



Female mountain log skinks are more likely to mate with males that court more, not males that are dominant

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To understand the evolution and exaggeration of male traits, we need to clarify the combined and separate contributions of male competition and mate choice to male reproductive success. Here, I tested whether female skinks discriminate between males based on morphological or behavioural traits in a sequential mate choice experiment to identify whether females prefer dominant males. A total of 48 females were tested of which, 26 mated with at least one male. Some females mated multiply with the same male or with both males. Females were more likely to mate with males that courted more and did not prefer males with orange ventral colour, which is indicative of male dominance. Females may use courtship as a cue to male quality because it was positively correlated with the duration of the mating grasp, during which time the male has to carry the female, and mating grasp is also positively correlated with mating duration. Interestingly, males courted smaller females more than larger females, despite the fact that larger females are more fecund. The results of this study suggest that the two processes of sexual selection may be favouring different male traits, resulting in male competition favouring male orange colour and mate choice favouring male courtship.

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Identifying the factors that underlie variation in male reproductive success is essential to explaining the evolution and exaggeration of male traits. In natural situations, both male competitive ability and female mate choice influence the skew in male reproductive success (Kokko et al. 2003). These two processes of sexual selection have each been the focus of much empirical and theoretical research, however, few studies have quantified the relative contributions of each to male reproductive success (for review see Wong & Candolin 2005). Understanding the evolution of male sexual traits requires that we disentangle the multiple factors underlying male reproductive success.

Dominant males are often more successful at securing paternity and in many cases dominant males are considered better quality mates. Females that mate with

dominant males may gain direct benefits from male-defended resources (Candolin & Voigt 2001) or indirect benefits if competitive ability is heritable and her sons enjoy similar competitive ability (e.g. Moore 1990). However, in several cases females prefer traits unrelated to dominance or discriminate against dominant males (Qvarnström & Forsgren 1998). Dominance related traits such as aggression and fighting ability could have negative effects on female fitness and reproductive success. These manifest as direct costs to the female such as reduced parental care (Forsgren 1997; Wong & Jennions 2003) or increased risk of injury (Le Boeuf & Mesnick 1991). They can also be the result of indirect costs, for example, traits that increase fitness of offspring of one sex but not the other (Pai & Yan 2002). Behavioural trade-offs may also reduce a dominant male's ability to secure matings. In cases where courtship displays are needed to attract females (Knapp & Kovach 1991; Wong 2004) or to overcome female resistance (Holland & Rice 1998), dominant/aggressive males may court females less, resulting in female preference for subordinate males (Sih et al. 2004).

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In the sexually dichromatic lizard *Pseudemoia entrecasteauxii* the presence of orange ventral colour, not body size, was the best predictor of male contest success (Stapley 2006). Orange males are more aggressive and dominant over larger males without orange venters, whereas larger males court more (Stapley 2006). In seminatural enclosures large males with orange venters sired the most offspring (Stapley & Keogh 2006). If females were simply mating with the most dominant males, then we would expect that both small and large males with orange venters would have similar reproductive success. The fact that small males with orange venters sired fewer offspring than their larger counterparts suggests that there is a reproductive advantage of body size that could be the result of a female mating bias towards either larger males or males that court more. The aim of this study was to test whether females discriminate between mates based on morphological traits related to dominance (orange ventral colour), morphological traits unrelated to dominance (body size and condition) or male courtship behaviour. To identify whether female mate choice and male competition act in unison to favour the exaggeration of male traits.

Traditionally, female mate choice has been tested in simultaneous two-choice tests. Females can view, without physical contact, two males who can in turn see the female but not the other male. This design controls for male–male aggression, which can interfere with female choice, however, there are several potential limitations to this method. First, females may encounter males sequentially and as a result cannot make simultaneous contrasts (Pitcher et al. 2003; Bissell & Martins 2006). Second, physical barriers such as glass can preclude chemical and tactile cues, which may be important during mate choice and/or it may alter male courtship behaviour (Schäfer & Uhl 2005; Shackleton et al. 2005). Another problem that arises in the simultaneous two-choice design is that female association, rather than mate choice, is usually measured. Few studies have verified that female association behaviour is a good proxy for female mate choice (but see Clayton 1990; Wong 2004) and this has never been confirmed in studies on lizards. For these reasons, I have used a sequential mate choice design and allowed pairs to mate, to unequivocally test mate choice.

