Variation in body size and sexual dimorphism across geographical and environmental space in the frogs \textit{Limnodynastes tasmaniensis} and \textit{L. peronii}

CHLOE S. SCHÄUBLE*

Department of Zoology and Entomology, The University of Queensland, Brisbane, Queensland 4072, Australia

Received 17 October 2002; accepted for publication 17 December 2003

This study aimed to identify potential factors responsible for geographically structured morphological variation within the widespread Australian frogs \textit{Limnodynastes tasmaniensis} Günther and \textit{L. peronii} Duméril & Bibron. There was support for James's rule, and both latitude and present climate explained large amounts of the variation in body size and shape (particularly in \textit{L. peronii}). There was also some support for the influence of several biogeographical barriers. Finally, both species were sexually dimorphic for body size and the degree of sexual size dimorphism (SSD) varied geographically. Climate was an important explanation for SSD variation in \textit{L. peronii}, while latitude was most important for \textit{L. tasmaniensis}. Geographical variations in sexual selection via male–male physical competition and climate-related resources are suggested as potential explanations for SSD variation in \textit{L. peronii}. © 2004 The Linnean Society of London, \textit{Biological Journal of the Linnean Society}, 2004, 82, 39–56.


INTRODUCTION

Body size is a fundamental morphological trait, important in a physiological, ecological and social context. Geographically structured variation in morphology, particularly body size, is common within many species (Avise, 2000). However, the causes and maintenance of geographical variation in morphology (including body size) are likely to be complex, and are not always well understood (Case & Schwaner, 1993; Partridge & French, 1996; Baez & Brown, 1997; Malhotra & Thorpe, 1997). Many macro- and microevolutionary processes, both adaptive and nonadaptive, have been proposed for the maintenance of variation in body size and shape. Examples of potential forces producing geographical variability in morphology include: (i) selection in response to geographical variation in prey type or predation pressure (e.g. Shine, 1987; Arnett & Gotelli, 1999a; Schneider \textit{et al}., 1999); (ii) effects of climate or other environmental parameters on growth rates (e.g. Riha & Berven, 1991; Castellano, Giacoma & Dujsebayeva, 2000; see also Van Der Have & De Jong, 1996); (iii) variation in the level and nature of sexual selection and sexual size dimorphism (e.g. Endler & Houde, 1995; Wiens, Reeder & Montes, 1999; Storz \textit{et al}., 2001); and (iv) non-selective genetic factors such as drift and founder effects (Baker, Peck & Goldsmith, 1990; Nussbaum & Wu, 1995; Demetrius, 2000).

Additionally, a range of general geographic rules for morphological variation has been developed. For example James’s rule (also known as Bergmann’s rule; see Blackburn, Gaston & Loder, 1999) predicts that body size within species increases with latitude (distance from the equator). The clines in body size predicted by James’s rule have been observed in many endotherms (Ashton, Tracy & de Queiroz, 2000) and ectotherms (Partridge & French, 1996; Arnett & Gotelli, 1999b), although some groups of ectotherms

*Current address: Queensland Parks & Wildlife Service, PO Box 1735, Bundaberg, Queensland 4670, Australia. E-mail: chloeschabule@yahoo.com.au
show reverse body-size clines (Mousseau, 1997; Sota et al., 2000).

Among anurans, analyses of intraspecific geographical variability in morphology have often revealed extensive variation in body size (Lee, 1993; Mendelson, 1998; Castellano et al., 2000). Previous work also indicates that body size varies among some populations of the widely distributed Australian frogs *Limnonectes tasmaniensis* Günther and *L. peronii* Duméril & Bibron (Moore, 1961; Wilson, 2000; Wilson, 2001). However, geographical variation in morphology has not been investigated at the scale of these species’ overall distributions. Accordingly, in this study I describe broad-scale geographical variation in body size and shape for *L. tasmaniensis* and *L. peronii* based on examination of a large number of museum specimens. Furthermore, I aim to gain an understanding of the relationships between morphology and several key environmental and evolutionary factors that potentially influence morphological variation at ecological and evolutionary time-scales. Thus, I address geographical variation in morphology with regard to four major issues; general ecorgraphic rules, climate variation, historical barriers to gene flow, and sexual selection.

First, given the broad east coast distribution of both species, I consider the variation of body size and shape in *L. tasmaniensis* and *L. peronii* in relation to latitude, a broad environmental index commonly congruent with morphological variation (e.g. Mousseau & Roff, 1995; Wigginton & Dobson, 1999; Loeschcke, Bundgaard & Barker, 2000). Specifically, I ask: how much of the observed variation in body size can be accounted for by variation in latitude, and does body size vary in accordance with James’s rule?

Secondly, I address the influence of environment on morphology in a more explicit way by asking: to what extent can body size and shape variation in *L. tasmaniensis* and *L. peronii* be explained by variation in precipitation, temperature and radiation? These three climate variables were chosen because some populations of the widely distributed Australian frogs *Limnonectes tasmaniensis* Günther and *L. peronii* Duméril & Bibron (Moore, 1961; Wilson, 2000; Wilson, 2001). However, geographical variation in morphology has not been investigated at the scale of these species’ overall distributions. Accordingly, in this study I describe broad-scale geographical variation in body size and shape for *L. tasmaniensis* and *L. peronii* based on examination of a large number of museum specimens. Furthermore, I aim to gain an understanding of the relationships between morphology and several key environmental and evolutionary factors that potentially influence morphological variation at ecological and evolutionary time-scales. Thus, I address geographical variation in morphology with regard to four major issues; general ecorgraphic rules, climate variation, historical barriers to gene flow, and sexual selection.

First, given the broad east coast distribution of both species, I consider the variation of body size and shape in *L. tasmaniensis* and *L. peronii* in relation to latitude, a broad environmental index commonly congruent with morphological variation (e.g. Mousseau & Roff, 1995; Wigginton & Dobson, 1999; Loeschcke, Bundgaard & Barker, 2000). Specifically, I ask: how much of the observed variation in body size can be accounted for by variation in latitude, and does body size vary in accordance with James’s rule?

Secondly, I address the influence of environment on morphology in a more explicit way by asking: to what extent can body size and shape variation in *L. tasmaniensis* and *L. peronii* be explained by variation in precipitation, temperature and radiation? These three climate variables were chosen because the first two have been shown to correlate with body size and shape divergence in other anurans (Nevo, 1973; Hemelaar, 1988; Lee, 1993; Castellano et al., 2000) and the third varies extensively across the range of both study species.

Thirdly, I examine the importance of several potential biogeographical barriers in the generation of morphological variation within *L. tasmaniensis* and *L. peronii*. Several geological and environmental features of the Australian east coast may represent barriers to gene flow, currently and/or historically, and are hypothesized to have influenced the evolution of morphological divergence in a range of Australian fauna (Schäuble, 2002; see Fig. 1). Assuming morphology has at least some genetic basis, increased genetic isola-
Figure 1. Maps for (A) Limnodynastes tasmaniensis and (B) L. peronii, showing the positions of biogeographical barriers (bold lines) and biogeographical regions (NBURDG, NMCPHERSON, NNSW, SNSW, EASTVIC, TAS, WESTVIC, WEST, and INLAND) used in analyses. Based on the museum specimens used for each species, I give mean latitude and longitude for biogeographical regions (this location is also marked with a dot), and male then female sample sizes (numbers in parentheses indicate sample size after removal of specimens whose position information placed them offshore; see text).
(1972). I randomly selected ten *L. tasmaniensis* museum specimens (from a jar containing more than a hundred frogs) and measured each of them ten times in random order to evaluate the repeatability (*r*) of the four measurements (Lee, 1982; Lessells & Boag, 1987; Lee, 1990; Hayek, Heyer & Gascon, 2001). Repeatability (*r*) was calculated as:

\[ r = \frac{\sigma^2_{\text{among}}}{\sigma^2_{\text{within}} + \sigma^2_{\text{among}}} \]

where \( \sigma^2_{\text{among}} \) and \( \sigma^2_{\text{within}} \) are the among-groups and within-groups variance components, respectively, and *r* falls between zero and one (Lessells & Boag, 1987).

