

Archived at the Flinders Academic Commons: http://dspace.flinders.edu.au/dspace/

This is the authors' version of an article published in the *Australian Journal of Zoology*. The original publication is available by subscription at:

http://www.publish.csiro.au/nid/90.htm

doi:10.1071/ZO13072

Please cite this article as:

Shamiminoori L, Fenner AL, Bull CM (2014) Weight watching in burrows: variation in body condition in pygmy bluetongue lizards. Australian Journal of Zoology 62, 284-293

Journal compilation © CSIRO 2014. All rights reserved.

Please note that any alterations made during the publishing process may not appear in this version.

- 1 Weight watching in burrows: variation in body condition in pygmy bluetongue lizards
- 2 Leili Shamiminoori^{A,B}, Aaron L. Fenner^A and C. Michael Bull^A
- ^ASchool of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, SA 5001
- 4 ^BCorresponding author: sham1012@flinders.edu.au

Abstract

The pygmy bluetongue lizard, *Tiliqua adelaidensis*, is an endangered scincid lizard which occurs in remnants of natural grasslands in the mid-north of South Australia. We assessed the factors affecting body condition of male and female lizards, using body size residuals as an index, over five sampling years. We included sex, phenotypic (patterned or plain morphs), temporal (sampling year and activity period within year), and climatic factors in our analyses. The results indicated that sampling year and activity period within the year were the two most important factors influencing variation in body condition of both male and female lizards over the period of the study. There were similar trends when we considered females separately in each of three stages of their reproductive cycle (pre-partum, gravid, post-partum). None of the analyses showed any significant effect of phenotype on body condition. Winter-spring rainfall was positively correlated with body condition of females in the pre-partum period, but showed no significant effect on mean body condition of any other grouping of adult lizards, nor a consistent direction of correlation among the different subsets of adult lizards that we considered. The substantial annual variations in the body condition of lizards, although of uncertain cause, provide important information for conservation managers who monitor persisting populations of this endangered species.

Introduction

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

In ecological studies, fitness is considered a fundamental factor in assessing the long term survival of a species. For endangered animal species, identifying the underlying causes of any observed changes in the mean levels of fitness over time is an essential component in the conservation management of natural populations (Sarre et al. 1994). Body condition is an indirect indicator of fitness that is often used when longer term data on survival and fecundity are not available. It usually refers to the amount of energy stored in the body relative to some measure of body size (Green 2001; Waye and Mason 2008). Estimates of body condition are typically derived from a ratio of body mass to body size, or from residuals in regressions of body mass against body size (Jakob et al. 1996; Green 2001; Connolly and Cree 2008). Individuals with higher body condition, derived from these estimates, are considered to have higher energy reserves to contribute towards the direct fitness generating processes of reproduction (Loehr et al. 2004; Coates et al. 2009; Vitousek 2009), growth (Madsen and Shine 2002), and survival (Shine et al. 2001). Although reproductive fitness is essential for population viability, and although each sex relies on energy reserves for activities related to reproduction, males and females employ different strategies in allocating their reserves (Aubret et al. 2002), and may have different allometric relationships. This means that direct comparisons of body condition between males and females, based on ratios of body mass and size, do not always translate into real fitness differences, and any comparative analyses are most relevant within a sex. A further complication is that reproductive females carrying developing eggs or young will weigh more than non-reproductive females with equivalent energy reserves. In that case, fitness comparisons within a sex, using ratios of body mass and size, are most effective when comparing individual females at similar stages in their reproductive cycle. Despite these issues, body condition can still

- be used as an indirect indicator of fitness, for comparative purposes, within males, within
- 47 reproductive females and within non-reproductive females.
- The use of mass-body size residuals as an index of body condition has been criticised by some
- 49 researchers for generating spurious relationships between body condition and other measures of
- 50 body size, particularly when the relationship between mass and body size is non-linear (Green
- 51 2001; Schulte-Hostedde *et al.* 2005). Ultimately the fitness of individuals of each sex must be
- 52 judged by their reproductive success. However, for many species, reproductive data are difficult
- or time consuming to derive, and body condition estimates can provide preliminary comparative
- 54 clues about fitness profiles in populations. This can be particularly important in conservation
- 55 programs where assessments of the consequences of various management interventions are
- 56 needed quickly.
- 57 Body condition indices have been used as a substitute for fitness in a wide variety of contexts in
- 58 conservation. Some studies have reported reductions in body condition indices with
- environmental degradation, resulting from habitat loss (Carter 1997; Hoare et al. 2006), from
- 60 overharvesting of the resources used by the population (Rosen and Trites 2000) or from climate
- 61 changes (Boersma 1998). Other studies have related body condition indices to more direct
- measures of fitness (reproduction and survival) (Bonnet and Naulleau 1995; Nagy et al. 2002) or
- to specific threatening ecological interactions, such as increased parasite loads (Whiteman and
- Parker 2004), across a range of different taxa (Stevenson and Woods 2006).
- For endangered species, conservation managers also need to have signals of when intervention
- will become important. One signal might be a decline in overall fitness of individuals in the
- 67 population. Body condition can be useful as an indirect assay of temporal trends in the fitness of

