Geographic variation in thermal sensitivity of jumping performance in the frog *Limnodynastes peronii*

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Summary

I compared the thermal sensitivity of jumping performance of five populations of the striped marsh frog (*Limnodynastes peronii*) over a wide geographic range extending from the cool-temperate south to the tropical north of Australia. Maximum jumping performance of adult *L. peronii* was assessed for each population at eight temperatures between 5°C and 32°C using a custom-designed force platform. From force recordings for each individual jump, maximum jumping force (F_{max}) and acceleration (A_{max}) and maximum power output (P_{max}), take-off velocity (U_{max}), jump distance (D_J) and contact time on the platform (T_C) were calculated. The body mass of adult *L. peronii* varied over their geographic range, from approximately 5g for the lowland tropical population to more than 22g for the cool-temperate populations. The thermal sensitivity of jumping performance varied over their geographic range, with the populations from the cooler climates generally performing better than those from the warmer climate populations at the cooler temperatures, and *vice versa* at the higher temperatures. However, not all parameters of jumping performance underwent parallel changes in thermal sensitivity amongst the populations of *L. peronii*. Only minor differences in the shape of the thermal sensitivity curves for F_{max} and A_{max} were detected amongst the populations, while the thermal sensitivities of U_{max}, D_J and P_{max} all displayed considerable variation amongst the populations. The optimal temperatures for U_{max}, D_J and P_{max} were generally lower in the cool-temperate populations than in the tropical populations of *L. peronii*. To determine whether this geographic variation was due to genetic variation, or merely reflected phenotypic plasticity, I also compared the thermal sensitivity of jumping performance between metamorph *L. peronii* from two different populations raised under identical conditions in the laboratory. The maximum jumping distance of the metamorph *L. peronii* was assessed at seven temperatures between 8°C and 35°C for the two latitudinally extreme populations (i.e. lowland tropical Proserpine and cool-temperate Gippsland populations). Like adult *L. peronii*, the metamorphs from the cool-temperate population jumped further than those from the lowland tropical population at the lower temperatures, although no differences were detected at the higher temperatures. Thus, geographic variation in thermal sensitivity of jumping performance in *L. peronii* probably has a genetic component, and the different populations appear to have undergone genetic adaptation of their thermal sensitivity to the varied thermal environments.

Key words: thermal dependence, geographic variation, evolution, population differentiation, temperature, locomotion, jumping, frog, *Limnodynastes peronii*.

Introduction

Physiological processes operate within the bounds of lethal temperature extremes, with the performance of a physiological trait gradually increasing with temperature from a lethal minimum to an optimum before dropping precipitously as temperature approaches a lethal maximum. Consequently, changes in environmental temperature can significantly influence the efficiency of physiological processes in ectotherms with a limited capacity for behavioural regulation of body temperature (Huey and Stevenson, 1979). Variation in the physiological performance of ectotherms as a result of changes in body temperature can affect survival and realised fitness through its influence on locomotion, foraging and mating (Huey and Stevenson, 1979; Christian and Tracy, 1981; Kingsolver and Watt, 1983). Studies examining the evolution of thermal sensitivity of ectotherm performance offer an opportunity to study the ecological and evolutionary consequences of variation in physiological performance (Kingsolver and Watt, 1983; Bauwens et al., 1995; Marden et al., 1996).

Traditionally, interspecific comparative studies have been

used to deduce historical evolutionary patterns of the thermal sensitivity of ectotherm performance. From gross interspecific comparisons (e.g. Antarctic *versus* tropical fish) (Johnston and Altringham, 1985; Franklin, 1998), thermal sensitivity of ectotherm performance has clearly evolved in response to different thermal environments. However, these interspecific comparisons reveal little about how readily thermal sensitivity of performance will evolve or the possible genetic correlations between different aspects of the thermal sensitivity curve and the likely responses of natural populations to short- or long-term thermal disturbances. Recently, several different approaches have been used to address these issues of the evolution of thermal sensitivity of ectotherm performance, including interspecific comparisons within a phylogenetic framework (Bauwens et al., 1995), comparisons amongst different populations of a single species (John-Alder et al., 1989; Van Damme et al., 1989; Bronikowski et al., 2001), laboratory natural selection (Bennett et al., 1990; Huey et al., 1991) and quantitative genetic studies (Gilchrist, 1996). Not surprisingly, these highly complementary approaches differ in their conclusions.