I calculated overall body size using a principal components analysis (STATISTICA: StatSoft Inc, 2000) on the covariance matrix of raw morphological measurements (SUL, HW, Jaw, Tibia). This was performed for each species separately. The first principal component (PC) calculated from a set of morphometric measurements generally expresses body size variation when all traits load largely and in the same direction (Reyment, Blackith & Campbell, 1984). Remaining variance describes relative shape differences that are not due to body size (and these are expressed in subsequent PCs). The relative contributions of the original variables to each principal component were determined from the matrix of factor-variable correlations. I used a single PCA on the total morphological dataset for each species as analysis of results from single sex PCAs showed that the subspaces defined by the first two principal components had the same orientation in both sexes. Specifically, the sums of the eigenvalues (S), were 1.92 and 1.98 for *L. peronii* and *L. tasmaniensis* (respectively) out of a possible range of 0–2, where 2 indicates identical subspaces (Krzanowski, 1979).

Amphibians and reptiles are assumed to show indeterminate growth (Duellman & Trueb, 1994). If body size does accurately reflect age (see Halliday & Verrell, 1988) in *L. tasmaniensis* and *L. peronii*, it is possible that observed geographical patterns result not from sampling populations that have intrinsically different body sizes, but instead from sampling populations that have markedly different age structures, e.g. lots of young (small) animals vs. lots of old (large) animals. Relevant information on demography is not available for these species. Therefore, I assume that the museum specimens represent samples from populations with relatively similar age structures, both presently and during the ~60-year period over which specimens were collected.

**LOCATION DATA**

Latitude and longitude location data for specimens were obtained from museum databases. Where this information was absent, I used data obtained from an Atlas of Australia (Reader’s Digest, 1994) and the online version of the Gazetteer of Australia 2000 (National Mapping Division, formerly AUSLIG: see http://www.auslig.gov.au/mapping/names/natgaz.htm). As most museum databases did not provide highly accurate positional data, the accuracy of the latitude and longitude data used in this study probably varies between hundreds of metres and several kilometres. Owing to a lack of suitable information, no attempt was made to correct the positional data of specimens that were placed offshore (*L. tasmaniensis*, *N* = 39; *L. peronii* *N* = 35). Despite the need for caution when using imperfect positional data, the large geographical scale on which this comparative study concentrates mitigates this potential problem to some extent.

**EAST COAST VARIATION IN MORPHOLOGY: LATITUDE AND CLIMATE**

**Latitude**

The distributions of both *L. tasmaniensis* and *L. peronii* are extremely large and encompass a wide range of habitats and environments. In order to most effectively compare correlates of morphological variation between the two species, I restricted my analyses to specimens distributed within approximately 150 km of the coast and east of the Murray River (South Australia). This allowed me to compare the response of body size and shape to location and climate variation across equal geographical areas for both species, and removed the confounding effects of the extended western distribution of *L. tasmaniensis*. Morphological changes across the whole range of *L. tasmaniensis* are discussed in terms of differences between biogeographical regions in a later section of this paper.

I used a regression approach to look for relationships between body size/shape and latitude, examining the sexes separately (Hayek et al., 2001). Latitude was categorized into one-degree-wide blocks (Table 1) and regression lines calculated through the block means for body size/shape. I tested for non-linearity of these relationships using the ‘test of significance in multiple regression’ procedure from Sokal & Rohlf (1995: 627) to determine if the amount of variance explained was significantly increased by including a quadratic term in the model, rather than a linear term alone.

Elevation can have important environmental and climatic consequences, and is often used as a general environmental index in much the same way as latitude. However, *L. tasmaniensis* and *L. peronii* specimens were not evenly distributed across elevations, and the non-linear relationships between body size/
shape and latitude prevented the use of latitude as a covariate in any analysis of elevation and morphology. For these reasons, I did not attempt to assess the effect of elevation on morphology, or to compare the effect of elevation with that of latitude. Likewise, I was unable to explicitly consider variation in elevation when conducting the latitudinal analyses presented in this study. Non-linear relationships between morphology and latitude precluded comparison of the relative contributions of variations in latitude, climate and biogeographical region to geographical variation in morphology, at least in terms of statistical techniques based on linear regression. Approaches such as those invoking non-linear regression were outside the scope of this study.

**Climate**

Next, I explored the relationship between body size/shape and more specific environmental factors. I calculated five raw climate variables for each specimen using data from AUSLIG (Annual mean temperature, Annual precipitation, Precipitation of wettest period, Precipitation of driest period and Annual mean radiation). Radiation (solar) provides an additional index of environmental temperature to that given by annual mean air temperature. Climate layers were created in BIOCLIM (Houlder et al., 2000) using a nine Second Digital Elevation Model (DEM) for Australia (AUSLIG, 2001). Climate variables could not be calculated for specimens whose collection locations erroneously appeared to be offshore. This included all *L. peronii* specimens from Tasmania and Western Victoria.

The five raw climate variables did not meet normality or homogeneity of variance assumptions of linear regression analysis, although I improved this by taking the natural log of all variables except Precipitation of driest period. Additionally, these raw climate variables are highly correlated with each other. Therefore, I produced new, orthogonal, climate variables through principal components analysis of the raw climate variables across all locations for both *L. tasmaniensis* and *L. peronii* together. The analyses were conducted on correlation matrices rather than covariance matrices, as measurement scales differed between variables (McGarigal, Cushman & Stafford, 2000). The relative contributions of the original variables to each principal component (PC) were determined from the matrix of factor-variable correlations. To assess the amount of body size/shape variation that could be explained by each climate PC, I performed best subsets multiple regression of body size on all PCs and used Mallows C_p statistic to determine the best regression model (for method, see p. 299 in Draper & Smith, 1981). The direction of the relationship between body size and each of the climate PCs retained in the final regression model was determined from the sign of the correlation coefficients, and the magnitude of these coefficients gave indications of the relative importance of each PC.

### BIOGEOGRAPHICAL BARRIERS

I coded the location data for the full set of specimens for both *L. tasmaniensis* and *L. peronii* into broad biogeographical regions reflecting the positions of postulated biogeographical barriers (Mackerras, 1962; Ford, 1986; Ford, 1987a; Ford, 1987b; Schodde, Mason & Wood, 1993; Crisp, Linder & Weston, 1995; James & Moritz, 2000; Schäuble & Moritz, 2001) and the areas of endemism described by Cracraft (1991). Relevant barriers were; the Burdekin Gap, the McPherson Range, the Hunter River Valley, the Eastern Highlands at the Victoria–New South Wales border, Bass Strait, the Bassian Volcanic Barrier, and the Murray River in South Australia. Codes and sample sizes for biogeographical regions, and positions of biogeographical

---

**Table 1.** Museum specimens of *Limnodynastes tasmaniensis* and *L. peronii* grouped into one-degree latitude blocks along the east coast of Australia. This table includes only those specimens used in latitude analyses (see text).