individuals or of populations overall (Bradshaw et al. 2000; Hoare et al. 2006; Loehr et al. 68 2007). That can in turn provide management clues about moderating or adjusting environmental 69 conditions for optimal persistence of an endangered species. This monitoring can also be used to 70 gauge the range of body conditions that can be tolerated in a normally variable environment, so 71 that times for appropriate conservation action can be more reliably identified. In the current 72 73 study we use body condition to assess the impact of biological, temporal and climatic factors on the fitness of an endangered Australian scincid lizard. 74 The pygmy bluetongue lizard *Tiliqua adelaidensis* is the smallest member of the genus *Tiliqua* 75 and is currently listed as endangered under the Australian Environment Protection and 76 Biodiversity Conservation Act 1999. The known populations of the species are restricted to a few 77 isolated fragments of remnant native grassland in a small area in the mid-north of South 78 Australia. Individual lizards occupy burrows constructed by lycosid and mygalomorph spiders 79 80 (Hutchinson et al. 1994; Fellows et al. 2009). Adult males are on average shorter than females and have wider heads (Hutchinson et al. 1994), a common phenomenon in skinks (Simbotwe 81 1985; Hutchinson and Donnellan 1992). 82 Annual rainfall within the current range varies substantially among years 83 (http://www.bom.gov.au), and individual populations have undergone major fluctuations in 84 density in the period since the species was re-discovered in 1992 (J. Schofield, personal 85 communication, 2011). A priority for conservation management is to understand how climate 86 and other factors impact demography. Our study uses variation in body condition across five 87 sampling years to provide an indirect indicator of fitness, and a pointer to factors that might 88

influence reproduction and survival in this endangered lizard.

Additionally, the lizard has two distinctive phenotypes, patterned and plain (with and without dorsal and lateral melanistic spots) (Hutchinson *et al.* 1994; Milne 1999). We included phenotype in the analyses to determine if body condition differences could be detected between the two forms. In ectotherms, darker coloured or more pigmented individuals may absorb heat more rapidly and perform better in cooler conditions. This is the thermal melanism hypothesis (Gates 1980). Other studies have reported that darker more melanistic individuals are more frequent in populations occupying cooler habitats (Forsman 1995a; Forsman 1995b). We compared body condition of the two phenotypes in the pygmy bluetongue lizard to provide possible additional insights into the responses of each phenotype to variable climatic conditions. Our analyses were designed to determine how body condition was influenced by varying conditions, and to infer fitness consequences for future conservation management.

Materials and methods

Study sites and field methods

Sampling was conducted at 10 populations of pygmy bluetongue lizards in remnant patches of native grasslands close to the town of Burra (33° 42'S, 138° 56'E) in the mid-north of South Australia (Fig.1). The population sites were separated from each other by 1 – 15 km of agricultural land, unsuitable for lizard occupancy. Sample sizes from many of the ten sampled populations were too small to explore geographic variation across the sampled sites, and we pooled the data from the ten populations. The area has hot, dry summers and cool, moist winters. The long-term average annual rainfall at Burra is 431.1 mm, although actual rainfall each year can range between 300 and 500 mm.

