
CAN WE USE HEAD SCALE SYMMETRY IN ENDANGERED PYGMY BLUETONGUE LIZARDS (*TILIQUA ADELAIDENSIS*) TO ALERT MANAGERS TO POPULATION CONDITION?

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Abstract.—Different levels of symmetry of individuals within a population or among populations are suggested to correlate positively with environmental or genetic stress by affecting the developmental stability of an organism during growth. However, the studies on the relationship between asymmetry and fitness have shown heterogeneous results. If stress increases the level of symmetry of an individual in a population, the measurement of asymmetry can be a valuable tool to assess the wellbeing of that population. In this paper we evaluated symmetry in head scales of Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) to establish if there was a relationship between a symmetry index and three indirect fitness measures, body condition, jaw width, and activity period (early and late in the season). We found that lizards captured in the late activity period had more symmetric head scales than those captured in the early activity period. Our results also demonstrated that females were less symmetric than males. Jaw width had a negative significant relationship with the symmetry index for all groups of lizards, where lizards with wider jaws were less symmetric. We did not find a significant correlation between body condition with either jaw width or with the symmetry level for any of the groups of lizards. The significant differences in symmetry of the head scalation between sexes and between samples collected during different periods of the year indicate that there are fitness differences associated with symmetry in Pygmy Bluetongue Lizard populations. Nevertheless, we did not find consistently strong evidence of an association between asymmetry and poor body condition in Pygmy Bluetongue Lizards. Therefore, at present, there is little value in assessing population well-being using asymmetry measures of head scalation in this species.

Key Words.—body condition; conservation; developmental stability; endangered species; fluctuating asymmetry; *Tiliqua adelaidensis*

INTRODUCTION

The growing rate of species extinction has prompted wildlife conservation managers to use biological indicators to identify species at risk, find underlying causes of decline and implement appropriate management programs to halt or reverse the decline. For endangered species that are restricted to small isolated patches of habitat, populations will face multiple threatening processes. These include ecological stresses from crowding, from habitat deterioration, and from climatic changes, and genetic stresses from elevated levels of inbreeding within small isolated populations (Soule 1979; Parsons 1992; Polak and Trivers 1994; Clarke 1998; Lens 2000).

Fluctuating asymmetry is considered to be one indicator of long-term stress (Sarre 1996). Fluctuating asymmetry is defined as random deviation from perfect symmetry in otherwise bilaterally symmetrical traits, and has become a commonly used measure of developmental stability that might be linked to stress conditions during growth (Palmer 1996; Palmer and Strobeck 2003; Van Valen 1962). As the two corresponding body sides share a single genome and experience similar external factors, differences in their development are unlikely to have

resulted from environmental or direct genetic effects. Rather, it is believed that asymmetry reflects the inability of individuals to buffer their development against small, random perturbations (Sarre et al. 1994; Palmer 1996). Different levels of asymmetry of individuals within a population, or among populations, are sometimes shown to correlate positively with environmental stress (Polak and Trivers 1994; Møller and Swaddle 1997), from factors such as extreme climate, degraded, fragmented or polluted habitat (Sarre 1996; Wright and Zamudio 2002; Helle et al. 2011), or inadequate nutrition (Vangestel and Lens 2011) with higher levels of asymmetry in more stressful conditions. Similarly, it has been suggested that genetic stress resulting from the loss of genetic diversity either by inbreeding or genetic drift, might increase the incidence and level of asymmetry in populations (Leung and Forbes 1997; Clarke 1998; Lens et al. 2002; Learnly and Klingenberg 2005; Pertoldi et al. 2006).

If stress increases asymmetry of individuals in a population, then measurements of symmetry might be a valuable tool to quickly assess the well-being of the population (Lemberget, 2009). A high proportion of asymmetric individuals may indicate that the population has experienced or is experiencing stress, and that

management intervention is required (Alford, 1999). If there is an established relationship between fluctuating asymmetry and fitness, it can be a useful monitoring tool to detect changing condition in populations.

As well as monitoring populations overall, fluctuating asymmetry may also relate to quality and fitness among individuals within a population (Leary and Allendorf 1989; Houle 1997; Brown and Brown 1998; Alford et al. 1999; Leung et al. 2000). Less symmetrical individuals may have lower fitness, especially where the trait measured directly affects performance (Møller 1991, 1992a). Females of the lizard *Lacerta monticola* preferred males that were more symmetric in the number and size of their femoral pores (Martin and Lopez 2000). Despite these findings, not all studies have reported negative relationships between fluctuating asymmetry and fitness (Lindell et al. 1993; Swaddle and Witter 1994; Bjorksten et al. 2000; Shine 2005; Lens and Eggermont 2008). Our aim in this paper was to explore the value of measuring symmetry in the dorsal head scales of an endangered Australian lizard, as a potential tool to monitor individual fitness and population condition.

The Pygmy Bluetongue Lizard (*Tiliqua adelaidensis*) is an endangered Australian scincid lizard, now restricted to a small number of isolated fragments of previously continuous native grassland in the mid-north region of South Australia (Milne et al. 2003). The species was thought to be extinct for 30 y until its unexpected re-discovery in the stomach of a Brown Snake (*Pseudonaja textilis*) near the town of Burra, South Australia, in 1992 (Armstrong and Reid 1992; Armstrong et al. 1993). Although a promiscuous mating system appears to have retained high levels of genetic diversity within some remaining populations (Schofield et al. 2014), there is now no detectable dispersal between even geographically close population sites (Smith et al. 2009) and a risk of losing genetic diversity in small populations. If head scale symmetry reflected genetic or ecological stress, it would be an easily applied tool for monitoring population condition.