METHODS

Study Species and Animal Maintenance

The mountain log skink is a small, diurnal, viviparous skink that inhabits cool temperate forest in southeastern Australia (Cogger 1996). The skink is sexually dimorphic for body size and colour. Females attain longer snout vent lengths than males (mean snout vent length (SVL): female = 51.7 mm; male = 49.1 mm) and some males develop orange breeding coloration on their ventral surface. Males mature at an SVL of 38 mm and females at 42-mm SVL (Pengilley 1972; Cogger 1996) and this takes 2–3 years in cool alpine habitats (S. Hudson, unpublished data). Age of *P. entrecasteauxii* is positively correlated with SVL until maturity, at which point the growth rate slows and age cannot be accurately estimated from SVL

(S. Hudson, unpublished data) similar to other reptiles (Halliday & Verrell 1988). Larger females have larger clutch sizes; of 41 field caught females that gave birth in the laboratory clutch size ranged from one to six and was related to female SVL: $\chi^2_{1,40} = 12.96$, $P = 0.001$ (unpublished data). The species is not territorial and there is a lot of home range overlap between males and females (Pengilley 1972). Males do, however, engage in aggressive behaviours and this results in the formation of dominance hierarchies. Observations of *P. entrecasteauxii* in seminatural enclosures and in the laboratory found that most interactions involved one male approaching the other with an aggressive display (tail wave) and the other male flees (Stapley 2006; Stapley & Keogh 2006). During these dominance interactions males with orange venters were more aggressive and dominated, and small males with orange venters dominated over large males without orange ventral colour (Stapley 2006; Stapley & Keogh 2006).

I collected lizards in January 2003 from Namadgi National Park by hand and transferred them to individual cloth bags for transport to the laboratory. In the laboratory, lizards were housed individually in plastic containers (42 × 32 cm and 22 cm high) in a temperature-controlled room maintained at 18–20°C. The floor of the container was covered in paper and a folded cardboard roll was provided as a retreat site. Between 0900 and 1700 hours a temperature gradient was established by placing heating tape under one half of the container to allow animals to thermoregulate freely. The room was under a 12:12 h light:dark cycle and water was provided ad libitum. The lizards were fed with live food (crickets and mealworms) dusted with vitamin powder every 2 days. Live food was used to reduce any acclimation of lizards to unnatural food items, which could reduce their survival when released. Animals were maintained in captivity for 2 months and released at their point of capture at the end of the study.

Before experiments, I measured lizard SVL to the nearest millimetre using a ruler, and weight to the nearest 0.01 g using a digital balance. Condition was calculated using the residuals from a linear regression of weight on SVL. I identified male ventral colour by visual comparison to Natural Colour Scheme (NCS) colour chart at normal incidence (full, morning sunlight). Most male's ventral colour was identified as orange or white (lacking in orange pigment), with fewer males having a ventral colour in between these two colours (Stapley & Keogh 2006). Because humans cannot see within the ultraviolet range, I measured the spectral reflectance of the venters of a subset of males. There was no evidence of reflectance within the UV range (320–400 nm) and the orange colour of the male's ventral surface appeared to have peak reflectance at 550–650 nm (J. Zeil & J. Stapley, unpublished data). Unfortunately, it was not possible to measure all the males before the experiment. In the absence of an accurate unbiased measure of male coloration it seems reasonable to discriminate based on the apparent dichotomy that exists in the species, which is the presence or absence of ventral colour, as described in previous study of 245 field caught males (Stapley & Keogh 2006).

Females are receptive following parturition in January–February. I tested the preferences of 48 postpartum females (SVL range = 43–61 mm) in a sequential mate choice trial in February 2003. The experiments took place in plastic enclosures with the same dimensions and conditions as the home enclosures. I randomly assigned 29 adult males to pairs (SVL range = 42–56 mm, 16 white ventral colour, 13 orange ventral colour). Males were used repeatedly but never in the same pair and were allowed a minimum of 4 days rest between trials. To begin a trial, one randomly chosen male of each pair was placed into a new enclosure with a female at 0800 hours and removed at 1800 hours on the following day (34 h later). On the third day at 0800 hours the other male of the pair was placed into a new enclosure with the female for 34 h and both lizards were removed at 1800 hours on the fourth day and placed back into their home enclosures. Thus, each female spent 34 h with each male. Lizards were provided with ad libitum water and food during the trials. Enclosures were monitored from 0800 to 1800 hours by a video camera mounted above and recorded with a video recorder onto VHS tape. Lizard activity was strongly influenced by their ability to obtain preferred body temperature and they are strictly diurnal (Pengilley 1972; Cogger 1996; Stapley 2006). In all cases the lizards had retreated and were no longer active when cameras were turned off at 1800 hours. In a few cases one lizard (usually the male) was outside the refuge in the morning before 0800 hours, but two lizards were never observed active before cameras were turned on.

