Received: 19 November 2019 | Revised: 23 January 2020 | Accepted: 25 January 2020
DOI: 10.1002/jez.2353

RESEARCH PAPER

JEZ-A ECOLOGICAL AND INTEGRATIVE PHYSIOLOGY WILEY

Reproductive phenotype predicts adult bite-force performance in sex-reversed dragons (*Pogona vitticeps*)

Marc E. H. Jones[1,2,3] | Jennifer C. A. Pistevos[2,4] | Natalie Cooper[5] | A. Kristopher Lappin[6] | Arthur Georges[7] | Mark N. Hutchinson[2,3] | Clare E. Holleley[7,8]

[1]Department of Cell and Developmental Biology, University College London, London, UK

[2]School of Biological Sciences, University of Adelaide, North Terrace, Adelaide, South Australia, Australia

[3]Vertebrates, South Australian Museum, North Terrace, Adelaide, South Australia, Australia

[4]Centre de Recherches Insulaires et Observatoire de l'Environnement CRIOBE - USR 3278: PSL Université Paris: EPHE-CNRS-UPVD, Laboratoire d'Excellence "CORAIL", Papetoai, Moorea, Polynésie Française

[5]Vertebrates, Department of Life Sciences, Natural History Museum, London, UK

[6]Department of Biological Sciences, Pomona, California

[7]Institute for Applied Ecology, Canberra, Australian Capital Territory, Australia

[8]Australian National Wildlife Collection, National Research Collections Australia CSIRO, Canberra, Australian Capital Territory, Australia

Correspondence
Marc E. H. Jones, Department of Cell and Developmental Biology, University College London, Gower Street, Main Anatomy Building, London, WC1E 6BT, UK.
Email: marc.jones@ucl.ac.uk

Funding information
Australian Research Council,
Grant/Award Numbers: DE130101567, DP110104377, DP170101147

Abstract

Sex-related differences in morphology and behavior are well documented, but the relative contributions of genes and environment to these traits are less well understood. Species that undergo sex reversal, such as the central bearded dragon (*Pogona vitticeps*), offer an opportunity to better understand sexually dimorphic traits because sexual phenotypes can exist on different chromosomal backgrounds. Reproductively female dragons with a discordant sex chromosome complement (sex reversed), at least as juveniles, exhibit traits in common with males (e.g., longer tails and greater boldness). However, the impact of sex reversal on sexually dimorphic traits in adult dragons is unknown. Here, we investigate the effect of sex reversal on bite-force performance, which may be important in resource acquisition (e.g., mates and/or food). We measured body size, head size, and bite force of the three sexual phenotypes in a colony of captive animals. Among adults, we found that males (ZZm) bite more forcefully than either chromosomally concordant females (ZWf) or sex-reversed females (ZZf), and this difference is associated with having relatively larger head dimensions. Therefore, adult sex-reversed females, despite apparently exhibiting male traits as juveniles, do not develop the larger head and enhanced bite force of adult male bearded dragons. This pattern is further illustrated in the full sample by a lack of positive allometry of bite force in sex-reversed females that is observed in males. The results reveal a close association between reproductive phenotype and bite force performance, regardless of sex chromosome complement.

KEYWORDS
Agamidae, bite force, lizard, performance, *Pogona vitticeps*, scaling, sex reversal, sexual dimorphism

1 | INTRODUCTION

Sexual differences, most notably of secondary sexual characteristics, are a key aspect of within-species variation impacting on anatomy, behavior, physiology, and life history (Chen, Stuart-Fox, Hugall, & Symonds, 2012; Deepak et al. 2016; Hoops et al., 2017; Littleford-Colquhoun et al., 2019; McLean, Chan, Dickerson, Moussalli, & Stuart-Fox, 2016; Stauber & Booth, 2003; Thompson & Withers, 2005; Wotherspoon & Burgin, 2011). Sex-determination mechanisms in reptiles are incredibly diverse, exhibiting a rich evolutionary history of repeated independent transitions between sex-determination modes (Alam, Sarre, Gleeson, Georges, &

Ezaz, 2018; Gamble et al., 2015; Pokorna & Kratochvil, 2016; Sarre, Ezaz, & Georges, 2011). The accumulating evidence of species that employ both primary cues (genes and environment) to determine sex (transitional systems; Hill, Burridge, Ezaz, & Wapstra, 2018; Holleley et al., 2015; Holleley, Sarre, O'Meally, & Georges, 2016; Radder, Quinn, Georges, Sarre, & Shine, 2008; Shine, Elphick, & Donnellan, 2002), points to the existence of a continuum of states from complete genetic control via sex chromosomes to complete dependence on environmental influence over sex (Sarre, Georges, & Quinn, 2004). The potential for naturally occurring sex reversal (Baroiller & D'Cotta, 2016; Ginot, Claude, Perez, & Veyrunes, 2017; Holleley et al., 2015; Jiménez, Burgos, Caballero, & De La Guardia, 1988) is the hallmark of transitional systems. A small number of studies of terrestrial vertebrates indicate that the de-coupling of chromosomal and phenotypic sex, via sex reversal, can result in individuals bearing a mixture of male-like, female-like, or novel traits (Deveson et al., 2017; Ginot et al., 2017; Li, Holleley, Elphick, Georges, & Shine, 2016). Such differences in phenotype may be associated with significant differences in fitness, and thus be informative for predicting the evolutionary stability of the sex-determination system (Holleley et al., 2015; Schwanz, Georges, Holleley, & Sarre, 2020). Therefore, to interpret the evolution of sex determination and associated life histories, we need to better understand how sexually dimorphic traits are manifested in sex-reversed individuals with discordant genotypic and phenotypic sex.

The central bearded dragon (*Pogona vitticeps*) provides an excellent model organism for studying sexually dimorphic phenotypic traits. The species is sexually dimorphic (Badham, 1976; Witten 1994), with a transitional mode of sex determination, exhibiting simultaneous genetic and environmental influence over sex (Ezaz et al., 2005; Quinn et al., 2007). Heterogametic individuals (ZW) are always female (ZWf). Homogametic individuals (ZZ) develop as males at moderate egg incubation temperatures (22–32°C; ZZm), but at higher incubation temperatures (≥32°C) a proportion of chromosomal males will develop into functional, reproductive females (ZZf; Holleley et al., 2015; Quinn et al., 2007). This temperature-induced sex reversal is known to occur in the wild and may be increasing in frequency as a result of climate change (Holleley et al., 2015).

The performance capacities of sex-reversed females are of great interest, because they may afford a positive fitness advantage that could further increase the proportion of ZZf individuals in the wild and accelerate the progressive loss of the female-specific W sex chromosome. Under such (directional) selection, the W chromosome could be driven to local extinction and thus the population would transition to temperature-dependent sex determination (Holleley et al., 2015). As juveniles, the sex-reversed female phenotype (ZZf) exhibits some male-like traits relative to the chromosomally concordant female phenotype (ZWf), such as a relatively long tail, greater boldness, higher activity levels, and warmer thermoregulatory preference (Li et al., 2016). As adults, sex-reversed ZZf individuals lay more eggs than their ZWf counterparts (Holleley et al., 2015). However, individuals of the two female groups can only be identified with certainty using genetic/chromosomal data (Whiteley et al., 2017). To date, potential differences in whole-organism performance characteristics among sexual phenotypes have not been examined.

Bite force is an important measure of whole-organism performance that may differ between males and females (Gvozdík & Van Damme, 2003; Lailvaux, Cespedes, & Houslay, 2019; Lappin, Hamilton, & Sullivan, 2006; Lappin & Husak, 2005; Lappin & Jones, 2014; McLean et al., 2016). Some male iguanian lizards use their jaws as a weapon to fight other males or to intimidate and restrain female lizards (Lailvaux et al., 2019; Lappin & Husak, 2005; Lappin, Brandt, Husak, Macedonia, & Kemp, 2006; Lappin, Hamilton et al., 2006; McLean et al., 2016; McLean & Stuart-Fox, 2015). In eastern collared lizards (*Crotaphytus collaris*), the bite force of adult males is a strong predictor of access to females, mating success, and genetic paternity, whereas body size is not; the greater bite force of males is associated with considerably greater head dimensions (likely related to having larger jaw muscles) than females (Husak, Lappin, & Van Den Bussche, 2009; Lappin & Husak, 2005). However, aggression between female lizards also is known to occur in some species, particularly when resources (such as perching or nesting sites) are patchy or limited (Baird & Sloan, 2003; Rauch, 1988). Therefore, having greater bite-force performance than other individuals of the same sex also can be beneficial for female lizards.

