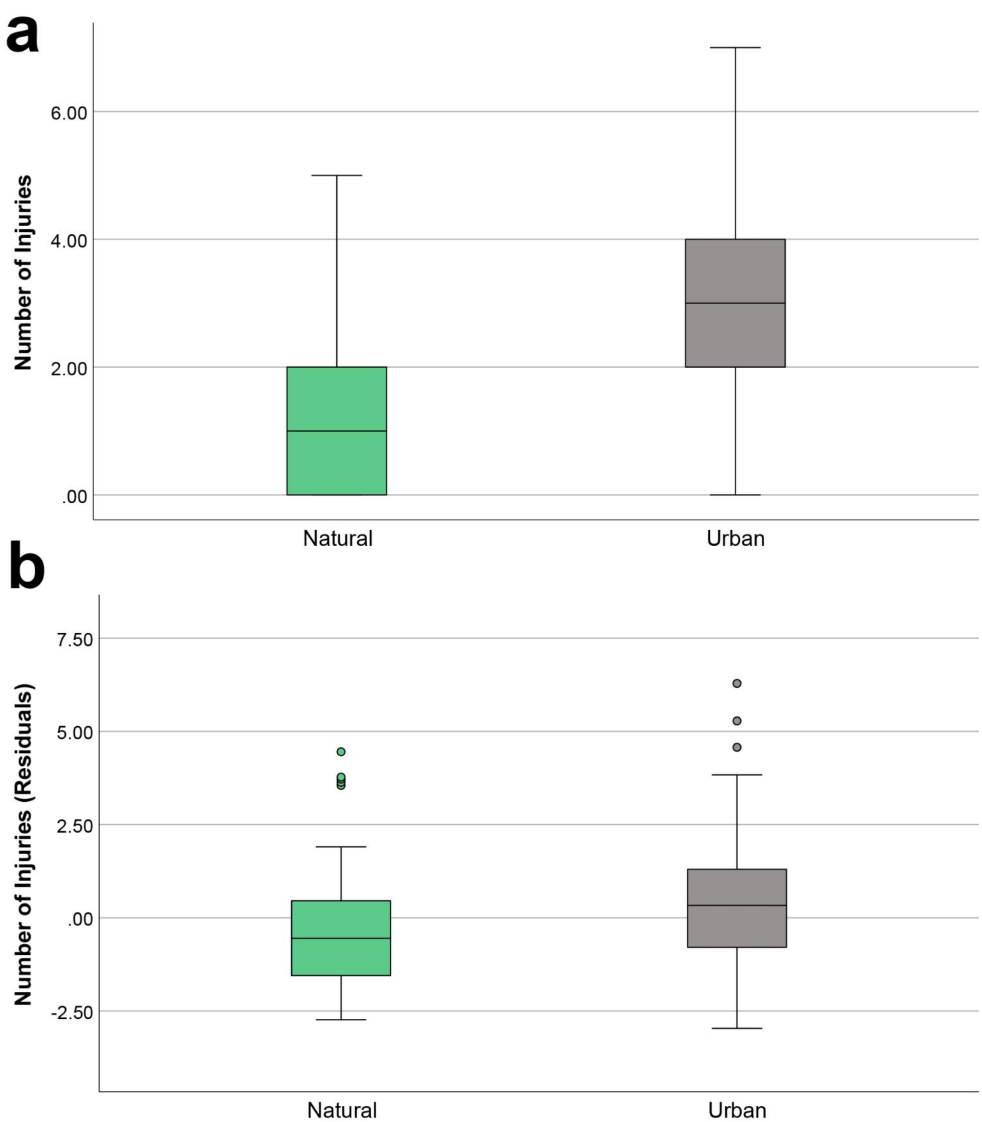

Fig. 4 Box and whisker plots for number of injuries between natural (green) and urban (grey) populations of females **(a)** and males **(b)** for *Bradypodion damaranum*. Outlier values (outside the 75th and 25th percentiles) retained in the analyses are shown by circles. Unstandardised residuals of a regression of number of injuries against snout-vent-length was used for males, as SVL was a significant covariate for this variable when performing a Poisson regression analysis

