Female aggression predicts mode of paternity acquisition in a social lizard

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Individual differences in behaviour are ubiquitous in nature. Despite the likely role of selection in maintaining these differences, there are few demonstrations of their fitness consequences in wild populations and, consequently, the mechanisms that link behavioural variation to variation in fitness are poorly understood. Specifically, the consequences of consistent individual differences in behaviour for the evolution of social and mating strategies have rarely been considered. We examined the functional links between variation in female aggression and her social and mating strategies in a wild population of the social lizard *Egernia whitii*. We show that female *Egernia* exhibit temporally consistent aggressive phenotypes, which are unrelated to body size, territory size or social density. A female's aggressive phenotype, however, has strong links to her mode of paternity acquisition (within- versus extra-pair paternity), with more aggressive females having more offspring sired by extra-pair males than less aggressive females. We discuss the potential mechanisms by which female aggression could underpin mating strategies, such as the pursuit/acceptance of extra-pair copulations. We propose that a deeper understanding of the evolution and maintenance of social and mating systems may result from an explicit focus on individual-level female behavioural phenotypes and their relationship with key reproductive strategies.

Keywords: *Egernia whitii*; extra-pair paternity; individual differences in behaviour; mating systems

1. INTRODUCTION

Aggression is widely regarded as an important component of an animal's behavioural repertoire, having strong and persistent effects on various fitness-related traits. These include territory acquisition and defence, mate acquisition, parental care, intra- and interspecific interactions, mode of reproductive success (within- versus extra-pair paternity) and anti-predation behaviour (e.g. Wingfield 1984; Huntingford & Turner 1987; Ketterson *et al.* 1992; Moss *et al.* 1994; Raouf *et al.* 1997; Duckworth 2006a). Consequently, aggression can exert a significant influence on both large-scale population dynamics and important evolutionary processes (e.g. Moss *et al.* 1994; Mougeot *et al.* 2003; Duckworth 2006b; Duckworth & Badyaev 2007).

To date, the majority of work on aggression has largely concentrated on the hormonal, behavioural and physiological links between aggression and fitness-related traits in males (see earlier references). Female aggression, on the other hand, is assumed to be either subtle or inconspicuous and has received relatively little attention (Gill *et al.* 2007). Recent work, however, suggests that female aggression may have important consequences in a number of functional contexts (Dunn & Hannon 1991; Slagsvold & Lifjeld 1994; Rosvall 2008), such as territory acquisition and eviction (e.g. Woodley & Moore 1999), the maintenance of monogamy (e.g. Sandell & Smith 1997; Sandell 2007), the pursuit/acceptance of extra-pair copulations (e.g. Sheldon 1993) and parental care (e.g. Wolff & Peterson 1998; Sinn *et al.* 2008). More recently, the proximate mechanisms underlying female

aggression, specifically the role of androgens such as testosterone, have been highlighted under both natural and experimental settings (e.g. Cristol & Johnsen 1994; Sandell 2007; Parn *et al.* 2008). Combined, these studies emphasize the importance of considering the effects of aggression on the reproductive strategies of both males *and* females when trying to understand how individual-level aggression results in population-level phenomena, such as dispersal, social spacing and mating systems (e.g. Sandell & Smith 1997; Sandell 2007).

Genetic and phenotypic variation in individual-level aggression is widespread within animal populations. In many cases, this individual-level variation in aggression shows considerable consistency (i.e. individuals have a distinctive aggressive phenotype; Sinervo *et al.* 2000; Gosling 2001; Sih *et al.* 2004; Duckworth 2006a). Thus, individuals often show some, but limited plasticity in their aggressive behaviour (i.e. some individuals are consistently more or less aggressive than others). Such consistency can generate trade-offs, such that levels of inherent aggressiveness may be appropriate in some functional contexts but not others. For example, aggressive individuals may be more successful in defending resources such as food or territories from conspecifics but these same individuals may also display inappropriate aggression towards potential mates (Sih *et al.* 2004; Johnson & Sih 2005). Recent work across a range of taxa that has explicitly focused on consistency in individual-level behavioural phenotypes suggests that aggression may play an important role in an individual's reproductive success and, to a lesser extent, its survival (Dingemanse & Reale 2005; Duckworth 2006a; Boon *et al.* 2007; Reale *et al.* 2007; Smith & Blumstein 2008). However, despite