<table>
<thead>
<tr>
<th>Latitude block</th>
<th>Sample size</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>L. tasmaniensis</em> (males, females)</td>
<td><em>L. peronii</em> (males, females)</td>
</tr>
</tbody>
</table>


To accommodate the extensive inland distribution of *L. tasmaniensis*, I created a large INLAND biogeographical region not bounded by specific physical features and containing all specimens collected more than ~150 km from the coast. I compared body size and shape among the biogeographical regions using ANOVA and Bonferroni-corrected *post hoc* tests.

**EAST COAST VARIATION IN SEXUAL DIMORPHISM**

I investigated sexual dimorphism and its relationship with latitude in two ways. First, I examined dimorphism in overall body size of *L. tasmaniensis* and *L. peronii*. Scatterplots confirmed that both male and female specimens of each species were similarly distributed across latitude and longitude in both species. Therefore, I used one-way ANOVA (Type IV sums of squares) to assess the significance of overall size difference between the sexes in each species. I then used the following general index of sexual size dimorphism between the sexes in each species: $I_{SSD} = \frac{\text{mean body size of the larger sex}}{\text{mean body size of the smaller sex}}$.

Because body sizes (PC1) were centred on zero, I added a positive constant (which was larger than absolute value of the most negative number) to both the male and female body size means for each latitude block before calculating the SSD ratio. I arcsine transformed the SSD ratio before performing linear regression to test the significance of the relationship between SSD and latitude in each species. As in the analyses of climate and body size, I excluded specimens taken more than 150 km from the coast (INLAND region) and those west of the Murray River (WEST region).

To assess the amount of SSD variation that could be explained by climate and latitude, I performed best subsets multiple regression for SSD and used Mallows $C_p$ statistic to determine the best regression model (see p. 299, Draper & Smith, 1981). In order to include latitude and climate in the same analysis, I calculated the mean value for each of the four climate components for each one-degree latitude block. The direction of the relationship between SSD and each of the variables retained in the final regression model was determined from the sign of the correlation coefficients, and the magnitude of these coefficients gave indications of the relative importance of each variable.

**RESULTS**

Mean values for raw morphological measurements are given in Table 2. Repeatabilities were high for all measurements ($r = 0.99$ (SUL), 0.78 (HW), 0.87 (Jaw), 0.95 (Tibia)), indicating their suitability for further analysis. In *L. tasmaniensis* the first PC (Body size) explained 93% of the total variance in the morphological data; in *L. peronii* the value was 94%. All original variables loaded heavily and in the same direction onto this component (Table 3). The second PC (PC2) explained 4% and 3% of the variance in the original data for *L. tasmaniensis* and *L. peronii*, respectively, and factor scores of this component were retained as the variable ‘body shape’. Original variables loaded onto this second component differently in each species (Table 3). PC2 correlated positively and most strongly with head width and jaw length in *L. tasmaniensis*, indicating that head robustness accounts for the dominant source of shape variation in this species. In con-

---

**Table 2.** Morphological measurements from *Limnodynastes tasmaniensis* and *L. peronii* museum specimens. Measurements are given as mean ± standard deviation (min-max) for males (M) and females (F). Morphological measurements: SUL, snout–urostyle length; HW, head width; Jaw, jaw length; Tibia, tibia length

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>N</th>
<th>SUL (mm)</th>
<th>HW (mm)</th>
<th>Jaw (mm)</th>
<th>Tibia (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. tasmaniensis</em></td>
<td>M</td>
<td>885</td>
<td>33.2 ± 3.7</td>
<td>12.1 ± 1.4</td>
<td>9.43 ± 1.0</td>
<td>11.7 ± 1.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(22.3–47.3)</td>
<td>(7.8–18.9)</td>
<td>(7.1–14.4)</td>
<td>(7.7–16.9)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>795</td>
<td>34.9 ± 3.7</td>
<td>12.3 ± 1.4</td>
<td>9.54 ± 1.0</td>
<td>11.9 ± 1.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(24.2–50.5)</td>
<td>(8.8–18.9)</td>
<td>(7.2–14.4)</td>
<td>(8.0–16.9)</td>
</tr>
<tr>
<td></td>
<td>Both</td>
<td>1680</td>
<td>34.0 ± 3.8</td>
<td>12.2 ± 1.4</td>
<td>9.5 ± 1.0</td>
<td>11.8 ± 1.3</td>
</tr>
<tr>
<td><em>L. peronii</em></td>
<td>M</td>
<td>337</td>
<td>51.7 ± 7.0</td>
<td>18.3 ± 3.0</td>
<td>13.7 ± 1.7</td>
<td>20.3 ± 2.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(34.1–72.8)</td>
<td>(11.1–28.6)</td>
<td>(9.8–19.5)</td>
<td>(14.0–27.1)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>309</td>
<td>46.6 ± 5.9</td>
<td>15.5 ± 2.0</td>
<td>12.2 ± 1.3</td>
<td>17.8 ± 2.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(34.5–66.6)</td>
<td>(11.6–22.3)</td>
<td>(7.5–16.7)</td>
<td>(11.2–24.0)</td>
</tr>
<tr>
<td></td>
<td>Both</td>
<td>646</td>
<td>49.2 ± 7.0</td>
<td>16.9 ± 2.9</td>
<td>13.0 ± 1.7</td>
<td>19.1 ± 2.5</td>
</tr>
</tbody>
</table>

© 2004 The Linnean Society of London, Biological Journal of the Linnean Society, 2004, 82, 39–56
trast, tibia length (in particular) and jaw length were the key factors in shape variation in L. peronii (and increased as PC2 increased).

EAST COAST VARIATION IN MORPHOLOGY:
LATITUDE AND CLIMATE

Latitude

Relationships between body size/shape and latitude for coastal eastern Australia were significantly curvilinear except in male L. tasmaniensis (Table 4, Figs 2, 3). It was not possible to straighten curvilinear relationships using logarithmic or other transformations. Body size was significantly and positively correlated with distance from the equator in both species for both sexes [L. tasmaniensis: males (linear regression), \( F_{1,22} = 4.60, \text{adjusted } R^2 = 0.13, \ P = 0.043, y = 1.144 - 0.030x \); females (quadratic regression), \( F_{2,21} = 25.14, \text{adjusted } R^2 = 0.70, \ P < 0.001, y = 3.916 - 0.297x + 0.005x^2 \); L. peronii: males (quadratic regression), \( F_{2,20} = 63.08, \text{adjusted } R^2 = 0.85, \ P < 0.001, y = 0.870 + 0.030x - 0.004x^2 \); females (quadratic regression), \( F_{2,22} = 22.71, \text{adjusted } R^2 = 0.64 \ P < 0.001, y = 0.266 + 0.153x - 0.007x^2 \)]. Moreover, within each species, latitude explained more variation in body size for the sex that was larger.

Body shape was also significantly correlated with latitude [L. tasmaniensis: males (linear regression), \( F_{1,22} = 4.33, \text{adjusted } R^2 = 0.12, \ P = 0.049, y = -0.712 + 0.025x \); females (quadratic regression), \( F_{2,18} = 6.36, \text{adjusted } R^2 = 0.35, \ P < 0.01, y = 2.233 - 0.237x + 0.007x^2 \); L. peronii: males (quadratic regression), \( F_{2,20} = 4.28, \text{adjusted } R^2 = 0.23, \ P = 0.029, y = 0.161 - 0.129x + 0.005x^2 \); females (linear regression), \( F_{1,21} = 22.57, \text{adjusted } R^2 = 0.47, \ P < 0.001, y = -1.304 + 0.084x \)]. Further south, L. tasmaniensis had relatively smaller heads and L. peronii had shorter tibias and jaw lengths. Overall, latitude explained more variation in shape in females than males.