reduced ornamentation in urban areas is supported. Given that 'town' did not show an effect for any of the analyses, chance differences between towns is a less tenable interpretation for the population differences. Other alternatives have yet to be explored in a hypothesis testing framework, including increased predation that could impact the proportion of scared individuals in the population. Alternatively, intraspecific competition and aggression could impact overall and localised chameleon population density and/or demand for scarce resources. Dietary differences between

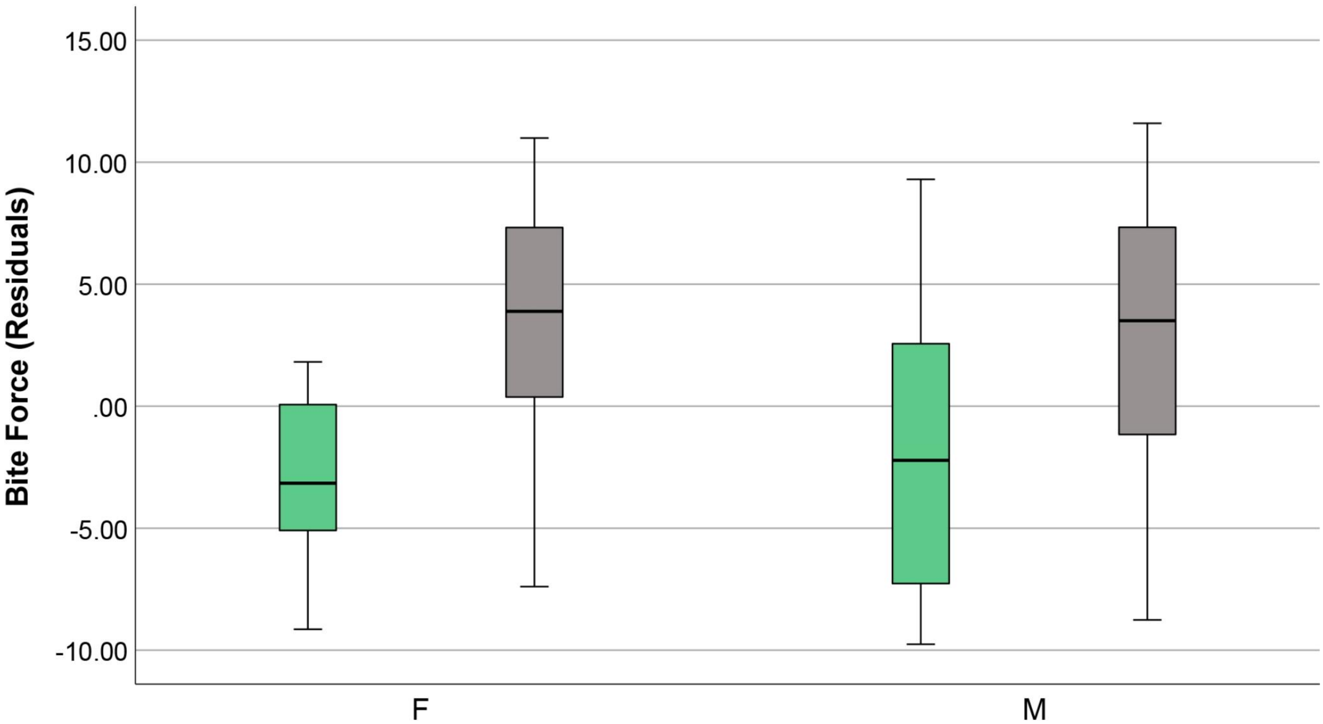

Fig. 5 Residuals of bite force (covariate – casque height; N – force in Newtons) for *Bradypodion damaranum* in Knysna from natural (green) and urban (grey) habitats with females (left) and males (right)

urban and natural populations could also potentially impact bite force (Dollion et al. 2017). These hypotheses provide a rich environment for future research.