Bite-force performance is unknown for *Pogona vitticeps*, but males reach a greater size and have larger and relatively wider heads than females (Badham, 1976; Witten, 1994). This pattern might indicate that males bite more forcefully and use biting to compete for access to females (Witten, 1994). Sexual dimorphism in head size (and possibly shape) may be common among agamid lizards (e.g., Hoops et al., 2017; Kuo, Lin, & Lin, 2009; Littleford-Colquhoun et al., 2019; Stauber & Booth, 2003; Thompson & Withers, 2005; Wotherspoon & Burgin, 2011), and greater bite force associated with greater head size has been found in male eastern water dragons (*Intellagama lesueurii*; Baxter-Gilbert & Whiting, 2019). Two species of spiny-tailed agamid *Uromastyx* do not show obvious sexual differences in head dimensions or bite force but comparisons may be limited by sample size: n = 7:5 and 1:5 (Herrel, Castilla, Al-Sulaiti, & Wessels, 2014). The only other reports of bite force in agamid lizards either include only males (McLean & Stuart-Fox, 2015) or do not explicitly report how individual data points correspond to sex or species (e.g., Herrel & De Vree, 2009; Herrel, Schaerlaeken, Meyers, Metzger, & Ross, 2007; Porro et al., 2014; Schaerlaeken, Herrel, Aerts, & Ross, 2008). The paucity of detailed bite force performance for Agamidae restricts comparisons within Agamidae as well as broader comparisons between Agamidae and other reptile groups such as Rhynchocephalia (Jones & Lappin, 2009).

Here, we analyze head dimensions and bite-force performance in *P. vitticeps*. Owing to the expected sexual dimorphism in head size and the likely association with male reproductive success, we predict that large heads and forceful bites are associated with only the male phenotype (ZZm), and that both concordant (ZWf) and sex-reversed females (ZZf) display similar, smaller heads and weaker bite force.

2 | MATERIALS AND METHODS

2.1 | Study taxon

The central bearded dragon (*P. vitticeps*) is an agamid lizard commonly found in the arid and semiarid regions of central Australia (Badham, 1976; Rej & Joyner, 2018) and internationally as a common pet (Johnson & Adwick, 2019; Raiti, 2012). It is also increasingly used as a reptilian model organism in a wide range of biological disciplines. Recent examples of research focused on this taxon include those related to thermal physiology (Couture, Monteiro, Aymen, Troncy, & Steagall, 2017; Smith et al., 2016), niche modeling (Rej & Joyner, 2018), behavior (Cadena & Tattersall, 2009; Cadena et al., 2017; Kis, Huber, & Wilkinson, 2015; Li et al., 2016), veterinary herpetology (Schmidt-Ukaj, Hochleithner, Richter, Brandstetter, & Knotek, 2017), development (Haridy, 2018; Melville et al., 2016; Ollonen, Da Silva, Mahlow, & Di-Poï, 2018; Whiteley et al., 2017), comparative brain anatomy (Tosches et al., 2018), gene expression (Capraro et al., 2019), and genomics (Deakin et al., 2016; Georges et al., 2015). The species *P. vitticeps* is also frequently included in broader comparative studies (e.g., Chen et al., 2012; Cubo, Hui, Clarac, & Quilhac, 2017; Geist, 2000; Gray, Hutchinson, & Jones, 2019; Gray, McDowell, Hutchinson, & Jones, 2017; Gray, Sherratt, Hutchinson, & Jones, 2019; Head & Polly, 2015; Herrel & De Vree, 2009; Herrel et al., 2007; Holliday, Gardner, Paesani, Douthitt, & Ratliff, 2010; Littleford-Colquhoun et al., 2019; Macrì, Savriama, Khan, & Di-Poï, 2019; Ross et al., 2010; Schaerlaeken et al., 2008; Watanabe et al., 2019; Witten, 1985, 1994; Woltering et al., 2009).

2.2 | Specimens

Our sample comprised 91 captive individuals (39 adults and 52 juveniles) of the central bearded dragon, *P. vitticeps*, from a previously studied breeding colony (at the Institute for Applied Ecology at the University of Canberra; Figure S1; Table S1). The genotypic and phenotypic sex had been characterized for all individuals (Holleley et al., 2015; Li et al., 2016). Animals represent three groups: 26 discordant sex-reversed females (ZZf), 33 genotypically and phenotypically concordant females (ZWf), and 32 males (ZZm) ranging from juveniles to large adults (snout-vent length [SVL] = 58.5–228 mm). An SVL of 150 mm or greater was used to define adults. This value is 20 mm greater than previous observations of sexual maturity (Badham, 1976) but helps ensure that the adult sample exhibits adult head proportions (see fig. 2 in Witten, 1994). Therefore, our adult sample comprised: 17 sex-reversed females (ZZf), 11 concordant females (ZWf), and 11 males (ZZm). We focus most of our analyses on adult animals to remove the influence of ontogeny, but we also examine scaling of bite force and head dimensions in the full samples to provide additional insight into differences among the groups.

2.3 | Morphometrics

For each individual, we measured mass, SVL, head length directly from the tip of the rostrum to the posterior end of the retroarticular process (HLrr), head length from the tip of the rostrum to the posteroventral corner of the tympanum (approximately the position of the quadrate-articular jaw joint; HLrq) (similar to st of Badham 1976), head width at the base of the tympanum (HWqu) (similar to wt of Badham 1976), head width at the midpoint of the temporal region (HWmt), and head depth at the midpoint of the temporal region including the lower jaw with the mouth closed (HDmt). Mass was measured using a digital scale, SVL was measured using a transparent plastic ruler, and head dimensions were measured using digital calipers.

2.4 | Bite-force performance

Bite force was measured using a Kistler piezoelectric force transducer (type 9203, Kistler, Switzerland) attached between two stainless steel bite plates and connected to a charge amplifier (type 5995, Kistler, Switzerland). One plate is straight whereas the other is sigmoid (cf. Herrel, Spithoven, Van Damme, & De Vree, 1999). To accommodate the size range of specimens tested, two different sized sets of bite plates were used (Figure S2) that differed in their width: 25 mm (also used here: Jones & Lappin, 2009; Lappin, Hamilton et al., 2006; Lappin & Husak, 2005; Lappin & Jones, 2014) and 20 mm wide (used here for the first time). The bite plates of the smaller transducer were shallower and more closely opposed so that the smallest animals did not have to use excessive gape angles, which might restrict maximum performance (Figure 1). Strips of leather (about 5 mm wide) were added to the outer tips of the bite

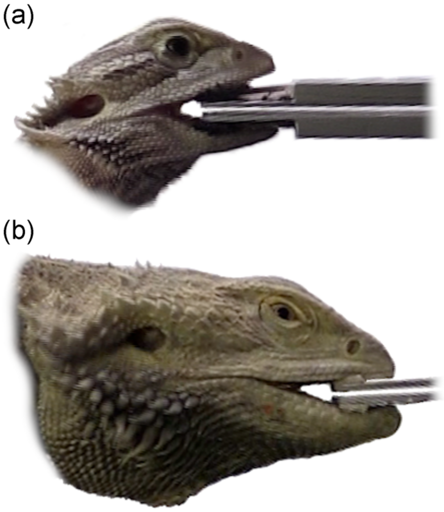

FIGURE 1 *Pogona vitticeps* biting the bite plates of the force transducer in lateral view: (a) Juvenile 008031 ZWf concordant female (45 g mass, 110 mm SVL, and HLqu = 27.1 mm) and (b) adult 002919 ZZf sex-reversed female (365 g mass, 228 mm SVL, and HLqu = 51.9 mm). SVL, snout-vent length [Color figure can be viewed at wileyonlinelibrary.com]

plates to protect the animal's jaws and teeth, to provide a naturalistic surface to bite, and to ensure that the bite force being applied was at a consistent point along the bite plates (Figure 1; Lappin & Jones, 2014). The output voltage of the devices was calibrated to bite force (Newtons) by hanging a series of weights by a string positioned at the center of the leather strip (cf. Dechow & Carlson, 1983; Lappin, Hamilton et al., 2006).

Before bite-force trials, we gave animals an opportunity to thermoregulate under heat lamps for at least 30 min to achieve preferred body temperature. We measured body temperature using a Digitech QM-7221 digital temperature gun with dual laser targeting between the first and second trials. The surface readings recorded (~31°C) were only slightly lower than the preferred or optimal body temperatures reported elsewhere (34–36°C; e.g., Cadena & Tattersall, 2009; Johnson & Adwick, 2019). Adult males tended to be slightly warmer than adults of the other two genotypes (Figure S3: ZZf = 30.59°C ± 0.32, ZWf = 30.08°C ± 0.71, ZZm = 31.57°C ± 0.72) but there is no obvious relationship between surface temperature and bite force (Figure S4).