I made scan samples of the video footage every 15 min to quantify behaviour. To record matings, I watched the video in fast forward to identify the exact timing and duration of mating. During the scan samples, I recorded the lizard's behaviour (within a 1-min window) and position. I recorded whether either lizard was in the refuge, whether they were next to each other (<50 mm) and whether the male was courting the female. During courtship the male waves his tail while approaching the female indirectly in an arc. The female responds by either behaving aggressively and rejecting the male or accepting the courtship and mating. During rejection the female waves her tail, moves away and/or bites the male. When the female accepts the courtship she allows him to grasp her neck and they mate (similar to behaviours described for *Lampropholis guichenoti*; Torr & Shine 1994). In the approach and courtship bout before mating, when a female accepts a male, females never tail waved. There was no other female behaviours observed in this study and female choice was determined by whether she mated with the male or not.

Courtship index was used as a measure of male courtship effort and was calculated using the following function: courtship intensity/activity. Where courtship intensity is the number of scans the male was observed courting the female minus the number of scans he was next to her (within 50 mm). Activity is the total number of observations minus the number of observations one or more lizard was in the retreat site. This provided a measure of courtship effort as a function of opportunity. Males only court when in close proximity (<50 mm), some males court at every opportunity (every time they are

near the female) whereas other males court at a much lower frequency despite ample opportunity, that is, next to the female. This measure is highly correlated with proportion of time spent courting but unlike proportion of time spent courting, courtship index could be transformed (square-root transformation) to meet normality.

Mating involves a premating grasp, where the male bites the female holding her across the neck/thoracic region and carries her around before mating (Pengilley 1972). Females normally go limp during the premating grasp with their limbs held close to their body, not making contact with the ground (personal observation). Mating occurs when the male inserts one of his hemipenes and releases his grasp on the female. It is unlikely that forced copulation is common in this species because females are larger than males (Pengilley 1972; Cogger 1996) and in one case, I observed a female struggle and free herself of a premating grasp before intromission. During this study, all females that mate appeared to cooperate with the male (i.e. she was limp and held her forelegs flush against the sides of her body). The premating grasp results in a mating scar and the number of mating scars is a reliable indicator of mating history (Pengilley 1972). At the end of each trial, I recorded the presence of a mating scar to confirm whether a mating had taken place. This was cross-referenced with the analysis of videotapes to ensure that no mating had taken place at night or very early in the morning before the cameras were turned on. The research described in this paper was approved by the Animal Experimentation and Ethics Committee of the Australian National University (Protocol number: F.BTZ.17.00) and is in accordance with the ASAB Guidelines for the use of Animals in Research.

Data Analysis

The continuous variables, male and female SVLs, male courtship index and male and female condition (residuals of a linear regression of weight on SVL), were standardized by subtracting the mean from each observation and then dividing this by the standard deviation. Data analysis was carried out using information theoretic (IT) model selection approach based on Akaike's Information Criterion (AIC) as outlined in Burnham & Anderson (2002). Although, in some cases it may be beneficial to use the global model containing all explanatory variables, the inclusion of nuisance variables often results in imprecise parameter estimates (Burnham & Anderson 2002). For this reason, I constructed a set of candidate models for each response term and compared the fit of each of these models. Each model represents a different hypothesis and these models were compared in their entirety (Burnham & Anderson 2002; Whittingham et al. 2006). In all the cases, AIC was corrected for small sample size (also called the second-order criterion AIC_c), this is necessary when the ratio of the number of observations (N) to the number of parameters (K) is small (<40; Burnham & Anderson 2002) and was calculated as:

$$AIC = AIC + ((2K(K + 1))/(N - K - 1)) \quad (1)$$

Model AIC was calculated and compared between the candidate models, the model with the lowest AIC (AIC_{\min}) is the best fitting model and the relative change in AIC (Δ_i) between models was calculated using:

$$\Delta_i = AIC_i - AIC_{\min} \quad (2)$$

To compare between R set of models the Akaike weights (ω_i) are calculated as follows:

$$\omega_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)} \quad (3)$$

These weights provide a useful way to compare between models, as ω_i is a relative estimate of the weight of evidence in favour of i being the best model (Burnham & Anderson 2002). Models with high Δ_i (>10) have low ω_i , and subsequently little evidence that this is the best model. In cases where there is a clear best model ($\omega_i \geq 0.90$), this model's parameter estimates are used (Burnham & Anderson 2002; Whittingham et al. 2006). The direction and magnitude of the explanatory variable's effect on the response term is based on the parameter estimate and its 95% confidence interval (CI). Confidence intervals were estimated using Markov chain Monte Carlo sampling method and Bayesian highest posterior density (Baayen et al., submitted for publication). If the CIs do not overlap with zero then the variable in question is said to be having a strong effect on the response term (Baayen et al., submitted for publication). Analyses were carried out using the statistical package R 2.4.2 and the models were fitted with the package lme4, with specific details given below for each model (R Development Core Team 2006).

