

# Individual variation in preferred body temperature covaries with social behaviours and colour in male lizards

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## Abstract

1. I tested if individual variation in preferred body temperature (PBT) covaried with behaviours and male phenotypic traits (size and colouration) in *Pseudemoia entrecasteauxii*.
2. Individuals varied in their PBT and this variation was repeatable across days. PBT was not related to body size but males with orange ventral colour had higher PBT.
3. Males with orange ventral colour were more aggressive and dominated males with white venters.
4. Male behaviours were correlated and they covaried with PBT. Correlated behaviours such as these may be related to a shy–bold continuum.

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## 1. Introduction

A prerequisite of selection is that there is heritable variation between individuals; however, most studies have focussed on the mean for a given species or population, effectively treating individuals as ecological equivalents (Bolnick et al., 2003; Sih et al., 2003). Studies that have considered individual variation in traits such as behaviour or metabolic rate have demonstrated that individual variation is consistent across different situations and repeatable between subsequent measurements, and this can have dramatic effects on many fitness-related traits (Metcalf et al., 1995; Brodie and Russell, 1999; Labocha et al., 2001; Dingemanse et al., 2004; Sih et al., 2004). Consistency in individual variation demonstrates that the behaviour of an organism in one context can be linked to their behaviour in another and this can limit the optimal expression of a trait and influence its evolution (Sih et al.,

2004). Variation in some aspect of physiology, such as metabolic rate or plasma testosterone levels, may cause correlations between traits (Metcalf et al., 1995; Sih et al., 2003; Schjolden et al., 2005). In ectotherms, body temperature is arguably the most important ecophysiological variable, influencing a variety of fitness-related traits including immune function, metabolic rate, digestive efficiency, sensory input and locomotion (for review, see Angilletta et al., 2002b). Thermoregulating ectotherms normally strive to maintain their internal temperature at a preferred body temperature (PBT) to maximise processes such as digestion and locomotion (Stevenson, 1985). However, studies have identified considerable variation between individuals in their PBT (Peterson and Arnold, 1986; Blouin-Demers et al., 2000), but to my knowledge none have considered if this variation is repeatable and if this is related to an individual's morphology or behaviour.

The main focus of many thermoregulatory studies has been to identify the PBT for a species or population and study the effects of deviation from this temperature on various performance measures (Huey et al., 1990; Mautz et al., 1992; Currin and Alexander, 1999; Blouin-Demers et al., 2000; Angilletta et al., 2002b). In most ectotherms,

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performance increases up to a thermal optimum and then falls away as body temperature approaches the critical maximum (Angilletta et al., 2002b). At lower temperatures, changes in locomotor performance can induce shifts in antipredator behaviours (Keogh and De Serto, 1994; Brodie and Russell, 1999; Whitaker and Shine, 1999; Cooper, 2000), foraging behaviour (Díaz, 1994), general activity (Melville and Schulte, 2001), social behaviours (Mautz et al., 1992; Stone et al., 1995; Stutt and Willmer, 1998) and interspecific aggression (Magoulick and Wilzbach, 1998). Interestingly, several of these studies identified that locomotor performance is optimised within a range of temperatures rather than a single optimum (Mautz et al., 1992; Angilletta et al., 2002a). Therefore, individuals that maintain lower PBTs are not necessarily at a disadvantage with respect to locomotion and may gain advantages in terms of reduced metabolic rate and energy expenditure (Angilletta, 2001). In contrast, other processes are more sensitive to changes in body temperature. For example, metabolisable energy intake varies greatly when temperature deviates from the optimum (Angilletta, 2001).

The fact that different physiological processes have different thermal sensitivities suggests that the optimal internal temperature may be under conflicting selection pressure. One of the proposed explanations for individual variation within a trait is the fact that selection may conflict across multiple contexts in this way (Sih et al., 2003). For example, high levels of aggression may be favoured in a competitive or foraging context, but may be under strong negative selection in a parental or inter-sexual context (Chapman et al., 2003; Sih et al., 2003). As a result, individuals within a population may diverge to maximise fitness under certain conditions. High body temperature may be favoured when food is abundant and predators are scarce, but may be a disadvantage when food is scarce and predators are abundant. Environmental or genetic variation could promote individual variation in PBTs. Other factors such as breeding colouration and male aggression may alter the energy requirements experienced by an individual (Metcalf et al., 1995), and create variation in PBT and behaviours. Considering the effects of temperature on ectotherm physiology and behaviour, it is likely that variation in PBT at the individual level may parallel variation in a suite of behaviours, in turn producing correlations between them across contexts. Here, I investigate individual variation in PBT in the Mountain Log skink *Pseudemoia entrecasteauxii* (*Lygosoma*, *Leiopisma entrecasteauxii*) and test if it is related to an individual's behaviours or morphology.