Ornamentation in chameleons is known to be important for communication during intraspecific encounters to indicate fighting ability and for mating displays to females, with large casques in males correlating with winning contests through signalling and thus avoiding a final escalation to a physical encounter (Stuart-Fox and Whiting 2005; Stuart-Fox et al. 2006). The urban populations of *B. damaranum* showed reduced head ornamentation and this could impact their ability to avoid aggressive encounters through display, potentially resulting in more frequent fighting. While it is not known if ornamentation size for lizards from urban environments influence fighting frequency, some species of birds show increased aggression with reduced ornamentation in urban habitats (e.g., Beck et al. 2018). Similarly, observations of *Bradypodion* suggest that open canopy ecomorphs have reduced ornamentation but probably more scarring than those from closed canopy (e.g., Measey et al. 2011), implying that escalation to aggressive encounters may occur more often in open habitats due to diminished capacity to signal conspecifics. While it is not currently possible to tease apart the source of injury (conspecific or predator), we propose that the higher number of injuries in urban dwarf chameleons could be due to increased number of aggressive encounters in the more open, urban habitat (e.g., Pattishall and Cundall 2009; Roe et al. 2011, Baxter-Gilbert and Whiting 2019) with scarcer sheltering sites. This thought-provoking notion could be advanced through targeted behavioural and observational studies of *Bradypodion*.

Assuming that alterations in the frequency of aggressive intraspecific encounters in urban habitats drives the adaptation for some traits, this could provide a fitness advantage to increase their performance during combat. Increased bite force has been attributed to a greater chance of success in contests for several lizard species (e.g., Herrel et al. 2001; Vanhooydonck et al. 2005; McLean and Stuart-Fox 2015), and although this has not been explicitly tested for chameleons, it is likely to be the case within the *Bradypodion* genus, as combat between individuals sometimes escalates to biting (Stuart-Fox et al. 2006; Stuart-Fox and Whiting 2005; Tolley and Burger 2007), and our data shows clear bite marks on the bodies of many individual chameleons. Bite force differences between populations were only observed when accounting for differences in casque height (i.e., ornamentation), not body or head size, with urban populations biting harder for their casque size than natural populations. Therefore, despite the general reduction in head ornamentation for urban populations, these chameleons bite harder than those with similarly sized casques from the natural populations. Thus, we reasoned that the reduced ornamentation would not be an honest signal for bite force and fighting performance, possibly an advantage in a landscape that is thought to drive more frequent aggressive encounters.

Although aggressive encounters likely have a bearing on bite force, we note that other factors could drive the differences observed. That is, bite force within the *Bradypodion* genus has also been linked to prey hardness, with species consuming harder prey also having higher bite forces (Dollion et al. 2017), although this does not appear to be universal across all species (e.g., da Silva et al. 2016). Invertebrates are the primary prey of *Bradypodion* species (Measey et al. 2011; Carne and Measey 2013; da Silva et al. 2016; Dollion et al. 2017) and urbanisation is known to reduce invertebrate species richness (Fenoglio et al. 2021), although the effects on arthropod abundance are varied depending on species and urban habitat (e.g., McIntyre et al. 2001; Chatelain et al. 2023). Whether urbanisation has a major influence on diet composition and therefore prey hardness, is unclear but could be assessed with detailed dietary studies allowing for a fuller assessment of the most important factors that contribute to differences in bite force between populations.