Laboratory natural selection and quantitative genetic studies (e.g. Bennett et al., 1990; Leroi et al., 1994; Gilchrist, 1996; Mongold et al., 1996) have dominated evolutionary studies of thermal sensitivity during the last decade because of their ability to document evolution in real time and/or their effectiveness in elucidating genetic correlations between certain aspects of the thermal sensitivity curve. These studies have demonstrated that ectotherms with short generation times possess the capacity to respond to changes in the thermal environment by adaptation of their thermal sensitivity (Huey et al., 1991; Bennett et al., 1992; Leroi et al., 1994). Similarly, several interspecific comparisons of the thermal sensitivity of ectotherm performance amongst closely related species from distinct thermal environments (including phylogenetic analyses) indicate that thermal sensitivity readily evolves in response to different thermal environments (John-Alder et al., 1988; Bauwens et al., 1995; Navas, 1996). In contrast, inter-population studies suggest that thermal sensitivity is evolutionarily conservative and does not readily undergo change (Hertz et al., 1983; Crowley, 1985; John-Alder et al., 1989; Van Damme et al., 1989). However, it is not clear whether these intraspecific studies are representative of the differentiation of thermal sensitivity of performance among natural ectotherm populations. Further comparative analyses of the thermal sensitivity of performance using several populations of an ectotherm species found over a wide range of thermal environments would help to elucidate general patterns of differentiation of thermal sensitivity among natural populations.

In this study, I determined the extent of geographic variation in thermal sensitivity of jumping performance in the striped marsh frog (*Limnodynastes peronii*). My study was designed to address several questions directly relating to the evolution of thermal sensitivity of ectotherm performance. First, is there any divergence amongst the populations in the thermal sensitivity curve of jumping performance? If

different populations of *L. peronii* have undergone thermal adaptation to their environment, I predict that populations from the cooler climates will perform better at cooler temperatures than those from the tropical populations, and *vice versa* at the warmer temperatures. Second, have all parameters of whole-animal jumping performance (maximum velocity and jump distance) and their underlying physiological traits (power output, acceleration and force) undergone parallel changes in thermal sensitivity amongst different populations? For example, only certain parameters of jumping performance and not others may have experienced selection in the different thermal environments. Finally, is the geographic variation in the shape of the thermal sensitivity curve among the populations of adult *L. peronii* similar to the variation that has been observed in laboratory natural selection and interspecific comparative studies?

Several factors make *L. peronii* an appropriate species for this intraspecific analysis of thermal sensitivity. First, striped marsh frogs (*L. peronii*) are distributed over a huge geographic range, from 16°S (tropics) to 42°S (cool-temperate). Moreover, differences in thermal characteristics amongst the different populations of *L. peronii* are enhanced further by geographic differences in their activity and breeding seasons. Also, like other predominantly terrestrial amphibians (Putnam and Bennett, 1981; Renaud and Stevens, 1983; Rome, 1983; Whitehead et al., 1989; Knowles and Weigl, 1990), adult *L. peronii* are incapable of modifying the thermal sensitivity of their jumping performance in response to long-term changes in their thermal environment (Wilson and Franklin, 2000); thus, any differences amongst populations can probably be attributed to genetic differences. However, to test this assumption further, the thermal sensitivity of jumping performance was also compared between newly metamorphosed *L. peronii* from the two latitudinal extreme populations raised under identical conditions in the laboratory.

Materials and methods

Adult male striped marsh frogs *Limnodynastes peronii* (Duméril and Bibron) (Fig. 1A) were collected from five study sites across an extensive geographic range over their natural distribution (from the tropical north to the cool-temperate regions of Australia) (Fig. 1B). Maximum jumping performance of *L. peronii* adults was compared amongst the five populations at eight temperatures between 5 °C and 32 °C. The jumping performance of metamorph *L. peronii* raised in the laboratory under constant conditions was also compared between the two latitudinal extreme populations (i.e. tropical lowland Proserpine and cool-temperate Gippsland) at seven temperatures between 8 °C and 35 °C.

Description of study sites

Five populations of *L. peronii* that represented the range of thermal environments experienced by this species over their distribution were selected for this study. The tropical lowland
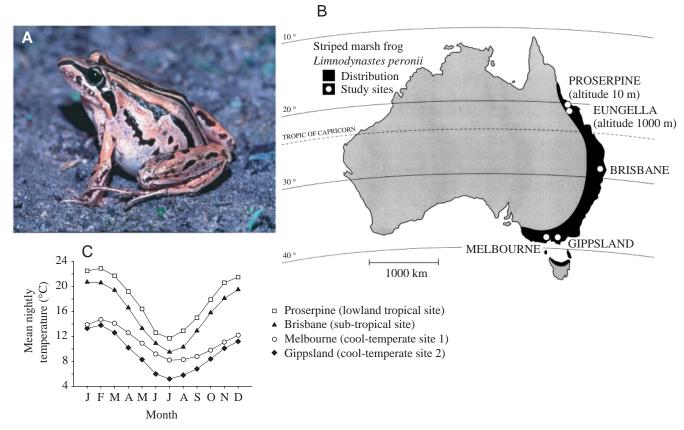
Fig. 1. (A) A striped marsh frog (*Limnodynastes peronii*) (photograph courtesy of E. Meyer). (B) Distribution of striped marsh frogs along the eastern regions of Australia. Symbols indicate sites where adult animals were collected. (C) Seasonal changes in average nightly temperature at four of the study sites (Australian Bureau of Meteorology).