In this paper, we measured symmetry in the head scales of the Pygmy Bluetongue Lizard and made three indirect assays of fitness, related to ecological stress. Those assays generated three specific hypotheses about the relationship between symmetry and lizard fitness, with the ultimate aim of determining if symmetry could be a useful indicator for monitoring overall population health in this endangered species. The first hypothesis was that adult individuals with different symmetry had different probability of survival over their spring and summer activity period. To assess this hypothesis we compared the symmetry of individuals caught early or late in the activity season. Any difference in mean symmetry between those two periods might indicate differential mortality, and hence, by implication,

different fitness of individuals with different levels of symmetry.

The other two hypotheses were that two indirect measures of adult lizard fitness were related to lizard symmetry. One of these hypotheses concerned a measure of jaw width, with an assumption that lizards with wider jaws were fitter because they might have a wider range of food items or might be better in conspecific agonistic encounters. Head size has been identified as important in both intra- and intersexual agonistic behaviors in many lizards (Mouton and Van Wyk 1993; Husack et al. 2006; Herrel et al. 1996). Males with larger heads and larger jaws are more effective in fights with other males (Bull and Pamula 1996), and can hold females more firmly, which gives them an advantage in both competition with other males and in copulation (Vitt and Cooper 1985; Herrel et al. 1999). Among insectivorous lizards, individuals of either sex with wider jaws may also have an advantage in being able to capture and ingest larger prey items (Siqueira et al. 2013; Herrel et al. 1999). The third hypothesis concerned a measure of body condition, derived from the relationship between body mass and snout-to-vent length (SVL), with the assumption that lizards with higher body condition were fitter.

Our aim was to establish if there were relationships between symmetry and fitness among individuals in a population that might allow the degree of symmetry to be used to indicate overall population condition. A more specific aim was to develop a simple examination of symmetry, based on body parts, which could be quickly assayed in an endangered species. Our chosen assay was by photography of the dorsal scales, so that population condition, if it was associated with symmetry, could be quickly monitored.

MATERIALS AND METHODS

Study site and sampling.—We collected samples from two isolated populations of Pygmy Bluetongue Lizards within 15 km of each other, near Burra, South Australia (33°42'S, 138°56'E). The area has hot, dry summers and cool, moist winters. The long-term average annual rainfall at Burra is about 400 mm. We located lizards in each population by inspecting burrows with an optical fiberscope (Provision Elite/ Olympus IF8D4X2-10L, Chicago Miniature Lighting LLC, Chicago, Illinois, USA), and captured them by hand after luring them out with a mealworm tethered to a fishing line (Strong et al. 1993; Milne 1999; Fenner 2009). Pygmy Bluetongue Lizards are active between September and April (the austral spring/summer; Milne 1999) and we call this seven month period the activity period. We sampled on 262 d over three activity periods (2008/2009 and 2010/2011). In the analyses we refer to these as three sampling years (2008, 2009, and 2010) related to the

TABLE 1. Count of lizards captured during each sampling year and the count of 30% of the most symmetric and 30% of the least symmetric Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*), Burra, South Australia.

Groups	2008/2009	2009/2010	2010/2011	Total
All Lizards				
Male	25	55	2	82
Female	24	50	9	81
Total Adults	49	105	11	163
30% of Most/Least Symmetric				
Male	16	32	2	50
Female	18	26	6	50
Total Adults	36	55	9	100

year of the spring start to the season. We divided the lizards each year into two groups, those sampled in the early part of the season (September to December), and the different group of lizards sampled in the later part of the season (December to April). Following Milne (1999), we defined adults as those with a snout to vent length (SVL) of more than 80 mm, and only included adults in the subsequent analyses. We assessed 163 adult lizards for symmetry (see below), and selected 100 individuals (30% of the most symmetric and 30% of the least symmetric; see below) for some analyses (Table 1).

For each lizard we recorded the date of capture, its sex (usually by cloacal examination), mass (to the nearest 0.5 g), SVL, and jaw width (JW; both to the nearest 1.0 mm). Jaw width was measured as the longest distance between left and right ears for each lizard (Fig. 1). We took digital photographs of the scales on the dorsal surface of the head of each adult lizard (Fig. 2) using a Canon SLR 450D camera (Canon Inc., Tokyo, Japan). We gave each lizard a unique toe clip identification marking, and then released them back into their burrows.

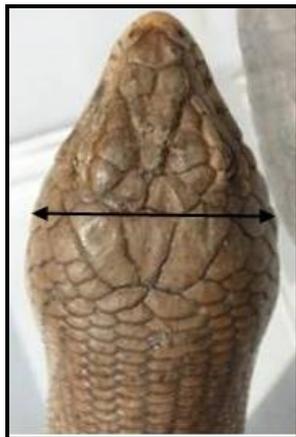


FIGURE 1. Head of a Pygmy Bluetongue Lizard (*Tiliqua adelaidensis*) showing the measurement of jaw width (JW) as the distance between two ears. (Photographed by Leili Shamiminoori).

We deliberately searched for independent samples and avoided recaptures by broadening the area of sampling on each new visit. For the small number of lizards that were captured more than once, we used only data from the first capture.