The Mountain Log skink is a small cool temperate ectotherm, found in alpine regions in Australia (Cogger, 1996). Their activity is strongly seasonal and limited to a relatively short season from December to March (Pengilly, 1972). This species provides a good system to investigate differences in PBT and potential behavioural correlations, as males differ in traits that may influence their energy expenditure. During the breeding season, male

reproductive strategies appear to diverge, approximately half the males develop orange ventral colouration that relates to aggression and dominance (Stapley, 2004). The aim of this study is to identify if there is consistent individual variation in PBT and test the hypothesis that this variation covaries with social behaviours and secondary sexual traits (breeding colour and body size) in male *P. entrecasteauxii*.

## 2. Methods

### 2.1. Animal care and husbandry

Lizards used in the study were collected by hand from Namadgi National Park in the Australian Capital Territory. Animals were transported back to the laboratory and housed individually in plastic tubs (420 mm *L* 320 mm *W* 220 mm *H*) in a temperature-controlled room maintained at 18–20 °C. The floor of the container was covered with paper towel and a ceramic tile was provided as a retreat site. Heat was supplied from 8:30 h to 17:30 h by heat tape that ran under each enclosure. The room was under a 12:12 h light:dark cycle. The lizards were fed *ad libitum* with live food (crickets and mealworms) dusted with vitamin powder.

### 2.2. Experimental procedure

A total of 32 male lizards were tested in three separate experiments, half of these (16) had orange ventral colour and the other half had white ventral colour. Colour was identified by visual comparison to a Natural Colour Scheme colour chart at normal incidence (full, morning sunlight). This method of colour assessment is biased toward the human visual system and we know from studies of *Anolis* that lizards can detect light at lower (ultraviolet) wavelengths than humans (Loew et al., 2002, 1580). Spectral measurements of a sub-sample of males failed to identify any reflectance within the UV range (320–400 nm) and the orange colour of the male's ventral surface had a peak reflectance at 550–650 nm (Zeil and Stapley, unpublished data). A little variation in the hue and chroma of the orange ventral colour exists between males. However, most males either have an orange venter or a white venter and can be easily characterised into these two groups (Stapley, 2004). Prior to experiments, male snout vent length (SVL) and weight were measured. Male condition was calculated as the residuals of the regression of weight on SVL. In experiment 1, each lizard's PBT was recorded in their home enclosure; in experiment 2, male aggressive behaviours were examined in staged male contests; and in experiment 3, I tested male courtship behaviours in staged encounters with a female. Experiments were carried out in this order for several reasons. Experiment 1 was conducted in December to measure male PBT just prior to the height of the breeding season (January–February) but when male colour development was complete (Pengilly, 1972).

Experiments 2 and 3 followed in January–February. In this species, the females mate in the 2–3 weeks after giving birth (Pengilley, 1972). Male contests preceded male–female interactions to replicate the succession of these social behaviours in the field. Male dominance hierarchies are already established prior to female sexual receptivity (Stapley, 2004), and colour, which is important in male dominance (Stapley, 2004), peaks prior to mating (Pengilley, 1972). This suggests that male contests are most common prior to courtship and mating in the field. It is possible that the order of experiments could influence a male's behaviour (Dugatkin, 1997). For example, the act of loosing in male contests may suppress male courtship behaviours (Kudryavtseva et al., 2000) or alternatively, enhance them (Kudryavtseva et al., 2004). To minimise any potential carryover effects, I separated each experiment by 2 weeks, and each male was presented with a “priming” female prior to the courtship experiments. A “priming” female was used because testosterone has been shown to increase dramatically following an encounter with a female in males that were previously housed individually (Kudryavtseva et al., 2004). In previous studies, I noted that when a male was placed with a female for the first time after being housed individually, his courtship behaviour was suppressed in comparison to his courtship of subsequent females (Stapley, unpublished data).

