

Behavioral syndromes influence mating systems: floater pairs of a lizard have heavier offspring

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Variation in correlated behaviors or behavioral syndromes could have interesting effects on mating systems, especially if the variation in syndrome exists in both sexes. Both males and females of the lizard *Eulamprus heatwolei* display two behavioral types of a behavioral syndrome, defined by correlations between territorial, exploratory, and predator avoidance behaviors. We tested how this variation in behavioral syndrome influences reproductive success, pairing patterns, and offspring weight. We used spatial behavior and residency in the field to identify territorial and floater individuals. Females were relocated to the laboratory to give birth, and all offspring, dams, and potential sires were genotyped to determine offspring paternity. During field surveys, 164 lizards were caught of which 27.5% were territorial and the rest were floaters. Paternity was assigned to 66% of the 104 offspring produced by 33 dams. Territorial sires fathered a greater proportion of the offspring of territorial dams than floater sires. Larger territorial males were more likely to sire the entire clutch or share paternity with fewer additional sires than smaller territorial males. Floater sire size, however, did not influence the number of fathers per litter. Floater females produced heavier offspring than their territorial counterparts, and offspring fathered by floaters were heavier than maternal half-sibs fathered by territorial males. We speculate that differences in offspring weight may be the result of differences in yolk provisioning by females and parent genetic compatibility. *Key words:* *Eulamprus heatwolei*, multiple paternity, offspring quality, personalities. [*Behav Ecol* 16:514–520 (2005)]

Correlations between behaviors across different contexts have been termed behavioral syndromes and recently have been identified as an important factor shaping the evolution of behaviors (Sih et al., 2004). For example, a bold/shy syndrome describes variation between individuals in their tendency to explore novel environments or to engage in predator inspection (Armqvist and Henriksson, 1997; Dingemanse et al., 2003; Sih et al., 2003; Stapley and Keogh, 2004; Wilson et al., 1994). Behavioral syndromes recognize links between behaviors across different contexts. Therefore, a syndrome involving nonmating behaviors may be linked with mating behaviors and influence various aspects of the mating system. For example, individual male sticklebacks (*Gasterosteus aculeatus*) that are bolder toward predators are also better at obtaining breeding sites through territorial aggression (Huntingford, 1976). Variation in foraging vigor of female spiders (*Dolomedes triton* and *Nephila plumipes*) predicts the occurrence of sexual cannibalism (Johnson, 2001; Schneider and Elgar, 2002). Individual male meadow voles (*Microtus pennsylvanicus*) that have greater spatial ability in a laboratory water maze trial are better at finding and remembering the location of female nest-boxes and as a result have greater reproductive success (Spritzer et al., 2004). In side-blotched lizards (*Uta stansburiana*), two female morphs exist that differ in stress-coping styles, clutch size, spatial distribution, and fitness (Comendant et al., 2003). These studies demonstrate that correlations between behaviors across different contexts can influence mating behaviors and strategies and are likely to affect the mating system.

When behavioral syndromes occur simultaneously in males and females, interesting questions can be addressed with regard to pairing patterns and reproductive success. For

example, in the great tit (*Parus major*), individuals vary in their exploratory behavior in a novel environment (“fast” and “slow” explorers) (Both et al., 2004). Fast explorers are bold in exploration, insensitive to external stimuli, and aggressive compared to slow explorers (Marchetti and Drent, 2000; Verbeek et al., 1994, 1999). Males and females did not pair with like partners but paired disassortatively according to personality (Dingemanse et al., 2004). Mother personality had a significant effect on the survival and local recruitment of offspring, although this varied between years (Dingemanse et al., 2004). The study demonstrated that behavioral syndromes in females and males can act independently and/or interact to influence the processes of sexual selection. Further work, however, is needed in the field to identify the generality of these findings and build on our understanding of the effects of behavioral syndromes on mating systems (Sih et al., 2004).