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these recent advances, we still know relatively little about the fitness consequences of aggressive phenotypes and, in general, the mechanisms that link variation in behaviour to variation in fitness (Both *et al.* 2005; Duckworth 2006*a*; Boon *et al.* 2007). Specifically, covariance between female aggression and reproduction has rarely been examined (Sih *et al.* 2004; Both *et al.* 2005; Sinn *et al.* 2006; Van Oers *et al.* 2008; Sih & Bell 2008), despite that the extent of variation between females in their behaviour towards conspecifics should have strong impacts on the strength of selection on fitness-related traits.

We addressed the above limitations by examining the links between a female's aggressive phenotype and her social and reproductive strategies in a wild population of the Australian lizard *Egernia whitii*. *Egernia* display relatively complex sociality, with considerable variation in social organization and mating systems both between and within species (reviewed in Chapple 2003). Importantly, within populations, *Egernia* display considerable individual variation in their social strategies relating to the mode of paternity acquisition (within- versus extra-pair paternity), social organization (monogamy versus polygyny) and parental care (e.g. Bull & Baghurst 1998; Gardner *et al.* 2002; O'Connor & Shine 2004; Chapple & Keogh 2005). However, the mechanisms by which variation in social strategies are maintained are poorly understood (Chapple 2003). As *Egernia* populations are typically highly saturated, characterized by intense competition over limited permanent shelter sites, high levels of conspecific aggression and high juvenile mortality (Chapple 2003; O'Connor & Shine 2004; Langkilde *et al.* 2005), conspecific aggression may be an ecologically important behavioural trait for female lizards that, through its effects on the development and maintenance of social strategies (including parental care), mediates reproductive success. Specifically, female aggression may influence both mate acquisition and pair bonding, which can affect reproductive efficiency (Bull 2000), parasite transmission (Bull 2000) and the vulnerability of offspring to conspecific infanticide (O'Connor & Shine 2004; Sinn *et al.* 2008). Thus, the aim of the present study is to investigate consistency in individual-level female aggressiveness and the extent to which female aggression covaries with social and reproductive strategies.

2. MATERIAL AND METHODS

(a) *Study species*

White's skink (*E. whitii*) is a medium-sized (up to 100 mm snout–vent length, SVL) viviparous lizard found throughout southeastern Australia. Male and female *E. whitii* are sexually monomorphic, become reproductively mature at approximately 3 years and have an overall lifespan of 9–10 years (Chapple 2003). We used *E. whitii* from a population on the east coast of Tasmania, Australia (42°57′ S, 147°88′ E). Individuals at the study site are found in a discrete patch of open grassland (200 × 200 m) in close association with excavated burrows or rock crevices, which they use as permanent retreat sites. Reproduction occurs annually, with males emerging from overwinter hibernation prior to females. As females emerge, individuals pair (in the majority of cases to the same partner as previous seasons) with mating occurring during the spring (September–October) and offspring born in the summer (January–February) following

a three- to four-month gestation (Chapple 2003; While *et al.* 2007). The social organization of this population is based on small family groups typically centred on a stable mono-gamous (70% of social groups) or polygynous (30% of social groups) male–female pair bond(s) (While *et al.* in press; see also Chapple & Keogh 2006). Adult pair bonds and home ranges are stable between years, with approximately 70 per cent of adults maintaining pair bonds from one year to the next, with extra-pair offspring occurring in approximately 35 per cent of litters (While *et al.* in press). Parental care extends to semi-independent juveniles remaining close to their parents potentially gaining access to resources and protection from infanticide (Bull & Baghurst 1998; O'Connor & Shine 2004).