### 2.3. Experiment 1: PBT

PBT was measured in the lizard's home enclosure (see above) where they were housed individually in a temperature-controlled room (18–20 °C). A thermal gradient was established by placing heat tape at one end of the enclosure width ways. At the hottest point, the floor of the enclosure was 40 °C, and at the coolest point, the temperature of the floor of the enclosure was equal to the ambient air temperature (18–20 °C). Prior to experimentation, lizards were housed in these enclosures for over a month, with ample time to learn the thermal gradient and use it in the most efficient manner (Brattstrom, 1974). Male PBT was measured on three experimental days. Each experimental day was separated by three rest days, and on the first of these rest days lizards were fed two crickets. Males were not fed again prior to each experimental day to ensure all males were postabsorptive (Bennett and John-Alder, 1986; Angilletta, 2001). This should remove variation between individuals in body temperature that is due to an increased metabolic rate during digestion and absorption of food (Niewiarowski and Waldschmidt, 1992; Robert and Thompson, 2000). On the experimental day, I remotely recorded the body temperature three times (Schwarzkopf and Shine, 1991), once at 10:00 h, 12:00 h and 14:00 h using a thermal imaging camera (FLIR ThermocamTM SC2000 PAL) (Stapley and Keogh, 2004). Temperature readings were recorded live from the camera, and they were always taken on the dorsal surface, between the lizard's shoulders. During a preliminary study, several positions were tested;

however, the chosen position was easy to locate repeatedly and provided accurate temperature measurement when compared to internal temperature readings taken from an anal probe (Stapley, unpublished data). The use of the thermal imaging camera was also robust to any physiological changes related to heating and cooling phases (e.g. vascular dilation or constriction) providing accurate measurements of the lizard's internal temperature regardless of these states (Stapley, unpublished data). From the observations, I calculated a daily PBT, which was the mean of the three recordings that day, and the overall PBT as the mean across all observations for an individual.

### 2.4. Experiment 2: male aggressive behaviour

I staged encounters between 16 randomly assigned pairs of males in open-topped plastic tubs (420 mm  $L \times$  320 mm  $W \times$  220 mm  $H$ ) maintained at a constant temperature of 36 °C using heating tape. Males were only tested once to avoid any potential influence of a winner–loser effect on the outcome of subsequent tests (Dugatkin, 1997). Males were placed into the experimental enclosure under separate opaque boxes and allowed to acclimate for 5 min, after which time the box was lifted from behind a blind and the lizards were free to move around the enclosure and interact. The activity of the lizard was monitored with a video camera suspended above and recorded on videotape for 30 minutes. During the analysis of the video, I recorded every interaction between males. Interactions between males were classified as “aggressive” or “non-aggressive”. The interaction was scored as aggressive when lizard A approached lizard B and lizard B retreated rapidly, or if either lizard displayed any aggressive behaviours such as a slow-walk approach with head arched, biting, wrestling or chasing (similar to behaviours described in *Lampropholis guichenoti* (Torr and Shine, 1996)). A “dominance” interaction was recorded if lizard A approached lizard B and lizard B retreated rapidly. A “bite” score was recorded when lizard A bit lizard B. The initiator and winner of the aggressive interactions were recorded. A winner was recorded if one male retreated rapidly immediately after the interaction. As there was the potential for an aggressive interaction whenever lizards were in close contact (within 2 cm of each other), I calculated an aggression index for each male, which was the number of aggressive interactions that a male initiated, divided by total number of observed interactions.

### 2.5. Experiment 3: Male courtship behaviour

I staged encounters as described above between males and randomly assigned females. Each male was paired with a receptive “priming” female, then a receptive “experimental” female and then a second receptive “experimental” female on three experimental days. Each experimental day was separated by two rest days. For a conservative estimate, females were considered receptive for up to 2

weeks after birth (Pengilley, 1972). Two “experimental” females were used to test for repeatability of courtship behaviours. Lizard behaviour was recorded remotely for 30 min using a video camera. During the analysis of the videotapes, I recorded all interactions between the pairs of lizards. Courtship was recorded when the male vibrated his tail while approaching the female. Similar to the male aggression index, I calculated a courtship index by dividing the number of times courtship was recorded by the total number of interactions. A mean courtship index, taken across the two females was used in analyses with male morphological traits, PBT and male aggression. In response to male courtship, females use a rejection behaviour, in which she vibrates her tail similar to the male courtship display (Stapley, 2004). If the female accepts the male there is no tail vibration and the male grasps the female in the premating grasp and they mate. Females never mated in these experiments, females were therefore consistent in their behaviour in the sense that they always rejected the males’ courtship. It is possible that females may encourage or discourage male courtship using very subtle behaviours and this may in turn influence male behaviour, but I have never observed any additional female behaviours in this or other studies.