Proserpine site was consistently warmer than every other site throughout the year, with nightly temperatures more than 6°C higher than at the two cool-temperate study sites year-round (Fig. 1C). The subtropical Brisbane site represented an intermediate thermal environment between the latitudinal extreme study sites (Fig. 1C).

Proserpine (20°27′S, 148°36′E; altitude 10 m)

This tropical lowland site consists of ephemeral pools of water on the periphery of a flood plain, which consistently receives rain between the months of December and April (Australian summer to mid-Autumn). The activity and breeding season of *L. peronii* in this region are during the hotter summer months, with their breeding pools drying up by the end of April.

Eungella (21°7′S, 148°29′E; altitude 1000 m)

This high-altitude tropical population receives consistent rain year-round and is characterised by large permanent ponds. The activity and breeding season of *L. peronii* from this study site are virtually year-round, with the exception of mid-winter.

Brisbane (27°28′S, 153°3′E; altitude 20 m)

This subtropical lowland site consists of both permanent and semi-permanent ponds. Given sufficient rain, *L. peronii* in the

areas surrounding Brisbane will breed almost year-round, except for mid-winter.

Melbourne (37°50′S, 145°7′E; altitude 20 m)

This cool-temperate site includes both permanent and semi-permanent ponds. The activity and breeding season of *L. peronii* inhabiting these ponds are predominantly from late-winter to early summer (late July to December). The paucity of rain during the warmer months generally precludes breeding during the hottest parts of the year.

Gippsland (38°52′S, 146°17′E; altitude 300 m)

The activity and breeding season of *L. peronii* from this second cool-temperate site are essentially very similar to those at the Melbourne site (i.e. late July to December). This site consists of permanent ponds only.

I used Tidbit Stowaway temperature loggers to record environmental temperature at the lowland tropical (Proserpine) and two cool-temperate (Melbourne and Gippsland) study sites to quantify and compare their thermal characteristics. Temperature loggers were placed in sheltered locations where calling males were captured, and temperature was recorded every hour during the months when *L. peronii* were typically active in each study site.

The force platform

The design of the force platform was based on that outlined by Katz and Gosline (1993) for measuring the jumping performance of locusts and is described in detail in Wilson et al. (2000). The calculations used to determine maximum jumping acceleration (A_{max}), maximum power output (P_{max}), take-off velocity (U_{max}) and jump distance (D_J) from the force platform data are also described in Wilson et al. (2000).

Effects of temperature on jumping performance

The jumping performance of each frog was assessed within 3 days of capture in the order 20, 12, 32, 26, 8, 28, 24 and 5 °C, and then again at 20 °C. The initial and final test temperature of 20 °C was non-randomly selected whilst the set order for all other test temperatures for all individuals was randomly selected. Data from individuals that did not produce at least 90 % of their initial maximum jumping force when retested at 20 °C were discarded. No more than two individuals from each population were removed from the analysis. As no difference in jumping performance for any population was detected between the initial and final testing at 20 °C, it was concluded that the jumping performance did not change over the course of the experiment. The body temperature of the frogs was changed at 4 °C h⁻¹ and was maintained by keeping each individual in a 300 ml plastic container that was half-filled with water and immersed in a temperature-controlled waterbath (±0.5 °C). The air temperature of the experimental room was kept within 5 °C of the experimental temperature at all times. The body temperature of the frogs did not change significantly during handling and jumping at any temperature and was kept within ±0.5 °C of the experimental temperature. Jumps were elicited by placing the frogs in the middle of the force platform and touching their urostyle, taking care to avoid applying forces to the platform. Each individual was stimulated to jump from the platform at least five times, with the jump that produced the greatest ground reaction force for each individual at each temperature used as a measure of maximum jumping performance.

Thermal sensitivity of jumping performance in laboratory-reared frogs

Eight clutches were collected from the two latitudinally extreme study sites, Proserpine and Gippsland. For each study site, clutches were collected within 12 h of being deposited and were immediately mixed, placed at 23 °C and transported to The University of Queensland campus. Eggs hatched within 52 h, and the tadpoles were then housed individually in 1 l plastic containers and fed daily on dried cat food until they metamorphosed. Developing larvae were kept in temperature-controlled rooms with the water temperature at 23 °C. The jumping performance of the frogs was tested on the day after their tail had been completely resorbed.

The jumping performance of these metamorphs was determined at seven temperatures between 8 °C and 35 °C. As metamorphs were too small to obtain accurate jumping data from the force platform, only maximum jump distance was recorded for these animals. Each metamorph was encouraged to jump along a wooden bench by lightly touching its urostyle, with at least five jumps from each individual recorded. The ventral surface of the metamorphs was kept damp at all times, allowing their jump distance to be recorded by measuring the distance between damp marks on the wooden bench. The longest jump for each individual metamorph at each temperature was used as a measure of maximum jumping distance. The jumping performance of metamorphs from both populations was assessed in the order 30, 18, 23, 8, 15, 12 and 35 °C, and then again at 30 °C. Like the adult jumping performance protocol, data from individuals that did not produce at least 90 % of their initial maximum jumping force when retested at 30 °C were discarded. No more than two individuals from each population were removed from the analysis.