Two behavioral types exist in the southern water skink (*Eulamprus heatwolei*), which are the result of a behavioral syndrome relating to exploratory and territorial defense behaviors. Most individuals (61%) adopt a floater strategy, while the rest adopt a territorial strategy (Morrison et al., 2002). Territorial lizards defend core areas where other animals are not tolerated and frequently display and chase other lizards (Morrison et al., 2002). Floater lizards, on the other hand, do not defend territories, they are characterized by a low number of sightings after initial capture, and if they are resighted, it is often a long distance from their initial capture (Morrison et al., 2002). In the laboratory, floater lizards have a greater tendency to explore novel environments, are more likely to retreat in response to a simulated attack of a predator, and spend more time in the refuge after such an attack than territorial individuals (Stapley and Keogh, 2004). These two behavioral types are not related to any measurable adult morphological character such as snout–vent length (SVL), head size, weight, condition, or fat stores (Morrison et al., 2002; Wilson, 2001).

The aim of this study was to use a natural population of the southern water skink to investigate the influence of variation in behavioral syndromes on the mating system and test the following predictions. (1) Floater males and females should

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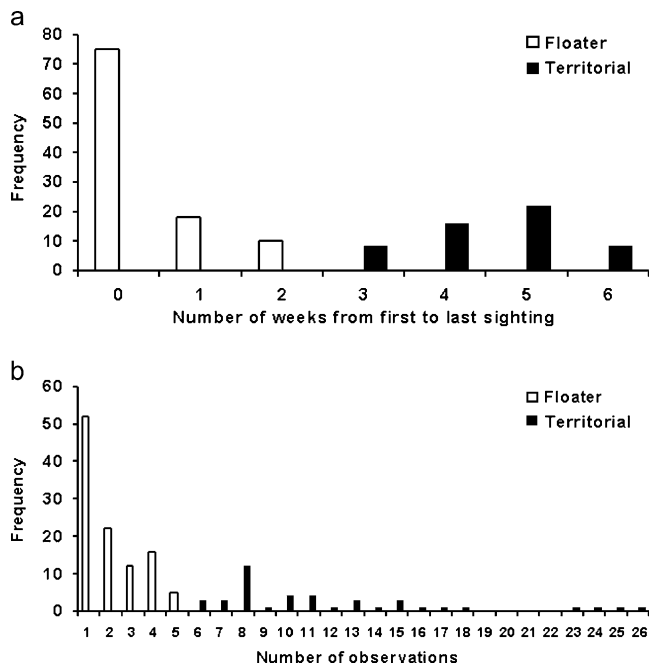


Figure 1
Frequency distributions of the (a) total number of observations for territorial and floater lizards during the study and (b) number of weeks separating the first and last sighting of territorial and floater lizards.

have reduced reproductive success because they do not defend resources and have greater dispersal. For females this may result in smaller clutches or smaller offspring, and in males this could result in a lower reproductive success. (2) As male territoriality is consistent with female defense polygyny (Morrison et al., 2002), territorial males should be more likely to sire the entire litter of territorial dams sharing his territory. As a result, litters of territorial dams will have fewer fathers and have proportionally more territorial sires. Floater dams will have litters sired by more males as they do not remain on the territories of males. (3) As male body size is often related to contest success in lizards (Olsson and Madsen, 1998), the number of fathers per litter will be negatively correlated to the territorial male body size.

METHODS

Study site and sampling

The study was conducted during September to March of 2001–2002 at the Tidbinbilla Nature Reserve, 25 km southwest of Canberra, Australia. The lizard population was studied previously in the spring and summer of 1999–2000, and the vegetation features and mapping technique are described elsewhere (Morrison et al., 2002). The study area was expanded from the previous study area and encompassed a 150-m-long section of the Mountain Creek and extended approximately 100 m either side of the creek. The water skink *E. heatwolei* is a large (up to 100 mm SVL), diurnal, conspicuous, easily caught, and a highly abundant skink (Greer, 1989). Yearly activity ranges from 6 to 8 months, and lizards hibernate during winter months (Pengilly, 1972). The species is long lived with individuals living up to 6–8 years; males mature in 2 years and females mature in 3 years (Tilley, 1984). Females are viviparous and give birth to a single litter of up to five offspring. Not all females reproduce each year and many skip reproductive years (Morrison et al., 2002).

Reproduction in a given year is determined by existing energy stores from the previous season (Doughty and Shine, 1998). Territorial behavior peaks during the breeding season, but chases also have been observed outside the breeding season (Stapley J and Keogh JS, unpublished data).