## 2.6. Data analysis

The effect of male body size and ventral colour on PBT, aggression index and courtship were tested using linear models. I then tested for relationships between aggression and PBT, courtship and PBT and aggression and courtship using linear models. Analysis was performed using Genstat Release 5.0.

## 3. Results

Male ventral colour was not related to mean SVL ( $t_{1,31} = -0.02, p = 0.482$ ), mean weight ( $t_{1,31} = -0.37, p = 0.356$ ) or mean condition ( $t_{1,31} = -0.26, p = 0.398$ ).

### 3.1. Experiment 1: Preferred body temperature

No lizards shed during the experiment. PBT on day one was highly correlated with PBT on days two (Fig. 1a;  $F_{1,31} = 42.34, p < 0.001, r^2 = 57.9$ ) and three (Fig. 1b;  $F_{1,31} = 29.21, p < 0.001, r^2 = 48.5$ ) demonstrating individual consistency in PBT across the three experimental days. The overall mean PBT varied from 24.5 to 36.1 °C and was not related to SVL ( $F_{1,31} = 0.00, p = 0.936$ ) or condition ( $F_{1,31} = 50.83, p = 0.370$ ), but was higher in males with an orange ventral colour ( $F_{1,31} = 4.33, p = 0.046$ ).

### 3.2. Experiment 2: Male aggressive behaviour

During staged encounters between males, aggressive interactions were common (150 aggressive, 67 non-aggressive).

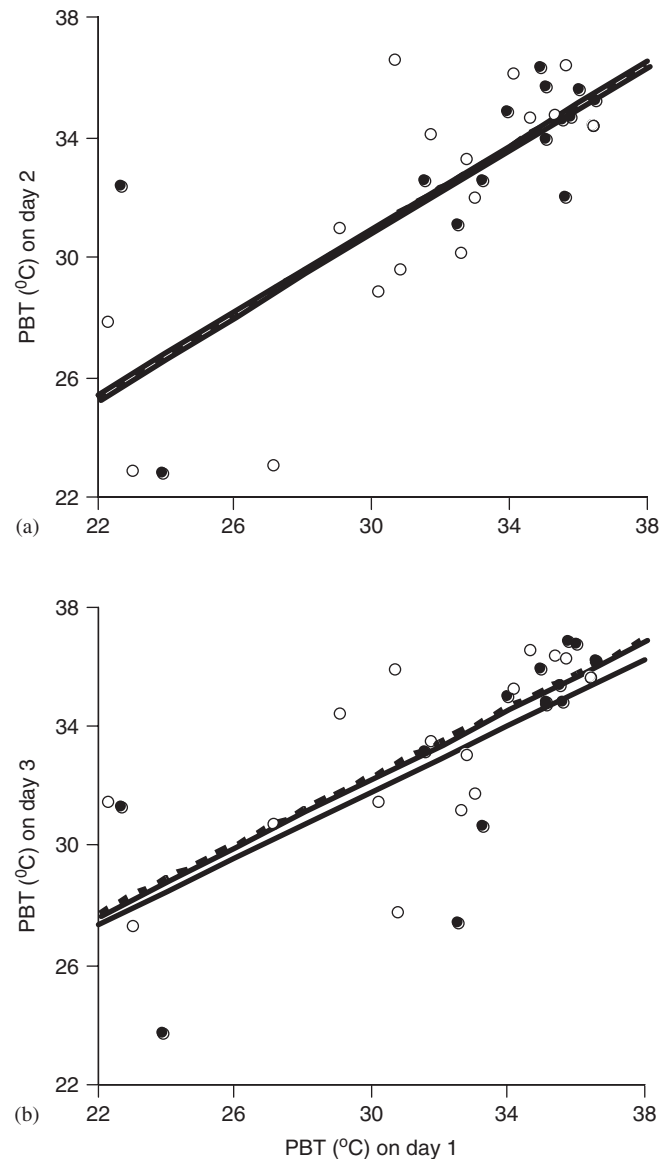


Fig. 1. Fitted and observed relationship between the preferred body temperature (PBT) of males with (solid line, solid circles) and without (dashed line, open circles) orange ventral colour on day one plotted against PBT; (a) day two and (b) day three.