Climate

The first three principal components (PCs) based on climate variables explained 51%, 34% and 8% of the total variation in climate. Loadings of original variables onto these principal components are given in Table 5. PC1 reflects a ‘tropical–temperate’ gradient, where PC1 decreases with decreasing precipitation (annual and wettest period) and solar radiation. For example, PC1 expresses a major climate difference between Eungella in Queensland and Tomahawk in Tasmania. Decreasing PC2 values correspond to decreasing dry period precipitation and increasing

Table 3. Factor-variable correlations between original morphological variables and the first two principal components, PC1 (body size) and PC2 (body shape), for Limnodynastes tasmaniensis and L. peronii. Morphological measurements: SUL, snout–urostyle length; HW, head width; Jaw, jaw length; Tibia, tibia length

<table>
<thead>
<tr>
<th>Species</th>
<th>Variable</th>
<th>PC1 (body size)</th>
<th>PC2 (body shape)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. tasmaniensis</td>
<td>SUL</td>
<td>0.99</td>
<td>-0.10</td>
</tr>
<tr>
<td></td>
<td>HW</td>
<td>0.87</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>Jaw</td>
<td>0.80</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>Tibia</td>
<td>0.87</td>
<td>0.25</td>
</tr>
<tr>
<td>L. peronii</td>
<td>SUL</td>
<td>0.99</td>
<td>-0.06</td>
</tr>
<tr>
<td></td>
<td>HW</td>
<td>0.95</td>
<td>-0.05</td>
</tr>
<tr>
<td></td>
<td>Jaw</td>
<td>0.88</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>Tibia</td>
<td>0.84</td>
<td>0.54</td>
</tr>
</tbody>
</table>

Table 4. Results of regression tests for non-linearity of relationships between morphology and latitude in male (M) and female (F) Limnodynastes tasmaniensis and L. peronii, based on one-degree latitude block means for east coast specimens. Significant P-values indicate cases where quadratic models better explain the relationship than linear ones

<table>
<thead>
<tr>
<th>Species</th>
<th>Dependent variable</th>
<th>Sex</th>
<th>N</th>
<th>( F^* )</th>
<th>P (blocks)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. tasmaniensis</td>
<td>Body size</td>
<td>M</td>
<td>24</td>
<td>0.86</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>21</td>
<td>5.23</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Body shape</td>
<td>M</td>
<td>24</td>
<td>0.96</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>21</td>
<td>8.84</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>L. peronii</td>
<td>Body size</td>
<td>M</td>
<td>23</td>
<td>8.30</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>25</td>
<td>13.16</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Body shape</td>
<td>M</td>
<td>23</td>
<td>4.72</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>25</td>
<td>4.22</td>
<td>0.05</td>
</tr>
</tbody>
</table>

\( F^* \), calculated using linear +quadratic terms vs. linear term
mean temperature; this is indicative of a cline between a hot, arid environment (where rain is limited for at least part of the year, e.g. St Lawrence in mid-east Queensland) and a cool environment with rainfall more evenly distributed throughout the year (e.g. Barrington Tops in New South Wales). Hence, I refer to PC2 as the ‘dry season wet-arid’ gradient. PC3 is more difficult to interpret, but appears to represent a ‘cool bright–warm dull’ gradient that contrasts high radiation with low mean annual temperature (sunny and cool vs. less sunny but warm). Inspection of the raw data suggests that PC3 represents a dichotomy between high elevation sites at medium latitudes (e.g. the northern tablelands of NSW) and coastal sites at lower latitudes (e.g. Warrnambool, Victoria).

Best subsets regression showed that climate was significantly correlated with body size in *L. tasmaniensis* (males: $F_{3,590} = 8.7$, adjusted $R^2 = 0.04$, $P < 0.001$; females: $F_{3,495} = 38.15$, adjusted $R^2 = 0.18$, $P < 0.01$) and *L. peronii* (males: $F_{3,310} = 85.90$, adjusted $R^2 = 0.45$, $P < 0.01$, females: $F_{3,274} = 45.12$, adjusted $R^2 = 0.32$, $P < 0.01$). Mallows $C_p$ statistics indicated that the models which explained most variation included all three climate PCs. The standardized regression coefficients indicated that male and female body sizes were correlated with climate variables in a generally similar way in both species (Table 6), although *L. peronii* body sizes were positively rather than negatively correlated with the ‘cool bright–warm dull’ gradient (PC3). Overall, male body size was most influenced by the ‘dry season wet–arid’ gradient, and body size increased in cold climates where rainfall was high in the driest period. In females, large size was predominantly correlated with less tropical climates. As was the case for latitude, climate explained the greatest amount of body size variation in the larger sex of each species.

Body shape was significantly, but relatively weakly, correlated with climate in both species (*L. tasmaniensis*: males, $F_{2,591} = 14.38$, adjusted $R^2 = 0.04$, $P < 0.001$; females, $F_{3,495} = 15.14$, adjusted $R^2 = 0.08$, $P < 0.001$; *L. peronii*: males, $F_{1,312} = 31.99$, adjusted $R^2 = 0.09$, $P < 0.001$; females, $F_{2,275} = 16.07$, adjusted $R^2 = 0.10$, $P < 0.001$). The models that explained most variation did not always include all three climate PCs. Variation in male *L. tasmaniensis* body shape (i.e. head shape and relative head size) was best explained by the ‘tropical-temperate’ and ‘cool bright–warm dull’ gradients only (PC1 and PC3; Table 5). For females, all three climate PCs were
employed in the best model, but this model had a \( C_p \) statistic only slightly closer to the number of variables than one including only PC1 and PC3. Overall, increasing relative size of \( L. \) tasmaniensis heads correlated most closely with increasing temperature and decreasing radiation, added to by reduced overall rainfall and temperature. In \( L. \) peronii males, variation in tibia length could be explained by the ‘tropical–temperate’ gradient alone (PC1; Table 5), tibias were larger in high radiation environments where overall, and wet period, rainfall was high (e.g. tropical areas). A similar pattern was apparent for females, but there was an added influence of radiation (PC3) indicating tibias were large both in tropical areas and in areas with cool temperatures and high radiation levels.

**Table 5.** Factor-variable correlations of original climate variables with climate principal components. These PCs were calculated using the position data from all individual museum specimens of east coast \( L. \) tasmaniensis and \( L. \) peronii. General descriptions of the way each PC might be interpreted as an environmental gradient are: PC1 = tropical – temperate; PC2 = dry season wet, cool – dry season arid, warm; PC3 = low radiation, warm – high radiation, cool. These interpretations are based on the factor-variable correlations for each PC, and are expressed to show the main type of climate change associated with moving from high values of the PC to low values.

<table>
<thead>
<tr>
<th>Original climate variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log (Annual mean temperature)</td>
<td>0.57</td>
<td>-0.69</td>
<td>0.35</td>
</tr>
<tr>
<td>Log (Annual precipitation)</td>
<td>0.87</td>
<td>0.38</td>
<td>0.13</td>
</tr>
<tr>
<td>Log (Precipitation of wettest period)</td>
<td>0.92</td>
<td>0.22</td>
<td>0.08</td>
</tr>
<tr>
<td>Precipitation of driest period</td>
<td>0.20</td>
<td>0.92</td>
<td>-0.04</td>
</tr>
<tr>
<td>Log (Annual mean radiation)</td>
<td>0.74</td>
<td>-0.43</td>
<td>-0.51</td>
</tr>
</tbody>
</table>

**Figure 3.** Body shape variation for east coast \( L. \) tasmaniensis and \( L. \) peronii, sexes displayed separately. Means, SE and SD are given for body shape (PC2) across one-degree latitude blocks. Whether a quadratic or linear relationship was most appropriate is also identified on each graph. Sample sizes for each block are given in Table 1.