Each lizard was given the opportunity to bite during four trials with a brief period of rest between each successive trial (~30 s). Four trials is similar to the number used in previous studies (five, e.g., Herrel et al., 2014, p. 172; three, e.g., Baxter-Gilbert & Whiting, 2019, p. 257). Lizards were encouraged to gape by touching the side or underside of the lower jaw. Bites were elicited by carefully placing the transducer in the animal's mouth. Of the 364 trials, only nine resulted in no bite. All trials were digitally video-recorded in lateral view to document the position along the jaws at which each bite was applied. The location along the jaws where the bite was applied to the leather strips was used to measure the proportional bite out-lever (the distance between the bite location and jaw joint along the jaw divided by the full length of the lower jaw). Voluntary bites were delivered with a range of proportional bite out-levers (mean = 0.85, maximum = 0.97, and minimum = 0.68). However, we standardized each bite to what it would be at the tips of the jaws, represented by a proportional bite out-lever of 1.0 (Lappin & Jones, 2014). As is convention, the greatest bite force among the trials was used in analyses (e.g., Baxter-Gilbert & Whiting, 2019; Herrel et al., 2014; Husak et al., 2009; Lappin & Husak, 2005; Lappin & Jones, 2014). We performed analyses using both the greatest standardized (BF) and greatest raw bite force (nonstandardized for lever, BF no lever) values but we focus on standardized bite force in the main text.

2.5 | Analyses

All statistical analyses were done using R version 3.6.1 (R Core Team, 2019) and code to reproduce the analyses is available at https://github.com/MarcEHJones/sex-reverse-pv.

2.5.1 | Bite force and morphometric comparison

To compare body size, dimensions, and bite force measures among adults of the three groups (ZZf, ZWf, and ZZm), we calculated the mean ± standard error for each untransformed variable (Table 1). We tested for significant differences among the groups using analysis of variance (fixed model) natural log-transformed variables (Tables 2 and S3). We used standard model checks for linear models (Q-Q plot, histogram of residuals, residuals vs. linear predictors, and response vs. fitted values) to assess model fit.

2.5.2 | Allometry and scaling

To test the scaling of bite force for allometry across ontogeny (including juveniles and adults) for each of the three groups (ZZf, ZWf, and ZZm) we fitted linear models of log10-transformed bite force as a function of log10-transformed SVL, mass, and each of the head dimensions to each group separately (Table 3). Maximum bite force performance should scale isometrically with the cross-sectional area of the jaw muscles contributing to the bite (Erickson, Lappin, & Vliet, 2003; Gans, 1982; Gröning et al., 2013; Santana, Dumont, & Davis, 2010; Sellers, Middleton, Davis, & Holliday, 2017). Therefore, if bite force performance in *Pogona* scales isometrically with the size it should scale to the square of linear measurements (e.g., SVL) with a slope of 2.000 and to the two-thirds power of volumes (e.g., body mass) with a slope of 0.667 (Erickson et al., 2003). We used the standard error to estimate upper and lower limits for the slope and to evaluate whether there was adequate evidence of negative or positive allometry respectively (Tables 3 and S3). To compare the scaling relationships between bite force and measures of body and head size

TABLE 1 Mean body size and head shape measures (with standard error) of adult *Pogona vitticeps* used in this study

	ZZf	ZWf	ZZm	Units
Mass	228.07 ± 19.73	236.38 ± 23.1	234.68 ± 13.71	g
SVL	183.85 ± 4.93	184.64 ± 6.09	187.82 ± 4.24	mm
HLrr	50.54 ± 1.55	52.20 ± 1.74	56.31 ± 1.23	mm
HLrq	42.51 ± 1.32	42.23 ± 1.31	46.37 ± 0.96	mm
HWqu	37.55 ± 1.30	37.89 ± 1.38	41.48 ± 0.96	mm
HWmt	36.12 ± 1.04	36.50 ± 1.20	38.64 ± 1.23	mm
HDmt	23.54 ± 0.75	24.62 ± 1.11	28.11 ± 0.83	mm
BF at tips	50.28 ± 4.04	52.66 ± 5.98	71.46 ± 6.46	N
BF no lever	62.20 ± 5.28	65.93 ± 8.27	90.37 ± 9.59	N
n	17	11	11	

Note: ZZf, sex-reversed females (*n* = 17), ZWf, concordant females (*n* = 11), ZZm, males (*n* = 11). Mass, body mass (g); SVL, snout-vent length (mm); HLrr, head length directly from the tip of the rostrum to the posterior end of the retroarticular process (mm); HLrq, head length from the tip of the rostrum to the posteroventral corner of the tympanum (approximately the position of the quadrate-articular jaw joint) (mm); HWqu, head width measured at the base of the tympanum (mm); HWmt, head width measured at the midpoint of the temporal region (mm); HDmt, and head depth measured at the midpoint of the temporal region (mm); BF at tips, bite force at the tips corrected for out lever (N; Lappin and Jones, 2014); BF no lever, bite force without lever correction (N).

TABLE 2 Results from analysis of variances testing for differences in variables across three genotypes in adults

			ZZf	ZZf and ZWf difference			ZZf and ZZm difference		
Response	*F*	*p*	Mean ± *SE*	Mean ± *SE*	*t*	*p*	Mean ± *SE*	*t*	*p*
log(Mass)	0.161	.852	5.370 ± 0.078	0.047 ± 0.124	0.376	.709	0.067 ± 0.124	0.538	.594
log(SVL)	0.197	.822	5.208 ± 0.025	0.004 ± 0.040	0.112	.911	0.024 ± 0.040	0.612	.544
log(Bite force)	3.710	.034*	3.865 ± 0.087	0.030 ± 0.138	0.214	.832	0.356 ± 0.138	2.581	.014*
log(Bite force nl)	3.388	.045*	4.066 ± 0.095	0.043 ± 0.152	0.284	.788	0.377 ± 0.152	2.492	.017*
log(HLroret)	3.669	.035*	3.916 ± 0.026	0.034 ± 0.042	0.807	.425	0.113 ± 0.042	2.695	.011*
log(HLroqu)	3.133	.056	3.743 ± 0.025	−0.004 ± 0.041	−0.106	.916	0.092 ± 0.041	2.258	.030*
log(HWqu)	2.749	.077	3.616 ± 0.030	0.012 ± 0.047	0.247	.806	0.106 ± 0.047	2.241	.031*
log(HWmt)	1.258	.297	3.580 ± 0.028	0.011 ± 0.044	0.260	.797	0.068 ± 0.044	1.541	.132
log(HDmt)	6.830	.003**	3.151 ± 0.031	0.042 ± 0.049	0.851	.400	0.180 ± 0.049	3.642	.001**

Note: ZZf, sex-reversed females ($n = 17$), ZWf, concordant females ($n = 11$), ZZm, males ($n = 11$). Degrees of freedom 2, 36 for all tests.
Abbreviation: *SE*, standard error.
*Significant at $p = .05$.
**Significant at $p = .01$.

TABLE 3 Bite force scaling results in full sample of *Pogona vitticeps* ($n = 91$)

Genotype	Predictor	Slope	*SE*	Upper limit	Lower limit	*df*	*t*	*p*	Predicted isometry	adj.r^2	Allometry
ZZf	SVL	1.747	0.186	1.933	1.560	24	9.37	<.001	2.000	.78	Negative
ZWf	SVL	1.799	0.137	1.937	1.662	31	13.11	<.001	2.000	.84	Negative
ZZm	SVL	2.222	0.130	2.352	2.092	30	17.11	<.001	2.000	.90	Positive
ZZf	Mass	0.567	0.052	0.619	0.515	24	10.81	<.001	0.667	.82	Negative
ZWf	Mass	0.581	0.039	0.620	0.541	31	14.73	<.001	0.667	.87	Negative
ZZm	Mass	0.729	0.035	0.764	0.694	30	20.83	<.001	0.667	.93	Positive
ZZf	log(HLroret)	1.983	0.187	2.170	1.795	24	10.58	<.001	2.000	.82	–
ZWf	log(HLroret)	1.939	0.144	2.082	1.795	31	13.50	<.001	2.000	.85	–
ZZm	log(HLroret)	2.262	0.117	2.379	2.145	30	19.33	<.001	2.000	.92	Positive
ZZf	log(HLroqu)	2.094	0.190	2.284	1.903	24	11.01	<.001	2.000	.83	–
ZWf	log(HLroqu)	2.206	0.162	2.369	2.044	31	13.62	<.001	2.000	.85	Positive
ZZm	log(HLroqu)	2.433	0.113	2.545	2.320	30	21.58	<.001	2.000	.94	Positive
ZZf	log(HWqu)	1.895	0.143	2.038	1.752	24	13.26	<.001	2.000	.87	–
ZWf	log(HWqu)	1.882	0.152	2.034	1.730	31	12.38	<.001	2.000	.83	–
ZZm	log(HWqu)	2.233	0.095	2.328	2.137	30	23.41	<.001	2.000	.95	Positive
ZZf	log(HWmt)	2.095	0.174	2.269	1.921	24	12.01	<.001	2.000	.85	–
ZWf	log(HWmt)	2.106	0.159	2.265	1.946	31	13.23	<.001	2.000	.84	–
ZZm	log(HWmt)	2.422	0.128	2.550	2.294	30	18.88	<.001	2.000	.92	Positive
ZZf	log(HDmt)	2.003	0.187	2.269	1.921	24	10.73	<.001	2.000	.82	–
ZWf	log(HDmt)	1.922	0.148	2.265	1.946	31	12.97	<.001	2.000	.84	–
ZZm	log(HDmt)	2.190	0.109	2.550	2.294	30	20.11	<.001	2.000	.93	Positive

Note: Adult and juvenile ZZf, sex-reversed females ($n = 26$), ZWf, concordant females ($n = 33$), and ZZm, males ($n = 32$). Standard error (*SE*) was used to define upper and lower limits. Allometry is considered positive when the lower limit of the slope is > 0.667 for mass and 2.0 for linear measurements (the isometric predictions) and negative when the upper limit of the slope is < 0.667 for mass and 2.0 for linear measurements.