(b) *Field and laboratory protocol*

All subject lizards were part of a larger life-history study, which has taken place over three reproductive seasons, 2004–2005 to 2006–2007 (see While *et al.* 2007; While *et al.* in press). All individuals in the population were therefore toe-clipped to allow for unique identification previous to our field study in 2006–2007 and genotyped for six polymorphic microsatellite markers (see below). Throughout the 2006–2007 field season, detailed positional and behavioural observations of all individuals were collected using a digitized map of the study area (average number of observations per individual = 15.20 ± 1.13). At the end of gestation, all pregnant females ($n = 30$) were captured, measured for length (±1 mm) and weight (±1 mg), and returned to the laboratory to give birth. Females were housed individually in temperature- and light-controlled rooms, with room lights set to the ambient day length. Basking lights were set on a timer to come on 1 hour after 'sunrise' and to turn off 1 hour before 'sunset'. Housing containers (30 × 60 × 40 cm), identical to those used for behavioural assays (see below), were opaque on all sides, included a basking rock and light at one end and a single shelter at the opposite end. Food (*Tenebrio* larvae, crushed fruit) and water were available ad libitum. At birth, offspring were temporarily removed from their mother to be marked, have their weight (±1 mg), SVL and total length (±1 mm) recorded, and a portion of their tail tip taken for later genetic analysis. We were unable to identify offspring sex as juvenile female *Egernia* retain their hemipenes until well after birth (Chapple 2003). Within 3 days of birth, offspring were released with their mother at their mother's site of capture. All the above field and laboratory protocols were carried out by a single experimenter (G.M.W.).

From the positional data collected throughout the season (August–April), we calculated adult home ranges using a fixed kernel analysis with a least-squares cross-validation smoothing parameter (Powell 2000). Within this estimator, we used 95 per cent isopleths to calculate total home range and 50 per cent isopleths to calculate core area. Where home ranges did not reach 80 per cent of the asymptote, that individual's home range data were removed from further analysis (Rose 1982). Home range overlap was calculated as the number, area (m²) and percentage overlap of males, females and all adults for each individual's total and core kernel home range. All positional data were analysed using ANIMAL MOVEMENT (Hooge & Eichenlaub 1997).

An individual's 50 per cent core area is associated with permanent shelter and crevice sites from which basking, feeding and social activities are undertaken (Chapple 2003); thus, social pairings were identified based on 50 per cent core

area overlap. Social pairings were determined when an adult male's core area home range overlapped any portion of a female's (or multiple females') core home range (94% of social groups). Where no females fulfilled this criterion (6% of social groups), a male's social grouping was assigned to the female(s) for which he had the greatest (>75%) total home range overlap and there were no other females with a similar level of overlap. In most cases (60%), this represented a single member of the opposite sex, with an average core area overlap between social pairs of 48.33 ± 5.99 per cent. The above social pairing data were confirmed by observational data related to pair bonding collected throughout the study period (i.e. basking, mating and parental care; Gardner *et al.* 2002; Chapple & Keogh 2006). As identical methodology was undertaken in multiple seasons, we could examine social group stability between years. Each female was assigned a score of 1 if their social partner in 2006–2007 was the same as that in 2005–2006, and a 0 if they were with a new social partner.

We characterized the source of paternity (within- versus extra-pair male) of a female's litter via molecular analysis of male paternity. DNA was extracted from the tail tip of all individuals within the population using a modified hexadecyltrimethyl ammonium bromide (CTAB) protocol. All individuals at the study site, including offspring born in the laboratory, were genotyped for six microsatellite loci (EST1, EST2, EST4 and EST12: Gardner *et al.* 1999; TruL12 and TruL28: Gardner *et al.* 2008) using standard molecular techniques. In *E. whitii*, these loci are unlinked, conform to the expectations of Hardy–Weinberg equilibrium and are highly variable and informative (Chapple & Keogh 2005; this study). Paternity was assigned using the computer program CERVUS v. 3.0 (Marshall *et al.* 1998) using the following simulation parameters: 10 000 cycles; 95 per cent of candidate parents sampled; 90 per cent loci typed; and a genotyping error of 1 per cent (calculated in CERVUS from our data). The one-parent-known option was used, with all adult males (SVL>70 mm) in the population included as possible fathers. Paternity was assigned to the male with the highest male–female–offspring trio logarithm of the odds score and the lowest number of mismatches (0 or 1). In cases where we were unable to separate two males based on the above methods (17% of cases), paternity was assigned to one of those males based on behavioural and home range observations (i.e. distance between male and female home ranges; see Foerster & Kempenears 2004 and Chapple & Keogh 2005 for similar approaches). Where no candidate fathers fulfilled the paternity criteria, we considered the father to be unknown or unsampled (5% of cases).