Conclusion

Overall, our study revealed that *Bradypodion damaranum* from urban populations have more injuries than those from natural habitats. There is also a concomitant reduction in head ornamentation, although urban populations have wider/higher heads and higher bite force for their ornamentation size. These differences might be driven by the less dense habitat in urban areas making shelter a scare resource. We suggest that this has led to selection pressures influencing the phenotype of chameleons to reduce conspicuousness, but with a trade-off for diminished interspecific communication resulting in more frequent interspecific interactions leading to injuries. Trait differences related to behaviour, communication and morphology may have their basis within standing genetic variation (e.g., phenotypic plasticity), or may be the result of changes in genetic architecture (e.g., adaptation). It is worth noting, however, the lack of evidence of developmental phenotypic plasticity in other *Bradypodion* (Miller and Alexander 2009). Certainly, there are many outstanding questions and other avenues to explore, which could be addressed by incorporating additional sites and other species of *Bradypodion* as well as other lines of inquiry. Our conclusions could be strengthened, or become more nuanced, by including an assessment of chameleon and predator abundance, behavioural differences, microhabitat structure, dietary differences, additional reciprocal common garden experiments, as well as genome-wide association studies to link adaptive traits with specific mutations. The present study can be viewed as the opening salvo to a fuller examination as to whether urban *Bradypodion* populations under similar environmental pressures show convergence of traits, such as ornamentation and head size, and whether such convergence might arise through standing genetic variation or if similar solutions to a common problem are underlain by new genetic architecture.

Acknowledgements We would like to thank Matthew Adair, Jessica da Silva, Azraa Ebrahim, Juan-Jacques Forgus, Devon Main, Jody Taft, and Bettine van Vuuren for assistance with field work and logistics, and Colleen Seymour for assistance with statical approaches and R coding. Research was funded by the National Research Foundation of South Africa, Dimensions of Biodiversity Program (Grant no. 136381). Permission to carry out this work was granted by CapeNature (CN44-59-11927) and South African National Parks under a research agreement. Ethical clearance was granted by the University of Witwatersrand (2019/10/56/B) and the University of Johannesburg (2019/10/10).

Author Contributions Funding for this study was generated by Krystal A. Tolley and Graham J. Alexander. All authors contributed to the study conception and design, and carried out field work for data collection. Melissa A. Petford and Krystal A. Tolley carried out analyses and wrote the initial drafts of the manuscript, and all authors contributed to the text, and edited all versions of the manuscript. All authors read and approved the final manuscript.

Funding Research was funded by the National Research Foundation of South Africa, Dimensions of Biodiversity Program (Grant no. 136381).

Data Availability Data are available from the corresponding author upon reasonable request.

Declarations

Ethics approval Ethical clearance was granted by the University of Witwatersrand (2019/10/56/B) and the University of Johannesburg (2019/10/10).

Competing interests The authors declare no competing interests.

References

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545

Anderson L, Burgin S (2008) Patterns of bird predation on reptiles in small woodland remnant edges in peri-urban north-western Sydney, Australia. Landsc Ecol 23:1039–1047. https://doi.org/10.1007/s10980-008-9252-5

Bamford M, Calver MC (2012) Cat predation and suburban lizards: a 22 year study at a suburban Australian property. The Open Conserv Biol Jl 6:25–29. https://doi.org/10.2174/1874839201206010025

Banks SC, Piggott MP, Stow AJ, Taylor AC (2007) Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. Can J Zool 85:1065–1079. https://doi.org/10.1139/Z07-094

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Baxter-Gilbert JH, Whiting MJ (2019) Street fighters: bite force, injury rates, and density of urban Australian water dragons (*Intellagama lesueurii*). Austral Ecol 44:255–264. https://doi.org/10.1111/aec.12670

Baxter-Gilbert J, Riley JL, Frère CH, Whiting MJ (2020) Shrinking into the big city: influence of genetic and environmental factors on urban dragon lizard morphology and performance capacity. Urban Ecosyst 24:661–674. https://doi.org/10.1007/s11252-020-01065-4

Beck ML, Davies S, Sewall KB (2018) Urbanization alters the relationship between coloration and territorial aggression, but not hormones, in song sparrows. Anim Behav 142:119–128. https://doi.org/10.1016/j.anbehav.2018.06.012