(all natural log-transformed) among the three groups, we used linear regressions again checking model fit as described above (Table S4).

2.5.3 | Head shape comparison

To compare head shape among the three groups (ZZf, ZWf, and ZZm) controlling for isometric size differences, the five head dimensions were converted to log shape ratios (Mossiman variables). This approach involves dividing each of the five head dimensions by the geometric mean of the five dimensions for each specimen (e.g., Sakamoto & Ruta, 2012). These new values were examined with a principal component analysis using the princomp function in R. We performed this analysis for both the full sample (Figures S7–S10) and adults (Figures 5, S11, and S12).

3 | RESULTS

For the entire sample (juveniles and adults, 58.5–228 mm SVL) bite force standardized at the tips of the jaws ranged from 5.59 N to 98.73 N and is positively correlated with body size (Tables 1–3).

3.1 | Adult bite force and morphometric comparison

At least among adult animals, males (ZZm) bite with greater force than both groups of phenotypically female individuals (ZZf and ZWf; Figure 2; Tables 1 and 2). The difference between males (ZZm) and sex-reversed females (ZZf) is significant ($p = .014$; Table 2) but between males (ZZm) and concordant females (ZWf) it is not ($p = .052$; Table S2). We did not observe any difference in bite force when comparing sex-reversed females (ZZf) and concordant females ($p = .832$; Figure 2; Table 2). Males (ZZm) have greater head dimensions than both sex-reversed (ZZf) and concordant females (ZWf; Table 1). The difference is significant for head length between the rostrum and tympanum (HLrq), head width at the tympanum (HWqu), head depth at the mid-temporal region (HDm; Tables 2 and S2), and, with sex-reversed females (ZZf) only: head length between the rostrum and posterior end of the retroarticular process (HLrr; Table 2). Sex-reversed females and concordant females do not differ significantly from each other in any measure of head size (Figure 3; Table 2). Mass and SVL do not differ significantly across the three groups (Figure 2; Tables 2 and S2).

3.2 | Allometry and scaling comparison

Sex-reversed females (ZZf) and concordant females (ZWf) exhibit negative allometry of standardized bite force on body size (SVL and mass) whereas males (ZZm) exhibit positive allometry of bite force on body size (Table 3). The positive allometric scaling of males (ZZm) is driven by the relatively greater bite force of adult males (Figures 4, S5, and S6). Using the standard error to estimate upper and lower limits for the slope, males (ZZm) show positive allometry of bite force on every head dimension, concordant females (ZWf) only show positive allometry for head length (HLqu), and sex-reversed females (ZZf) show no obvious allometry with respect to any head dimension (Table 3). Standardized bite force scales with body size (SVL and mass) with a significantly lower slope in sex-reversed females (ZZf) than it does in males (ZWf; $p = .035$ and $p = .039$, respectively; Table S4), but no significant difference was found between the slopes of sex-reversed females (ZZf) and concordant females (ZWf; Table S4). We did not detect any significant differences among the

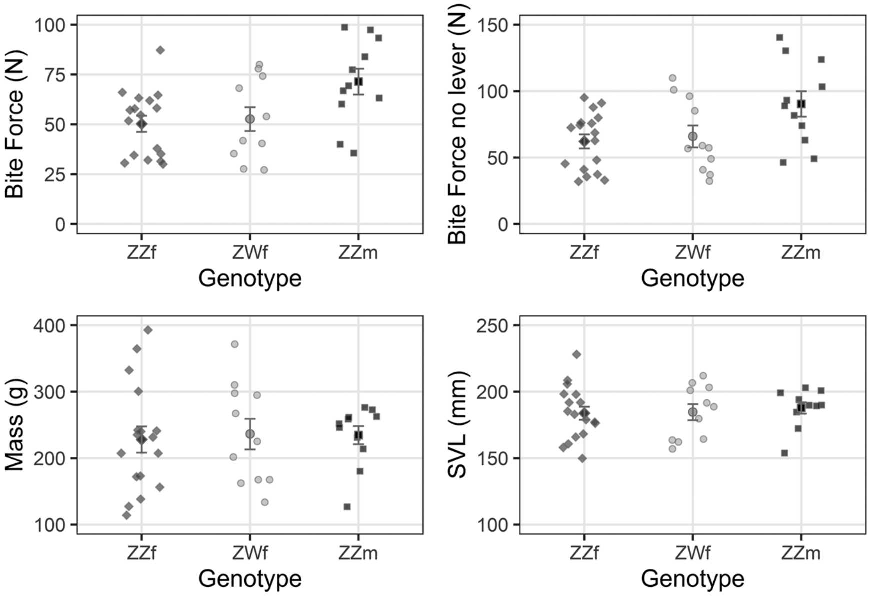

FIGURE 2 Bite force, mass, and snout-vent length (SVL) in adult *Pogona vitticeps* ($n = 39$) according to genotype ZZf, sex-reversed females ($n = 17$), ZWf, concordant females ($n = 11$), and ZZm, males ($n = 11$)

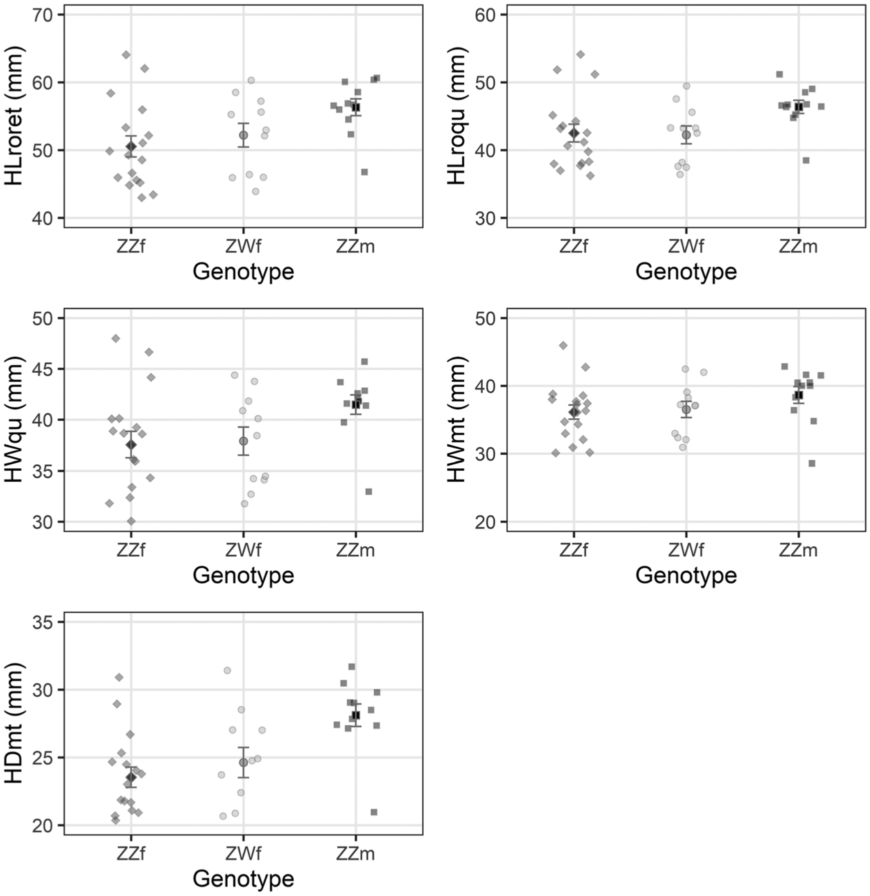

FIGURE 3 Basic head dimensions in adult *Pogona vitticeps* ($n = 39$) according to genotype: ZZf, sex-reversed females ($n = 17$), ZWf, concordant females ($n = 11$), and ZZm, males ($n = 11$). HLrr, head length directly from the tip of the rostrum to the posterior end of the retroarticular process (mm); HLrq, head length from the tip of the rostrum to the posteroventral corner of the tympanum (approximately the position of the quadrate-articular jaw joint; mm); HWqu, head width measured at the base of the tympanum (mm); HWmt, head width measured at the midpoint of the temporal region (mm); HDmt, and head depth measured at the midpoint of the temporal region (mm)

three groups in the scaling of bite force with respect to any head dimension (Table S4).