All animals observed on the study site were caught by noosing or in pitfall traps. Pitfall traps were placed opportunistically next to logs to supplement noosing and remained there for the entire study. Pitfall traps were checked twice a day. Animals caught were measured and marked permanently by toe clipping and temporarily by painting numbers on their back using a nontoxic pen. Measurements included SVL and tail length to the nearest millimeter, head length and head width to the nearest 0.1 mm, and weight to the nearest 0.1 g. Sex was determined by everting the hemipenes of males. Clipped toes were retained in 70% ethanol for genetic analysis. Toe clipping was chosen because it provides a long-term individual mark and a DNA sample simultaneously. The alternative marking method for this species is passive integrated transponder (PIT) tagging. We opted against PIT tagging because we would have needed to collect tissue for DNA analysis as well, resulting in more total distress to the subject than toe clipping. During the procedure, care was taken to minimize pain and the possibility of infection. Toes were removed with sharp dissecting scissors that were rinsed in ethanol between each lizard. Toe clipping has been used successfully in this species and other species with no obvious negative effects on survival or reproduction (Borges Landáez, 1999; Hudson, 1996; Morrison et al., 2002). The study was approved by the Australian National University Animal Experimentation Ethics Committee (protocol number F.BTZ.01.99).

Sampling consisted of twice daily censuses that involved walking through the study area recording the locations of lizards. The entire study site was surveyed every weekday from 27 September to 16 November (35 days). During observations, the location of each sighted lizard was recorded on a map of the study site. These points were converted to x- and y-coordinates, and home range size was calculated using the kernel method on Arcview 3.0. Although this method can sometimes overestimate home range size, it is stable to changes in sample size (Samietz and Berger, 1997), and the home range estimates from the kernel method closely matched home range estimates using the minimum convex polygon method.

As in Morrison's (2002) study, we categorized lizards as territorial or floater based on the number of times they were observed on the study site. If adults were observed six or more times, they were categorized as territorial and if observed less, they were deemed a floater. Although this may appear arbitrary, this classification is supported by the distribution of the data and the length of residency of lizards on the study site (see Results, Figure 1). Residency was calculated as the number of days separating the first and last sighting of each lizard. The classification of floaters and territorial lizards was used in additional laboratory studies that found differences in exploratory and predator avoidance behaviors, suggesting that the classification accurately identifies individuals according to their behavioral syndrome (Stapley and Keogh, 2004). In a separate experiment conducted in large outdoor enclosures and using lizards from another population, similar variation in territorial behavior was found. A proportion of individuals maintained and defended territories, whereas others moved randomly around the enclosure (Wilson, 2001). Territorial lizards have been recaptured occupying the same territories during repeated sampling spanning 3 years (Stapley J, unpublished data). This suggests that the observed variation in spatial behavior between floaters and territorial lizards is consistent in adults. In contrast, no

Table 1

Summary of field observations of *Eulamprus heatwolei* describing the total number of lizards caught during the study, the mean SVL, mean number of observations, the residency (number of days separating the first and last sighting of a lizard), the mean home range size (HRS), and home range overlap with females (HROF) and males (HROM) of territorial lizards

	Total	Floater female	Territorial female	Floater male	Territorial male
Number of individuals	164	65	22	43	19
Mean SVL	88.2 ± 5.52	89.00 ± 4.12	90.04 ± 3.98	86.89 ± 5.21	88.21 ± 4.75
Number of observations	5.23 ± 5.42	2.76 ± 1.75	10.04 ± 3.41	1.76 ± 1.29	13.57 ± 6.47
Residency	—	4.80 ± 0.27	36.08 ± 1.22	5.83 ± 0.37	39.35 ± 1.40
Mean HRS (m ²)	—	—	137.7 ± 34.67	—	222.3 ± 47.53
Mean HROF	—	—	2.48 ± 0.40	—	2.62 ± 0.72
Mean HROM	—	—	3.06 ± 0.70	—	1.93 ± 0.72

All means presented with 95% confidence intervals (mean ± 95% CI)

floaters were recaptured during this time. A detailed observation of lizard behavior was not carried out in this study because evidence from previous work was comprehensive and our effort in the present study was focussed on catching and genotyping all animals on the study site to ensure good paternity estimates.