Bomblies K, Peichel CL (2022) Genetics of adaptation. Proc Natl Acad Sci USA 119(3): e2122152119

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R J 9:378–400. https://doi.org/10.3929/ethz-b-000240890

Carne L, Measey GJ (2013) Chameleons on the cruise: seasonal differences in prey choice of two dwarf chameleons. Herp J 23(4):221–227

Chatelain M, Rüdisser J, Traugott M (2023) Urban-driven decrease in arthropod richness and diversity associated with group-specific changes in arthropod abundance. Front Ecol Evol 11. https://doi.org/10.3389/fevo.2023.980387

Core Team R (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

da Silva JM, Carne L, Measey GJ, Herrel A, Tolley KA (2016) The relationship between cranial morphology, bite performance, diet and habitat in a radiation of dwarf chameleon (*Bradypodion*). Biol J Linn Soc 119:52–67. https://doi.org/10.1111/bij.12819

Dollion AY, Measey GJ, Cornette R, Carne L, Tolley KA, da Silva JM, Boistel R, Fabre AC, Herrel A (2017) Does diet drive the evolution of head shape and bite force in chameleons of the genus. Bradypodion? Funct Ecol 31:671–684. https://doi.org/10.1111/1365-2435.12750

Ellis EC (2011) Anthropogenic transformation of the terrestrial biosphere Philos Trans A Math. Phys Eng Sci 369:1010–1035. https://doi.org/10.1098/rsta.2010.0331

Fenoglio MS, Calviño A, González E, Salvo A, Videla M (2021) Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. Ecol Entomol 46:757–771. https://doi.org/10.1111/een.13041

Fox J, Weisberg S (2018) An R Companion to Applied Regression, Third Edition. Los Angeles: Sage Publications

French SS, Webb AC, Hudson SB, Virgin EE (2018) Town and country reptiles: a review of reptilian responses to urbanization. Integr Comp Biol 58:948–966. https://doi.org/10.1093/icb/icy052

Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Func Ecol 21(3):394–407. https://doi.org/10.1111/j.1365-2435.2007.01283.x

Hammond TT, Ortiz-Jimenez CA, Smith JE (2020) Anthropogenic change alters ecological relationships via interactive changes in stress physiology and behavior within and among organisms. Integr Comp Biol 60:57–69. https://doi.org/10.1093/icb/icaa001

Hendry AP, Farrugia TJ, Kinnison MT (2008) Human influences on rates of phenotypic change in wild animal populations. Mol Ecol 17:20–29. https://doi.org/10.1111/j.1365-294X.2007.03428.x

Herrel A, Spithoven L, Van Damme R, De Vree F (1999) Sexual dimorphism of head size in Gallotia galloti: testing the niche divergence hypothesis by functional analyses. Funct Ecol 13:289–297. https://doi.org/10.1046/j.1365-2435.1999.00305.x

Herrel A, De Grauw ED, Lemos-Espinal JA (2001) Head shape and bite performance in xenosaurid lizards. J Exp Zool 290:101–107. https://doi.org/10.1002/jez.1039

Hopkins KP, Tolley KA (2011) Morphological variation in the Cape dwarf chameleon (*Bradypodion pumilum*) as a consequence of spatially explicit habitat structure differences. Biol J Linn Soc 102:878–888. https://doi.org/10.1111/j.1095-8312.2011.01618.x

Irschick DJ, Meyers JJ (2007) An analysis of the relative roles of plasticity and natural selection in the morphology and performance of a lizard (*Urosaurus ornatus*). Oecologia 153:489–499. https://doi.org/10.1007/s00442-007-0726-y

Koenig J, Shine R, Shea G (2002) The dangers of life in the city: patterns of activity, injury and mortality in suburban lizards (*Tiliqua scincoides*). J Herpetol 36:62–68. https://doi.org/10.1670/0022-1511(2002)036[0062:TDOLIT]2.0.CO;2