If nonstandardized bite force is used, males (ZZm) still show positive allometry of bite force on both measures of body size and all head dimensions (Table S3). Sex-reversed females (ZZf) and concordant females (ZWf) show negative allometry of bite force on body mass. Sex-reversed females (ZZf) show positive allometry on head width at the mid-temporal region whereas concordant females (ZWf) show positive allometry on head width at the mid-temporal region and head length between the rostrum and base of the tympanum (Table S3). We did not detect any significant differences among the three groups in the scaling of unstandardized bite force with respect to body size or head dimension (Table S4).

3.3 | Isometric head shape

There was no clear difference in head shape (isometric size removed) among the three groups (Figures 5 and S7).

For the full sample, PC1 (34.1% of total variation) mainly reflects the relative head depth, PC2 (26.7%) mainly reflects relative head width, and PC3 (21.8%) reflects differences in head width at the tympanum (quadrates) and head width at the mid-temporal region. The distribution of the three genotypes extensively overlaps (Figure S7). Individuals with greater bite forces appear to plot with lower PC1 scores and higher PC3 scores: heads that are relatively deep at the mid-temporal region and wide at the base of the tympanum (Figures S7 and S8). This pattern parallels body size: adults plot with lower PC1 scores and high PC3 scores (Figures S9 and S10).

In the analysis of just adults, PC1 (36.6%) mainly reflects relative head width, PC2 (31.7%) mainly reflects the relative head depth, and PC3 (21.2%) reflects differences in head width and length at the tympanum (quadrates) relative to the other dimensions (Figure 5). Again the distribution of the three groups overlaps but the distribution of sex-reversed females (ZZf) tends to overlap concordant females (ZWf) more than concordant males (ZZm; Figure 5). The sex-reversed females (ZWf) tend to plot with narrower heads compared to males. However, this distribution does not obviously reflect body size or bite force (Figures S11 and S12).

4 | DISCUSSION

We show that adult male (ZZm) bearded dragons (*P. vitticeps*) can bite more forcefully and in general, have larger heads than adult females whether they are sex-reversed (ZZf) or concordant (ZWf) females. This result is consistent with our prediction based on the sexually dimorphic head size in this species. It suggests that male

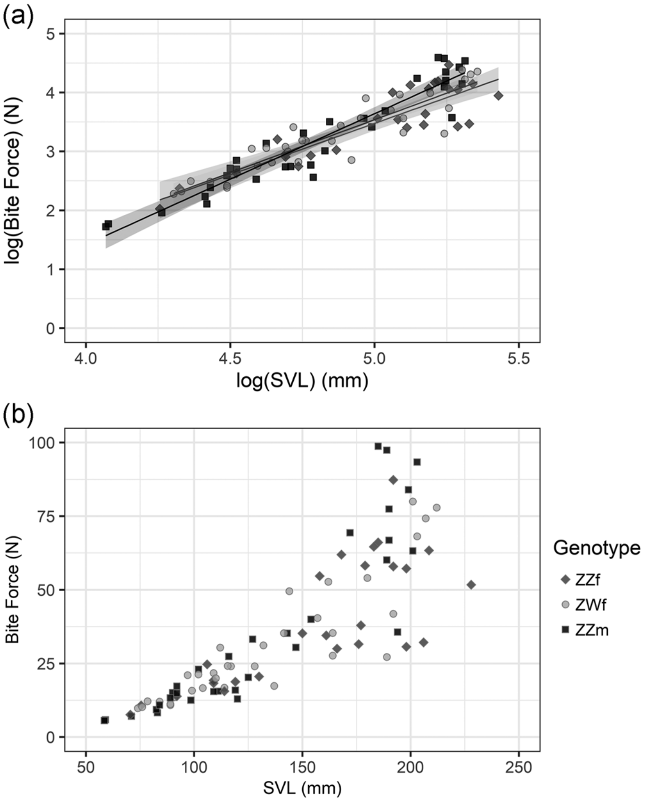

FIGURE 4 Relationship between snout-vent length (SVL) and bite force in *Pogona vitticeps* (*n* = 91) from three different genotypes shown in log (a) and non-log (b). Adult and juvenile ZZf, sex-reversed females (*n* = 26), ZWF, concordant females (*n* = 33), and ZZm, males (*n* = 32)

bearded dragons, like some other iguanian lizards, use their jaws and bite force to secure access to females at the expense of other males (Baxter-Gilbert & Whiting, 2019; Lappin, Brandt et al., 2006; Lappin & Husak, 2005; Lappin, Hamilton et al., 2006). This enhanced bite-force performance may also incidentally allow males access to a wider range of food items.

Despite sex-reversed *P. vitticeps* (ZZf) reportedly exhibiting several male (ZZm) traits as juveniles (Li et al., 2016), we found no evidence that they possess the enhanced bite force and larger heads of adult males (ZZm; Table 2). Concordant (ZWf) and sex-reversed female (ZZf) bearded dragons have similar bite-force performance, despite the two groups of females being initiated by different primary mechanisms (sex chromosomes and temperature, respectively) enacted on different genetic backgrounds (ZW and ZZ, respectively). The adult phenotype of this sexually dimorphic trait reflects reproductive phenotype, not sex chromosome complement, suggesting that either environmental cues are pivotal to the development of this trait, and/or (more likely) that bite force (and head size) is controlled exclusively by a common downstream sexual differentiation cascade and sex hormone production. Interindividual levels of testosterone in the (noniguanian) lizard *Gallotia gallotia* have been found to correlate with bite force performance (Huyghe et al., 2010). More work is required to determine the relative fitness of sex-reversed females, which will allow us to predict the evolutionary stability of sex chromosomes and the likelihood of transitions to temperature-dependent sex determination.

The only other study of intraspecific bite-force performance in a species with sex reversal was conducted on adults of the African pygmy mouse (*Mus minutoides*; Ginot et al., 2017). In contrast to the situation in *P. vitticeps*, sex-reversed female mice (X*Y) were found to have greater bite-force performance than both concordant females and males (Ginot et al., 2017). However, as in *P. vitticeps*, the greater bite force is associated with greater head size, thus highlighting the close relationship between head size and bite force (related to jaw muscle physiological cross-sectional area, e.g., Erickson et al., 2003; Gans, 1982; Gröning et al., 2013; Santana et al., 2010; Sellers et al., 2017). The results for both taxa hint at the diversity of phenotypic responses to sex reversal that may exist in nature. A full understanding of the fitness of sex-reversed individuals in a suite of phenotypic traits will be crucial to our understanding of key evolutionary processes, such as the birth and death of sex chromosomes in response to rapidly changing environmental stimuli.

The positive allometry of bite force performance in male *P. vitticeps* relative to SVL and mass is similar to that reported in other reptiles (Erickson, Gignac et al., 2014; Erickson, Lappin et al., 2003; Herrel & O'Reilly, 2006; Jones & Lappin, 2009) but it is greater than would be expected given that bite force should scale according to muscle cross-sectional area. This result likely reflects a range of factors (Erickson, Lappin et al., 2003; Herrel & O'Reilly, 2006; Jones & Lappin, 2009) including a disproportional increase in jaw muscle size (=cross-sectional area). Correspondingly, the postorbital region of the skull (which houses the jaw muscles) lizards does increase disproportionally during ontogeny in *Pogona* (Gray, Sherratt, Hutchinson, & Jones, 2019b) as it does in many lepidosaurs (e.g., Jones, 2008; Jones & Lappin, 2009). Other factors may include ontogenetic changes in muscle quality and skeletal stiffness involved in the transmission of muscle forces (Erickson, Lappin et al., 2003).

The result that males generally have greater head dimensions compared to females matches the results of previous studies (Badham, 1976; Witten, 1994). In particular, males tend to have deep heads that are relatively wide at the quadrates. However, substantial intraspecific variation limits distinguishing between individuals of the three genotypes using isometric head shape alone. As previously reported, the ontogeny of various head dimensions (e.g., head width and head depth) relative to body size are not necessarily linear or similar to each other (Witten, 1994, fig. 2). This variation clouds comparisons using isometric shape alone. Although some head dimensions differ on average between males and females, head shape and size are unlikely to be a reliable predictor of sex for an individual unless that individual is a very large male (where differences have the potential to be most exaggerated).