Pygmy bluetongue lizards are active and can be sampled in the period between September and April (the austral spring/summer) of each year (Milne 1999). Populations were surveyed during this sampling period over five seasons (2005/06 -2009/10). Although each sampling period contained months in two calendar years, in our analyses we refer to the separate sampling periods as 'sampling years'. We further divided each sampling year into two activity periods early [September-December] and late [January-April]. Lizards were located in each population by looking down their refuge burrows with an optical fiberscope (Provision Elite), and were captured by luring them out of their burrows with a mealworm (Strong et al. 1993; Milne 1999; Fenner 2009). For each lizard we recorded the date of capture (and its activity period), its sex as determined by relative head size and cloacal examination, and its mass and snout to vent length (SVL). We only included adult lizards, defined as having SVL> 80mm (Milne 1999) in this study. Each lizard was assigned to one of two phenotypic groups, 'Patterned' or 'Plain', based on the presence or absence of dark spotting on the dorsal and lateral surfaces (Hutchinson et al. 1994). The lizard was given a unique toe clip identification marking, and then released back to its burrow. The data were collected by random sampling and the recapture rate within and between sampling years was low. Each of the 783 adult lizards sampled (Table 1) was included in the analysis only once. For the 11 lizards that were captured more than once we used data from the first occasion the lizard was captured. Body condition analyses were conducted on the sample of all adult lizards, then on male and female lizards separately, then on females separately from each of three different times within the sampling period to allow for different reproductive condition. In this lizard, mating occurs in early November, and litters of live young are produced in early February (Hutchinson and Donnellan 1992; Milne 1999). We considered females sampled before November 7 as pre-

111

112

113

114

115

116

117

118

119

120

121

122

123

124

125

126

127

128

129

130

131

132

partum, and after February 15 as post-partum. The sample of females from between those dates was considered to contain some gravid females, with those females at different stages of litter development during that period. In each analysis for each sub-set of adult lizards, body condition was calculated separately, from the residuals of the linear regression between natural log-transformed mass and natural log-transformed SVL for all lizards in that subset. In our study, there were highly significant positive relationships between ln mass and ln SVL in each subset of the data (Fig. 2). Under these conditions this index can be a powerful indicator of spatial and temporal differences in body condition that does not require destructive sampling (Bradshaw *et al.* 2000; Hoare *et al.* 2006; Peig and Green 2010). This body condition index has been commonly used in studies of other reptile species (Lebas and Marshall 2001; Connolly and Cree 2008; Godfrey *et al.* 2010) and of other vertebrates (Jakob *et al.* 1996; Dubiec and Cichon 2001; Blackwell 2002; Cattet *et al.* 2002).

Statistical analysis

All adult lizards

Analyses were designed to determine factors that influenced patterns of variation in body condition among the sampled lizards. Data were checked for normality and are presented with standard errors where applicable. We used the general linear model in 'R', version 2.13.0. We first investigated the variation in body condition of all adult lizards. Body condition was the dependent variable and fixed factors were sex, sampling year, lizard phenotype (plain, patterned), and activity period (early season, late season).

This led to 23 models to explain variation in body condition of adult pygmy bluetongue lizards.

The full list of models is summarised in Appendix 1. They included all combinations of factors,

and all of their two-way and three-way interactions, and the null model of intercept only.

Akaike's Information Criterion (AIC) was used to rank the models for their ability to explain the observed variation in body condition index (Burnham and Anderson 2002). Subsequently we used analyses of variance to explore the interactions between factors that appeared in the best AIC model.

Male and female lizards

We next analysed separately the subsets of all adult males and all adult females. We used the same approach as before, but omitted phenotype, which had been shown to play no role in any of the top ranked models used to explain variation of body condition of the whole sample. For males and for females we considered only two explanatory factors, sampling year and activity period (early or late season), and developed five alternative models (Appendix 2) including all combinations of the two factors, their interaction and the null model of intercept only. Akaike's Information Criterion (AIC) was used, as before, to rank the models for their ability to explain the observed variation in body condition index.

Pre-partum, post-partum and gravid female lizards

We performed separate analyses of covariance (ANCOVA) to explore the variation in body condition for each of the three groups of females sampled at different reproductive times (prepartum, post-partum and gravid). Body condition was the dependent variable, and sampling year was a factor. In these analyses we included day of sampling (number of days after Sept 1) as a covariate, to allow for changes in body condition over time within each reproductive phase. This provided a finer scale of temporal resolution than the use of early and late activity period categories in the previous analyses. Note that no females were collected in the pre-partum period

(before Nov 7) in the 2008/2009 sampling year so only four years were included for that analysis. Similarly, for the gravid period, only three females were collected, all very late in the gravid period of 2007/2008, so that year was omitted from that analysis (although those females are included in the graphical representation of the trend). And in both 2006/2007 and 2007/2008 only three and two females were collected in the post-partum period, in each case at one time in that period, so the analysis of this group of females included data from only three years.