To investigate the influence of male traits on female mate choice, I constructed generalized linear mixed models (GLMMs) to test the following hypothesis: Model 1: mate traits interact to influence mate choice (model contained all morphological and behavioural traits measured: SVL, colour, condition and courtship index and their second-order interactions); Model 2: females mate with dominant males (model contained male colour; Stapley 2006; Stapley & Keogh 2006); Model 3: females discriminate between males based on morphological traits unrelated to dominance (model contained SVL, condition and their interaction); Model 4: females discriminate between males based on their courtship (model contained courtship index); Model 5: males and females mate size assortatively (model contained male and female body size); and Model 6: female body size influences her probability of mating (model contained female body size). All GLMMs contained three random terms, male identity, female identity and male number (first or second), were fitted with a Binomial error structure with a logit link function using the Laplace method (which is an approximation of the Maximum Likelihood).

To investigate factors influencing male courtship index, I constructed linear mixed models (LMMs) to test the following hypothesis: Model 1: courtship index was related to male morphological traits (model contained all male traits measured: SVL, colour and condition and their second-order interactions); Model 2: courtship index is

related to male dominance (model contained male colour); Model 3: courtship index is related to male traits unrelated to dominance (model contained SVL, condition and the interaction); Model 4: courtship index is related to male body size because this has previously been shown to be correlated with courtship index (Stapley 2006; model contained male SVL); and Model 5: males court larger, more fecund females (model contained female SVL). All models contained three random terms: male identity, female identity and male number (first or second), the LMMs were fitted using the Maximum Likelihood method.

For each mating, the grasp latency (from the beginning of the trial until the male grasps the female), the grasp duration (time from when the male grasps the female to intromission) and mating duration (time from intromission to separation) were recorded and were log transformed to meet normality. Any relationship between grasp latency, grasp duration and mate duration was tested with Pearson correlations. In the case where a pair was observed mating more than once the mean for that pair was used. To investigate how male and female traits were related to grasp latency, grasp duration and mating duration I used the IT approach outlined above and constructed LMMs for each response variable and included the random terms, male and female identity. These models were fitted using the Maximum Likelihood method.

For grasp latency, I constructed LMMs to test the following hypothesis: Model 1: grasp latency is related to female traits (model contained female SVL, female condition and the interaction term); Model 2: grasp latency is related to male behaviour (model contained courtship index); Model 3: grasp latency is related to male traits that confer dominance (male colour); and Model 4: grasp latency is related to male morphological traits unrelated to dominance (model contained male SVL, condition and the interaction).

For grasp duration, I constructed LMMs testing the following hypotheses: Model 1: the difference between male and female body size will effect grasp duration because smaller males will have difficulty in carrying larger females (model contained male SVL–female SVL); Model 2: traits that confer dominance will influence grasp duration (model contained male colour); Model 3: grasp duration is related to male morphological traits unrelated to dominance (model contained male SVL, condition and the interaction); and Model 4: grasp duration is related to male behaviour (model contained courtship index).

For mating duration, I constructed LMMs to test the following hypotheses: Model 1: mating duration is related to female traits (model contained female SVL, female condition and the interaction term); Model 2: mating duration is related to male traits that confer dominance (model contained male colour); Model 3: mating duration is related to male morphological traits unrelated to dominance (model contained male SVL, condition and the interaction); Model 4: mating duration is related to behaviour (model contained courtship index); and Model 5: mating duration is longer if the female has previously mated (model contained mating history, mated/unmated).

As each male was observed with a female for 2 days and males were used repeatedly with different females, I could test how repeatable male courtship behaviour was.

Repeatability was calculated using equations (2)–(5) from Lessells & Boag (1987). Two measures of repeatability were calculated, the first one measured how repeatable male behaviour was between the first and second day he was paired with the same female (repeatability was calculated for each male only once $N = 28$). The second repeatability estimate was calculated for each male between trials with a different female ($N = 28$). I used the mean courtship index (across day 1 and day 2) for each male with the first female compared to the mean courtship index for the second female he was observed with. This gives two repeatability estimates, one quantifies repeatability across days with the same female, and the other quantifies repeatability across different females.

RESULTS

In total 26 (54%) females mated, five females mated more than once and a total of 34 matings were recorded. Of those females to mate more than once, three females mated with both males, one female mated twice with the same male once with the other male, and one female mated three times with the one male and once with the other male.

Excluding females that mated more than once, females were not more likely to mate with the first male (12) than the second (9; Exact binomial test: $P = 0.66$), but more females mated on the first day she was paired with the male (24) than on the second day (10; $P = 0.02$). Female snout vent length was not related to the number of times she mated (generalized linear model, GLM, with Poisson error: $\chi^2_{1,23} = 0.79$, $P = 0.37$) or the likelihood that she mated during the trials (Table 1). In a total of 18 cases, the male's body size was equal to or larger than the female, compared to 11 when the male's body size was less than the female, but there was no evidence of size-assortative mating between pairs (Table 1).