(c) *Female conspecific aggression tests*
All females were captured at two periods during their reproductive cycle in 2006–2007 and assayed for conspecific aggression. The first capture period (21 September–11 October) occurred during the mating season ($n=45$). A second collection of a subset of these individuals occurred at the end of female gestation (10–24 January; $n=31$). At both periods, females were subjected to two conspecific aggression tests given by a single experimenter (D.L.S.) on two testing days, 24 and 48 hours after their capture. Behavioural tests were conducted between 14.00 and 17.00, allowing lizards to obtain preferred body temperatures before tests, and the test order was randomized on each test day.

Table 1. Loadings of discrete behaviours of *Egernia* observed during conspecific aggression tests on principal components analyses during test ($n=45$) and retest ($n=31$) periods.

behaviour	test	retest
number of touches	0.89	0.93
number of back arches	0.85	0.92
number of mouth opens	0.77	0.88
number of bites	0.72	0.86
cumulative variance explained (%)	65	81

Behavioural tests consisted of the experimenter touching the lizard with a realistic conspecific clay model attached at the end of a fishing rod (model dimensions: head width 15.7 mm; head depth 12.3 mm; head length 17.6 mm; SVL 87 mm; see Lopez *et al.* 2005 and Sinn & Moltschaniwskyj 2005 for similar approaches). Models were scented with male and female *Egernia* urine and faeces collected from unrelated laboratory animals. During the first test period, we maintained distinct 'male' and 'female' models by using only one type of scent on two separate but otherwise physically identical models (within 0.3 mm for all dimensions above). Mean levels of conspecific aggression scores (see below) were not different for individual female *Egernia* when given the two 'sex' models (paired *t*-test: $t_{38}=-0.28$, $p=0.78$); therefore, for subsequent tests, we used a single model scented with a mixture of both male and female scents, and assumed that our tests measured a generalized response to a conspecific independent of the sex of the intruder.

Subject lizards were presented with the conspecific model only if they were found on, and remained on, the basking rock for a 60 s acclimatization period at the start of tests. Lizards were touched on the centre of the snout by the model up to 10 times, or until they fled into, or on top of, the shelter. Four behaviours were measured in these tests: the number of touches required before the lizard fled; the number of back arches (a display whereby the spine of the lizard is bent in a concave manner); the number of times the lizard displayed with an open mouth; and the number of times the subject actively bit the model. These behaviours closely resemble those recorded in antagonistic interactions within this and other species of *Egernia* (e.g. Langkilde & Shine 2004; O'Connor & Shine 2004; Langkilde & Shine 2005; Langkilde *et al.* 2005; Langkilde & Shine 2007; J. McEvoy 2008, unpublished data). Behaviours in tests were recorded for the duration of stimulus presentation (i.e. the number of touches). Multiple frequencies of each behaviour were possible since lizards could perform behaviours anew after each touch with the model.

The four behaviours were highly intercorrelated and loaded strongly on a single common component in PCA at each collection period (table 1). Therefore, to reduce the number of variables used in subsequent analyses and to facilitate the use of a reliable single score (e.g. Buss & Craik 1983), we computed aggregate scale scores (Tabachnick & Fidell 1996). A unique scale score for each lizard for each collection period was computed by summing the normalized frequencies of the observed variables in the two tests given within each collection period. Normalization was according to the grand mean of all tests in both collection periods. This method resulted in each behavioural variable contributing equally to scale scores, and it also allowed for meaningful

mean-level comparisons between scale scores across collection periods. This procedure resulted in higher scale scores representing more aggressive overall responses.