Descriptive traits of the thermal sensitivity curve

Several descriptive traits of the thermal sensitivity curve were calculated for all parameters of jumping performance from the adult and metamorph data sets. These are the traditional traits used to describe the thermal sensitivity curve outlined originally by Huey and Stevenson (1979). The optimal temperature for performance (T_{opt}) was defined as the single temperature at which an individual produced its peak performance. Peak performance was defined as the value at T_{opt}. As the decrease in performance at high temperatures was not always observed for each individual, thermal performance breadths were not calculated. However, the lower extremity of the thermal performance breadth, defined as the lowest temperature at which performance was at least 80 % of peak performance (LL_{80}), was calculated.

At the end of the jumping protocol, morphological measurements were taken from each adult and metamorph. Snout-to-vent length (L_{SV}) was measured with calipers (to ±0.02 mm), while the mass of each frog was measured with an A200S Sartorius analytical balance (to ±0.01 g).

Statistical analyses

The effects of population on the relationship between temperature and measures of performance (thermal sensitivity curves) were analysed using two-way repeated-measures analysis of variance (ANOVA). All data were log-transformed before analyses. Measures of peak performance, T_{opt} and LL_{80}, were compared amongst the populations using a one-way ANOVA for the adult frogs and a Student's t-test for the metamorphs. Body mass and L_{SV} were compared amongst the adults from the five populations using a one-way ANOVA and a Student's t-test for metamorphs. All results are presented as means ± S.E.M. Statistical significance was taken at $P<0.05$.

Results

Thermal environments of the different study sites

The temperature profiles of the lowland tropical study site and the two cool-temperate study sites were compared during

Table 1. *Morphometrics for the striped marsh frogs (*Limnodynastes peronii*) from the five populations studied*

Population	Locality	Mass (g)	Snout–vent length (mm)	N
Tropical lowland	Proserpine	5.14±0.3	38.6±0.72	16
Tropical highland	Eungella	9.5±0.7	49.6±1.0	15
Sub-tropical	Brisbane	7.5±0.43	43.8±0.9	26
Cool-temperate 1	Melbourne	23.3±2.0	57.3±2.0	13
Cool-temperate 2	Gippsland	22.7±1.4	57.6±1.0	20

Values are means ± S.E.M.

the months when adult *L. peronii* are active at each study site. Average nightly temperature during their months of activity in the lowland tropical Proserpine site varied from 25.4±1.0 and 26.9±1.4 °C in December and January, respectively, to 22.6±1.4 °C in May. In contrast, average nightly temperature increased from 9.7±0.9 °C in July to 18.1±2.0 °C in November for the cool-temperate Melbourne site and ranged from 8.9±0.6 °C in July to 17.6±1.8 °C in November for the Gippsland site.

Geographic variation in thermal sensitivity of adult jumping performance

The body mass of adult *L. peronii* varied across their geographic range (one-way ANOVA; $P<0.01$), increasing from 5.14±0.3 g for the tropical lowland population to 23.3±2.0 g for the Melbourne population (Table 1). As adult *L. peronii* from the tropical lowland Proserpine population did not jump at 5 °C, all comparisons amongst the populations are between 8 °C and 32 °C.

The thermal sensitivity of maximum jumping performance for adult *L. peronii* varied over their geographic range, with the populations from the cooler climates generally performing better than the populations from the warmer climates at the cooler temperatures, and *vice versa* at the higher temperatures (Figs 2, 3). The thermal sensitivity of U_{max} varied significantly among the populations of *L. peronii* (repeated-measures ANOVA; $P<0.01$), with the populations from the cooler climate generally attaining higher velocities than the more tropical populations at low temperatures and *vice versa* at temperatures higher than 24 °C (Fig. 2A). The optimal temperature for peak take-off velocity (U_{opt}) differed significantly amongst the populations of *L. peronii* (one-way ANOVA; $P<0.01$), with the Melbourne population possessing the lowest optimal temperature (21.5±1.2 °C) and the lowland tropical population the highest U_{opt} (30.6±2.3 °C) (Table 2).