**Table 5.** Factor-variable correlations of original climate variables with climate principal components. These PCs were calculated using the position data from all individual museum specimens of east coast \( L. \) tasmaniensis and \( L. \) peronii. General descriptions of the way each PC might be interpreted as an environmental gradient are: PC1 = tropical – temperate; PC2 = dry season wet, cool – dry season arid, warm; PC3 = low radiation, warm – high radiation, cool. These interpretations are based on the factor-variable correlations for each PC, and are expressed to show the main type of climate change associated with moving from high values of the PC to low values.

**Figure 3.** Body shape variation for east coast \( L. \) tasmaniensis and \( L. \) peronii, sexes displayed separately. Means, SE and SD are given for body shape (PC2) across one-degree latitude blocks. Whether a quadratic or linear relationship was most appropriate is also identified on each graph. Sample sizes for each block are given in Table 1.

**Table 5.** Factor-variable correlations of original climate variables with climate principal components. These PCs were calculated using the position data from all individual museum specimens of east coast \( L. \) tasmaniensis and \( L. \) peronii. General descriptions of the way each PC might be interpreted as an environmental gradient are: PC1 = tropical – temperate; PC2 = dry season wet, cool – dry season arid, warm; PC3 = low radiation, warm – high radiation, cool. These interpretations are based on the factor-variable correlations for each PC, and are expressed to show the main type of climate change associated with moving from high values of the PC to low values.

**Biogeographical barriers**

Body size and shape varied significantly between biogeographical regions, and therefore across at least some biogeographical barriers, in both species (Figs 4, 5, Body size: ANOVA: \( L. \) tasmaniensis: males, \( F_{6,876} = 29.15, P < 0.001; \) females, \( F_{6,727} = 32.83, P < 0.001; \) \( L. \) peronii: males, \( F_{7,329} = 43.64, P < 0.001; \) females, \( F_{7,301} = 28.72, P < 0.001. \) Body shape: ANOVA: \( L. \) tasmaniensis: males, \( F_{6,876} = 14.10, P < 0.001; \) females, \( F_{6,727} = 16.49, P < 0.001; \) \( L. \) peronii: males, \( F_{7,329} = 8.24, P < 0.001; \) females, \( F_{7,301} = 11.08, P < 0.001.\) Figures 4 and 5 indicate that these results may reflect the same relationships between morphol-
ogy and latitude described in previous analyses, at least along the east coast. Nevertheless, the biogeographical region analyses provide some important additional information.

Table 6. Standardized regression coefficients from best subsets regression of body size and shape onto climate PCs for *Limnodynastes tasmaniensis* and *L. peronii*. Best subsets models included one, two or three climate PCs (see text). Hence, the number of regression coefficients presented here for each species and sex indicates how many (and which) climate PCs were present in the best model.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Coefficient for climate component</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>PC1</td>
</tr>
<tr>
<td><em>L. tasmaniensis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body size</td>
<td>M</td>
<td>-0.11</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>-0.38</td>
</tr>
<tr>
<td>Body shape</td>
<td>M</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.14</td>
</tr>
<tr>
<td><em>L. peronii</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body size</td>
<td>M</td>
<td>-0.36</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>-0.37</td>
</tr>
<tr>
<td>Body shape</td>
<td>M</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>-0.32</td>
</tr>
</tbody>
</table>

In *L. tasmaniensis* there was a general tendency for INLAND frogs to be larger than coastal frogs. However, a key finding was the sharp divergence in body size and shape across the Murray River barrier in *L. tasmaniensis* (WEST vs. WESTVIC; Fig. 4). *Limnodynastes tasmaniensis* head size increased significantly from east to west for both sexes, and in relation to all other biogeographical regions; WEST frogs were particularly large and WESTVIC frogs particularly small (Fig. 4). The Eastern Highlands barrier (EASTVIC vs. SNSW) was also correlated with significant size and shape changes. North of the Eastern Highlands barrier, head size increased in *L. tasmaniensis* and body size decreased in *L. peronii* (Fig. 5). Additionally, the tibia and jaw lengths of female, but not male, *L. peronii* increased significantly across this barrier. Further north, female body size of *L. peronii* decreased across the Hunter Valley barrier (Fig. 5), and both male *L. peronii* and female *L. tasmaniensis* body sizes decreased significantly north of the McPherson Range (Figs 4, 5).

**EAST COAST VARIATION IN SEXUAL DIMORPHISM**

Female *L. tasmaniensis* were significantly larger than males (all specimens, $F_{1,1678} = 64.94$, $P < 0.001$), although body size ranges overlapped considerably. Examination of means indicated that, overall, female SULs were larger by around 1.5 mm (Table 2). Sexual

![Figure 4](image-url)
size dimorphism was also evident in *L. peronii*, but it occurred in the opposite direction. Females were significantly smaller than males (all specimens, PC1, $F_{1,644} = 125.30, P < 0.001$) by around 5 mm SUL (Table 2). Furthermore, male and female body sizes showed less overlap in *L. peronii* than in *L. tasmaniensis*. There was a trend for sexual size dimorphism (SSD = larger sex:smaller sex) to vary with latitude in both species (INLAND and WEST specimens not included). Sexual size dimorphism became more pronounced in the southern end of the species’ ranges, although the relationship was non-significant in *L. peronii* ($F_{1,16} = 9.03, \text{adjusted } R^2 = 0.32, P = 0.008$; *L. peronii*: $F_{1,21} = 4.23, \text{adjusted } R^2 = 0.13, P = 0.052$). In addition to size, body shape varied between sexes. Male *L. tasmaniensis* had larger heads than females, and male *L. peronii* had larger tibias than females ($L. tasmaniensis$: $F_{1,1678} = 147.10, P < 0.001$; *L. peronii*: $F_{1,644} = 52.90, P < 0.001$).

Best subsets regression of SSD on latitude plus climate variables indicated that, for *L. tasmaniensis*, the model explaining most variation in SSD was significant and included only latitude ($F_{1,14} = 7.03, \text{adjusted } R^2 = 0.29, P = 0.019$; Table 7). In contrast, the best subsets model for *L. peronii* comprised of climate variables PC2 and PC3, and latitude. This model explained almost 60% of the variation in SSD ($F_{3,19} = 12.27, \text{adjusted } R^2 = 0.59, P < 0.001$; Table 7). More specifically, sexual size dimorphism in *L. peronii* was most affected by the ‘dry season wet–arid’ climate gradient (PC2), with SSD increasing with increasing

---

**Figure 5.** Body size variation for *Limnodynastes peronii* across biogeographical regions, sexes displayed separately. Labels indicate the direction of interpretation for the x-axis. Means, SE and SD are shown and sample sizes are given above box whiskers in the top graph. See Fig. 1 for locations of biogeographical regions. There are no *L. peronii* samples for the WEST biogeographical region, as their distribution does not extend that far west.