In most cases, the maximum level reached between two males was a “dominant” interaction (23 trials, 71%) and bites were observed less frequently (nine trials, 19%). Male condition was weakly positively correlated with male aggression during the staged encounters ( $F_{1,31} = 3.56, p = 0.06$ ). Male SVL was not related to aggression index, but males with orange ventral colour were more aggressive (Fig. 2; SVL:  $F_{1,31} = 3.39, p = 0.07$ ; badge:  $F_{1,31} = 22.46, p < 0.001$ ). In most cases the male that initiated the aggressive interaction won that interaction (initiator won = 136, initiator lost = 14,  $\chi^2 = 94.20, p < 0.001$ ), suggesting that more aggressive males dominate less aggressive males.

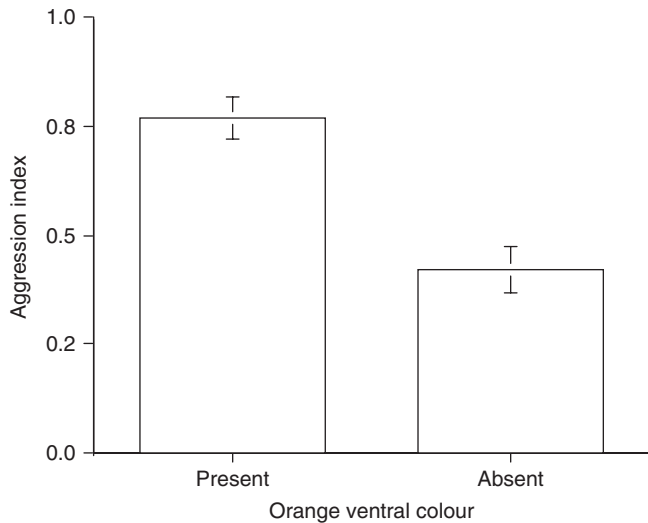


Fig. 2. Mean ( $\pm$ standard error) aggression index of males with and without orange ventral colour measured during staged encounters between randomly assigned pairs.

### 3.3. Experiment 3: Male courtship behaviour

During staged encounters with females, male courtship index of the first female correlated with his courtship of the second (Fig. 3;  $F_{1,31} = 10.57$ ,  $p = 0.005$ ,  $r^2 = 43.2$ ), demonstrating that male courtship behaviour was repeatable. Mean male courtship index was not related to female body size ( $F_{1,31} = 0.00$ ,  $p = 0.995$ ), male ventral colour ( $F_{1,31} = 1.32$ ,  $p = 0.263$ ) or male condition ( $F_{1,31} = 1.77$ ,  $p = 0.205$ ). However, larger males courted females more (Fig. 4;  $F_{1,31} = 4.48$ ,  $p = 0.047$ ,  $r^2 = 14.2$ ).

### 3.4. Individual variation and consistency

In all experiments, considerable variation in male behaviour was observed and this variation was correlated across experiments. Males that had a higher PBT were more aggressive (Fig. 5a;  $F_{1,31} = 9.43$ ,  $p = 0.005$ ,  $r^2 = 21.2$ ) and courted more (Fig. 5a;  $F_{1,31} = 8.41$ ,  $p = 0.012$ ,  $r^2 = 16.1$ ). Male aggression index was positively correlated with mean courtship index (Fig. 6;  $F_{1,31} = 20.49$ ,  $p < 0.001$ ,  $r^2 = 53.0$ ) and there was a significant interaction between aggression index and colour on mean courtship index ( $F_{1,31} = 25.22$ ,  $p < 0.001$ ).