Genotyping and paternity assignment

Females were caught in January (approximately 3 weeks prior to parturition) and housed individually in plastic containers (30 l × 21 w × 9 h cm) in a temperature-controlled room (18°C) with a natural light cycle. Paper towel was provided as bedding, and two cardboard rolls provided refuges. A temperature gradient was established by placing heating tape under one half of the container to allow animals to thermoregulate freely. Animals were provided with ad libitum water and food in the form of mealworms, crickets, and canned dog food. Females were checked daily until parturition. On their day of birth, offspring were toe-clipped, weighed, and SVL and tail length measurements were taken. Offspring gender was not determined due to the difficulties in accurately determining sex in small individuals using morphological characters. Dams and offspring were released at the dam's point of capture approximately 1–2 weeks after parturition.

All dams and their offspring, and all males that were caught during the study, were genotyped for four microsatellite loci (the number of alleles are provided in parentheses) (Ek17(14), Ek100(19), Ek107(18), Ek37(17)) (Scott et al., 2001). Paternity was assigned using the CERVUS program (Marshall et al., 1998). A conservative approach was taken to paternity assignment, sires were only assigned paternity if there were no genetic mismatches and only a single father was assigned to each offspring. Initially, three loci were used, but because several offspring were assigned more than one sire, an additional locus was added. These four polymorphic loci provided enough resolution to exclude sires with mismatched genotypes and assign paternity. Pairwise relatedness also was calculated between mated pairs because relatedness has been shown to strongly influence offspring phenotype in a variety of taxa (Jennions and Petrie, 2000). Pairwise relatedness between parents was calculated using the program MER, which uses the formula of Wang (2002). The estimate is well suited to highly variable markers such as microsatellites (Wang, 2002). All allele frequencies for CERVUS and MER were estimated using adult genotypes only.

Data analysis

Data were analyzed using Generalized Linear Models (GLM) with a logarithmic link function. GLMs were used to fit both

continuous and categorical explanatory variables. Data with a normal distribution were analyzed with a GLM with a normal model [GLM(n)]. These included the relationship between body size, sex, and behavioral syndrome and variables associated with offspring weight. Count data were analyzed using a GLM with a Poisson model [GLM(p)] (Grafen and Hails, 2002). These included the influence of dam body size and behavioral syndrome on litter size, the influence of sire body size and behavioral syndrome on number of offspring sired, and factors affecting the number of sires per litter. The relationship between female behavioral syndrome, litter size, and body size on the ratio of territorial sires to floater sires of each litter was analyzed with a binomial GLM. A half-sib comparison was made to compare offspring weight between territorial and floater sires using a *t* test (two tailed). The significance of each factor in a GLM was estimated from the analysis of accumulated deviance and the associated *F*-statistic. All main effects, but only significant interactions (<0.05), were reported in the results, and the order of factors presented in the text corresponds with the order used in the model. Statistical analysis was carried out with Genstat (Release 5) and R (version 1.9.1). Post hoc power calculations were calculated for nonsignificant results using G*Power. Power was estimated for a small effect size of 0.15 (15% variation) (Cohen, 1988). This was chosen as it provides a conservative estimate of power and is comparable to the average effect size of evolutionary and ecological studies as calculated from 44 meta-analyses (Møller and Jennions, 2002).

RESULTS

A total of 164 lizards were captured in the spring of 2001 with 62 males, 87 females, and 15 juveniles. Home range size was calculated for 27.5% of adults, and the remainder were classified as "floaters" and not resident on the study site (Table 1). The residency of each lizard on the study site, calculated as the number of days between the first and last observation, was greater in territorial lizards and greater in males. Differences between the sexes were attributed to the fact that the males emerged from hibernation earlier than females and were more active on colder days than females (Stapley J, personal observations). Territorial lizards were resident on the study site for more than 29 days, whereas floaters were never resident on the site for more than 25 days and the majority (63%) were sighted only once (Figure 1b).