We calculated a body condition index from the residuals of the linear regression for all adults between the natural log-transformed mass and the natural log-transformed SVL (Shamiminoori et al. 2014). This measure of body condition is commonly used in reptile population studies (Green 2001; Madsen and Shine 2000). In our study system, there is a highly significant positive relationship between (ln) mass and (ln) SVL (Shamiminoori et al. 2014), a condition that makes this index a powerful indicator of fitness (Bradshaw et al. 2000; Peig and Green 2010).

Development of a symmetry index.—We developed a symmetry index by comparing the size and shape of each of six pairs of dorsal head scales (Fig. 2). Before making those comparisons, we needed to correct the digital images for the impact of variation in image size, in horizontal tilt and in luminance. This process has been formally described by Tohl et al. (2013). First, we transformed color images of the head of each lizard to grayscale so that any seasonal changes in dorsal color would not affect interpretation of the outline of the scales. Then we inserted a vertically centered line of symmetry from the tip of the snout to the middle of the neck for each photo, positioned so that the mirror image of the head scales across the line produced the highest cross-correlations. Next we corrected the image for any angle of head tilt in the posture of the lizard while it was being photographed. To achieve this, we split the image into left and right halves using the line of symmetry, and then tilted through various degrees. The left half of the image was mirrored and then cross-correlated with the

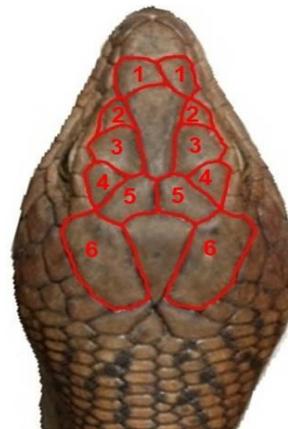


FIGURE 2. Diagram of the six pairs of scales used in deriving the symmetry index (SI) of the head of a Pygmy Bluetongue Lizard (*Tiliqua adelaidensis*). (Photographed by Leili Shamiminoori).

right half at each 0.5 degree angle of tilt. We deemed the angle with the highest correlation value as the angle for tilt correction. Next we applied edge detection techniques to the image to extract scale pattern edges of the head as binary images. Edge detection removed features from in between the scale patterns that might affect individual scale measurements. Finally, we calculated a symmetry index as the normalized correlation between extracted scale outlines of the left and right images. This resulted in a value between one and zero. Values closer to one were more symmetrical, while values closer to zero were less symmetrical (Tohl et al. 2013).

Statistical analysis.—We pooled samples from all years and from both populations in the analyses, but we included each lizard only once. To investigate changes in the symmetry index among individuals sampled at different times within a sampling year, we divided the data into an early activity period (between September and December) and a late activity period (between January and April the following year), as described previously (Shamiminoori et al. 2014). If the degree of symmetry directly affected survival of lizards across the spring and summer, we expected that the distribution of symmetry index values should change from early to late in the season, and that this should be reflected in the lizards we sampled at different times. To test this, we performed a two-way ANOVA of the symmetry index, with sex and activity period (early or late in the season) as factors.

If the degree of symmetry was indirectly related to lizard fitness, we expected to find a relationship between the symmetry index and an indicator parameter of fitness. To test this, we conducted Pearson's correlation analyses between the symmetry index and either jaw width or body condition index in the adult lizards. We first analyzed data from all adult lizards, then from adult males and females separately to allow for any effects of sexual size dimorphism (Hutchinson et al. 1994). For analysis of body condition in females, we also considered separately individual females at two different reproductive stages, pre-parturition (before 7 November), and post-parturition (after 15 February of the following year) to allow for reproductive changes in body condition (Shamiminoori et al. 2014). We omitted analyses of females collected in between these dates because inclusion of both gravid and non-gravid individuals might confuse interpretation of any trends in body condition. In each analysis of a separate group of lizards, we derived new body condition index values based on the residuals from the regression of natural logs of body mass against SVL for just that group of lizards.

In further analyses, we used a general linear model in 'R', version 2.13.0 (Symonds and Mousalli 2011) to determine the relative importance of sex, sampling year,

TABLE 2. Results of two-way ANOVA of symmetry index with sex and activity period as factors. Significant results are shown in bold.

	df	F	P
Sex	1	7.863	0.006
Activity period	1	6.829	0.010
Activity period × Sex	1	0.007	0.935
Error	96		

and symmetry index on jaw width (in one analysis) and body condition index (in a second analysis). In these analyses, jaw width or our body condition index were the dependent variables and the symmetry index, sampling year, and lizard sex were fixed factors. For the factor symmetry index, we categorized lizards into two groups of Symmetrical or Asymmetrical individuals describing the level of symmetry in their head scales. In this paper we report analyses using the 30% most symmetrical and the 30% least symmetrical lizards (Table 1). For separate analyses on only males or only females, we chose 30% of the most symmetric and 30% of the least symmetric males or females separately. Equivalent analyses using the 20%, 40% and 50% most and least symmetrical individuals produced similar results and are reported in Supplementary Tables 1.

For these general linear model analyses of all adult lizards, we followed a model selection approach (Burnham and Anderson 2002) comparing 10 models for the data set including all three main effects (sex, symmetry level [most symmetric and least symmetric] and year) and different combinations and interactions of those effects, plus a null model with only an intercept. For data sets with just males or just females, we compared five models with different combinations of symmetry level and year. We used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to select the models that best explained the observed variation in jaw width or in body condition index. We calculated AIC_c values for all models and then the Akaike weight (*w_i*) of each, to rank them and evaluate model fit. For each variable considered, we also calculated the model-averaged coefficient and confidence intervals using the modavg package in R 2.13.0. We considered model-averaged coefficients that had confidence intervals that did not overlap zero to have a strong effect on the dependent variable. The full list of models is given in Supplementary Tables 2.