## 4. Discussion

The results of this study identified relationships between male traits, behaviours and PBT. Males with orange ventral colour were more aggressive and dominated males with white venters. This is consistent with the findings of a previous study carried out in semi-natural enclosures (Stapley, 2004). Larger males had a higher courtship rate and there was no effect of female body size on male courtship. A large degree of individual variation was

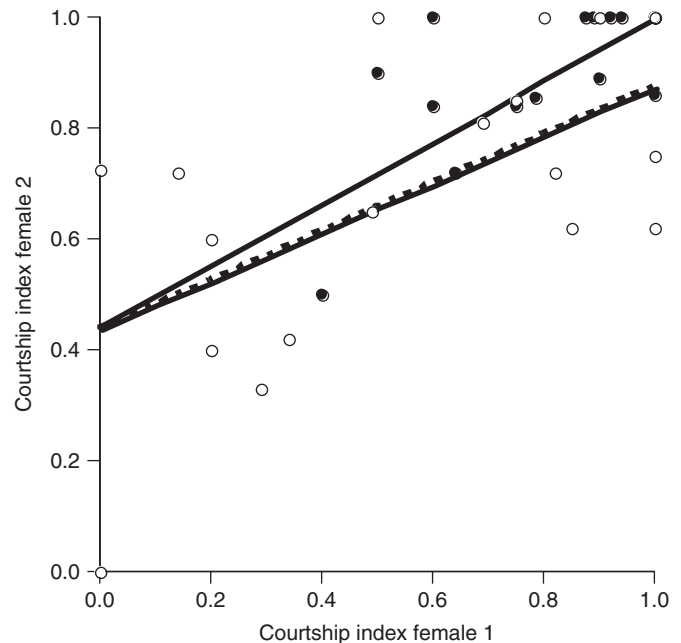


Fig. 3. Fitted and observed relationship between the courtship index of the first female by males with (solid line, solid circles) and without (dashed line, open circles) orange ventral colour with his courtship of the second female.

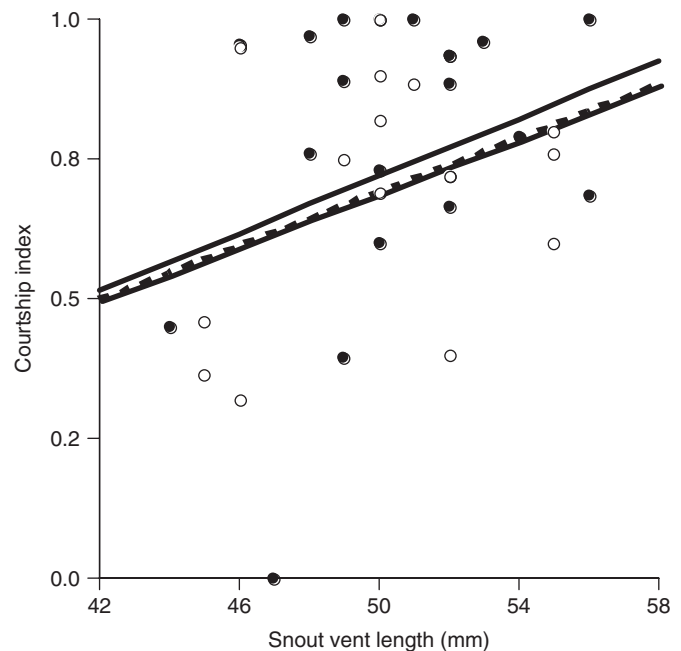


Fig. 4. Fitted and observed relationship between snout vent length and mean courtship index of males with (solid line, closed circles) and without (dashed line, open circles) orange ventral colour. Mean ( $\pm$ standard error) courtship index of males with ( $0.78 \pm 0.091$ ) and without ( $0.65 \pm 0.070$ ) orange ventral colour.

observed in PBT, aggression levels and courtship behaviours of *P. entrecasteauxii* males, and individual PBT and courtship was repeatable. PBT was not related to male body size. Males with higher PBT were more aggressive in