The new bite force data here permits some limited comparisons with other agamids and lepidosaurs. Our bite force values for *P. vitticeps* do not appear to be substantially different from others reported for agamids (Herrel et al. 2007, fig. 4; Herrel & De Vree, 2009, fig. 2). Our results suggest that among agamids, *P. vitticeps* has a bite force

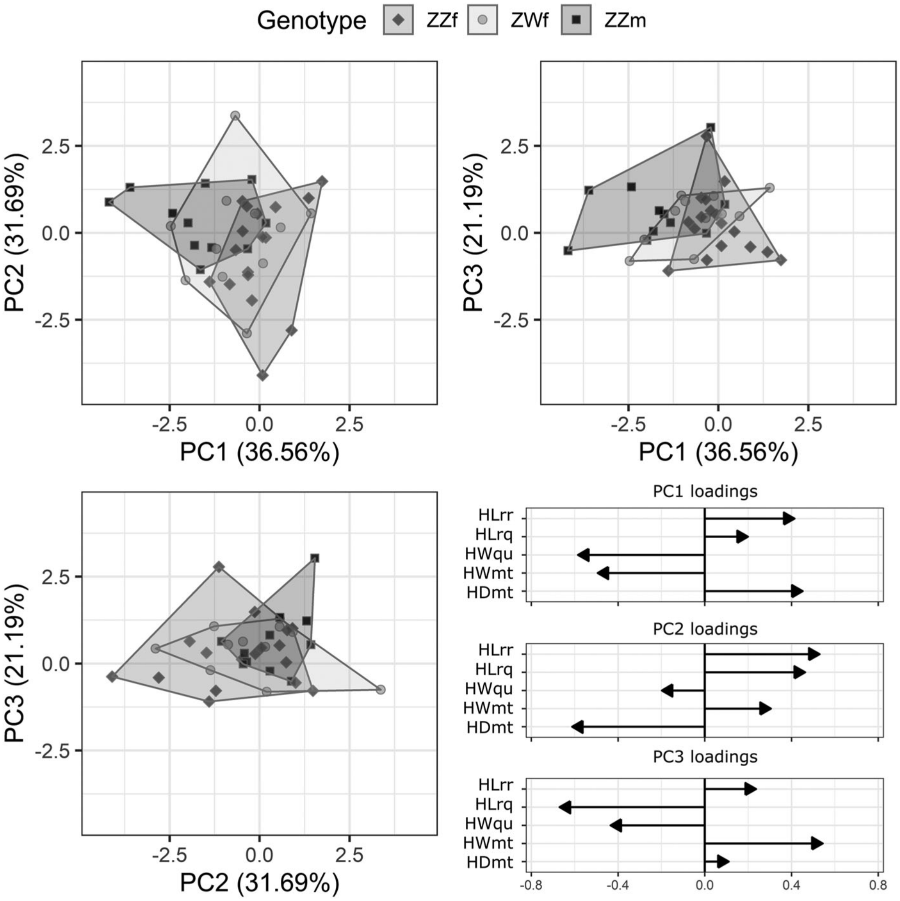

FIGURE 5 Isometric head shape variation among adult *Pogona vitticeps* (*n* = 39) of known genotypes (>150 SVL mm, *n* = 39) according to a principal components analysis of log shape ratios of five head dimensions. Arrows indicate the relative loading of each head dimensions for each PC axis. ZZf, sex-reversed females (*n* = 17), ZWF, concordant females (*n* = 11), and ZZm, males (*n* = 11)

similar to that of *Uromastyx acanthinura* (Herrel et al. 2014), greater than *Ctenophorus maculosus* (McLean & Stuart-Fox, 2015), but much less than *Intellagama lesueurii* (Baxter-Gilbert & Whiting, 2019). This pattern broadly reflects differences in body and head size, with larger taxa having greater bite force. However, such broad comparisons remain problematic due to differences in the exact method used (e.g., standardization of out lever, biting substrate, number of trials, and rest period between trials). Perhaps more important, comparisons are inhibited by nondisclosure (publication) of raw measurement data for individual animals which means comparisons are limited to plots of values from a range of taxa (Herrel et al. 2007; Herrel & De Vree, 2009), mean values (Baxter-Gilbert & Whiting, 2019, p. 259) or maxima (McLean & Stuart-Fox, 2015, table 1). In the spirit of open data and reproducibility, we advocate that future studies should provide explicit methods and publication of raw individual measurement data.

ACKNOWLEDGMENTS

We thank Wendy Ruscoe for assistance with animal husbandry and handling, Andy Duncan for help with filming, Wolf and Sebastian Carius for help constructing equipment, Vera Weisbecker, and one anonymous reviewer for comments on a previous version of the manuscript, Brett A. Goodman, Mike S. Y. Lee, and Kyle N. Armstrong for general advice, and The Institute for Applied Ecology at the University of Canberra for housing the reptile colony. M. E. H. J. was supported by Australian Research Council grant DE130101567. C. E. H. and A. G. were supported by Australian Research Council Discovery grants DP110104377 and DP170101147, both led by A. G.

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The raw data as well as the code to reproduce the analyses is available at https://github.com/marcehjones/sex-reverse-pv (Jones & Cooper, 2020).

ETHICAL STATEMENT

All research was conducted under the University of Canberra animal ethics Protocol CEAE 15-01 and the University of Adelaide animal ethics Protocol 2013/37.

ORCID

Marc E. H. Jones http://orcid.org/0000-0002-0146-9623
Jennifer C. A. Pistevos http://orcid.org/0000-0001-8081-7069
Natalie Cooper http://orcid.org/0000-0003-4919-8655
A. Kristopher Lappin http://orcid.org/0000-0002-5386-0069
Arthur Georges http://orcid.org/0000-0003-2428-0361

Mark N. Hutchinson http://orcid.org/0000-0003-2910-1983
Clare E. Holleley http://orcid.org/0000-0002-5257-0019

REFERENCES

Alam, S. M. I., Sarre, S. D., Gleeson, D., Georges, A., & Ezaz, T. (2018). Did lizards follow unique pathways in sex chromosome evolution? *Genes*, *9*(5), 239.

Badham, J. (1976). The *Amphibolurus* species-group (Lacertilia: Agamidae). *Australian Journal of Zoology*, *24*, 432–443.

Baird, T. A., & Sloan, C. L. (2003). Interpopulation variation in the social organization of female collared lizards, *Crotaphytus collaris*. *Ethology*, *109*, 879–894.

Baroiller, J. F., & D'Cotta, H. (2016). The reversible sex of gonochoristic fish: Insights and consequences. *Sexual Development*, *10*(5-6), 242–266.

Baxter-Gilbert, J. H., & Whiting, M. J. (2019). Street fighters: Bite force, injury rates, and density of urban Australian water dragons (*Intellagama lesueurii*). *Austral Ecology*, *44*(2), 255–264.

Cadena, V., Smith, K. R., Endler, J. A., Porter, W. P., Kearney, M. R., & Stuart-Fox, D. (2017). Geographic divergence and colour change in response to visual backgrounds and illumination intensity in bearded dragons. *Journal of Experimental Biology*, *220*, 1048–1055.

Cadena, V., & Tattersall, G. J. (2009). The effect of thermal quality on the thermoregulatory behavior of the bearded dragon *Pogona vitticeps*: Influences of methodological assessment. *Physiological and Biochemical Zoology*, *82*, 203–217.

Capraro, A., O'Meally, D., Waters, S. A., Patel, H. R., Georges, A., & Waters, P. D. (2019). Waking the sleeping dragon: Gene expression profiling reveals adaptive strategies of the hibernating reptile *Pogona vitticeps*. *BMC Genomics*, *20*(460), 1–16.

Chen, I. P., Stuart-Fox, D., Hugall, A. F., & Symonds, M. R. (2012). Sexual selection and the evolution of complex color patterns in dragon lizards. *Evolution*, *66*, 3605–3614.

Couture, E. L., Monteiro, B. P., Aymen, J., Troncy, E., & Steagall, P. V. (2017). Validation of a thermal threshold nociceptive model in bearded dragons (*Pogona vitticeps*). *Veterinary Anaesthesia and Analgesia*, *44*, 676–683.

Cubo, J., Hui, M., Clarac, F., & Quilhac, A. (2017). Static osteogenesis does not precede dynamic osteogenesis in periosteal ossification of *Pleurodeles* (Caudata, Amphibia) and *Pogona* (Squamata, Lepidosauria). *Journal of Morphology*, *278*, 621–628.

Deakin, J. E., Edwards, M. J., Patel, H., O'Meally, D., Lian, J., Stenhouse, R., … Li, Q. (2016). Anchoring genome sequence to chromosomes of the central bearded dragon (*Pogona vitticeps*) enables reconstruction of ancestral squamate macrochromosomes and identifies sequence content of the Z chromosome. *BMC Genomics*, *17*, 447.

Dechow, P. C., & Carlson, D. S. (1983). A method of bite force measurement in primates. *Journal of Biomechanics*, *16*, 797–802.

Deepak, V., Giri, V. B., Asif, M., Dutta, S. K., Vyas, R., Zambre, A. M., Bhosale, H., & Karanth, K. P. (2016). Systematics and phylogeny of Sitana (Reptilia: Agamidae) of Peninsular India, with the description of one new genus and five new species. *Contributions to Zoology*, *85*(1), 67–111.