Rainfall

Because sampling year was a significant factor contributing to all of the analyses (see results), we considered that climatic factors within each year may have influenced body condition. We did not have enough sample years to explore multiple climatic indicators, but our prediction was that rainfall during the winter and early spring (May - October), before and at the beginning of the sampling period each year, might influence both germination of annual plants, and subsequently the invertebrate food levels for the lizards. Thus, indirectly, rainfall could influence lizard body condition, and we expected body condition to be higher in years with more winter and spring rainfall. Rainfall data from Burra for May – Oct in each sampling year of the study were obtained from the Bureau of Meteorology website (http://www.bom.gov.au) (Fig.3). We explored correlative relationships between the winter-spring rainfall and mean lizard body condition in that year for all adult lizards and for each subset of adult lizards separately, to help explain observed patterns in body condition.

Results

All adult lizards

The best model to explain variation in body condition among all adult lizards contained the three way interaction between sampling year, sex and activity period (Table 2). The Akaike weight ($w_{i=}$ 0.9946) of this model was considerably higher than the next best model, and we rejected all of the alternative models as having low support (Appendix 1).

Analysis of Variance including lizard body condition as the dependent variable and sex, sampling year and activity period as fixed factors, exhibited two significant two-way interactions (Table 3). The interaction between sampling year and lizard sex resulted from females having poorer body condition than males in each of four sampling years, according to the index derived from the pooled sample, but equivalent body condition to males in the 2005/2006 sampling year (Fig. 4).

The interaction between sampling year and activity period, resulted because mean body condition was normally higher in samples from early than from late in the season, but the seasonal decline in body condition was greater in some sampling years (e.g. 2008/2009) than in others (e.g. 2006/2007) (Fig. 5).

Male and female lizards

Each of the analyses, for males and for females, identified two models involving combinations of, and interactions between sampling year and activity period, which together accounted for over 99% of the Aikake weight (Table 4; Appendix 2). For each sex, the independently derived body condition varied both between activity periods and among years with patterns similar to those derived from the analysis of all adults (Fig. 6).

Pre-partum, post-partum and gravid female lizards

Analysis of covariance (ANCOVA) revealed a significant effect of day of sampling for gravid females, but not for pre-partum or post-partum females (Table 5). For females sampled during the gravid period body condition tended to decline with later days of sampling (Fig 7). There were no significant main effects of sampling year, nor any interaction effects between sampling year and day of sampling for any of the three groups of females (Table 5).

Rainfall

Correlation analyses showed a significant positive association between mean body condition and total winter-early spring rainfall in pre-partum female lizards (Table 6; Fig. 8). No other group of adult lizards showed any significant correlation with rainfall; nor was there any consistent trend for correlations to be positive or negative among the different groups of adults analysed (Table 6). Further analysis (data not shown) of males caught before November, and of males and females (separately) in the early activity period, failed to show any significant correlation with winter – spring rainfall.

Discussion

In our study the model that best explained variation in body condition of the sample that included all adult pygmy bluetongue lizards, *Tiliqua adelaidensis*, included lizard sex, and the activity period and sampling year when the lizard was sampled. The analysis indicated that this model was substantially better than any of the many alternative models, and we have inferred that these three factors were more important in determining body condition over the period of the study than the other factors we considered.

Effect of lizard sex

In general, males of *T. adelaidensis* displayed a higher body condition index than females (Fig.4). There are three probable sources of intersexual variation in our measure of body condition. One is based on the differences in body and head size between male and female pygmy bluetongue lizards. Male lizards have a larger head and a shorter and bulkier body than female lizards (Hutchinson *et al.* 1994). A shorter male will record a higher ratio of mass to length and thus a higher body condition than a female of equivalent mass. Hence, the allometric size difference, rather than any difference in overall fitness, will be reflected in the body condition index we have used.

The second source of intersexual variation comes from female fecundity. Gravid females, with developing embryos contributing to their body mass, are expected to register higher body condition than males of equivalent SVL with the index we have used. However, our results showed a consistently higher body condition for males than for females. The overall mean body condition for females will be influenced by the proportion of females that are gravid in our sample, but the trend in our data suggests female fecundity has a relatively low influence on the patterns of intersexual variation.

A third possible source is the real differences in the body condition between males and females resulting from differences in their responses to environmental conditions. Because we cannot separate the three explanations for this intersexual variation, we do not explore these patterns any more deeply, except to suggest that females may suffer greater loss of body condition each season as a result of producing litters. A demographic study of *T. adelaidensis* reported that females do not always reproduce in successive years, and that in each year, some females are non-reproductive (Milne 1999). This suggests that there are significant fitness costs for females in reproduction, and that they may not have recovered sufficiently from previous litters to be able

to reproduce every year. That explanation is consistent with the observed lower mean body condition of females in the sample. In other reptiles, body growth is related to the availability of food (Cox *et al.* 2007), and females with below-average body condition show lower sexual receptivity (Aubret *et al.* 2002).