A total of 27 lizards were recaptured from the 83 (66 adults, 18 subadults, and juveniles) caught and marked in 1999 (Morrison et al., 2002). All but one of those recaptured were categorized as territorial in the present study, and 85.5% (23) of these were caught within 2 m of the site of their original

Table 2

Summary of the genetic mating system in *Eulamprus heatwolei* as determined by microsatellite markers, describing the total number of clutches and offspring born in the laboratory, according to sex and tactic of parents

	Total	Territorial female	Floater female
Clutches	33	11	22
Offspring	104	36	68
Multiple paternity clutch	19	8	11
Offspring sired by territorial males	29	19	10
Offspring sired by floater males	40	17	23
Offspring sired by unknown males	35	0	35

capture. This demonstrates that territorial lizards remain in the same territories over time. There was no difference in body size between males and females or between territorial or floater lizards (GLM(n) sex: $F_{1,148} = 0.00, p = .98$, syndrome: $F_{1,148} = 0.15, p = .69$, power = 0.99; Table 1). The mean home range size was larger for males than females (GLM(n) $F_{1,40} = 411.39, p < .01$; Table 1). Female home ranges overlapped with an average of two to three other lizards, and male home ranges overlapped with two to three females and one to two males (Table 1).

A total of 33 dams gave birth in the laboratory, resulting in 104 offspring. Paternity was assigned to 66% of the offspring (Table 2). The remaining 34% were from litters of floater females and were sired by unknown males. Unknown males may be either floater or territorial males outside of the study site. All offspring of territorial females had their paternity assigned to known sires, suggesting that all males that came onto the study site and sired offspring were caught and genotyped during the study. For 81% of territorial females, the male whose territory overlapped hers sired at least one offspring. Only 27 of the 62 males caught obtained any paternity; two males (one territorial, one floater) sired a high number of offspring (13 and 11, respectively), and the rest sired between one and six offspring. Multiple paternity of litters was high with 57% of litters sired by more than one male (Table 2).

Litter size was not related to dam body size or behavioral syndrome (GLM(p) SVL: $F_{1,32} = 0.28, p = .59$; syndrome: $F_{1,32} = 1.18, p = .29$, power = 0.58). Territorial males sired more offspring (GLM(p) syndrome: $F_{1,68} = 7.10, p < .01$; Table 2), but this was not influenced by sire body size (SVL: $F_{1,68} = 0.33, p = .57$, power = 0.88). Number of sires per litter was not related to the litter size ($F_{1,68} = 2.39, p = .21$, power = 0.88), but an interaction between sire syndrome and sire body size influenced the number of sires per litter (sire syndrome: $F_{1,37} = 0.28, p = .59$; sire SVL: $F_{1,37} = 1.18, p = .29$; sire syndrome \times sire SVL: $F_{1,37} = 31.37, p < .001$; Figure 2). The proportion of territorial sires per litter was greater for larger litters and for territorial dams (litter size: $F_{1,24} = 11.09, p < .001$; dam syndrome: $F_{1,24} = 40.34, p < .001$; dam SVL: $F_{1,24} = 0.52, p = .47$, power = 0.45; Figure 3). Between mated individuals, dam body size was not related to sire body size (GLM(n): $F_{1,68} = 0.06, p = .81$, power = 0.88), suggesting that there was no size-assortative mating in this species.

The relationship between pair relatedness, litter size, dam syndrome, dam body size, sire syndrome, sire body size, and all interactions was tested against offspring weight in a single GLM, and only two variables showed significant relationships;

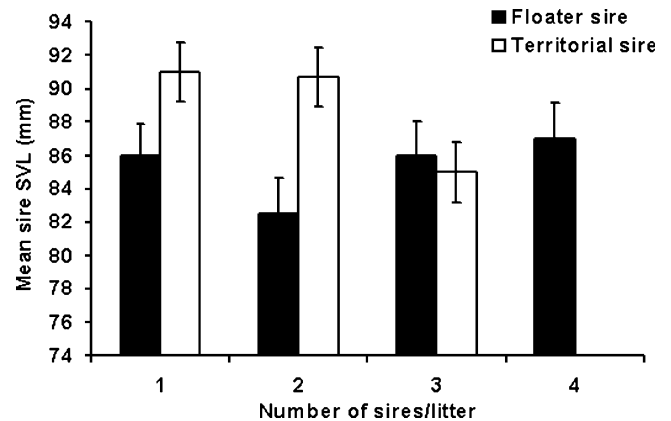


Figure 2
Mean (\pm SE) SVL of sires plotted against the number of sires per litter for territorial and floater males.

litter size and dam's syndrome (GLM clutch size: $F_{1,68} = 8.99, p < .01$; syndrome: $F_{1,68} = 13.75, p < .01$). Not surprisingly, there was a negative relationship between litter size and offspring weight, but offspring of floater dams were heavier (Figure 4a). In addition, maternal half-sib comparisons revealed that offspring of territorial sires weighed less than their half-sibs sired by floaters (two tailed, paired t test $t_{11} = 2.72, p = .01$; Figure 4b). As a result, pairs of floaters had heavier offspring than pairs of territorial lizards.