RESULTS

The symmetry index calculated from all adults had a mean and SE of 0.389 ± 0.13 (range, 0.152–0.648). Males (mean = 0.406 ± 0.13 ; range, 0.181–0.647) were significantly more symmetrical than females (mean = 0.368 ± 0.134 ; range, 0.152–0.610; Table 2; Fig. 3a). We found significant differences in the symmetry index

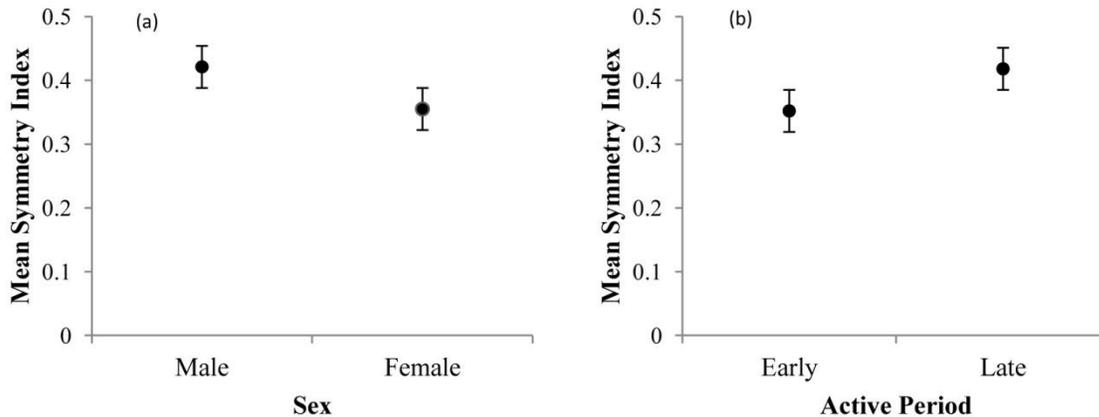


FIGURE 3. Comparisons of symmetry index between (a) male and female adult Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*), and (b) early and late activity periods.

between individuals that were sampled early and the different group of individuals that were sampled late in the season (Table 2), with a higher symmetry in lizards sampled in the late activity period (January to April) than in the early activity period (September to December; Fig. 3b). There was no significant interaction between sex and activity period, indicating that both males and females sampled late in the season were more symmetric than those sampled early in the season.

Jaw width.—We found significant negative correlations between the symmetry index and jaw width for all adults, and for both males and females (Table 3). Lizards that were less symmetric in their head scales had

significantly wider jaws. Analysis of Covariance for jaw width on all adult lizards using the symmetry index as a covariate, also showed a significant effect of the symmetry index on jaw width ($F_{1,96} = 13.71$; $P < 0.001$), but no effect of sex ($F_{1,96} = 1.25$; $P = 0.260$), and no significant interaction between sex and symmetry index ($F_{1,96} = 1.88$, $P = 0.200$). Changes in jaw width with the symmetry index occurred equally in each sex.

The most parsimonious AIC models to explain the variation of jaw width among individuals contained only the symmetry level (Table 4). In all lizards, and in both

TABLE 3. Results of the correlations (r) with sample size (n) and P values between jaw width and symmetry index (JW-SI), jaw width and body condition (JW-BC), and body condition and symmetry index (BC-SI) of Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*), Burra, South Australia. Acronyms are SI, Symmetry Index; JW, Jaw Width; and BC, Body Condition. Correlations with asterisks are significant at 0.05 (2-tailed).

Lizard group	r	n	t -value	P -value
JW-SI				
All adults	-0.370**	100	3.94	0.001
Males	-0.426**	50	3.26	0.001
Females	-0.298*	50	2.16	0.035
JW-BC				
All adults	-0.030	100	0.30	0.768
Males	-0.021	50	0.15	0.886
Females	-0.016	50	0.11	0.913
BC-SI				
All adults	0.113	100	1.12	0.262
Males	0.163	85	1.51	0.257
Females	-0.045	80	0.40	0.756

TABLE 4. Summary of the best-ranked AIC models examining the effect of the level of symmetry (sym), sampling year, and sex on jaw width in the 30% of data of all adults, males, and females Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*), Burra, South Australia. Acronyms are K, the number of fitted parameters; AIC, Akaike's Information Criteria; Δ AIC, difference between AIC value of the best model and AIC value of other models; w_i , Akaike model weight; cum w_i , Cumulative Akaike weights; \times refers to the interaction between factors; + represents the inclusion of main factors in the model.