Effect of activity period

In four of the five sampling years, body condition of *T. adelaidensis* was higher in the early activity period (September-December) than in the late activity period (January-April), although there was annual variation in the extent of the difference. This result was consistent whether we analysed all adults together, or adult males and females separately. Within females there was also a significant decline in body condition over the gravid period. The latter result is surprising in that we expected gravid females to become increasingly heavy over that period as their embryos developed, leading to predicted increases in body condition index. However, not all females sampled in the gravid period were necessarily gravid, and even gravid females may be transferring their own body reserves to the developing embryos rather than increasing body mass (Wapstra and Swain 2001; Cadby *et al.* 2011; Itonaga *et al.* 2012).

The general seasonal decline in body condition can be explained by ecological factors. Spring growth of annual grassland plants, and moister conditions during spring, may encourage higher invertebrate prey abundances earlier in the season (Milne 1999; Souter 2003). Also during spring, there are fewer days with high temperatures, allowing lizards to remain emerged at their burrow entrances, and able to detect passing prey for longer periods (Milne *et al.* 2003). Thus lizards could have more feeding opportunities in the early than the late activity season.

286

287

288

289

290

291

292

293

294

295

296

297

298

299

300

301

302

303

304

305

306

307

An over-riding feature of the analyses, whether they were of all adult lizards or of males and females separately, was the substantial variation in the body condition from one year to the next. Among the factors that have varied across the study years, the most obvious was climate (for instance rainfall) (Fig.3), and we asked whether climatic variation may explain some of this temporal variation in body condition of pygmy bluetongue lizards. A climate effect may have been direct, through the influence of climate on how often conditions were suitable for lizard activity, or indirect by influencing the levels of plant growth or invertebrate prey at the population sites. Many studies have demonstrated that annual climatic variation can impact body condition of other reptiles (Nagy and Bradshaw 1995; Wapstra 2000; Nagy et al. 2002; Lourdais et al. 2004; Shine 2005; Chamaille-Jammes et al. 2006) either by shifts in the mean temperature or through year to year variation in thermal regimes (Aubret and Shine 2010). Rainfall and temperature are sometimes used as indirect indicators of food availability for reptiles (Hanson and Weltzin 2000; Loehr et al. 2007). Nagy and Bradshaw (1995) found seasonal differences in body condition in an agamid lizard Ctenophorus nuchalis that were significantly correlated with rainfall. Their lizards had significantly lower body condition in years with low winter rainfall. Similarly, Madsen and Shine (2000) found year to year body condition variation in Arafura filesnakes (Acrochordus arafurae) that correlated with varying amount of rainfall and food availability in different years. Loehr et al. (2007) showed that rainfall, through its impact on food resources, impacted body condition of male and female *Hompus signatus* tortoises, but reported that the timing and frequency of rainfall events were important as well as the amount of rainfall. Both male and female tortoises had low body condition in years with low rainfall.

We chose one rainfall parameter, rainfall in winter and early spring, as the most likely to affect the fitness of the lizards in our study. Despite the small sample size of years, we found one group of lizards, adult females sampled in the pre-partum period, to have a strong positive correlation between body condition and winter spring rainfall, consistent with the patterns found for other reptiles. More rainfall in the period just before lizards start to become active led to females being in better condition in the early part of the season, perhaps because of higher prey densities. However, with a limited sample of only five years of data, we detected no significant effect of winter-spring rainfall on the body condition of any other grouping of adult lizards, and the directions of correlations of body condition with rainfall showed no consistent pattern among the different subgroups of adult lizards. Perhaps the lack of response by males early in the season reflects the fact that female condition is lower than males, and that they can respond more positively to periods of resource abundance. We did not explore the impact of other climatic parameters. Some factors not influenced by local climate may also have varied sufficiently among years to

have generated the substantial annual variation in body condition that we observed. Invertebrate prey abundance may not always be driven by local climate. In the years 2010 and 2011, after our sampling was completed, pulses of plague locusts, *Chortoicetes terminifera*, invaded the study sites, providing abundant food. Those locust pulses were generated by rainfall events in western Queensland, hundreds of kilometres away and many months earlier. Additionally, local stochastic events, such as a grass fire in one population in December 2005, can cause immediate and dramatic reductions in the invertebrate prey, in the amount of time lizards spend at their burrow entrance, and in lizard body condition (Fenner and Bull 2007).