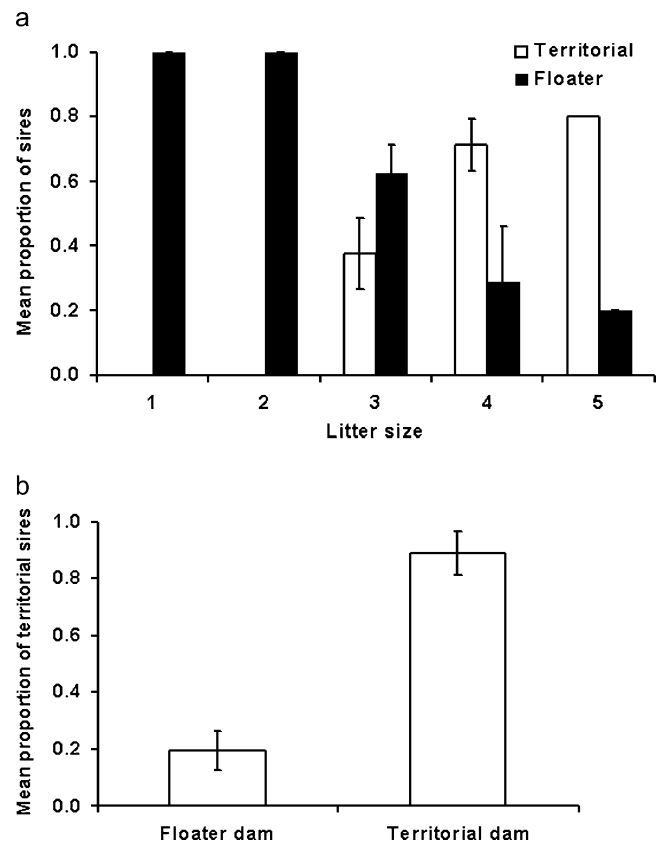


Figure 3
The mean proportion (\pm SE) of territorial and floater sires of (a) litters of varying size (no error bars for litter size = 1, 2, and 5 where $n = 1$) and (b) litters of territorial and floater dams.

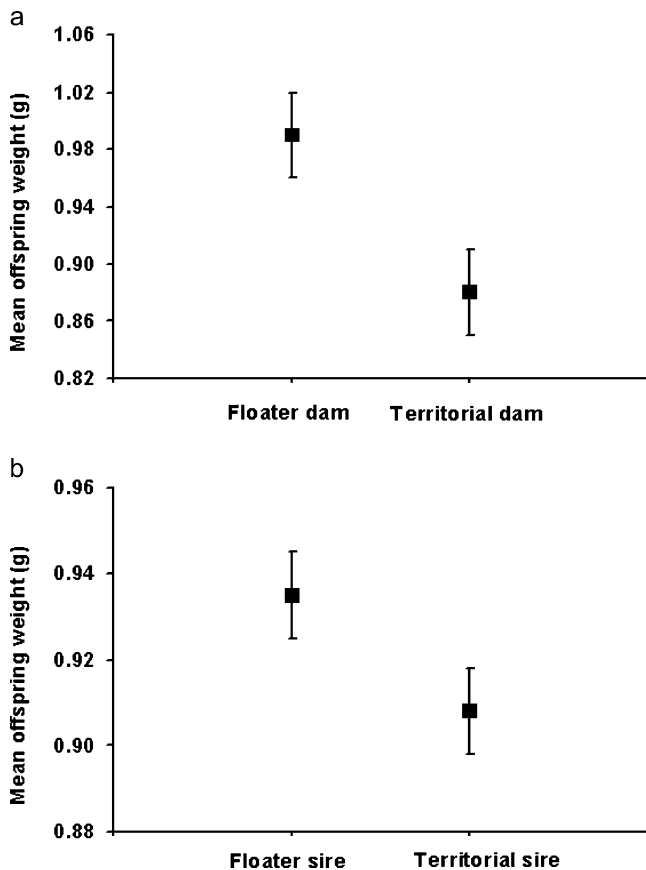


Figure 4 Mean (\pm SE) weight of offspring from (a) territorial and floater dams and (b) half-sibs sired by floater and territorial males.