Comparing between models constructed to explain female mate choice, the best model ($\omega_i \geq 0.90$) for explaining variation in the probability of mating was the model that contained courtship index (Table 1). The slope estimate (95% CI) of courtship index is 1.13 (0.35–1.20) suggesting that courtship index is having a positive effect on a male's probability of mating (Fig. 1). Male colour a trait that predicts male dominance performed poorly as an explanatory variable, suggesting that females do not prefer to mate with dominant males. When

considering variables that influenced male courtship index (Table 2), the model containing female body size was the best model ($\omega_i \geq 0.90$). But, contrary my prediction the relationship was negative with an estimated slope of -0.34 (95% CI: -0.54 to -0.13), suggesting that male courtship index was higher for smaller females (Fig. 2).

When paired with different females, an individual male's courtship index was repeatable across the two observational days ($r = 0.95$), in other words individual males that courted more on day 1 also courted more on day 2. Males showed similar repeatability in individual courtship rates when paired with different females ($r = 0.93$). As a result, individual males that had a high courtship index when paired with one female also showed relatively high courtship rates with a different female (Fig. 3). Similar repeatability in male behaviour was also found in a previous study (Stapley 2006).

The average time to mating (grasp latency) was over 5 h (mean \pm SE: 397.25 ± 147.8 min). The mean number (\pm SE) of times a male was observed courting a female before the grasp was 3.59 ± 0.61 . Males carried females in the premating grasp for 4–33 min (mean = 13.72 ± 1.39) and mating took between 1 and 41 min (mean = 9.92 ± 1.71). Considering the three mating behaviours, (grasp latency, grasp duration and mating duration), a positive correlation was found between grasp duration and mating duration (Table 3, Fig. 4), but no other correlations were observed. Of the candidate models constructed to explain variation in grasp latency and mating duration, no single best model could be identified ($\omega_i \geq 0.90$; Table 4). This suggests that the variation in male and female traits measured in this study did not influence grasp latency or mating duration. In contrast, a single best model was identified to explain variation in grasp duration (Table 4). Males with high courtship index also had longer grasp durations (Fig. 5).

DISCUSSION

Female mating decisions were influenced by male behaviour, but not by the male's morphological traits. Females were more likely to mate with males that courted more. Male body size, condition and/or ventral colour did not influence the probability of mating. In this species, males with orange ventral colour are more aggressive and dominate males with white venters irrespective of male body size (Stapley 2006). These results suggest that

Table 1. Generalized linear mixed models* constructed to explain female mate choice

Model	Explanatory variables	logLik	K	AIC	Δ_i	ω_i
4	Male behaviour	-51.86	4	114.13	0	0.99
6	Female body size	-57.22	4	124.83	9.91	0.006
5	Size-assortative mating	-56.44	6	127.84	13.71	0.001
3	Male traits unrelated to dominance (size*condition)	-56.54	6	128.04	13.91	0.00091
2	Dominance related trait (male colour)	-59.01	4	128.43	14.3	0.00078
1	All male traits and second order interactions	-46.14	13	134.3	20.07	0.00004

Model in bold is the best fit $\omega_i > 0.90$ (Burnham & Anderson 2002).

*Binomial errors structure, logit link function, Laplace estimation method, random terms: male identity; female identity; male number (first or second).

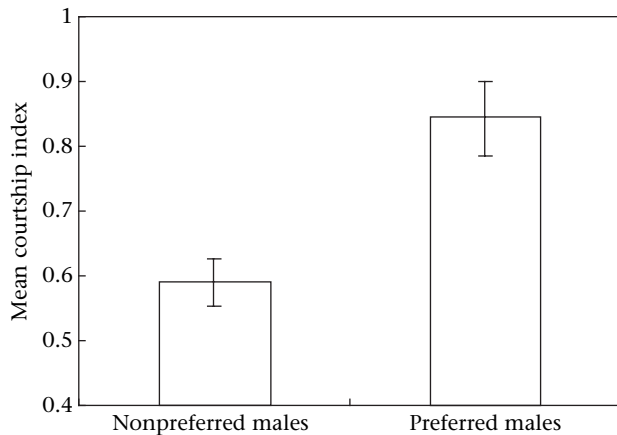


Figure 1. Mean square-root transformed (SRT) courtship index of nonpreferred and preferred males.

females do not prefer dominant males and it is likely that female mate choice and male competition favour the exaggeration of different male traits. Dominant orange males are presumably able to restrict subordinate male's access to females particularly when lizards are congregated around basking sites. After reaching preferred body temperatures, however, lizards disperse and actively forage in the leaf litter (Pengilley 1972). It is then that subordinate males may gain access to females and through greater courtship effort secure matings. This is supported by the paternity data, which showed that subordinate males lacking orange colour were not completely excluded from siring offspring (Stapley & Keogh 2006). These results confirm theoretical predictions that multiple male traits may be maintained by a combination of different selective mechanisms (Wong & Candolin 2005). Results of experimental mate choice studies such as this, where male competition can be excluded, enable us to disentangle the multiple factors underlying male reproductive success.