Deveson, I. W., Holleley, C. E., Blackburn, J., Graves, J. A. M., Mattick, J. S., Waters, P. D., & Georges, A. (2017). Differential intron retention in *Jumonji* chromatin modifier genes is implicated in reptile temperature-dependent sex determination. *Sciences Advances*, *3*(6), 1–8.

Erickson, G. M., Gignac, P. M., Lappin, A. K., Vliet, K. A., Brueggen, J. D., & Webb, G. J. W. (2014). A comparative analysis of ontogenetic bite-force scaling among Crocodylia. *Journal of Zoology*, *292*, 48–55.

Erickson, G. M., Lappin, A. K., & Vliet, K. A. (2003). The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *Journal of Zoology*, *260*, 317–327.

Ezaz, T., Quinn, A., Miura, I., Sarre, S., Georges, A., & Marshall Graves, J. (2005). The dragon lizard *Pogona vitticeps* has ZZ/ZW micro-sex chromosomes. *Chromosome Research*, *13*, 763–776.

Gamble, T., Coryell, J., Ezaz, T., Lynch, J., Scantlebury, D. P., & Zarkower, D. (2015). Restriction site-associated DNA sequencing (RAD-seq) reveals an extraordinary number of transitions among gecko sex-determining systems. *Molecular Biology and Evolution*, *32*, 1296–1309.

Gans, C. (1982). Fiber architecture and muscle function. *Exercise and Sport Sciences Reviews*, *10*(1), 160–207.

Geist, N. R. (2000). Nasal respiratory turbinate function in birds. *Physiological and Biochemical Zoology*, *73*(5), 581–589.

Georges, A., Li, Q., Lian, J., O'Meally, D., Deakin, J., Wang, Z., … Zhang, G. (2015). High-coverage sequencing and annotated assembly of the genome of the Australian dragon lizard *Pogona vitticeps*. *GigaScience*, *4*, 45.

Ginot, S., Claude, J., Perez, J., & Veyrunes, F. (2017). Sex reversal induces size and performance differences among females of the African pygmy mouse, *Mus minutoides*. *Journal of Experimental Biology*, *220*, 1947–1951.

Gray, J. A., Hutchinson, M. N., & Jones, M. E. H. (2019). Exceptional disparity in Australian agamid lizards is a possible result of arrival into vacant niche. *Anatomical Record*, *302*, 1536–1543.

Gray, J. A., McDowell, M. C., Hutchinson, M. N., & Jones, M. E. H. (2017). Geometric morphometrics provides an alternative approach for interpreting the affinity of fossil lizard jaws. *Journal of Herpetology*, *51*(3), 375–382.

Gray, J. A., Sherratt, E., Hutchinson, M. N., & Jones, M. E. H. (2019). Changes in ontogenetic patterns facilitate diversification in skull shape of Australian agamid lizards. *BMC Evolutionary Biology*, *19*(1), 7.

Gröning, F., Jones, M. E. H., Curtis, N., Herrel, A., O'Higgins, P., Evans, S. E., & Fagan, M. J. (2013). The importance of accurate muscle modelling for biomechanical analyses: A case study with a lizard skull. *Journal of the Royal Society Interface*, *10*(84), 1–10.

Gvozdík, L., & Van Damme, R. (2003). Evolutionary maintenance of sexual dimorphism in head size in the lizard *Zootoca vivipara*: A test of two hypotheses. *Journal of Zoology*, *259*(1), 7–13.

Haridy, Y. (2018). Histological analysis of post-eruption tooth wear adaptations, and ontogenetic changes in tooth implantation in the acrodontan squamate *Pogona vitticeps*. *PeerJ*, *6*, 1–25.

Head, J. J., & Polly, P. D. (2015). Evolution of the snake body form reveals homoplasy in amniote Hox gene function. *Nature*, *520*(7545), 86–89.

Herrel, A., Castilla, A. M., Al-Sulaiti, M. K., & Wessels, J. J. (2014). Does large body size relax constraints on bite-force generation in lizards of the genus *Uromastyx*? *Journal of Zoology*, *292*, 170–174.

Herrel, A., & O'Reilly, J. C. (2006). Ontogenetic scaling of bite force in lizards and turtles. *Physiological and Biochemical Zoology*, *79*(1), 31–42.

Herrel, A., Schaerlaeken, V., Meyers, J. J., Metzger, K. A., & Ross, C. F. (2007). The evolution of cranial design and performance in squamates: Consequences of skull-bone reduction on feeding behavior. *Integrative and Comparative Biology*, *47*(1), 107–117.

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. *Functional Ecology*, *13*(3), 289–297.

Herrel, A., & De Vree, F. (2009). Jaw and hyolingual muscle activity patterns and bite forces in the herbivorous lizard *Uromastyx acanthinurus*. *Archives of Oral Biology*, *54*(8), 772–782.

Hill, P., Burridge, C. P., Ezaz, T., & Wapstra, E. (2018). Conservation of sex-linked markers among conspecific populations of a viviparous skink, *Niveoscincus ocellatus*, exhibiting genetic and temperature dependent sex determination. *Genome Biology and Evolution*, *10*, 1079–1087.

Holleley, C. E., O'Meally, D., Sarre, S. D., Graves, J. A. M., Ezaz, T., Matsubara, K., … Georges, A. (2015). Sex reversal triggers the rapid transition from genetic to temperature-dependent sex. *Nature*, *523*, 79–82.

Holleley, C. E., Sarre, S. D., O'Meally, D., & Georges, A. (2016). Sex reversal in reptiles: Reproductive oddity or powerful driver of evolutionary change? *Sexual Development*, *10*, 5–6.

Holliday, C. M., Gardner, N. M., Paesani, S. M., Douthitt, M., & Ratliff, J. L. (2010). Microanatomy of the mandibular symphysis in lizards: Patterns in fiber orientation and Meckel's cartilage and their significance in cranial evolution. *The Anatomical Record*, *293*(8), 1350–1359.

Hoops, D., Ullmann, J. F. P., Janke, A. L., Vidal-Garcia, M., Stait-Gardner, T., Dwihapsari, Y., … Keogh, J. S. (2017). Sexual selection predicts brain structure in dragon lizards. *Journal of Evolutionary Biology*, *30*(2), 244–256.

Husak, J. F., Lappin, A. K., & Van Den Bussche, R. A. (2009). The fitness advantage of a high-performance weapon. *Biological Journal of the Linnean Society*, *96*(4), 840–845.

Huyghe, K., Husak, J. F., Moore, I. T., Vanhooydonck, B., Van Damme, R., Molina-Borja, M., & Herrel, A. (2010). Effects of testosterone on morphology, performance and muscle mass in a lizard. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *313*(1), 9–16.

Jiménez, R., Burgos, M., Caballero, L., & De La Guardia, R. D. (1988). Sex reversal in a wild population of *Talpa occidentalis* (Insectivora, Mammalia). *Genetics Research*, *52*(2), 135–140.

Johnson, R., & Adwick, S. (2019). Central bearded dragons (*Pogona vitticeps*). In J. Yeats (Ed.), *Companion Animal Care and Welfare* (pp. 395–411). Oxford, UK: Wiley Blackwell.

Jones, M. E. H. (2008). Skull shape and feeding strategy in *Sphenodon* and other Rhynchocephalia (Diapsida: Lepidosauria). *Journal of Morphology*, *269*, 945–966.

Jones, M. E. H., & Cooper, N. (2020). MarcEHJones/sex-reverse-pv: Code for sex-reverse-pv (Version v1.0). Zenodo. Retrieved from https://doi.org/10.5281/zenodo.3623100

Jones, M. E. H., & Lappin, A. K. (2009). Bite-force performance of the last rhynchocephalian (Lepidosauria: *Sphenodon*). *Journal of the Royal Society of New Zealand*, *39*(2-3), 71–83.

Kis, A., Huber, L., & Wilkinson, A. (2015). Social learning by imitation in a reptile (*Pogona vitticeps*). *Animal Cognition*, *18*(1), 325–331.

Kuo, C. Y., Lin, Y. T., & Lin, Y. S. (2009). Sexual size and shape dimorphism in an agamid lizard, *Japalura swinhonis* (Squamata: Lacertilia: Agamidae). *Zoological Studies*, *48*, 351–361.

Lailvaux, S. P., Cespedes, A. M., & Houslay, T. M. (2019). Conflict, compensation, and plasticity: Sex-specific, individual-level trade-offs in green anole (*Anolis carolinensis*) performance. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *331*, 280–289.

Lappin, A. K., Brandt, Y., Husak, J. F., Macedonia, J. M., & Kemp, D. J. (2006). Gaping displays reveal and amplify a mechanically-based index of weapon performance. *American Naturalist*, *168*, 100–113.