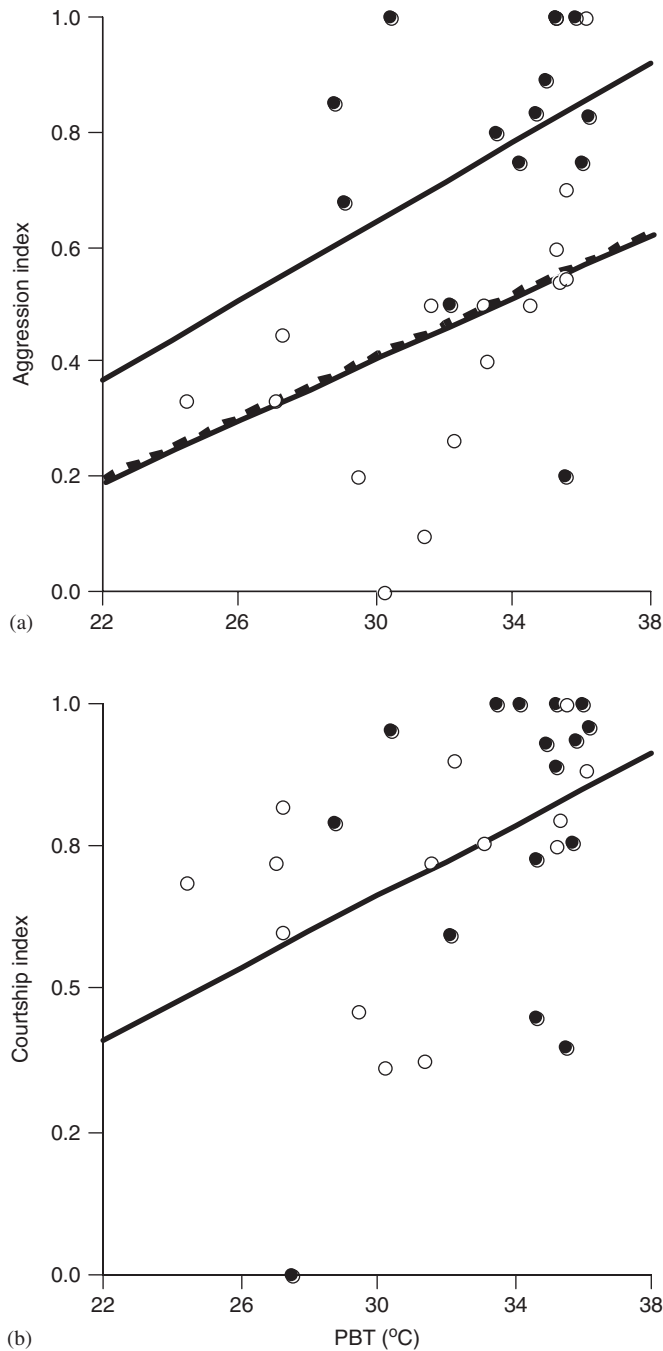


Fig. 5. The fitted and observed relationship between the preferred body temperature with (a) aggression index and (b) mean courtship index of males with (solid line, closed circles) and without (dashed, open) orange ventral colour. Note that the fitted relationship of the mean courtship index for males with and without orange badge colour is not distinguishable at this scale.

male contests and were more active in courtship. Suggesting males with higher PBT tend to be more active in social situations. A correlation between these two behaviours is consistent with a shy–bold continuum where bold individuals demonstrate a greater tendency to be proactive in a social context (Wilson et al., 1994). The observations from this study also suggest that individuals at the bold end of

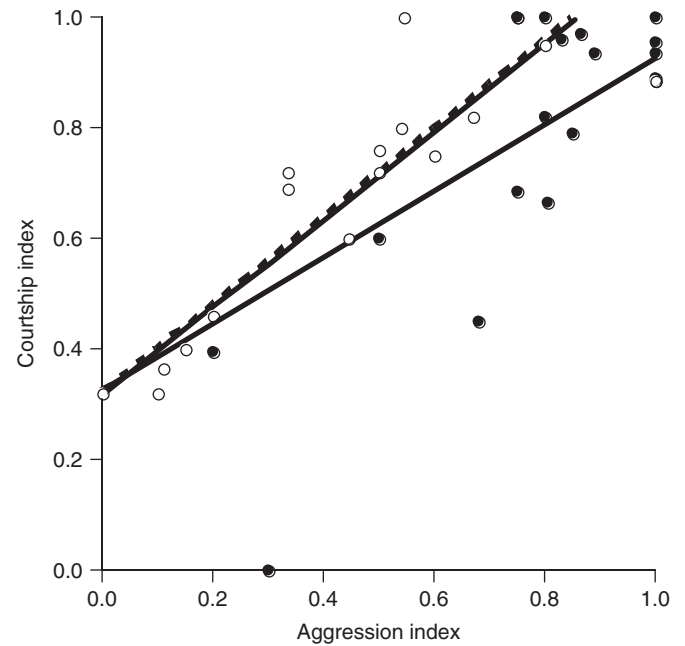


Fig. 6. Fitted and observed relationship between aggression index and mean courtship of males (solid line, closed circles) and without (dashed, open) orange ventral colour.

the continuum were more likely to have orange ventral colour. The presence of a shy–bold continuum in male *P. entrecasteauxii* is consistent with results from a wide variety of taxa (Wilson et al., 1994; Dall, 2004; Dingemanse et al., 2004; Lopez et al., 2005; Schjolden et al., 2005). Fewer studies, however, have demonstrated a link between male colour and boldness, although a link between personality types and male mating strategy has been demonstrated in another Australian lizard *Eulamprus heatwolei* (Stapley and Keogh, 2004).