Kolbe JJ, Losos JB (2005) Hind-limb length plasticity in Anolis carolinensis. J Herpetol 39:674–678. https://doi.org/10.1670/87-05N.1

Lacy KE, Martins EP (2003) The effect of anthropogenic habitat usage on the social behaviour of a vulnerable species, *Cyclura nubila*. Anim Conserv 6:3–9. https://doi.org/10.1017/S1367943003003020

Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D (2021) Performance: an R package for assessment, comparison and testing of statistical models. J Open Source Softw 6. https://doi.org/10.21105/joss.03139

Magidi J, Ahmed F (2022) Monitoring vegetation phenology using MODIS NDVI 250m in the City of Tshwane, South Africa. S Afr J Geomat 11:176–189. https://doi.org/10.4314/sajg.v11i2.1

Marnocha E, Pollinger J, Smith TB (2011) Human-induced morphological shifts in an island lizard. Evol Appl 4:388–396. https://doi.org/10.1111/j.1752-4571.2010.00170.x

McDonnell MJ, Hahs AK (2015) Adaptation and adaptedness of organisms to urban environments. Annu Rev Ecol Evol Syst 46:261–280. https://doi.org/10.1146/annurev-ecolsys-112414-054258

McIntyre NE, Rango J, Fagan WF, Faeth SH (2001) Ground arthropod community structure in a heterogeneous urban environment. Landsc Urban Plan 52:257–274. https://doi.org/10.1016/S0169-2046(00)00122-5

McLean CA, Stuart-Fox D (2015) Rival assessment and comparison of morphological and performance-based predictors of fighting ability in Lake Eyre dragon lizards, *Ctenophorus maculosus*. Behav Ecol Sociobiol 69:523–531. https://doi.org/10.1007/s00265-014-1863-z

Measey GJ, Rebelo AD, Herrel A, Vanhooydonck B, Tolley KA (2011) Diet, morphology and performance in two chameleon morphs: do harder bites equate with harder prey? J Zool 285:247–255. https://doi.org/10.1111/j.1469-7998.2011.00861.x

Miller AK, Alexander GJ (2009) Do dwarf chameleons (Bradypodion) show developmental plasticity? Afr Zool 44:45–54. https://doi.org/10.3377/004.044.0105

Morris RJ (2010) Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. Philos Trans R Soc Lond B Biol Sci 365:3709–3718. https://doi.org/10.1098/rstb.2010.0273

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4(2):133–142

Palamuleni LG, Turyahikayo AK (2015) Vegetation density assessment in the Upper Molopo River Catchment, South Africa. J Food Agric Environ 13:190–196

Pattishall A, Cundall D (2009) Habitat use by synurbic watersnakes (*Nerodia sipedon*). Herpetologica 65:183–198. https://doi.org/10.1655/08-038R2.1

QGIS.org (2022) QGIS Geographic Information System. QGIS Association. http://www.qgis.org

Rebelo AD, Altwegg R, Katz EM, Tolley KA (2022) Out on a limb: female chameleons (*Bradypodion pumilum*) position themselves to minimise detection, whereas males maximise mating opportunity. Afr J Herpetol. https://doi.org/10.1080/21564574.2021.1998233. 71:39–50

Roe JH, Rees M, Georges A (2011) Suburbs: dangers or drought refugia for freshwater turtle populations? J Wildl Manag 75:1544–1552. https://doi.org/10.1002/jwmg.219

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. https://doi.org/10.1038/nmeth.2089

Schoener TW (1979) Inferring the properties of predation and other injury-producing agents from injury frequencies. Ecology 60:1110–1115. https://doi.org/10.2307/1936958