**Figure 6.** Sexual size dimorphism (SSD, mean body size of larger sex divided by mean body size of the smaller sex) across one-degree wide latitude blocks for *Limnodynastes tasmaniensis* and *L. peronii*. An SSD value of 1.00 would indicate sexes of equal size. Linear regression equations are given for each species.
larger in opposing directions in the two species (females were change. Sexual size dimorphism (SSD) operated in the sites most clearly associated with morphological Eastern Highlands at the Victoria/NSW border were the Bassian Volcanic Barrier, Bass Strait and the ever, this may be partly due to insufficient fine-scale variation, my findings can only be interpreted within populations may reflect genetic and/or environmental gradients, although climate was a stronger correlate of logical variation was at least partly related to climate. This was particularly marked in L. peronii. Appearance of the SSD variation in morphology for L. peronii. Overall body size. The consequences of particular environmental characteristics for ecological and life history characteristics can have significant influence on the mean body size within a population. Physiologically critical variables such as temperature, humidity, seasonality and length of growing season can directly affect growth rates and contribute to interpopulation differences in mean body size. Reeve, Fowler & Partridge (2000) found evidence that thermal selection for larger adult males was at least partly responsible for producing larger body size in Drosophila melanogaster at low temperatures, and Hemelaar (1988) found Bufo bufo from France grew much faster than northern (Norwegian) or high (Swiss) elevation populations. Yet climate variation does not always explain body size variation. Growth and age of maturation of Rana macronemis vary across some populations in the Near

precipitation in the dry season. The presence of PC3 and latitude in the model indicates that SSD also increased with increased annual mean radiation, cooler temperature and decreased distance from the equator.

**DISCUSSION**

This study confirms significant geographical variation in the body size, shape and extent of sexual dimorphism of Limnodynastes tasmaniensis and L. peronii. Relationships between body size and latitude provide support for James’s rule and body size variation appeared highly influenced by variation in climate. This was particularly marked in L. peronii. Morphological variation was at least partly related to climate gradients, although climate was a stronger correlate of morphology in L. peronii than L. tasmaniensis. Few of the landscape features proposed as historical barriers to gene flow were congruent with significant changes in morphology for L. tasmaniensis or L. peronii. However, this may be partly due to insufficient fine-scale sampling across barriers. Overall, the Murray River, the Bassian Volcanic Barrier, Bass Strait and the Eastern Highlands at the Victoria/NSW border were the sites most clearly associated with morphological change. Sexual size dimorphism (SSD) operated in opposing directions in the two species (females were larger in L. tasmaniensis), was more pronounced in L. peronii. Climate and latitude explained around 60% of the SSD variation in L. peronii.

While observed morphological differences between populations may reflect genetic and/or environmental variation, my findings can only be interpreted within the limitations of a correlational framework (rather than an experimental one). Future studies of L. tasmaniensis and L. peronii might aim to use reciprocal/common environment experiments and quantitative genetic approaches to estimate the relative contributions of genetic and environmental factors to the generation of the geographical variation in morphology observed in the current study.

**EAST COAST VARIATION IN MORPHOLOGY:**

**Latitude and Climate**

**Latitude**

As predicted, latitude explained a large amount of the observed variation in body size (L. tasmaniensis males 13%, females 70%; L. peronii males 85%, females 64%) with southern frogs larger than northern frogs, in accordance with the predictions of James’s rule (Blackburn et al., 1999). The similar latitude–body size association observed in L. tasmaniensis and L. peronii prompts the question: are there causative factors in common? This is not simple to address because latitude potentially indexes a complex mix of environmental and ecological factors. However, latitudinal variation in climate parameters such as temperature, precipitation and humidity are frequently thought to drive morphological variation in many taxa, e.g. copepods (Lonsdale & Levinton, 1985), ants (Arnett & Gotelli, 1999b), fruit flies (Robinson & Partridge, 2001; Hallas, Schiffer & Hoffman, 2002), frogs (Jameson et al., 1973), lizards (Michaud & Echternacht, 1995), squirrels (Lindsay, 1987), and gliders (Quin, Smith & Norton, 1996). Therefore, additional insight into the mechanisms behind geographical body size variation in L. tasmaniensis and L. peronii may be gained by considering relationships between body size and specific climate gradients.

**Climate**

Table 7. Standardized regression coefficients from best subsets regression of larger sex body size:smaller sex body size (SSD) onto climate PCs and one degree latitude blocks for Limnodynastes tasmaniensis and L. peronii. Best subsets models potentially included one to four variables. Hence, the number of regression coefficients presented here for each species indicates how many (and which) variables were present in the best model. A negative latitude coefficient indicates absolute SSD was reduced away from the equator, and vice versa.

<table>
<thead>
<tr>
<th>Species</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>Latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. tasmaniensis</td>
<td>-1.30</td>
<td>0.43</td>
<td>-0.58</td>
<td>0.58</td>
</tr>
<tr>
<td>L. peronii</td>
<td>-0.45</td>
<td>0.42</td>
<td>0.57</td>
<td>-0.86</td>
</tr>
</tbody>
</table>

© 2004 The Linnean Society of London, Biological Journal of the Linnean Society, 2004, 82, 39–56
East and Caucasus irrespective of climatic conditions (Tarkhnishvili, Hille & Böhme, 2001). So, is climate a likely explanation for the latitudinal variation in body size observed for *L. tasmaniensis* and *L. peronii*?

Body size in east coast populations of *L. tasmaniensis* and *L. peronii* varied in the same direction along two climate gradients. First, body size increased from tropical to temperate areas, i.e. along the ’tropical–temperate’ gradient. Second, body size decreased as mean temperature increased and dry period precipitation decreased (along the ‘dry period wet–dry’ gradient). However, there was a direct contrast in the way *L. tasmaniensis* and *L. peronii* body sizes correlated with the third, ’cool bright–warm dull’ gradient. *Limnodynastes tasmaniensis* became larger in cool, high radiation climates while *L. peronii* became smaller.

Climate appears to be an important correlate of body size in *L. tasmaniensis* and *L. peronii*, so how might it act on body size? In general, small body size in both species was associated with warm, high radiation climates that are wet overall but receive little rain during the driest period of the year (and are therefore probably highly seasonal in terms of moisture availability). Currently, the tropics of Australia – particularly open savannah country and grasslands – experience pronounced and extensive dry seasons during which standing water supplies become depleted (Anon, 1986; Dingle, Rochester & Zalucki, 2000). If activity seasons are shorter in such areas, this might produce smaller body sizes by simply reducing the time available for growth.

Alternatively or additionally, the increased body size of *L. tasmaniensis* and *L. peronii* in southern Australia (cooler, rain more evenly spread throughout the year) may improve their ability to withstand seasonal food shortages during winter or summer dry periods (but see Wikelski & Trillmich, 1997; Wikelski & Thom, 2000). Improved starvation resistance has been hypothesized previously as a general adaptive explanation for increased body size in temperate vs. tropical areas (Blackburn et al., 1999), and supporting evidence has come from *Drosophila* flies (Parkash & Munjal, 1999; but see Halls, Schiffer & Hoffman, 2002), the ant lion *Myrmeleon immaculatus* (Arnett & Gotelli, 1999a), and ant colonies (Kaspari & Vargo, 1995).

Larger adult size in southern *L. tasmaniensis* and *L. peronii* might also reflect climatic impacts on larvae or juveniles. James & Partridge (1995) and Robinson & Partridge (2001) found that cooler temperatures improved larval growth rates and growth efficiency (i.e. better use of limited food supplies) in *Drosophila melanogaster*, resulting in larger adult body size. The same may be true for *L. tasmaniensis* and *L. peronii*. It is not currently known whether *L. tasmaniensis* and *L. peronii* forage within breeding seasons (but see Humphries, 1979), if they are active throughout the year, or how activity patterns vary with latitude. However, this information would be particularly useful in facilitating further investigation of the ideas outlined above.