Lack of effect of phenotype

Whether lizards were the patterned or the plain phenotype had no impact on their body condition, suggesting no obvious advantage for one or the other form in gaining resources for growth in the years of our sampling. That leaves unanswered the questions of how this polymorphism is maintained within populations, and why the frequency of patterned individuals varies among populations. The thermal melanism hypothesis of Gates (1980) is not supported by our analyses. Given that the darker spots of the patterned individuals in *T. adelaidensis* are relatively small and positioned laterally as well as dorsally, they are probably unlikely to have much influence on thermoregulation.

Conservation implications

Other reptile studies have shown that body condition is dependent on a number of climatic and seasonal factors, and that body condition is positively correlated with fitness parameters such as survival (Shine *et al.* 2001), and reproduction (Naulleau and Bonnet 1996). Identifying factors that affect variation in body condition within and among seasons will shed light on the demographic processes of reptile populations over time.

The conservation implications from this study are that there are substantial annual variations in the body condition of *T. adelaidensis*, and presumably in the factors that influence body condition. The body condition in populations and its variation should be monitored by conservation managers in order to recognise what are the normally tolerated ranges of body condition, and to identify any deteriorating trend in the body condition of the current populations of *Tiliqua adelaidensis*. To do that we need to know more about what causes the variation that we have observed.

An immediate concern is to determine any impact of changing climate that might affect these lizards either directly, through thermoregulatory constraints on the amount of time lizards can remain at their burrow entrances, or indirectly by climatic influences on surrounding vegetation and available prey. The impact of changes in climate on survival and persistence can only be determined with longer-term field studies that document annual climatic variation and demographic traits and other associated variables such as food availability over more years than the current study (Brown and Shine 2007). A future development with practical application for *T. adelaidensis* would be to determine any influence of the body condition index as measured in this study, and fitness parameters such as survival and fecundity of the lizards. The results of this study stress the need of monitoring by conservation managers to determine any possible declining trend in fitness of the current populations of pygmy bluetongue lizards. Those monitoring programs may, additionally detect body condition declines that indicate population sites that can no longer support viable populations, and where translocation of individuals at those sites might be considered (Fordham *et al.* 2012).

Acknowledgements

This research was funded by the Australian Research Council, Nature Foundation of South Australia and the Holsworth Wildlife Research Endowment Fund. We thank the landholders, Chris and Maria Reed, for allowing access to their property. The study was conducted according to the guidelines of Flinders University Animal Welfare Committee (approval no. E206) and in compliance with the Australian Code of Practice for the Use of Animals for Scientific Research.

References Aubret, F., Bonnet, X., Shine, R., and Lourdais, O. (2002) Fat is sexy for females but not males: the influence of body reserves on reproduction in snakes (Vipera aspis). Hormones and Behavior , 135-147. Aubret, F., and Shine, R. (2010) Thermal plasticity in young snakes: how will climate change affect the thermoregulatory tactics of ectotherms? Journal of Experimental Biology 213, 242-248. Blackwell, G.L. (2002) A potential multivariate index of condition for small mammals. New Zealand Journal of Zoology 20, 195-203. Boersma, P.D. (1998) Population trends of the galapagos penguins: impacts of El Nino and La Nina Condor 100, 245-253. Bonnet, X., and Naulleau, G. (1995) Estimation of body reserves in living snakes using a body condition index. . In 'Scientia Herpetologia.' (Eds. GS Loirebte, A Montori, X Santos and MA Carretero) pp. 237-240)

Bradshaw, C.J.A., Davis, L.S., Lalas, C., and Harcourt, R.G. (2000) Geographic and temporal variation in the condition of pups of the New Zealand fur seal (Arctocephalus foresteri): evidence for density dependence and differences in the marine environment. Journal of Zoology , 41-51. Brown, G.P., and Shine, R. (2007) Rain, prey and predators: climatically driven shifts in frog abundance modify reproductive allometry in a tropical snake. *Oecologia* **154**, 361-368. Burnham, K.P., and Anderson, D.R. (2002) 'Model selection and multimodel inference.' 2nd edn. (Springer: New York) Cadby, C.D., Jones, S.M., and Wapstra, E. (2011) Potentially adaptive effects of maternal nutrition during gestation on offspring phenotype of a viviparous reptile. *Journal of* Experimental Biology **214**, 4234-4239. Carter, S.I. (1997) 'The habitat ecology of bog turtles (*Clemmys muhlenbergii*) in southwestern Virginia '(Blacksburg, VA: Virginia Polytechnic Institute and State University)