One potential issue with our behavioural assay is that the behaviours used to calculate aggression scores may be highly correlated not because they accurately represent an individual's inherent aggressiveness, but rather because only females that were more persistent (i.e. females that did not flee upon 'attack' by the model conspecific) could display the other three observed behaviours. In other words, individuals who had fewer touches before they fled also had less opportunity to display aggressively. Thus, our behavioural assays may have confounded persistence and aggression. To account for this possibility, we recalculated aggression scores using only three of the aggressive behaviours (number of back arches, mouth opens and bites), each divided by the number of touches required before the lizard fled previous to the creation of a normalized aggregate score as above. We then reran all models (see below), and, in all cases, our interpretation of the results held irrespective of the method for calculating aggression score. An individual's tendency to flee is likely to be a key component of an *Egernia* lizard's overall aggressive response, where agonistic conspecific interactions are over limited permanent shelter sites from which the majority of an individual's social activities are undertaken (e.g. Duffield & Bull 2002; Chapple 2003; Langkilde *et al.* 2005; While *et al.* in press). In other words, defence of a physical location is a key component of many fitness-related activities in this species, so it is likely that aggressive behaviours (biting and displaying) are closely related to an individual's tendency to remain stationary when attacked. Therefore, we retained aggression scores calculated using all four observed behaviours for all subsequent analyses. Statistically, the number of pokes before an individual fled was strongly correlated with an individual's aggression scores calculated using the three other observed behaviours corrected for the number of touches previous to fleeing (time 1, Spearman's $r = 0.63$, $p < 0.01$; time 2, Spearman's $r = 0.84$, $p < 0.01$). Thus, more aggressive individuals tended not to flee when being poked and exhibited more aggressive acts per poke.

Aggression scores at both times were right-skewed; therefore, log-transformed scores or non-parametric statistics were used for subsequent analyses. We used the one-way random-effects intraclass correlation coefficient (hereafter referred to as 'repeatability'; Boake 1989; McGraw & Wong 1996) to establish whether female aggression showed consistent between-individual variation across the three-month reproductive period. We also examined mean-level patterns of female aggression using repeated-measures ANOVA on log-transformed aggression scores, with collection period as a within-individual factor (two levels: at mating and at the end of gestation).

(d) *Linking aggressive phenotype to reproductive parameters*

Data analysis examining the effect of aggression on reproductive and social parameters in female *Egernia* was carried out using general and generalized linear models with the PROC GLM and the PROC GENMOD procedures, respectively, in SAS STAT v. 9.2. All models included an individual's log-transformed conspecific aggression score as a fixed factor and their SVL as a covariate. These two traits, aggressive phenotype and female body size, were not related

(Spearman's $r = -0.10$, $p = 0.51$). We used log-transformed aggression score assayed during the first testing period, as this time period corresponded to the mating season when aggression is likely to exert its strongest influence on reproductive parameters. The first three models examined the influence of female aggression and body size on an individual's home range characteristics; this included a single model with an individual's log-transformed core home range size as the response variable, and two models with sex-specific 95 per cent home range overlap as the response (i.e. one model for each overlapping sex). The fourth and fifth models examined the effects of female aggression on the sexual composition of the social group (monogamous versus polygynous) and the stability of the male–female pair bond. The sixth model examined the influence of female aggression on female clutch mass. Finally, we examined the influence of female aggression on the extent of extra-pair paternity within her litter. For this model, we ran a main-effects model including female aggression and male home range overlap as predictors, and the number of extra-pair offspring divided by a female's clutch size as the response. We included male overlap as a predictor because availability of males predicts extra-pair paternity in other reptiles (Uller & Olsson 2008). A main-effects-only model was fitted for extra-pair paternity, since female aggression and male density were not related (see §3), and we were interested primarily in determining what proportion of unique variance female aggression and male density explained in extra-pair paternity. As a female's aggressive phenotype was not related to her partner's body size (Spearman's $r = -0.32$, $p = 0.07$), we did not include partner size in any of the models.