DISCUSSION

Behavioral syndrome as determined by the residency of lizards on the study site influenced male reproductive success, pairing patterns, and offspring weight. In contrast to our predictions, floater dams gave birth to heavier offspring and half-sibs sired by floater males were heavier than those sired by territorial males. As a result, floater pairs had heavier offspring. In accordance with our second and third predictions, however, territorial dam litters had a higher proportion of territorial sires, suggesting assortative mating between lizards based on their behavioral syndrome. Territorial male body size influenced the number of sires per litter, larger territorial males were more likely to sire the entire litter or share the paternity with fewer males compared to smaller territorial males. No relationship between body size and the number of sires per litter was evident for floater males, and floater males had greater paternity of smaller litters.

Parental behavioral type influenced offspring weight. Floater dams gave birth to heavier babies, and offspring fathered by floater sires were heavier than half-sibs fathered by territorial sires. Although offspring sex was not determined, the difference in weight is not likely to be due to differences between the sexes as a sex difference in weight has never been recorded in this or closely related species (Borges Landáez, 1999; Morrison et al., 2002; Wilson, 2001). These weight differences are likely to influence offspring survival. Differences in offspring weight of just 0.03 g were found to strongly influence offspring survival during the first year of life in *Eulamprus quoyii* (Borges Landáez, 1999), and difference in

offspring weight between floater and territorial pairs observed in this study ranged from 0.01 to 0.09 g. This suggests an effect of behavioral type on offspring survival, similar to that found in great tits in which offspring survival was higher for fast-exploring females in poor years and slow-exploring females in rich years (Dingemanse et al., 2004).

Why floater females would produce heavier offspring is puzzling. Floater females may be able to produce larger offspring by provisioning more yolk to their eggs prior to fertilization. Energy stored in the preceding season largely determines the litter size, whereas energy intake just prior to and during ovulation influences offspring weight (Doughty and Shine, 1998). As there was no difference in litter size between floater and territorial females, it is unlikely that stored energy reserves differed between these two groups. Higher energy intake during ovulation and greater yolk provisioning by floater dams could have resulted in different offspring weights. Increased energy intake of floater dams may be the result of greater access to basking sites, greater foraging area, and/or flexibility in responding to localized increases in prey abundance. Territorial dams, on the other hand, may be constrained by their territory boundaries. Although high-quality territories are thought to contain quality feeding, basking, and refuge sites (Olsson and Madsen, 1998), territorial defense can ensue various survival costs such as increased energetic demands (for e.g., Matt et al., 1997; Wikelski et al., 1999) and greater vulnerability to predation (for e.g., Diaz-Uriarte, 1999; Veiga et al., 2002). An alternative explanation may lie in the trade-off between current and future reproduction and may represent differences between females in how they partition energy acquired during gestation. In the closely related species, *Eulamprus typanum*, the probability that a female will breed in any given year is not related to whether she bred in the previous year but is dependent on the amount of energy stored in the previous season (Doughty and Shine, 1998). Territorial females may store energy acquired during gestation to ensure reproduction in the following year, whereas floater females may invest heavily in offspring in the current season and forgo reproduction in the following year. Unfortunately, there is no information from previous breeding season.

The persistence of both types within this species is intriguing. Environmental heterogeneity may maintain fluctuating selection pressures and favor alternative behavioral syndromes. In the great tit (*P. major*), the fast explorers benefited by defending clumped resources in poor years, whereas slow explorers benefited in rich years (Dingemanse et al., 2004). Alternatively, stochastic events such as the intense bushfire in 2003 that ravaged the study site may play an important role. To survive such a fire, lizards would need access to large damp logs that would buffer them against the heat and smoke. Such logs did survive the fire (Stapley J, personal observations), and many territories are centered around such logs (Morrison et al., 2002). A third explanation may rest in opposing selection acting on each type across the sexes. Selection may favor territorial males that have higher reproductive success and floater females that have heavier offspring. If the syndrome were autosomally inherited, then opposing selection in males and females would maintain the two types. It is impossible to reconcile between these alternative explanations without long-term data on survival and fitness and without more accurate measures of male reproductive success.