Male variation in courtship rate may be indicative of variation in male quality. In other species, courtship index is indicative of male quality, relating to fat reserves (Knapp & Kovach 1991) or male parental ability (Östlund & Ahnesjö 1998; Wong 2004). The courtship index of male *P. entrecasteauxii* was positively correlated with grasp duration, which may be related to male quality. The act of carrying the female in the mating grasp may require considerable strength endurance and/or energy expenditure. Males that carried the female for longer in the

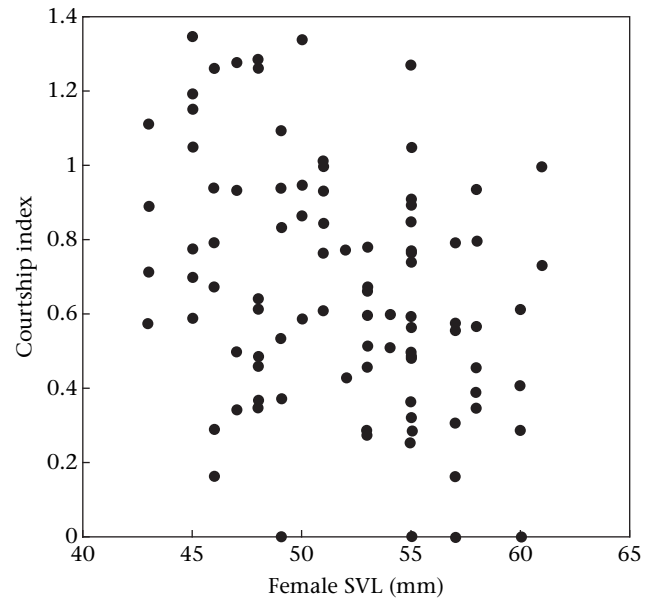


Figure 2. Observed relationship between male SRT courtship index and female SVL.

premating grasp also had longer mating times, which may result in greater ejaculate volume and/or better fertilization success (Simmons et al. 1996; Vermette & Fairbairn 2002). Ejaculate quantity or quality may be very important in this species because females store sperm over a 6-month winter hibernation period and do not fertilize their eggs until the following spring (Pengilley 1972; Cogger 1996). In a previous study, males with a greater courtship index were larger and maintained higher preferred body temperatures (Stapley 2006). In the current study, male body size explained little variation in courtship index. Greater courtship index and preferred body temperature of some males observed in the previous study were thought to be related to a shy–bold continuum, males at the upper end of this continuum are bolder and more likely to engage in social interactions (Stapley 2006). In the previous study, males were only observed for 30 min and it is possible that this may account for the disparity between studies. Over a short period of time in a novel environment, as in the previous study, differences between bold and shy individuals may be more pronounced. Over a longer period of time other factors such as female body size and male acclimation may override the shy–bold effect.

It is possible that females provided males with subtle cues to encourage courtship, and as a result, females

Table 2. Linear mixed models* constructed to explain the variation in male courtship index

Model	Explanatory variables	logLik	K	AIC	Δ_i	ω_i
5	Female body size	-132.8	4	275.95	0	0.958
4	Male size	-136.5	4	283.43	7.48	0.022
2	Dominance related trait (male colour)	-137.2	4	284.93	8.98	0.010
3	Male traits unrelated to dominance (size*condition)	-135.5	6	285.84	9.89	0.006
1	All male traits and second order interactions	-134.7	9	291.19	15.24	0.004

Model in bold is the best fit $\omega_i > 0.90$ (Burnham & Anderson 2002).

*Random terms: male identity; female identity; male number (first or second).