All data were checked for violations of assumptions, including homogeneity of slopes where covariates were used. Sample sizes differ slightly between tests as not all target traits could be measured for all individuals. To adjust for multiple comparisons, we adjusted α for parameters associated with female aggression using the false discovery rate procedure (Benjamini & Hochberg 1995). Assessing significance at the adjusted experiment-wise α did not change the interpretation of any of our results.

3. RESULTS

(a) *Consistency of aggressive response*

Females responded to behavioural tests in a distinctive manner. Some individuals acted aggressively towards conspecific models by actively displaying towards models (mouth open and back arch), biting models and tending not to flee. Conversely, others were less aggressive, and fled after fewer touches with the model while not displaying aggressively towards it. Individually, female aggression scores were highly repeatable across the duration of the study ($\rho = 0.58$, $F_{27,27} = 2.37$, $p = 0.01$). Combined with this maintenance of rank-order aggressiveness among females, there were also significant population-level changes in female aggression during the reproductive cycle, with a twofold population-level increase in aggression throughout gestation ($t_{27} = -3.27$, $p = 0.01$).

(b) *Home range size and overlap*

Home ranges were estimated for 80 per cent of the females given behavioural assays, with insufficient observations for the remaining females precluding accurate estimation of
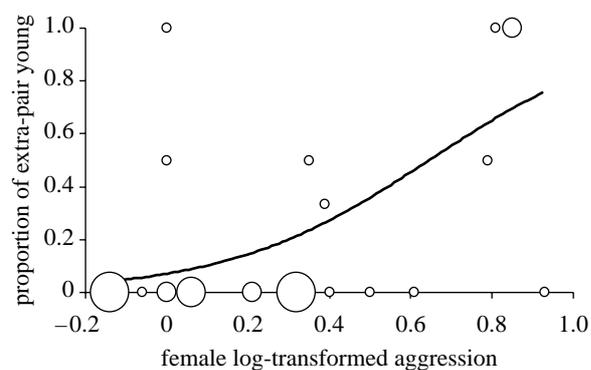
Figure 1. The relationship between a female *Egernia whitii*'s log-transformed aggression score and the proportion of her litter sired by extra-pair males ($n=28$). Points represent actual proportions of extra-pair paternity within litters; the solid line represents the increase in probability of extra-pair offspring with increasing female aggression. Circle size indicates sample size at each point (smallest circles $n=1$; largest circles $n=4$).

home range analyses. Core home range size for females was 9.29 ± 1.42 m^2, with an average of 1.24 ± 0.13 individuals overlapping the home range. Home range size was not related to a female's aggressive phenotype ($F_{1,32}=1.05$, $p=0.31$) or to her SVL ($F_{1,32}=0.03$, $p=0.87$). Examination of the links between aggression and sex-specific home range overlap suggests that there was no relationship between female aggression and the number of males ($\chi_1^2=0.42$, $p=0.52$) or females ($\chi_1^2=0.77$, $p=0.38$) overlapping their home range.

(c) Social groupings
Of the 45 adult females at the study site that were given behavioural assays, 40 occurred in a social group, as determined by home range overlap and observations of pairing. This included females in both monogamous (25 out of 40) and polygamous (15 out of 40) social groups, with no females being observed to have multiple male social partners. In line with this, females had an average of 1.00 ± 0.07 males and 0.21 ± 0.09 females overlapping their core area home range. Female aggression was not linked to the sexual composition of her social group (monogamous versus polygynous; $\chi^2=1.57$, $p=0.21$). Stability of social pairings for females was high between years, with 74 per cent of females remaining with the same social partner(s) as the previous year. A female's aggressive phenotype did not predict the stability of her pair bond ($\chi^2=1.47$, $p=0.23$).