The thermal sensitivity of D_J also varied significantly among the different populations of *L. peronii* (repeated-measures ANOVA; $P<0.001$) (Fig. 2B). Both the cool-temperate populations generally produced a longer D_J than the warmer-climate populations at the lower temperatures and *vice versa* at temperatures higher than 24 °C. For example, at 8 °C, both cool-temperate

populations had values of D_J that were more than 200 % greater than those of the tropical lowland population. In contrast, at the test temperature of 32 °C, the tropical lowland population reached a D_J that was more than 25 % greater than those of the cool-temperate populations. The optimal temperature for peak jump distance (D_{opt}) differed among the populations of *L.*
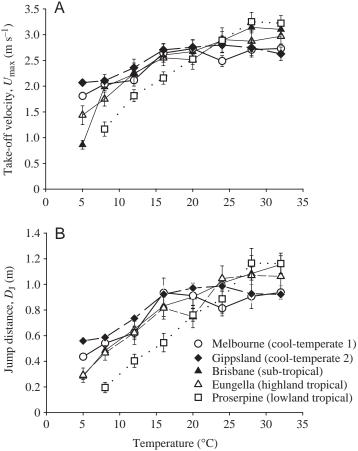

Fig. 2. Thermal sensitivity of (A) maximum take-off velocity (U_{max}) and (B) maximum jump distance (D_J), for adult striped marsh frogs (*Limnodynastes peronii*) from five populations across a wide geographic range. The relationship between temperature and each parameter of jumping performance was significantly different amongst the populations (two-way repeated-measures ANOVA) ($P<0.05$). Values are means ± S.E.M. (Melbourne, $N=12$; Gippsland, $N=24$; Brisbane, $N=22$; Eungella, $N=13$; Proserpine, $N=14$).

Table 2. *Comparison of the descriptive traits of the thermal sensitivity curve of jumping performance for five populations of striped marsh frog (*Limnodynastes peronii*)*

	Gippsland (cool-temperate 1)	Melbourne (cool-temperate 2)	Brisbane (sub-tropical)	Eungella (highland tropical)	Proserpine (lowland tropical)
Maximum jumping force, F_{max}					
Peak (N)	1.26±0.05	1.23±0.05	0.73±0.03	0.78±0.04	0.49±0.02
Optimal temperature (°C)	28.2±0.6*	27.3±0.8	30.2±1.1	28.3±0.7	29.9±0.6
LL_{80} (°C)	23.4±0.6	21.1±0.8	22.3±1.0	22.4±1.1	23.7±0.7
Maximum jumping acceleration, A_{max}					
Peak (m s^{-2})	47.4±2.2	36.3±3.7	81.7±2.9	71.6±3.4	87.6±3.4
Maximum jumping velocity, U_{max}					
Peak (m s^{-1})	3.09±0.11*	3.12±0.09	3.32±0.09	3.23±0.09	3.47±0.12
Optimal temperature (°C)	21.7±1.3*	21.5±1.2	25.5±1.6	24.3±1.2	30.6±2.3
LL_{80} (°C)	13.3±0.9*	16.7±0.8	17.9±1.2	18.9±1.3	22.7±0.8
Maximum jump distance, D_J					
Peak (m)	1.15±0.06*	1.16±0.04	1.23±0.06	1.23±0.07	1.31±0.06
Optimal temperature (°C)	22.9±1.2*	21.2±1.1	24.9±1.1	25.4±0.9	29.3±0.8
LL_{80} (°C)	16.2±0.8*	18.9±0.9	17.1±1.4	20.6±1.0	24.8±1.4
Maximum instantaneous power output, P_{max}					
Peak (W kg^{-1})	108.8±7.0*	110.1±7.5	190.7±9.5	175.9±12.9	205.9±12.4
Optimal temperature (°C)	26.3±0.9*	25.1±1.1	25.8±1.0	26.2±1.1	29.9±0.9
LL_{80} (°C)	20.0±1.1*	19.6±1.2	23.3±1.2	22.7±1.1	26.8±0.8
N	24	12	22	13	14

For maximum acceleration, only peak measures are provided because all other descriptive traits for this parameter are identical to maximum jumping force.

Significant population effects for each thermal sensitivity trait are denoted by an asterisk. Statistical significance is taken at the level of $P<0.05$.

Values are means ± S.E.M.

LL_{80}, the lowest temperature at which performance was at least 80 % of peak performance.

peronii (one-way ANOVA; $P<0.01$), with the lowland tropical population possessing the highest D_{opt} of 29.3±0.8 °C and the lowest of 21.2±1.1 °C for the Melbourne population (Table 2).
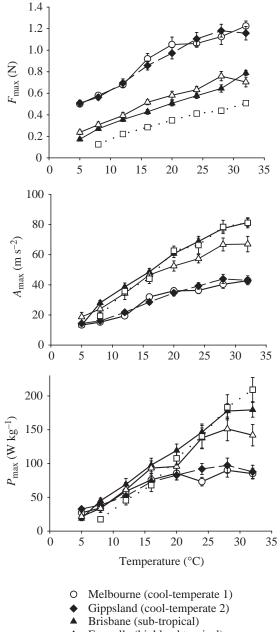
The thermal sensitivity of F_{max} significantly varied across the geographic range of *L. peronii* (repeated-measures ANOVA; $P<0.05$) (Fig. 3A). F_{max} for both cool-temperate populations was greater than for all other populations at each temperature, while the lowland tropical population possessed the lowest F_{max} at each temperature. For the cool-temperate Melbourne population, F_{max} increased from 0.50±0.02 N at 5 °C to 1.23±0.05 N at 32 °C, while that for the tropical lowland population increased from 0.13±0.01 N at 8 °C to 0.51±0.01 N at 32 °C. Optimal temperatures for F_{max} (F_{opt}) differed among the populations (one-way ANOVA; $P<0.01$), with the Gippsland and Melbourne populations possessing the lowest F_{opt} values (28.2±0.6 and 27.3±0.8 °C, respectively) and the Brisbane population the highest F_{opt} of 30.2±1.1 °C (Table 2). The thermal sensitivity of A_{max} also varied significantly across the geographic range of *L. peronii* (repeated-measures ANOVA; $P<0.05$) (Fig. 3B). Although the cool-temperate populations possessed the lowest A_{max} at each temperature, the difference between the populations was less than 10 % at the low temperatures but was greater than 100 % at the higher temperatures.