Candidate models	K	AIC _c	Δ AIC _c	w_i	Cum. w_i
All adults					
Sym	3	311.912	0.000	0.404	0.404
Sym + Year	4	313.719	1.807	0.164	0.567
Sym+ Sex	4	313.807	1.895	0.157	0.724
Males					
Sym	3	176.140	0.000	0.491	0.491
Sym + Year	4	176.701	0.560	0.371	0.863
Sym x Year	5	179.056	2.916	0.114	0.977
Females					
Sym	3	128.334	0.000	0.417	0.417
Year	3	129.549	1.214	0.227	0.644
Sym + Year	4	130.136	1.801	0.169	0.814

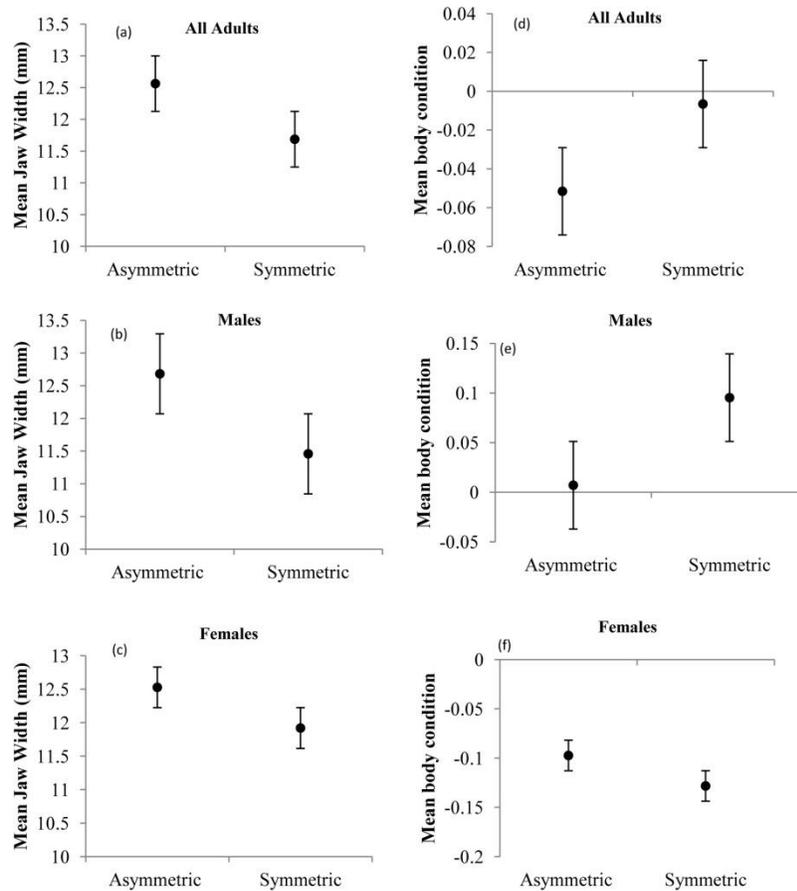


Figure 4. Comparisons of the mean jaw width (a-c) and mean body condition (d-f) between the most symmetric and the most asymmetric all adults, male, and female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*).

males and females separately, symmetry level had the highest predictor weight; with negative model average coefficients that were significant for all lizards and for males (Table 5). The 30% of lizards with the least

symmetric heads had wider jaws than the 30% of lizards with the most symmetrical heads (Fig. 4). Sampling year appeared in the second-best models for all adults, and for both males and females. However, the predictor weight was not strong enough in any data set to show a significant effect of sampling year on jaw width.

TABLE 5. Results of the AIC model averaging for jaw width in 30% of all lizards, male, and female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*), Burra, South Australia. Significant results are shown in bold.

	Jaw Width		
	Predictor w_i	Model Av. β	95% CI
All adults			
Sym	0.995	-0.867	-1.315, -0.419
Sex	0.361	-0.124	-0.583, 0.335
Males			
Sym	0.976	-4.552	-8.319, -0.785
Year	0.497	0.276	-0.133, 0.687
Females			
Sym	0.645	-1.614	-4.313, 1.084
Year	0.455	0.265	-0.167, 0.698

Body condition.—Our lizard body condition index was not significantly correlated with either jaw width (Table 3), or with the symmetry level (Table 3) for any of the groups of lizards. For the body condition index, the best AIC model for all adults included only sex (Table 6) with females showing lower body condition values than males. The symmetry level appeared as a factor that explained body condition in models with a ΔAIC of < 2 for all lizards, for males and for females (Table 6), and there were positive predictor coefficients in each case (Table 7). However, none of the coefficients were significant, indicating weak effects of the symmetry index on body condition (Fig. 4). Symmetry level did not appear in any of the highest ranked models for body condition in either pre-partum or

TABLE 6. Summary of the best-ranked AIC models examining the effect of level of symmetry (sym), sampling year and sex on the body condition of the 30% of the data of all adults, males, females, pre-partum, , and post-partum females of Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*), Burra, South Australia. Acronyms are K, the number of fitted parameters; AIC, Akaike’s Information Criteria; Δ AIC, difference between AIC value of the best model and AIC value of other models; w_i , Akaike model weight; cum w_i , Cumulative Akaike weights; \times refers to the interaction between factors; + represents the inclusion of main factors in the model.

Candidate model	<i>K</i>	AICc	Δ AICc	w_i	Cum. w_i
All adults					
Sex	3	-18.36	0.000	0.383	0.383
Sym+ Sex +	5	-17.37	0.994	0.233	0.616
Year					
Sym + Sex	4	-16.32	2.053	0.137	0.753
Males					
Null	2	-4.219	0.000	0.520	0.520
Sym	3	-2.496	1.723	0.219	0.740
Year	3	-1.994	2.225	0.171	0.911
Females					
Sym + Year	4	-23.13	0.000	0.370	0.370
Year	3	-22.89	0.241	0.328	0.698
Sym x Year	5	-22.10	1.039	0.220	0.918
Pre-partum					
Year	3	-19.43	0.000	0.398	0.398
Null	2	-19.27	0.153	0.369	0.767
Sym	3	-16.28	3.144	0.082	0.850
Post-partum					
Null	2	0.392	0.000	0.604	0.604
Year	3	2.361	1.968	0.225	0.830
Sym	3	2.957	2.564	0.167	0.997

post-partum females.