410 Cattet, M.R.L., Caulkett, N.A., Obbard, M.E., and Stenhouse, G.B. (2002) A body condition index for ursids. Canadian Journal of Zoology 80, 1156-1161. 411 412 Chamaille-Jammes, S., Massot, M., Aragon, P., and Clobert, J. (2006) Global warming and 413 positive fitness response in mountain populations of common lizards Lacerta vivipara. Global 414 Change Biology 12, 392-402. 415 416 Coates, P.S., Wylie, G.D., Halstead, B.J., and Casazza, M.L. (2009) Using time-dependent 417 models to investigate body condition and growth rate of the giant gartersnake. Journal of 418 419 Zoology 279, 285-293. 420 Connolly, J.D., and Cree, A. (2008) Risks of late start to captive management for conservation: 421 422 phenotypic differences between wild and captive individuals of a viviparous endangered skink (Oligosoma otagense). Biological Conservation 141, 1283-1292. 423 424 Cox, R.M., Butler, M.A., and John-Alder, H.B. (2007) The evolution of sexual size dimorphism 425 in reptiles. In 'Sex, size, and gender roles: evolutionary studies of sexual size dimorphism.'. (Eds. 426 DJ Fairbarin, WU Blanckenhorn and T Szekely). (Oxford University: Oxford) 427 428

429 Dubiec, A., and Cichon, M. (2001) Seasonal decline in health status of Great Tit (*Parus major*) nestlings. Canadian Journal of Zoology 79, 1829-1833. 430 431 Fellows, H.L., Fenner, A.L., and Bull, C.M. (2009) Spiders provide important resources for an 432 endangered lizard. Journal of Zoology 279. 433 434 Fenner, A.L. (2009) The biology, ecology and social structuring of the endangered pygmy 435 bluetongue lizard, Tiliqua adelaidensis: considerations for long term conservation. Ph.D. Thesis., 436 Flinders Unversity Adelaide 437 438 Fenner, A.L., and Bull, C.M. (2007) Short-term impact of grassland fire on the endangered 439 pygmy bluetongue lizard. Journal of Zoology 272, 444-450. 440 441 Fordham, D.A., Watts, M.J., Delean, S., Brook, B.W., Heard, L., and Bull, C.M. (2012) 442 Managed relocation as an adaptation strategy for mitigating climate change threats to the 443 444 persistence of an endangered lizard. Global Change Biology 18, 2743-2755. 445 Forsman, A. (1995a) Opposing fitness consequences of colour pattern in male and female 446 snakes. Journal of Evolutionary Biology 8, 53-70. 447

Hutchinson, M.N., and Donnellan, S.C. (1992) Taxonomy and genetic variation in the Australian lizards of the genus Pseudemoia (Scincidae: Lygosominae). Journal of Natural History 26, 215-264. Hutchinson, M.N., Milne, T., and Croft, T. (1994) Redescription and ecological notes on the pygmy bluetongue, Tiliqua adelaidensis (Squamata: Scincidae). Transactions of the Royal Society of South Australia 118, 217-226. Itonaga, K., Edwards, A., Wapstra, E., and Jones, S.M. (2012) Interpopulation variation in costs of reproduction related to pregnancy in a vivparous lizard. Ethology Ecology and Evolution (367-376). Jakob, E.M., Marshall, S.D., and Uetz, G.W. (1996) Estimating fitness: a comparison of body condition indices. Oikos 77, 61-67. Lebas, N.R., and Marshall, N.J. (2001) No evidence of female choice for a condition-dependent trait in the agamid lizard, Ctenophorus ornatus. Behaviour 138, 965-980.

- Loehr, V.J.T., Henen, B.T., and Hofmeyr, M.D. (2004) Reproduction of the smallest tortoise, the
- Namaqualand speckled padloper, *Homopus signatus signatus*. *Herpetologica* **60**, 444-454.

487

- Loehr, V.J.T., Hofmeyr, M.D., and Henen, B.T. (2007) Annual variation in the body condition of
- a small, arid-zone tortoise, *Homopus signatus signatus*. *Journal of Arid Environments* **71**(4),
- 490 337-349.