The thermal sensitivity of P_{max} also differed among the populations of *L. peronii* (two-way ANOVA; $P<0.001$) (Fig. 3C). The optimal temperature for peak power output (P_{opt}) varied significantly across the populations of *L. peronii*, with the lowest P_{opt} exhibited by the Melbourne population (25.1±1.1 °C) and the highest by the lowland tropical population (29.9±0.9 °C) (Table 2). The thermal sensitivity of T_C varied significantly among the populations of *L. peronii* (two-way ANOVA; $P<0.05$), with the T_C of both cool-temperate populations being consistently longer at all temperatures than the other populations (Fig. 4).

Thermal sensitivity of jumping performance in laboratory-reared frogs

The body mass of the laboratory-raised metamorph *L. peronii* was significantly different between the cool-temperate Gippsland frogs (0.35±0.02 g) and the tropical lowland Proserpine frogs (0.27±0.01 g) (t-test; $P<0.01$). Metamorphs from the tropical lowland population did not jump at 8 °C, so all comparisons between the two populations were made at temperatures between 12 and 35 °C.

The thermal sensitivity of D_J for the laboratory-raised *L. peronii* metamorphs differed significantly between the populations (repeated-measures ANOVA; $P<0.001$) (Fig. 5).

Fig. 3. Thermal sensitivity of (A) maximum jumping force (F_{max}), (B) maximum jumping acceleration (A_{max}) and (C) maximum instantaneous jumping power (P_{max}) for adult striped marsh frogs (*Limnodynastes peronii*) from five populations across a wide geographic range. The relationship between temperature and both parameters of jumping performance was significantly different amongst the populations (two-way repeated-measures ANOVA) ($P<0.05$). Values are means ± S.E.M. (See Fig. 2 for *N* values.)

For the Gippsland metamorphs, D_J increased from 8.1 ± 0.5 cm at $8\,°C$ to 25.7 ± 1.0 cm at $35\,°C$, while D_J for the tropical lowland population increased from 9.2 ± 0.4 cm at $12\,°C$ to 25.6 ± 0.9 cm at $35\,°C$.
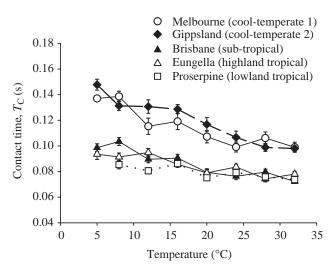
D_J of the Gippsland frogs was generally greater at cool

Fig. 4. Thermal sensitivity of contact time on the platform during a jump (T_C) for adult striped marsh frogs (*Limnodynastes peronii*) from five populations across a wide geographic range. The relationship between temperature and T_C was significantly different amongst the populations (two-way repeated-measures ANOVA) ($P<0.05$). Values are means ± S.E.M. (See Fig. 2 for *N* values.)
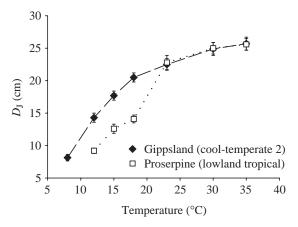

Fig. 5. Thermal sensitivity of maximum jump distance (D_J) for metamorph striped marsh frogs (*Limnodynastes peronii*) raised under identical conditions in the laboratory from the cool-temperate Gippsland and lowland tropical Proserpine population. Thermal sensitivity of D_J differed significantly between the two populations (two-way repeated-measures ANOVA) ($P<0.05$). Values are means ± S.E.M. (Gippsland, $N=19$; Proserpine, $N=13$).

temperatures, but there were no differences between the populations at temperatures greater than $24\,°C$ (Fig. 5). At $12\,°C$, D_J of the Gippsland metamorphs was $40\,\%$ higher than that of the tropical lowland populations (Fig. 5). The optimal temperature for D_J was not significantly different between the two populations (Table 3).