DISCUSSION

We documented variation in the level of symmetry in the head scalation among adult Pygmy Bluetongue Lizards and found three significant trends. First, females showed significantly less symmetry than males. Second, symmetry was lower in lizards sampled in the early activity period (September-December) than in those sampled in the late activity period (January-April). And third, there was a significant negative relationship between the index of symmetry and jaw width.

One explanation for the difference in symmetry between males and females may be that females were under more stress during development. Alternatively, there may be higher selection pressure on males to be symmetric. Other studies, in other species, have reported a female preference for more symmetrical males even when the mating cues are olfactory with no obvious reference to the visual aspects of the symmetry (Thornhill 1992; Lopez et al. 2002). Although the pattern of head scale symmetry is unlikely to represent a secondary sexual character, symmetry in that aspect may

TABLE 7. Results of the AIC model averaging of 30% of data for body condition in all adults, males, females, pre-partum, and post-partum females of Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*), Burra, South Australia. Significant results are shown in bold.

	Body condition		
	Predictor w_i	Model Av. β	95% CI
All adults			
Sym	0.623	0.299	-0.656, 1.256
Sex	0.865	0.112	-0.239, 0.464
Year	0.412	0.100	0.123, 0.325
Males			
Sym	0.306	0.180	-0.388, 0.748
Year	0.258	-0.006	-0.075, 0.063
Females			
Sym	0.610	0.596	-0.427, 1.620
Year	0.918	0.120	0.021, 0.218*
Pre-partum			
Sym	0.306	0.180	-0.388, 0.748
Year	0.258	-0.006	-0.075, 0.063
Post-partum			
Sym	0.169	-0.594	-1.506, 0.316
Year	0.227	0.101	-0.022, 0.224

be correlated with another character used as a sexual cue. Pygmy Bluetongue Lizard females can mate multiple times and apparently randomly with respect to genetic relatedness (Schofield et al. 2012), although video recordings have shown that not all courting males are accepted by females (Ebrahimi et al. 2014). Thus, although it is not yet established, there may be some mate choice by females, and, as in other species, symmetrical males may be preferred.

The trend for lower symmetry early in the activity season may reflect higher mortality in less symmetrical adult lizards over the activity season. Previous studies have shown that lizards are more likely to be moving on the surface, either seeking new burrows or looking for mating partners, in the early period (Schofield et al. 2014) and much more likely to remain in their burrow in the late period (Ebrahimi 2013). When lizards are outside of their burrows they are most susceptible to predation (Fenner et al. 2008) and populations suffer a decline in resident adults during the whole activity period (Fellows et al. 2009). An interpretation for the increase in symmetry over the season is that there is higher mortality among less symmetric individuals. An implication is that more symmetric individuals are fitter. This trend was equivalent for both sexes.

An explanation of why lizards with wider jaws were less symmetric in their head scalation could relate to the ontogenetic origins of symmetries. Symmetry relies on developmental stability (Palmer and Strobeck 1986, 2003). Higher investment into growth of one trait, such as the jaw, may reduce control on the stability of development of other traits, allowing developmental noise to cause random asymmetries in biosynthesis of

the two sides in those other traits (Aparicio 1998). In that case, variation of symmetry in one trait could correlate with different investments to the growth in another, without directly influencing overall developmental stability. The origin of variation in symmetry of particular traits in a species could be better deduced from patterns of change in symmetry as individuals grow. In this case, lizards that develop wider jaws may do so at the expense of symmetry in other characters, like the head scales. This is not an entirely satisfactory explanation as lizards with wider jaws may be able to compensate by increasing food consumption, so there would be no need to reallocate energy between both traits.

In some lizards, jaw width is considered an indirect measure of fitness in that lizards of both sexes with wider jaws can handle a wider range of prey item sizes (Vitt and Cooper 1985; Vitt and Pianka 1994; Herrel et al. 1999; Siqueira et al. 2013), and male lizards with wider jaws can fight conspecific rivals better (Bull and Pamula 1996), or can grasp females for mating more strongly (Milne 1999). Thus, our finding that the widest jaws belonged to the lizards with the least symmetry might be seen to potentially contradict our earlier conclusion that more symmetric lizards were fitter. Nevertheless, the temporal trend for lizards in the population to show higher symmetry later in the season is a stronger indication of a real fitness advantage for symmetry, than any indirect measure of fitness.

Our measure of body condition similarly provided no support for an association between symmetry and fitness, because there was no relationship between the symmetry index and body condition index. In contrast to some other studies, we found no evidence that individuals with less symmetrical head scalation had reduced fitness in terms of body growth or jaw width. In a range of species, the relationship between asymmetry and fitness can be sex, trait or species specific (Clarke 1995; Leung and Forbes 1997). In our system we did not explore symmetry in other traits (e.g., left and right limb measurements; number of lamellae in toes) because we considered investigating those traits would take more handling time and would be more intrusive. Although the general hypothesis is that symmetry manifests an overall phenotypic quality (e.g., Palmer and Strobeck 2003), the literature shows very mixed results. The lack of correlation between symmetry and indirect fitness measurements that we report is not without precedent in the literature (Møller 1992a, 1993a; Dufour and Weatherhead 1998a, b). In Pygmy Bluetongue Lizards, head scalation is neither a sexual trait nor a performance trait, although it is plausible head scale symmetry may reflect other developmental stabilities, and, more broadly, overall fitness.