491

- Lourdais, O., Shine, R., Bonnet, X., Guillon, M., Naulleau, G., and (2004) Climate affects
- 493 embryonic development in a viviparous snake, *Vipera aspis. Oikos* **104**, 551-560.

494

- Madsen, T., and Shine, R. (2002) Short and chubby or long and slim? Food intake, growth and
- body condition in free-ranging pythons. *Austral Ecology* **27**, 672-680.

497

- 498 Milne, T. (1999) Conservation and ecology of the endangered pygmy bluetongue lizard *Tiliqua*
- 499 *adelaidensis*. Flinders University, Adelaide

500

- Milne, T., Bull, C.M., and Hutchinson, M.N. (2003) Use of burrows by the endangered pygmy
- 502 bluetongue lizard *Tiliqua adelaidensis*. *Wildlife Research* **30**, 523-528.

Nagy, K.A., and Bradshaw, S.D. (1995) Energetics, osmoregulation, and food consumption by free-living desert lizards, Ctenophorus (equals Amphibolorus nuchalis). Amphibia-Reptilia 16, 25-35. Nagy, K.A., Henen, B.T., Vyas, D.B., and Wallis, I.R. (2002) A condition index for the desert tortoise (Gopherus agassizii). Chelonian Conservation and Biology 4, 425-429. Naulleau, G., and Bonnet, X. (1996) Body condition threshold for breeding in a viviparous snake. Oecologia 107, 301-306. Peig, J., and Green, A.J. (2010) The paradigm of body condition: a critical reappraisal of current methods based on mass and lenght. Functional Ecology 24, 1323-1332. Rosen, D.A., and Trites, A.W. (2000) Pollock and the decline of Steller sea lions: testing the junk food hypothesis Canadian Journal of Zoology 78, 1243-1250. Sarre, S., Dearn, J.M., and Georges, A. (1994) The application of fluctuating asymmetry in the monitoring of animal populations. Pacific Conservation Biology 1, 118-122.

523 Schulte-Hostedde, A.I., Zinner, B., Millar, J.S., and Hickling, G.J. (2005) Restitution of masssize residulas: validating body condition indices. *Ecology* **86**, 155-163. 524 525 Shine, R. (2005) Life-history evolution in reptiles. Annual Review of Ecology, Evolution, and 526 *Systematics* **36**, 23-46. 527 528 Shine, R., LeMaster, M.P., Moore, I.T., Olsson, M.M., and Mason, R.T. (2001) Bumpus in the 529 snake den: effects of sex, size, and body condition on morality of red-sided garter snakes. 530 Evolution 55, 598-604. 531 532 Simbotwe, M.P. (1985) Sexual dimorphism and reproduction of Lampropholis guichenoti 533 (Lacertilia: Scincidae). In 'The biology of Australian frogs and reptiles '. (Eds. G Grigg, R Shine 534 535 and H Ehmann) pp. 11-16. (Surrey Beatty & Sons: Sydney) 536 Souter, N.J. (2003) Habitat requirements and conservation of the endangered pygmy bluetongue 537 538 lizard Tiliqua adelaidensis. Flinders University of South Australia, Adelaide 539 Stevenson, R.D., and Woods, J., W. A. (2006) Condition indices for conservation: new uses for 540 evolving tools. *Integrative and Comparative Biology* **46**, 1169-1190. 541

Strong, D., Leatherman, B., and Brattstrom, B.H. (1993) Two new simple methods for catching small fast lizards. Herpetological Review 24, 22-23. Vitousek, M. (2009) Investment in mate choice depends on resource availability in female Galápagos marine iguanas (Amblyrhynchus cristatus). Behavioral Ecology and Sociobiology 64, 105-113. Wapstra, E. (2000) Maternal basking opportunity affects juvenile phenotype in a viviparous lizard. Functional Ecology 14, 345-352. Wapstra, E., and Swain, R. (2001) Reproductive correlates of abdominal fat body mass in Niveoscincus ocellatus, a skink with asynchronous reproductive cycle. Journal of Herpetology , 403-409. Waye, H.L., and Mason, R.T. (2008) A combination of body condition measurements is more informative than conventional condition indices: temporal variation in body condition and corticosterone in brown tree snakes (Boiga irregularis). General and Comparative Endocrinology **155**, 607-612.

Whiteman, N.K., and Parker, P.G. (2004) Body condition and parasite load predict territory
ownership in the Galapagos hawk. *Condor* 106, 915-921.