Discussion

The thermal sensitivity of maximum jumping performance varied over the geographic range of the striped marsh frog (*L.*

Table 3. *Comparison of thermal sensitivity traits for maximum jump distance between laboratory-raised metamorph striped marsh frogs (*Limnodynastes peronii*) from the cool-temperate Gippsland and lowland tropical Proserpine populations*

	Gippsland (cool-temperate 2)	Proserpine (lowland tropical)
Maximum jump distance, D_J		
Peak (cm)	27.3±1.0	26.8±1.0
Optimal temperature (°C)	32.6±0.6	32.7±0.6
LL_{80} (°C)	21.6±1.1*	25.5±1.0
N	19	13

Significant differences between the populations are denoted by an asterisk. Statistical significance is taken at the level of $P<0.05$.

Values are means ± S.E.M.

LL_{80}, the lowest temperature at which performance was at least 80 % of peak performance.

peronii). Cool-temperate populations of *L. peronii* consistently outperformed the warmer climate populations at the lower temperatures, and the tropical lowland population generally outperformed the more temperate populations at the higher temperatures. Moreover, optimal temperatures for jumping were lower in the cool-temperate populations than in the tropical populations of *L. peronii*. The thermal sensitivity of jumping performance in adult *L. peronii* is not affected by long-term exposure to different thermal environments (Wilson and Franklin, 2000), so differences in thermal sensitivity of jumping performance amongst populations of *L. peronii* probably reflected genetic differences. To strengthen this suggestion, I also compared the thermal sensitivity of jumping performance of metamorph *L. peronii* from two populations (lowland tropical and cool-temperate) raised under identical conditions in the laboratory. The thermal sensitivity of jumping performance in metamorph *L. peronii* differed between the two populations, with the cool-temperate Gippsland population jumping further than the lowland tropical population at the lower temperatures. Thus, geographic variation in thermal sensitivity of jumping performance in *L. peronii* probably has a genetic component and the different populations have undergone genetic adaptation of their thermal sensitivity to the varied thermal environments.

Most other intraspecific comparative studies have reported very little geographic variation in thermal sensitivity of performance, indicating that this trait is evolutionarily conservative and does not readily undergo differentiation amongst populations (Hertz et al., 1983; Crowley, 1985; Van Damme et al., 1989; John-Alder et al., 1989; Bronikowski et al., 2001). However, the data from the present study show that the thermal sensitivity of ectotherm performance can clearly diverge amongst different populations of a single species. Why some species and not others exhibit geographic variation in the thermal sensitivity of performance is not clear. One possibility is that geographic variation in active body temperatures may not be great enough to result in selection for changes in thermal

sensitivity. Although John-Alder et al. (1989) found no differences in thermal sensitivity of swimming and muscle contractile performance between northern and southern populations of the tree frog *Hyla crucifer*, geographic variation in the seasonal timing of breeding activity results in their activity periods occurring at similar environmental temperatures (John-Alder et al., 1989). In contrast, differences in active body temperatures were substantial amongst the different populations of *L. peronii*, with animals from the lowland tropical population commonly captured with body temperatures in excess of 25 °C, while calling male *L. peronii* from the Gippsland population were captured with body temperatures of less than 15 °C (R. S. Wilson, unpublished data).

Not all examples of conservative geographic variation in thermal sensitivity within an ectotherm species can be attributed to a lack of interpopulational variation in body temperature. No differences were detected in thermal sensitivity of running performance between different populations of *Sceloporus undulatus* (Crowley, 1985), *Podarcis tiliguerta* (Van Damme et al., 1989) or several agamid lizards (Hertz et al., 1983) despite significant differences in field body temperatures observed amongst the populations. Many other factors may also be important determinants of population differentiation of thermal sensitivity. One possibility for studies comparing different populations across altitudinal ranges (Crowley, 1985; Van Damme et al., 1989; Hertz et al., 1983) is that gene flow may be too great across this narrow range to allow differentiation of thermal sensitivity. To obtain a more comprehensive picture of the pattern of population differentiation of thermal sensitivity, further studies are necessary on ectotherms with a limited capacity for thermoregulation that are also distributed over wide latitudinal and altitudinal ranges.

In contrast to previous intraspecific studies, laboratory natural selection studies have shown that ectotherms with short generation times can respond rapidly to changes in their thermal environment by adaptation of their thermal sensitivity of performance (Bennett et al., 1990; Huey et al., 1991). Interspecific comparisons of the thermal sensitivity of performance between closely related species also indicate that this physiological trait readily undergoes adaptation to different thermal environments (Van Berkum, 1988; John-Alder et al., 1988; Navas, 1996). For example, John-Alder et al. (1988) found that several North America species of hylid frog inhabiting the higher latitudes or that bred during the cooler parts of the year performed relatively better at low temperatures than did species from lower latitudes or that reproduced during the warmer seasons. Similarly, Navas (1996) compared the thermal sensitivity of locomotor performance amongst different species of neotropical anurans over an altitudinal range in the Colombian Andes. The locomotor performance of the high-elevation species (above 2900 m) was almost thermally independent over the temperature range 5–35 °C, while the performance of the low-altitude species was considerably reduced at temperatures below 15 °C.