An explanation for the lack of relationship between body condition and symmetry in head scales may be that

all of the lizards in the populations have developed under relatively benign and unstressed conditions. Associations between symmetry and fitness may become stronger under high stress levels (Lens et al. 2002; Woods et al. 2002; Hendrickx et al. 2003). In the two Pygmy Bluetongue Lizard populations we studied, the lizards may not be under high levels of stress, despite the fact that they are now isolated in small fragments of native grassland and classed as Endangered. Schofield et al. (2014) showed that high genetic heterogeneity was sustained by promiscuous mating patterns in these populations, and a natural cycle of abundance and decline may have evolved in the stochastic natural conditions of their semi-arid habitat, before habitat fragmentation led to their current endangered status. In conditions where there is little ecological or genetic stress, attempts to use measures of symmetry as assays of population health may be unrewarding.

In conclusion, we found significant differences in symmetry of the head scalation between sexes, and between samples collected at different periods of the year. Both of these relationships indicate that there could be fitness differences associated with symmetry in Pygmy Bluetongue Lizard populations. The adjustment of levels of symmetry by sexual and natural selection is probably a continuing normal process in this species, as in most other animal species. Nevertheless, we did not find consistently strong evidence of an association between asymmetry and poor body condition. The lower symmetry in lizards with wider jaws may indicate that a healthy population of Pygmy Bluetongue Lizards should show some level of asymmetry. Current populations of Pygmy Bluetongue Lizards are not inbred or lacking genetic heterozygosity (Schofield et al. 2014), so we do not expect the extreme high levels of asymmetry that might trigger conservation concern. This is an important finding both from the perspective of the biology of isolated populations in general, and from the more specific perspective of conservation management of Pygmy Bluetongue Lizards. In the case of this species and at this point in time, there is little value in trying to assess population well being using asymmetry measures of head scalation. Further work may establish a stronger relationship between symmetry and body condition using a multi-trait approach.

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SUPPLEMENTARY DATA I

TABLE 1. Summary of the best-ranked AIC models examining the effect of level of symmetry (Sym), sampling year and sex on body condition of 20% of the most symmetrical and most asymmetrical all adults, male, and female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) in Burra, South Australia.

Candidate model	<i>K</i>	AICc	Δ AICc	w_i	Cum. w_i
All Adults					
Sex	3	-13.535	0.000	0.282	0.282
Sym x Year x Sex	9	-13.313	0.222	0.252	0.534
Sym + Year + Sex	5	-11.996	1.538	0.130	0.665
Males					
Null	2	-5.615	0.000	0.536	0.536
Year	3	-3.849	1.766	0.221	0.757
Females					
Sym + Year	4	-13.933	0.000	0.411	0.411
Year	3	-13.438	0.494	0.321	0.732

TABLE 2. Summary of the best-ranked AIC models examining the effect of level of symmetry (Sym), sampling year and sex on body condition of 40% of the most symmetrical and most asymmetrical all adults, male, and female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) in Burra, South Australia.

Candidate model	<i>K</i>	AICc	Δ AICc	w_i	Cum. w_i
All Adults					
Sex	3	-32.750	0.000	0.282	0.282
Sym + Year + Sex	5	-31.726	1.023	0.252	0.534
Sym x Year x Sex	4	-30.682	2.067	0.130	0.665
Males					
Null	2	-10.861	0.000	0.522	0.522
Year	3	-9.045	1.815	0.210	0.733
Females					
Null	2	-17.739	0.000	0.321	0.321
Year	3	-17.712	0.026	0.316	0.637
Sym + Year	4	-16.324	1.414	0.158	0.796

TABLE 3. Summary of the best-ranked AIC models examining the effect of level of symmetry (Sym), sampling year and sex on body condition of 50% of the most symmetrical and most asymmetrical all adults, (male, and female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) in Burra, South Australia.

Candidate model	K	AICc	Δ AICc	w_i	Cum. w_i
All Adults					
Sex	3	-50.936	0.000	0.535	0.535
Sym + Sex	4	-48.848	2.088	0.188	0.723
Males					
Null	2	-15.191	0.000	0.490	0.490
Sym	3	-13.599	1.591	0.221	0.712
Year	3	-13.114	2.076	0.173	0.885
Females					
Null	2	-25.557	0.000	0.345	0.345
Year	3	-25.319	0.237	0.306	0.651
Sym+ Year	4	-23.636	1.921	0.132	0.783

TABLE 4. Summary of the best-ranked AIC models examining the effect of level of symmetry (Sym), sampling year and sex on jaw width of 20% of the most symmetrical and most asymmetrical all adults, male, and female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) in Burra, South Australia.

Candidate model	K	AICc	Δ AICc	w_i	Cum. w_i
All Adults					
Sym	3	212.204	0.000	0.420	0.420
Sym + Year	4	214.058	1.853	0.166	0.587
Sym x Sex	4	214.241	2.036	0.151	0.739
Males					
Sym	4	122.699	0.000	0.585	0.585
Sym x Sex	3	125.185	2.485	0.168	0.753
Females					
Year	3	83.543	0.000	0.315	0.315
Null	2	83.552	0.008	0.314	0.630
Sym	3	84.056	0.512	0.244	0.874

TABLE 5. Summary of the best-ranked AIC models examining the effect of level of symmetry (Sym), sampling year and sex on jaw width of 40% of the most symmetrical and most asymmetrical all adults, male, and female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) in Burra, South Australia.