**Intersexual differences.** Female size in both *L. tasmaniensis* and *L. peronii* was correlated most highly with the ’tropical–temperate’ gradient. Why might female body size be especially responsive to the amount of annual radiation and wet period/annual precipitation? Clutch size is commonly linked with body size in anurans (Berven, 1988; Townsend & Stewart, 1994), and temperature can have implications for the size and number of eggs and clutches produced (Kaplan, 1987; Jørgensen, 1992; Williamson & Bull, 1995). Additionally, the availability of breeding sites is probably also influenced by the amount of precipitation. Theoretically, females could be smaller in tropical compared to temperate areas because it is favourable (i) to produce multiple, small clutches (requiring only small body size) in warm locations where aquatic spawning sites are readily available, and (ii) to produce larger clutches/eggs (requiring larger body size) in cooler areas where precipitation during the breeding season is less predictable or large clutches do better than small ones. Preliminary data suggest *L. peronii* around temperate Sydney produce larger clutches than those in the Wet Tropics of Queensland (Keith McDonald, pers. comm.; Hengl & Burgin, 2002), but total yearly clutch number is not known for either *L. tasmaniensis* or *L. peronii*.

For males of both species, the key climatic correlate of body size was the ’dry period wet–dry’ gradient. Males became larger as the amount of precipitation in the dry period increased and mean annual temperature decreased. Why does male body size vary along this gradient? The breeding activities of males are energetically expensive (Prestwich, 1994), and male anurans commonly arrive at breeding sites before females and remain there longer, e.g. *Hyla regilla* (Jameson, Mackey & Anderson, 1973), *L. tasmaniensis* and others (Humphries, 1979), *Adelotus brevis* (Katsikaros & Shine, 1997). This means that males may be more sensitive than females to climate factors that affect breeding season length. For example, large body size could be favourable when breeding seasons are long (i) if large males have greater energy storage or efficiency abilities than small males, (ii) if individuals reproduce over a long periods, and (iii) if calling sites are defended throughout the season. Therefore, if dry period precipitation and mean temperature affect breeding season length in *L. tasmaniensis* and *L. peronii* by extending it in cool climates with relatively even year-round precipitation, then larger body size may be predicted in these areas.

---

© 2004 The Linnean Society of London, Biological Journal of the Linnean Society, 2004, 82, 39–56
Shape. Body shape and climate were only weakly correlated. However, an obvious pattern was that long tibias in *L. peronii* were associated with northern latitudes and tropical climates. Possibly this variation represents adaptation of morphology associated with escape behaviour in response to latitudinal variation in predator type and density.

**BIOGEOGRAPHICAL REGIONS**

Because increased genetic isolation potentially facilitates evolution of phenotypic divergence, morphological differences between adjacent biogeographical regions may indicate reduction of historical gene flow between regions by the barrier that divides them. Body size and shape varied significantly among biogeographical regions for both species, with several biogeographical barriers geographically consistent with broad-scale changes in morphology. Of particular note were differences across the Murray River and the Eastern Highlands barriers (see Fig. 1).

Body size in *L. tasmaniensis* changed dramatically across the Murray River, and specimens from the WEST biogeographical region were particularly big and had large heads. This corresponds well with mtDNA evidence, which indicates that specimens from this area are highly divergent from those in Victoria (Schäuble & Moritz, 2001). The Bassian Volcanic Barrier and Bass Strait were congruent with detectable changes in *L. tasmaniensis* body size (but not shape), mainly due to the fact that western Victorian (WESTVIC) specimens tended to be smaller than those in other southern biogeographical regions. Other authors have noted morphological distinctiveness in the WESTVIC region, with some *L. tasmaniensis* females having reduced finger flanges (Roberts & Seymour, 1989). Head size in *L. tasmaniensis* and tibia length and body size in *L. peronii* all changed significantly across the Eastern Highlands, and the body size of the largest sex of both species changed across the McPherson Range. These were the only two barriers congruent with morphological change in more than one species. Congruent changes in abiotic or biotic factors may provide alternative explanations for morphological divergence that coincides with proposed biogeographical barriers. Indeed, many of the morphological changes in *L. tasmaniensis* and *L. peronii* observed across barriers distributed along the east coast of Australia may simply reflect the latitudinal patterns discussed in earlier sections. However, it was not within the scope of this study to disentangle the effects of region and latitude because of non-linear relationships between morphology and latitude.

Overall, WEST and INLAND *L. tasmaniensis* had larger bodies and heads than those from other regions. Much of the WEST and INLAND regions are arid or semiarid, so this pattern may reflect adaptation to arid environments. Nevo (1972) showed that populations of *Bufo viridis* in Israel exhibited an increase in body size concomitant with an increasingly arid climate, explaining the change as an adaptation for reducing desiccation (see also, Jameson *et al.*, 1973). Similarly, Castellano & Giacoma (1998) found *Bufo viridis* from drier Italian habitats were larger, and had proportionally larger heads.

**EAST COAST VARIATION IN SEXUAL DIMORPHISM**

In this study, I found there were opposing patterns of overall sexual size dimorphism (SSD) in *L. tasmaniensis* and *L. peronii*. Females were larger than males in *L. tasmaniensis*, which is the usual pattern for amphibians (Shine, 1979; Duellman & Trueb, 1994; Halliday & Tejedo, 1995); however, the difference was small and there was considerable overlap between the size ranges for each sex. In contrast, males were the larger sex in *L. peronii* and size ranges had limited overlap. As *L. peronii* is the larger species, my results follow a trend, observed in a range of taxa, for females to be larger in smaller species and males to be larger in large species (Rensch’s rule; Abouheif & Fairbairn, 1997; Kratochvil & Frynta, 2002). Particularly interesting was that the extent of body size dimorphism increased along a north–south latitudinal cline for *L. tasmaniensis*. My findings raise several questions.

*Why do L. tasmaniensis and L. peronii show opposing patterns of overall sexual size dimorphism?*

If fighting is important in male–male competition, and has a greater effect on mating success, then males may be expected to be larger than females (Darwin, 1871; Shine, 1979, 1990) (but see Halliday & Tejedo, 1995; Karubian & Swaddle, 2001). So perhaps sexual selection via male–male physical aggression has more importance in *L. peronii* than *L. tasmaniensis*, and has only led to male biased size dimorphism in the former.

*Limnodynastes peronii* males have wider heads than females (this study; Schäuble, 2002) and male–male physical aggression is known to occur in both *L. tasmaniensis* and *L. peronii*. Roberts (1976) indicates that male *L. tasmaniensis* from South Australia wrestle during aggressive interactions, and Clyne (1967) briefly details wrestling between breeding male *L. peronii*. Breeding *L. peronii* males develop bony excrescences on their thumbs (similar to spines) and have hypertrophied forearms compared to females (Moore, 1961; Martin & Littlejohn, 1982) that may be used as weapons against other males (Shine, 1979; Katsikaros & Shine, 1997; Emerson, 2001). Indeed,
Why does the extent of SSD vary with geography?

One possibility is that SSD variation is associated with climate variation. Indeed, several climate gradients and latitude were identified as important correlates of SSD variation in *L. peronii*. Specifically, absolute SSD was strongly and negatively correlated with the ‘dry season wet–arid’ climate gradient, i.e. males were likely to be increasingly larger than females as dry season precipitation increased and temperature decreased.