Maternal half-sib comparisons revealed measurable differences in the weight of offspring sired by territorial and floater sires, although the magnitude of differences was less than that associated with female behavioral syndrome alone. There are two possible explanations for the observed pattern: parental

genetic effects or differential allocation of resources by females to floater male offspring. Although differential allocation by dams to floater sire offspring cannot be excluded, it is unlikely in this system. There is no evidence that dams are able to discriminate between half-sibling offspring. This seems implausible (Birkhead et al., 2000; Sheldon, 2000), and even if dams could detect paternity of fertilized eggs, there is little opportunity to provide additional resources to particular embryos. Female *E. heatwolei* fertilize the entire clutch synchronously after they have yoked their follicles (J. Stewart, personal communication). After fertilization, little embryonic transfer takes place, only inorganic nutrients such as phosphorus, calcium, and sodium are transported across the placenta, and the yolk provides most of the nutrients to the offspring (Stewart, 1992). Therefore, the total allocation of energy to each embryo is determined prior to ovulation and cannot be influenced by the phenotype of the embryo after fertilization (Olsson and Madsen, 1998). A more parsimonious explanation is that differences in offspring weight are the result of the effects of genetic compatibility. This does not require that a genetic component relating to behavioral syndrome exists but rather some combinations of genes are better than others, and male-female pairings yield offspring that vary in their genetic compatibility and fitness (Jennions and Petrie, 2000). Within *E. heatwolei*, it is possible that the limited movements of territorial dams restricted their access to mates. As a result, a territorial dam will mate with the overlapping territorial male and may mate with floater males that move through her territory, even if these males do not provide the greatest benefits to her offspring. Our data indicating that territorial males sired a greater proportion of litters from territorial dams provide support to this hypothesis. Similar constraints on mate choice of territorial females have been demonstrated in other taxa (reviewed in Jennions and Petrie, 2000). Floater dams may be less constrained in their access to mates and able to choose the most suitable territorial and floater mates, either pre- or postcopulation. If this is the case, then it suggests that female behavioral syndromes in *E. heatwolei* may influence a female's ability to obtain genetically compatible mates.

Although territorial males sired more offspring, it is likely that individual male reproductive success has been underestimated in this study. Because of the extensive movements of floater males and females, the exact number of offspring sired by any male is unknown. Floater males could sire additional offspring to either territorial or floater dams outside the study site, and territorial males may sire offspring to floater dams not caught and brought into the laboratory. The movements of floaters made it difficult to determine male reproductive success in this study. However, 100% of territorial female litters were assigned fathers, and the relationships between territorial pairs were established. In birds, it is common that territorial males and females make extended forays outside their territories in search of mates (e.g., Double and Cockburn, 2000; Kempenaers et al., 1992; Stutchbury et al., 1997). Although it cannot be excluded without further study, it is unlikely that floater lizards are territorial individuals making extended forays outside their territory. Firstly, the boundaries of the study site reflect sharp decreases in lizard abundance in relation to vegetation type and distance from the creek (Morrison et al., 2002). Few lizards are observed more than 100 m from the creek or in the man-made open grassland downstream of the study site. Secondly, territorial lizards were never observed making long distance forays from their territory, and their space use was highly predictable each day of sampling. The study site was large enough that if territorial lizards did make any extended movements, they would be sighted again within the study site at locations other than those within their territories. Thirdly, no lizards identified as floaters

in 1999 were ever caught again in the current study or in 2002 during a third study. If they were territorial lizards from nearby habitat that commonly make forays outside their territories, we might expect to catch them between years.

The results of this study suggest that parental genetic effects related to behavioral syndromes can influence offspring weight. Studies have tended to focus on male behaviors, and while these have important implications for the mating system and male reproductive success, the results of this study demonstrated that we should pay equal attention to female behaviors. Considering that genetic fitness benefits to offspring do not accrue to males and females separately but to the pair, understanding the interactions between behavioral syndromes in both sexes will have important implications for our understanding of mating system evolution.

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