Candidate model	K	AICc	Δ AICc	w_i	Cum. w_i
All Adults					
Sym	3	411.509	0.000	0.320	0.320
Sym + Year	4	412.410	0.900	0.204	0.525
Sym x Sex	5	412.576	1.066	0.188	0.713
Sym + Sex	4	413.220	1.710	0.136	0.850
Males					
Sym	4	225.132	0.000	0.429	0.429
Sym + Year	3	225.138	0.006	0.428	0.857
Females					
Sym + Year	3	154.001	0.000	0.447	0.447
Sym	4	155.637	1.635	0.197	0.645
Year	3	155.715	1.713	0.190	0.835

TABLE 6. Summary of the best-ranked AIC models examining the effect of level of symmetry (Sym), sampling year and sex on jaw width of 50% of the most symmetrical and most asymmetrical all adults, male, and female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) in Burra, South Australia.

Candidate model	K	AICc	Δ AICc	w_i	Cum. w_i
All Adults					
Sym + Year	4	525.663	0.000	0.370	0.370
Sym	3	527.086	1.422	0.182	0.552
Sym + Sex + Year	5	527.565	1.901	0.143	0.695
Sym x Sex	5	527.737	2.073	0.131	0.827
Males					
Sym	3	271.550	0.000	0.505	0.505
Sym + Year	4	272.209	0.658	0.363	0.869
Females					
Year	3	211.734	0.000	0.480	0.480
Sym+ Year	4	213.130	1.396	0.238	0.718

SUPPLEMENTARY DATA II

TABLE 1. A full list of alternative models tested for the effect of level of symmetry and sampling year on body condition of 30% of the most symmetrical and most asymmetrical all adults, male, female, pre-partum, and post-partum Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) in Burra, South Australia.

Candidate model	K	AICc	Δ AICc	w_i	Cum. w_i
All adults					
Sex	3	-18.369	0.000	0.383	0.383
Sym+ Sex + Year	5	-17.374	0.994	0.233	0.616
Sym + Sex	4	-16.316	2.053	0.137	0.753
Sym x Sex	5	-15.218	3.151	0.079	0.832
Sym x Year x Sex	9	-14.340	4.028	0.051	0.883
Sym x Year	5	-13.695	4.673	0.037	0.920
Sym + Year	4	-13.818	4.550	0.034	0.956
Year	3	-12.812	5.556	0.023	0.976
Null	2	-11.922	6.446	0.015	0.991
Sym	3	-10.816	7.552	0.008	1.000
Males					
Null	2	-4.219	0.000	0.520	0.520
Sym	3	-2.496	1.723	0.219	0.740
Year	3	-1.994	2.225	0.171	0.911
Sym + Year	4	-0.139	4.074	0.067	0.979
Sym x Year	5	2.236	6.455	0.020	1.000
Females					
Sym + Year	4	-23.135	0.000	0.370	0.370
Year	3	-22.894	0.241	0.328	0.698
Sym x Year	5	-22.096	1.039	0.220	0.918
Null	2	-19.546	3.589	0.061	0.980
Sym	3	-17.302	5.833	0.020	1.000
Pre-partum					
Year	3	-19.426	0.000	0.398	0.398
Null	2	-19.272	0.153	0.369	0.767
Sym	3	-16.281	3.144	0.082	0.850

Sym +Year	4	-16.076	3.349	0.074	0.925
Sym x Year	4	-16.076	3.349	0.074	1.000
Post-partum					
Null	2	0.392	0.000	0.604	0.604
Year	3	2.361	1.968	0.225	0.830
Sym	3	2.957	2.564	0.167	0.997
Sym +Year	4	11.410	11.018	0.002	1.000
Sym x Year	5	29.878	29.485	0.000	1.000

TABLE 2. A full list of alternative models tested for the effect of level of symmetry and sampling year on jaw width of 30% of the most symmetrical and most asymmetrical all adults, male, female Pygmy Bluetongue Lizards (*Tiliqua adelaidensis*) in Burra, South Australia.

Candidate models	K	AIC_c	ΔAIC_c	w_i	Cum. w_i
All adults					
Sym	3	311.912	0.000	0.404	0.404
Sym + Year	4	313.719	1.807	0.163	0.567
Sym+ Sex	4	313.807	1.895	0.156	0.724
Symx Sex	5	314.075	2.163	0.137	0.861
Sym x Year	5	315.428	3.516	0.069	0.931
Sym + Year + Sex	5	315.535	3.623	0.066	0.997
Year	3	323.861	11.949	0.001	0.998
Null	2	324.550	12.638	0.000	0.999
Sex	3	324.814	12.901	0.000	0.999
Sex + Year	5	325.706	13.793	0.000	1.000
Males					
Sym	3	176.140	0.000	0.491	0.491
Sym + Year	4	176.701	0.560	0.371	0.863
Sym x Year	5	179.056	2.916	0.114	0.977
Year	3	183.522	7.382	0.012	0.989
Null	2	183.893	7.753	0.010	1.000

Females

Sym	3	128.334	0.000	0.417	0.417
Year	3	129.549	1.214	0.227	0.644
Sym + Year	4	130.136	1.801	0.169	0.814
Null	2	130.729	2.394	0.126	0.940
Sym x Year	5	132.234	3.899	0.059	1.000