Sexton JO, Song X-P, Feng M, Noojipady P, Anand A, Huang C, Kim D-H, Collins KM, Channan S, DiMiceli C, Townshend JRG (2013) Global, 30-m resolution continuous fields of tree cover: landsat-based rescaling of MODIS Vegetation continuous fields with lidar-based estimates of error. Int J Digit Earth 6:427–448. https://doi.org/10.1080/17538947.2013.786146

Seymour CL, Simmons RE, Morling F, George ST, Peters K, O'Riain MJ (2020) Caught on camera: the impacts of urban domestic cats on wild prey in an African city and neighbouring protected areas. Glob Ecol Conserv 23:e01198. https://doi.org/10.1016/j.gecco.2020.e01198

Stickler MM, Shackleton CM (2015) Local wood demand, land cover change and the state of Albany thicket on an urban commonage in the Eastern Cape, South Africa. Environ Manage 55:411–422. https://doi.org/10.1007/s00267-014-0396-6

Stotz GC, Salgado-Luarte C, Escobedo VM, Valladares F, Gianoli E (2021) Global trends in phenotypic plasticity of plants. Ecol Lett 24(10):2267–2281. https://doi.org/10.1111/ele.13827

Stuart-Fox D (2006) Testing game theory models: fighting ability and decision rules in chameleon contests. Proc R Soc B Biol Sci 273(1593):1555–1561. https://doi.org/10.1098/rspb.2006.3468

Stuart-Fox D, Moussalli A (2008) Selection for social signalling drives the evolution of chameleon colour change. PLoS Biol 6:e25. https://doi.org/10.1371/journal.pbio.0060025

Stuart-Fox DM, Whiting MJ (2005) Male dwarf chameleons assess risk of courting large, aggressive females. Biol Lett 1:231–234. https://doi.org/10.1098/rsbl.2005.0299

Stuart-Fox DM, Firth D, Moussalli A, Whiting MJ (2006) Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. Anim Behav 71:1263–1271. https://doi.org/10.1016/j.anbehav.2005.07.028

Stuart-Fox D, Moussalli A, Whiting MJ (2007) Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. Am Nat 170:916930. https://doi.org/10.1086/522835

Stuart-Fox D, Moussalli A, Whiting MJ (2008) Predator-specific camouflage in chameleons. Biol Lett 4(4):326–329. https://doi.org/10.1098/rsbl.2008.0173

Tolley KA, Burger M (2007) Chameleons of Southern Africa. Struik-Penguin Random House, Cape Town

Tolley KA, Measey GJ (2007) Chameleons and vineyards in the Western Cape of South Africa: is automated grape harvesting a threat to the Cape dwarf chameleon (*Bradypodion pumilum*)? Afr J Herpetol 56:85–89. https://hdl.handle.net/10520/EJC19231

Tyler RK, Winchell KM, Revell LJ (2016) Tails of the city: caudal autotomy in the tropical lizard, *Anolis cristatellus*, in urban and natural areas of Puerto Rico. J Herpetol 50:435–441. https://doi.org/10.1670/15-039

Urban MC, Richardson JL, Freidenfelds NA (2014) Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. Evol Appl 7:88–103. https://doi.org/10.1111/eva.12114

Vanhooydonck B, Herrel AY, Van Damme R, Irschick DJ (2005) Does dewlap size predict male bite performance in Jamaican Anolis lizards? Funct Ecol 19:38–42. https://doi.org/10.1111/j.0269-8463.2005.00940.x

West-Eberhard MJ (1989) Phenotypic plasticity and the origins of diversity. Annu Rev Ecol Syst 20(1):249–278

Western Cape Government (2021a) Socio-Economic Profile: George Municipality. Western Cape Government, South Africa

Western Cape Government (2021b) Socio-Economic Profile: Knysna Municipality. Western Cape Government, South Africa

Winchell KM, Carlen EJ, Puente-Rolón AR, Revell LJ (2018) Divergent habitat use of two urban lizard species. Ecol Evol 8:25–35. https://doi.org/10.1002/ece3.3600