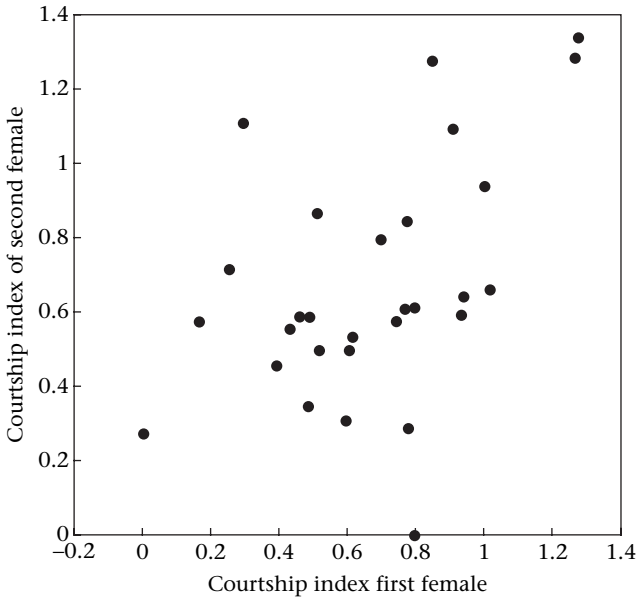


Figure 3. Relationship of individual male’s SRT courtship index of the first female with the SRT courtship index of a second female. Each point represents a single male.

encouraged preferred males to court more rather than directly preferring males that courted more. The consistency and repeatability of male courtship behaviour, however, would suggest that male courtship was mostly male driven and less influenced by female behaviour. In line with the findings of a previous study (Stapley 2006), there was large individual variation in courtship index and repeatability in individual male courtship index, both between days when paired with the same female and between observations when a male was paired with a different female. Together, this suggests that the inter-individual variation in male courtship index represents actual differences between males in their propensity to court rather than differences in the female’s receptivity to the courting male. Repeatability in behaviour is often considered to set the upper bounds of heritability (Boake 1989), behaviours that are repeatable are more likely to have higher heritability and respond to natural selection faster than behaviours with low repeatability (Brodie & Russell 1999). Dominant males are often considered better quality mates because they may give females access to

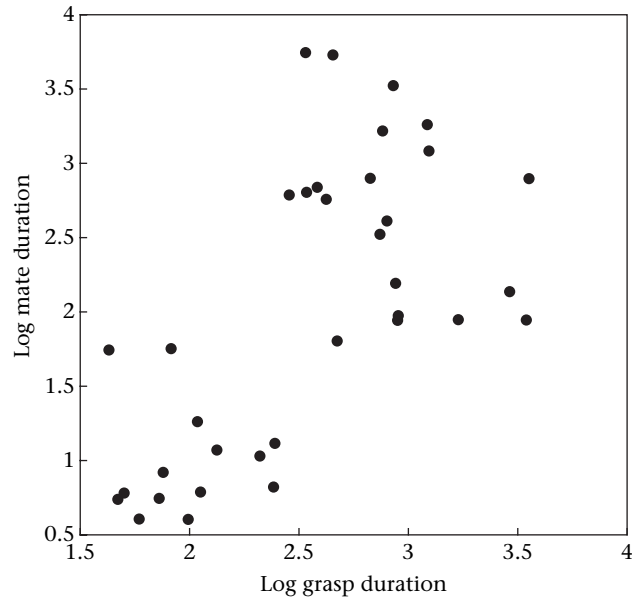


Figure 4. Mating duration was positively correlated with grasp duration. Points represent observed relationship between the log of mating duration and the log of grasp duration.

defended resources and/or if dominance is inherited her sons will enjoy a similar competitive ability. The results of this study suggest that dominant males are not necessarily better quality mates and courtship may be a consistent, and therefore, reliable indicator of other aspects of quality.

What is surprising is that males courted smaller females more. In many taxa female body size is positively correlated with clutch size (Honek 1993; Brana 1996; Bonduriansky 2001; Prado & Haddad 2005). This pattern is also present in *P. entrecasteauxii* (unpublished data). In dwarf chameleons, males court smaller females more because of the risk of injury from large aggressive females (Stuart-Fox & Whiting 2005). In *P. entrecasteauxii*, similar to dwarf chameleons, females can attain longer snout vent lengths than males, but little aggressive behaviour was observed during this study. One possible explanation for increased courtship of smaller females relates to the premating grasps. Males may not be physically capable of biting/carrying females larger than themselves. Certainly, matings were more common when the male was of similar or larger size than the female. Alternatively, there may be differences between small and large females in their choosiness or mating frequency. If smaller females mated more frequently then it could be beneficial for males to allocate more effort to courting smaller females. Females that mated three and four times were two of the smallest females in this study (45 mm), but there was no evidence of a relationship between mating number and female snout vent length, or a relationship between the latency to mating and female snout vent length.

The fact that male courtship varied with female body size and that courtship index was a strong predictor of male mating success suggests that male and female mate choices may interact to influence a male’s mating success. Mutual mate choice, although considered rare (Kokko & Johnstone 2002), is likely to be influencing male

Table 3. Pearson correlations between mating behaviours

	Grasp latency*	Grasp duration*	Mating duration*
Grasp latency*	—	0.04	0.18
Grasp duration*	0.82	—	0.67
Mating duration*	0.33	<0.001	—

Correlations in bold are significant at $P < 0.05$ after Bonferroni correction.