Lappin, A. K., Hamilton, P. S., & Sullivan, B. K. (2006). Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chuckwalla [*Sauromalus ater* (=*obesus*)]. *Biological Journal of the Linnean Society*, *88*, 215–222.

Lappin, A. K., & Husak, J. F. (2005). Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalis*, *166*, 426–436.

Lappin, A. K., & Jones, M. E. H. (2014). Reliable quantification of bite-force performance requires use of appropriate biting substrate and standardization of bite out-lever. *Journal of Experimental Biology*, *217*, 4303–4312.

Li, H., Holleley, C. E., Elphick, M., Georges, A., & Shine, R. (2016). The behavioural consequences of sex reversal in dragons. *Proceedings of the Royal Society B*, *283*, 1–7.

Littleford-Colquhoun, B. L., Clemente, C., Thompson, G., Cristescu, R. H., Peterson, N., Strickland, K., … Frere, C. H. (2019). How sexual and natural selection shape sexual size dimorphism: Evidence from multiple evolutionary scales. *Functional Ecology*, *33*, 1446–1458.

Macrì, S., Savriama, Y., Khan, I., & Di-Poï, N. (2019). Comparative analysis of squamate brains unveils multi-level variation in cerebellar architecture associated with locomotor specialization. *Nature Communications*, *10*, 1–16.

McLean, C. A., Chan, R., Dickerson, A. L., Moussalli, A., & Stuart-Fox, D. (2016). Social interactions generate mutually reinforcing selection for male aggression in Lake Eyre dragons. *Behaviour Ecology*, *27*(4), 1149–1157.

McLean, C. A., & Stuart-Fox, D. (2015). Rival assessment and comparison of morphological and performance-based predictors of fighting ability in Lake Eyre dragon lizards, *Ctenophorus maculosus*. *Journal of Experimental Biology*, *69*, 531–533.

Melville, J., Hunjan, S., McLean, F., Manziou, P., Boysen, K., & Parry, L. J. (2016). Expression of a hindlimb-determining factor Pitx1 in the forelimb of the lizard *Pogona vitticeps* during morphogenesis. *Open Biology*, *6*, 1–17.

Ollonen, J., Da Silva, F. O., Mahlow, K., & Di-Poï, N. (2018). Skull development, ossification pattern, and adult shape in the emerging lizard model organism *Pogona vitticeps*: A comparative analysis with other squamates. *Frontiers in Physiology*, *9*, 1–26.

Pokorna, M. J., & Kratochvil, L. (2016). What was the ancestral sex-determining mechanism in amniote vertebrates? *Biological Reviews*, *91*, 1–12.

Porro, L. B., Ross, C. F., Iriarte-Diaz, J., O'Reilly, J. C., Evans, S. E., & Fagan, M. J. (2014). In vivo cranial bone strain and bite force in the agamid lizard *Uromastyx geyri*. *Journal of Experimental Biology*, *217*(11), 1983–1992.

Quinn, A. E., Georges, A., Sarre, S. D., Guarino, F., Ezaz, T., & Graves, J. A. M. (2007). Temperature sex reversal implies sex gene dosage in a reptile. *Science*, *316*, 411.

R Core Team (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Radder, R. S., Quinn, A. E., Georges, A., Sarre, S. D., & Shine, R. (2008). Genetic evidence for co-occurrence of chromosomal and thermal sex-determining systems in a lizard. *Biology Letters*, *4*, 176–178.

Raiti, P. (2012). Husbandry, diseases, and veterinary care of the bearded dragon (*Pogona vitticeps*). *Journal of Herpetological Medicine and Surgery*, *22*(3), 117–131.

Rauch, N. (1988). Competition of marine iguana females (*Amblyrhynchus cristatus*) for egg-laying sites. *Behaviour*, *107*, 91–106.

Rej, J. E., & Joyner, T. A. (2018). Niche modeling for the genus *Pogona* (Squamata: Agamidae) in Australia: Predicting past (late Quaternary) and future (2070) areas of suitable habitat. *Peer J*, *6*, 1–22.

Ross, C. F., Baden, A. L., Georgi, J., Herrel, A., Metzger, K. A., Reed, D. A., … Wolff, M. S. (2010). Chewing variation in lepidosaurs and primates. *Journal of Experimental Biology*, *213*(4), 572–584.

Sakamoto, M., & Ruta, M. (2012). Convergence and divergence in the evolution of cat skulls: Temporal and spatial patterns of morphological diversity. *PLoS One*, *7*(7), 1–13.

Santana, S. E., Dumont, E. R., & Davis, J. L. (2010). Mechanics of bite force production and its relationship to diet in bats. *Functional Ecology*, *24*(4), 776–784.

Sarre, S. D., Ezaz, T., & Georges, A. (2011). Transitions between sex-determining systems in reptiles and amphibians. *Annual Review of Genomics and Human Genetics*, *12*, 391–406.

Sarre, S. D., Georges, A., & Quinn, A. (2004). The ends of a continuum: Genetic and temperature-dependent sex determination in reptiles. *BioEssays*, *26*, 639–645.

Schaerlaeken, V., Herrel, A., Aerts, P., & Ross, C. F. (2008). The functional significance of the lower temporal bar in *Sphenodon punctatus*. *Journal of Experimental Biology*, *211*(24), 3908–3914.

Schmidt-Ukaj, S., Hochleithner, M., Richter, B., Brandstetter, D., & Knotek, Z. (2017). A survey of diseases in captive bearded dragons: A retrospective study of 529 patients. *Veterinární Medicína*, *62*, 508–515.

Schwanz, L. E., Georges, A., Holleley, C. E., & Sarre, S. D. (2020). Climate change, sex reversal and lability of sex determining mechanisms. *Journal of Evolutionary Biology*, https://doi.org/10.1111/jeb.13587

Sellers, K. C., Middleton, K. M., Davis, J. L., & Holliday, C. M. (2017). Ontogeny of bite force in a validated biomechanical model of the American alligator. *Journal of Experimental Biology*, *220*, 2036–2046.

Shine, R., Elphick, M. J., & Donnellan, S. (2002). Co-occurrence of multiple, supposedly incompatible modes of sex determination in a lizard population. *Ecology Letters*, *5*, 486–489.

Smith, K. R., Cadena, V., Endler, J. A., Kearney, M. R., Porter, W. P., & Stuart-Fox, D. (2016). Color change for thermoregulation versus camouflage in free-ranging lizards. *American Naturalist*, *188*(6), 668–678.

Stauber, A., & Booth, D. J. (2003). Allometry in the bearded dragon *Pogona barbata* (Sauria: Agamidae): Sex and geographic differences. *Australian Zoologist*, *32*, 238–245.

Thompson, G. G., & Withers, P. C. (2005). Size-free shape differences between male and female Western Australian dragon lizards (Agamidae). *Amphibia-Reptilia*, *26*, 55–63.

Tosches, M. A., Tracy, M. Y., Naumann, R. K., Jacobi, A. A., Tushev, G., & Laurent, G. (2018). Evolution of pallium, hippocampus, and cortical cell types revealed by single-cell transcriptomics in reptiles. *Science*, *360*(6391), 881–888.

Watanabe, A., Fabre, A. C., Felice, R. N., Maisano, J. A., Müller, J., Herrel, A., & Goswami, A. (2019). Ecomorphological diversification in squamates from conserved pattern of cranial integration. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(29), 14688–14697.

Whiteley, S. L., Holleley, C. E., Ruscoe, W. A., Castelli, M., Whitehead, D. L., Lei, J., … Weisbecker, V. (2017). Sex determination mode does not affect body or genital development of the central bearded dragon (*Pogona vitticeps*). *Evolution and Devolopment*, *8*, 25.

Witten, G. J. (1985). Relative growth in Australian agamid Lizards: Adaptation and evolution. *Australian Journal of Zoology*, *33*(3), 349–362.

Witten, G. J. (1994). Relative growth in *Pogona* (Reptilia: Lacertilia: Agamidae). *Memoirs of the Queensland Museum*, *37*, 345–356.

Woltering, J. M., Vonk, F. J., Müller, H., Bardine, N., Tuduce, I. L., de Bakker, M. A., … Richardson, M. K. (2009). Axial patterning in snakes and caecilians: Evidence for an alternative interpretation of the Hox code. *Developmental Biology*, *332*(1), 82–89.

Wotherspoon, D., & Burgin, S. (2011). Allometric variation among juvenile, adult male and female eastern bearded dragons *Pogona barbata* (Cuvier, 1829), with comments on the behavioural implications. *Zoology*, *114*, 23–28.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Jones MEH, Pistevos JCA, Cooper N, et al. Reproductive phenotype predicts adult bite-force performance in sex-reversed dragons (*Pogona vitticeps*). *J. Exp. Zool.* 2020;333:252–263. https://doi.org/10.1002/jez.2353