(d) Female reproductive success
Twenty-nine of the females gave birth in the laboratory resulting in 57 offspring (average litter size 1.90 ± 0.12, range 1–3); all but one of these females had also been given a behavioural assay. Seventy-six per cent of offspring were sired by the females' social partner(s) with the remaining 24 per cent of offspring sired by extra-pair males. This resulted in 31 per cent ($n=9$) of litters containing extra-pair offspring. Female body size and aggressiveness explained 31 per cent of the variation in female clutch mass ($F_{3,28}=3.83$, $p=0.02$), but this was largely due to female body size ($F_{1,25}=3.88$, $p=0.06$) and not female aggressiveness ($F_{1,25}=0.47$, $p=0.50$) or their

interaction ($F_{1,25}=0.49$, $p=0.49$). However, a female's aggressive phenotype did predict the proportion of extra-pair paternity in her litter. More aggressive females had a greater proportion of offspring sired by extra-pair males, while less aggressive females had a greater proportion of their offspring sired by within-pair males ($\chi_1^2=9.99$, $p=0.002$; figure 1). Specifically, the odds of offspring sired by extra-pair males within a female's litter increased 3.99 times with a one unit increase in female aggressiveness (lower 95% CI$=1.76$ times, upper 95% CI$=6.84$ times; figure 1). We found no relationship between the number of males overlapping a female's home range and the proportion of extra-pair offspring within her litter ($\chi_1^2=0.03$, $p=0.87$).

4. DISCUSSION
The importance of female aggression in shaping social and reproductive parameters linked to large-scale population processes has started to gain increased attention (Sandell & Smith 1997; Gill *et al.* 2007; Sandell 2007; Smith & Blumstein 2008). However, to date, few studies have elucidated patterns of observed consistent individual differences in female aggression, and how this behavioural consistency may impact on an individual's social and reproductive strategies. We show that female *E. whitii* exhibit consistent individual variation in aggression (i.e. they have an aggressive phenotype), with the level of consistency comparable with that found for other functional behavioural traits in a diverse range of taxa (e.g. Gosling 2001; Sih & Bell 2008). Importantly, our data suggest that a female's aggressiveness may also largely determine her mode of paternity acquisition (i.e. within-versus extra-pair offspring) independent of the absolute availability of males. Below, we discuss the implications for consistent female aggression with regard to understanding social and mating strategies.

Our results indicated that a female's level of aggression was largely independent of her size, age or social environment (number of conspecifics overlapping, family mating system and stability of her pair bond). We also found no relationships between a female's aggressive phenotype and her reproductive output (clutch mass). However, we did find that a female's aggressive phenotype had strong links with the manner in which she acquired males for mating. Offspring from less aggressive females had a greater probability of being sired by within-pair males, whereas offspring from more aggressive females had a greater probability of being sired by extra-pair males. While links between aggressive phenotype and paternity acquisition have been documented in males (Wingfield 1984; Raouf *et al.* 1997), only recently have studies shown that individual-level aggression can also positively influence the proportion of extra-pair paternity within a female's clutch/litter (Van Oers *et al.* 2008). A positive effect of female aggression on promiscuity is in contrast with mean-level studies in avian systems, which indicate that female aggression typically reduces levels of promiscuity, albeit of males, by discouraging the settlement of additional females and thus promoting social monogamy (Sandell & Smith 1997; Sandell 2007). Similarly, female aggression can also serve as a mechanism to avoid/refuse extra-pair copulations (see Olsson 1995), where such

copulations are costly, for example, through increased risk of venereal disease (Sheldon 1993).