Not all parameters of jumping performance in adult *L. peronii* underwent parallel changes in thermal sensitivity amongst the populations. Both whole-animal performance traits (U_{max} and D_J) displayed considerable geographic variation in thermal sensitivity among populations of *L. peronii*. U_{max} and D_J were almost independent of temperature between 12 and 32 °C for adult *L. peronii* from the cool-temperate populations. It is the whole-animal traits that are exposed to direct selection, so it is not surprising that these traits displayed the greatest variation amongst populations. The low level of temperature compensation observed in the cool-temperate populations was not related to parallel changes in F_{max} or A_{max}: both these parameters were highly temperature-sensitive between 12 and 32 °C for all populations. However, adult *L. peronii* from the cool-temperate populations possessed greater total contact times whilst jumping at temperatures between 5 and 20 °C, thus allowing acceleration of their mass over an extended period. Maintenance of F_{max} and A_{max} relative to those of the other populations, coupled with increases in contact time and power output, may have led directly to higher take-off velocities and longer jump distances at the lower temperatures.

The body mass of adult male *L. peronii* varied across their geographic range, from approximately 5 g in the lowland tropical population to more than 22 g in the cool-temperate populations in southern Australia. As differences in body mass were also observed between metamorph *L. peronii* from high- and low-latitude populations raised under identical conditions in the laboratory, the latitudinal cline in body size appears to have a genetic component. An increase in body size with increasing latitude is often referred to as Bergmann's rule. Although originally proposed for body size clines in endotherms (Bergmann, 1847), ectotherms also exhibit similar clines in body size with increasing distance from the equator. Many studies have reported latitudinal or altitudinal clines in body size; for example, in the anuran *Rana sylvatica* (Berven, 1982), in several species of *Drosophila* (Coyne and Beecham, 1987; Imasheva et al., 1994; James et al., 1995) and in the house fly *Musca domestica* (Bryant, 1977). However, most studies do not address the functional consequences of these variations in body size (Partridge and French, 1996). The measures of jumping performance reported in the present study allow an examination of the functional consequences of latitudinal and altitudinal clines in body mass. The larger adult body mass of the cool-temperate populations of *L. peronii* allowed the production of greater ground reaction forces but substantially lower accelerations and longer contact times. As a consequence, take-off velocity and jump distance were not substantially influenced by body mass in adult *L. peronii* (Wilson et al., 2000), and variations in body mass alone amongst the populations did not affect these parameters.

Evolutionary theory predicts there should be a trade-off between specialist and generalist phenotypes, whereby the ability to perform well over a wide range of environments can be achieved only at the expense of maximal performance. Although this Principle of Allocation hypothesis (Levins, 1968) underlies much of evolutionary theory, it has seldom been empirically tested using physiological traits. Within the field of thermal physiology, a few studies have used the thermal sensitivity of ectotherm performance to investigate the generality of this evolutionary prediction (Huey and Hertz, 1984; Van Berkum, 1988; Gilchrist, 1996). Referred to as the 'Jack-of-all-temperatures is a master of none' hypothesis, it predicts that phenotypes that can perform a physiological function well over a wide range of temperatures (i.e. generalist) relative to other phenotypes will perform relatively poorly at their optimal temperature relative to the specialist phenotypes (Huey and Hertz, 1984). A corollary of this hypothesis is that tropical ectotherms (less variable environment) should possess specialist phenotypes that maximise peak performance, while more temperate ectotherms (more variable environment) should possess generalist phenotypes that maximise performance breadth (Van Berkum, 1988).

I could not calculate the thermal performance breadths of jumping performance for the different populations of *L. peronii* because the performance of the adults was only tested up to a maximum of 32 °C. However, several lines of evidence appear to indicate there may have been a trade-off between maximising thermal performance breadth (populations from cooler climates) and maximising peak jumping performance (populations from warmer climates) in *L. peronii*. Peak measures of jumping performance tended to decrease with increasing latitude. For example, peak U_{max} decreased from 3.47 m s^{-1} in the tropical lowland Proserpine population to 3.09 m s^{-1} in the Gippsland population. Similarly, minimum thermal performance breadth temperatures (T_{min}) generally decreased with latitude and altitude, possibly indicating an extension of the thermal performance breadth for the populations from cooler climates. For example, LL_{80} for U_{min} was 22.7 °C in the tropical lowland population and 13.3 °C for the Gippsland population. Although this difference may be negated by similar differences amongst the populations in maximum thermal performance breadth, it is likely that this difference would be much lower at the higher temperatures. Data on the critical thermal maxima of different populations of *L. peronii* (Brattstrom, 1968) suggest that a significant decrease in performance would occur in all populations just above 35 °C, making differences in thermal performance breadth amongst the populations smaller than indicated from T_{min} data, but still real.

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