#### 4.1. Preferred body temperature

PBT recorded in this study ranged from 24.5 to 36.1 °C, which is comparable to the results of a previous study on this species that found mean PBT for three lizards to be  $33.9 \pm 0.78$  °C (Bennett and John-Alder, 1986). The range is within the critical maximum (40–42.8 °C) and minimum recorded (2.5 °C) for this species (Brattstrom, 1971; Bennett and John-Alder, 1986). Although, most studies only consider the mean for a population or species, similar individual variation has been shown in northern water snakes *Nerodia sipedon* (Blouin-Demers et al., 2000) and female southern water skinks *E. heatwolei* (Schwarzkopf and Shine, 1991). The range reported here is consistent with the range of temperatures at which lizards can maintain maximal locomotor performance (Mautz et al., 1992; Angilletta et al., 2002a). In contrast, digestive processes are much more sensitive to fluctuations in temperature (Angilletta et al., 2002a). The variation in PBT observed in this study may only be detectable when lizards are not digesting and absorbing food. Nonetheless,

the results suggest that in a postabsorptive state, some lizards maintain a lower PBT. This reduction in PBT may reduce metabolic rate and energy expenditure (Angilletta et al., 2002a). In ectotherms, there appears to be a strong correlation between body temperature and metabolic rate. In the desert lizard *Sceloporus merriami*, energy expenditure increased by 6–10% for every hour that a lizard's body temperature was 5.5 °C warmer (Grant, 1990). In the tropics, where ectotherms can maintain PBT all year round, seasonality in PBT has been observed. For example, dragon lizards (*Lophognathus temporalis*) reduce their PBT in the dry season when food is limited, in order to reduce overall energy expenditure (Christian et al., 1999). Increases in metabolic rate could influence dominance (Bryant and Newton, 1994; Metcalfe et al., 1995) and status signalling badges (Whiting et al., 2003). These differences in metabolic rate do not necessarily result in differences in growth rates or adult body size, but rather the individuals with higher metabolic rates have a greater capacity for energetically expensive behaviours, such as aggression (Marler et al., 1995; Metcalfe et al., 1995). Male *P. entrecasteauxii* that had higher PBT may have an elevated metabolic rate, enabling them to be more aggressive and develop orange ventral colour. The change in PBT could be mediated by thyroid concentrations (Dupré et al., 1986) or the result of different maternal incubation temperatures (Blouin-Demers et al., 2000). Male *P. entrecasteauxii* with different thermal history or hormonal levels may maintain different body temperatures, which can influence a suite of behaviours important to fitness.

#### 4.2. Individual variation and consistency in behaviours

Aggression, courtship and PBT were correlated at the individual level. Some individuals were consistently more active in a social context compared with others and these individuals maintained higher PBT and were more likely to have orange ventral colouration. Manipulation of a physiological state such as circulating testosterone has provided the most conclusive evidence of a common physiological mechanism linking courtship and aggression. For example, in two species of quail (*Callippla gambelii* and *C. squamata*), castration resulted in a decrease in both male-male aggression and male courtship rates (Hagelin, 2001). However, in some cases, this relationship is not always present; for example, testosterone implants increased courtship but not aggression in the buff-banded rail (*Gallirallus philippensis*) (Wiley and Goldizen, 2003). The fact that multiple male traits important in reproduction can interact and may be under conflicting selection pressure is at the forefront of sexual selection studies (Chapman et al., 2003). Inter- and intra-sexual selection may favour different traits but when traits are linked, then conflicting selection pressure may limit their plasticity. The results of this study would suggest that male courtship behaviours could not increase without a subsequent

increase in aggression, which may in turn require an increase in energy assimilation, metabolic rate and PBT. Interestingly, large males courted females more and colourful males were more aggressive, despite the fact that courtship and aggression were correlated. This suggests that some behavioural plasticity persists despite the correlation between aggression and courtship.

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