The correlation coefficients are in the top diagonal of the matrix and P values in bottom half.

*Data were square-root transformed.

Table 4. Linear mixed models* constructed to explain the variation in (a) grasp latency, (b) grass duration and (c) mating duration

Model	Explanatory variables	logLik	K	AIC	Δ_i	ω_i
(a) Grasp latency						
1	Female traits (size*condition)	-42.17	5	97.13	0	0.57
2	Courtship	-44.86	3	99.08	1.95	0.21
3	Male colour	-44.96	3	99.28	2.15	0.19
4	Male traits (size*condition)	-42.84	3	106.81	9.68	0.004
(b) Grasp duration						
4	Courtship index	8.76	3	-8.71	0	0.90
1	Size difference	6.00	3	-3.10	5.61	0.05
2	Male colour	5.61	3	-2.42	6.29	0.03
3	Male traits (size*condition)	5.83	5	2.47	11.18	0.003
(c) Mating duration						
4	Courtship index	-15.69	3	40.19	0	0.45
2	Male colour	-15.94	3	40.67	0.48	0.35
1	Female traits (size*condition)	-14.70	5	43.53	3.34	0.08
5	Mated/unmated	-18.01	3	44.01	3.82	0.06
3	Male traits (size*condition)	-15.82	4	45.87	5.38	0.03

Model in bold is the best fit $\omega_i > 0.90$ (Burnham & Anderson 2002).

*Random terms: male identity; female identity.

reproductive success. Smaller females are courted intensely by small and large males, but larger females are only courted by larger males. This does not result in size-assortative mating, but it may limit the number of potential mates available for larger females, thereby constraining larger female reproductive options. An important goal of evolutionary biology is to understand what factors may constrain female mate choice (Jennions & Petrie 1997; Kokko et al. 2003). Male competition can limit female reproductive options if dominant males exclude subordinate males from access to females (Jennions & Petrie 1997; Stapley & Keogh 2005). The results of this study suggest that male preference for smaller females may similarly constrain female reproductive options.

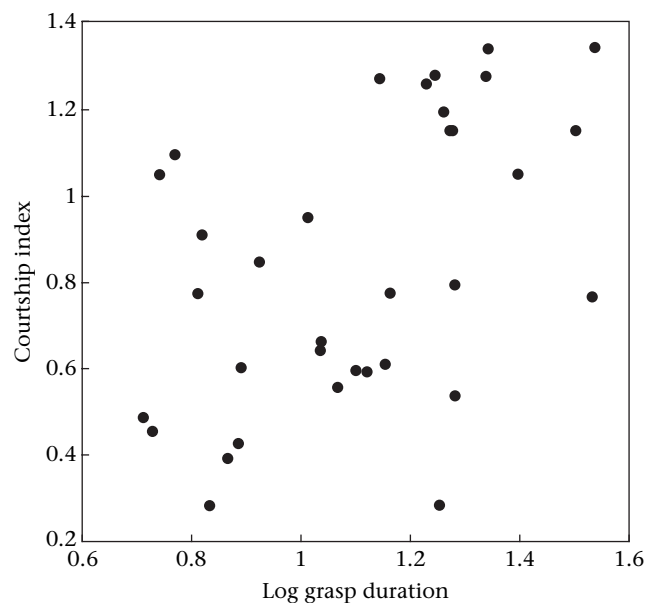


Figure 5. Observed relationship between log of grasp duration and SRT male courtship index.

There has been little success in identifying female mate choice for male traits in lizards compared to other taxa such as insects and birds. Of 17 published studies experimentally testing mate choice in lizards (Greenberg & Noble 1944; Crews 1975; Sigmund 1983; Andrews 1985; Olsson & Madsen 1995; Baird et al. 1997; Smith & Zucker 1997; Martín & López 2000; Lebas & Marshall 2001; Olsson 2001; Kwiatkowski & Sullivan 2002; López et al. 2002; Tokarz 2002; Olsson et al. 2003; Hamilton & Sullivan 2005; Bissell & Martins 2006), only one study has convincingly showed female mate choice (as measured by actual mating) and this used a sequential mate choice design (Cooper & Vitt 1993). There have been several arguments made as to why mate choice is rare in lizards (Olsson & Madsen 1995; Tokarz 1995; Olsson & Madsen 1998), but I propose that experimental design has been partly at fault. Most importantly, studies have failed to verify that female association behaviour accurately represents mate choice. It is probably that female lizards do not necessarily search for, or associate with, preferred mates but discriminate between males that court them. As such simultaneous two-choice tests where mating is prohibited are likely to be unsuccessful. These fundamental differences in how female lizards discriminate between mates may provide a base for novel advances in our understanding of the evolution of mate choice and male traits.

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