A potential explanation for geographical variation in SSD is increased competition for mates, linked to climate factors. Few quantitative data are available on basic reproductive, life history and social behaviour for *L. peronii*. However, it is possible that realized breeding seasons in areas of Australia with high dry season precipitation and cooler temperatures are more unpredictable than in northern, tropical areas. Similarly, altered population sex ratios may make females less available in such places. If so, heightened importance of male–male physical competition might explain an increase in male body size compared to female size. For example, Jenssen et al. (1995) noted a latitudinal cline in sexual size dimorphism in the American lizard *Anolis carolinensis*. On the basis of information on sex ratios and mating system, those authors concluded their data were best explained by sexual selection. Jenssen et al. (1995) also hypothesized that shorter breeding seasons at high (cold) latitudes caused increased frequency and intensity of aggression among males and selected for increased body size. Extensive geographical variation in SSD consistent with variation in male–male combat has also been observed within the Australian carpet python, *Morelia spilota* (Shine & Fitzgerald, 1995; Pearson, Shine & Williams, 2002).

In contrast to *L. peronii*, the best regression model for SSD in *L. tasmaniensis* contained only latitude. As male body size was only weakly associated with latitude in this species, variation in SSD for *L. tasmaniensis* may predominantly reflect latitudinal changes in female body size. Factors driving this latitudinal variation are yet to be clearly identified, but may include selection for production of more or larger eggs at southern latitudes.

This study has demonstrated that patterns of geographical variation in SSD within *L. tasmaniensis* and *L. peronii* are both interesting and complex. Naturally, my interpretations are tempered by sampling limitations. Future studies could redress these limitations via explicit comparisons of SSD between well-sampled, individual populations spread across latitude, elevation or climate gradients.

ACKNOWLEDGEMENTS

I thank Mark Blows, Ian Owens, Mark Hamann and Fiona Manson for their comments on this manuscript, and Mark Blows for invaluable statistical advice. Much appreciation is extended to the generous museum curators at the Australian Museum (Ross Sadlier and Alan Greer), the Queensland Museum (Andrew Amey and Patrick Couper), the South Australian Museum (Adrienne Edwards), the Museum of Victoria (John Coventry), and the Queen Victoria Museum Launceston (Tim Kingston). This study was conducted with monetary support from the following sources: a Department of Zoology University Research Grant, a University of Queensland Graduate School Travel Grant, and the Ethel Mary Read Research Grant Fund.

REFERENCES


Lee JC. 1982.
© 2004 The Linnean Society of London,
Kratochvil L, Frynta D. 2002. Body size, male combat and
the evolution of sexual dimorphism in eublepharid geckos
(Squamata: Eublepharidae). Biological Journal of the Lin-
Kranowksi WJ. 1979. Between-group comparisons of prin-
cipal components. Journal of the American Statistical
Lee JC. 1982. Accuracy and precision in anuran morphomet-
281.
Lee JC. 1990. Sources of extraneous variation in the study of
meristic characters: The effect of size and of inter-observer
Lee JC. 1993. Geographic variation in size and shape of neo-
tropical frogs: A precipitation gradient analysis. Occasional
Papers of the Museum of Natural History, University of Kan-
Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities: a
Lindsay SL. 1987. Geographic size and non-size variation in
Rocky Mountain (Canada and USA) Tamiasciurus hudsoni-
cus: Significance in relation to Allen’s rule and vicariant biog-
Loeschke V, Bundgaard J, Barker J. 2000. Variation in
body size and life history traits in Drosophila aldrichi and D.
buzzatii from a latitudinal cline in eastern Australia. Hered-
ity 85: 423–433.
Lonsdale DJ, Levinton JS. 1985. Latitudinal differentiation in
copepod (Scototolana canadensis) growth: an adaptation to
Mackerras IM. 1962. Speciation in Australian Tabanidae. In:
Leeper GW, ed. The evolution of living organisms: a symposium to mark the centenary of Darwin’s Origin of Specie
and of the Royal Society of Victoria, held in Melbourne, December, 1959. Parkville: Melbourne University Press,
328–358.
Malhotra A, Thorpe RS. 1997. Size and shape variation in a
Lesser Antillean anole, Anolis oculatus (Sauria: Iguanidae)
in relation to habitat. Biological Journal of the Linnean Socie-
ty 60: 53–72.
Hobart: University of Tasmania.
statistics for wildlife and ecology research. New York:
Springer.
Mecham JS. 1960. Introggressive hybridization between two
Mendelson JR III. 1998. Geographic variation in Bufo valli-
ceps (Anura: Bufonidae), a widespread toad in the United
States and middle America. Scientific Papers of the Natural
History Museum, The University of Kansas 8: 1–12.
Michaud EJ, Echternacht AC. 1995. Geographic variation in
the life history of the lizard Anolis carolinensis and sup-
port for the pelvic constraint model. Journal of Herpetology
Monnet J-M, Cherry MI. 2002. Sexual size dimorphism in
269: 2301–2307.
of the American Museum of Natural History 121: 149–386.
Mousseau TA, Roff DA. 1995. Genetic and environmental
contributions to geographic variation in the ovipositor length
Nevo E. 1972. Climatic adaptation in size of the green toad
(Bufo viridis). Israel Journal of Medical Sciences 8: 1010.
y 54: 1271–1281.
Nussbaum RA, Wu SH. 1995. Distribution, variation, and
systematics of the Seychelles treefrog, Tachycentris sechel-
lensis (Amphibia: Anura: Hyperoliidae). Journal of Zoology,
and desiccation resistance in populations of some tropical
drosophilids. Journal of Zoological Systematics and Evolution-
Partridge L, French V. 1996. Thermal evolution of ecto-
therm body size: why get big in the cold?. In: Johnston IA,
Bennett AF, eds. Animals and temperature: phenotypic and
evolutionary adaptation. Cambridge: Cambridge University
Press, 265–292.
in sexual size dimorphism within a single snake species
Prestwich KN. 1994. The energetics of acoustic signalling in
Quin DG, Smith AP, Norton TW. 1996. Eco-geographic vari-
sion in size and sexual dimorphism in sugar gliders and
squirrel gliders (Marsupialia: Petauridae). Australian Jour-
nal of Zoology 44: 19–45.
Digest (Australia).
Reeve MW, Fowler K, Partridge L. 2000. Increased body
size confers greater fitness at lower experimental tempera-
ture in male Drosophila melanogaster. Journal of Evolution-
Reyment RA, Blackith RE, Campbell NA. 1984. Multivariate
Riha VF, Berven KA. 1991. An analysis of latitudinal vari-
ation in the larval development of the wood frog (Rana sylvat-
Roberts JD. 1976. Call differentiation in the Limnodynes-
tas tasmaniensis complex (Anura: Leptodactylidae). Unpub-
lished PhD Thesis, Department of Zoology, The University of
Adelaide.
Roberts JD, Seymour RS. 1989. Non-foamy egg masses in
Limnodynastes tasmaniensis (Anura: Myobatrachidae) from
Robinson SJW, Partridge L. 2001. Temperature and clinal
variation in larval growth efficiency in Drosophila melano-
Schauble CA. 2002. Geographic variation in the widespread
Australian frogs Limnodynastes tasmaniensis and L. peronii.
Unpublished PhD, Department of Zoology and Entomology,
The University of Queensland.

© 2004 The Linnean Society of London, Biological Journal of the Linnean Society, 2004, 82, 39–56