Clearly, the benefits for extra-pair copulations in females, which are expected to revolve around offspring quality rather than quantity (reviewed by Jennions & Petrie 2000), would need to outweigh any costs associated with female promiscuity if the positive relationship between female aggression and extra-pair copulations, found here, is the result of adaptive evolution. However, the adaptive value of extra-pair copulations in reptiles has recently been questioned, with the suggestion that extra-pair paternity is driven primarily by opportunity rather than direct or indirect benefits (Uller & Olsson 2008). Therefore, the link between aggression and extra-pair paternity could be simply explained if a female's aggressive phenotype influences her opportunity for multiple mating, for example, through social density. However, we found no links between female aggression and male social density, nor did male social density explain significant variation in the proportion of extra-pair offspring within a female's litter. The lack of a link between social density and extra-pair paternity, coupled with the socially monogamous mating system characteristic of *Egernia* (see Chapple 2003), suggests that there may be real consequences of pursuing/accepting extra-pair copulations. While we know little of the exact costs and benefits of multiple mating for female *Egernia*, there is currently little evidence to suggest that pursuing/accepting extra-pair copulations is beneficial in terms of offspring quality. Given that sociality in *E. whitii* is based on a long-term male–female pair bond (Chapple & Keogh 2006; this study), which may be important for enhancing reproductive efficiency (Bull 2000), reducing parasite transmission (Bull 2000) or reducing infanticide risk to offspring (O'Connor & Shine 2004), there may actually be significant costs to pursing/accepting extra-pair copulations. This is particularly likely given that paternity influences male parental effort in this species (While *et al.* 2009; see also Neff & Gross 2001; Hunt & Simmons 2002).

Given the potential consequences of pursuing extra-pair copulations in this system, how might one explain the positive relationship between female aggression and promiscuity? One explanation could be that female aggression and an extra-pair mating strategy are part of a wider suite of correlated phenotypic traits (Bell 2007; Van Oers *et al.* 2008). In this scenario, the links between aggression and extra-pair paternity could represent either an evolutionary constraint or, alternatively, a suite of behaviours favoured by selection (Sih *et al.* 2004). In the case of the former, the links between female aggression and promiscuity may be a result of carry-over effects of aggression favoured in other functional contexts. For example, aggression in female *Egernia* has significant benefits for offspring survival, with offspring from more aggressive females having higher survival rates over their first year of life than offspring from less aggressive females (Sinn *et al.* 2008), a pattern which is potentially driven by enhanced offspring protection from conspecific infanticide (Sinn *et al.* 2008; see also O'Connor & Shine 2004). Thus, even if promiscuity is costly, the effect of aggression on reproductive strategies observed in this study could

simply be a result of selection for aggression in a parental care context. Such links, albeit in the opposite direction, have been observed in avian systems. For example, in western bluebirds (*Sialia mexicana*), the benefits of male aggression in nest defence from intra- and interspecific intrusions are offset by the costs of reduced parental care (Duckworth 2006a). In the case of the latter adaptive hypothesis, aggressive females have a greater proportion of extra-pair offspring within their litters because extra-pair paternity is beneficial and aggressive females actively solicit extra-pair copulations. Such correlations may be unlikely given that selection favouring the correlated evolution of aggression and an extra-pair reproductive strategy would require the benefits of pursuing extra-pair copulations to outweigh the costs outlined above. However, even in the face of strong costs associated with extra-pair paternity (e.g. reduced parental care; While *et al.* 2009), the correlated evolution of aggression and extra-pair paternity could still occur if more aggressive females are better able to 'pay' the costs associated with male pair-bond abandonment of young (i.e. their phenotype allows them to provide sufficient parental care to their young, while less aggressive females are not able to do so; Sinn *et al.* 2008). This behavioural syndrome hypothesis may explain the intrinsic variation in the propensity to engage in extra-pair paternity observed in some avian species (e.g. Forstmeier 2007).

Similarly, the relationship between female aggression and promiscuity could represent an indirect by-product of several non-independent components of the mating system. For example, female aggression may influence the strength of adult pair bonds, specifically male defence of his social partner. Such defence of females by males is likely to exert a strong influence on the opportunity for females to undertake extra-pair copulations (e.g. Olsson 1993), if less aggressive females are more easily defended by their male social partner. Although our results suggest that female aggression did not influence pair-bond stability *per se* (i.e. divorce or social monogamy across reproductive seasons), our study may not have detected the more subtle influences on the strength of pair bonds suggested above. Additionally, from a mate choice perspective, females that are more aggressive may also be more attractive to males than less aggressive females, if aggressiveness is an honest signal for parental care abilities, and therefore may simply receive more visits from extra-pair males than less aggressive females (see also Godin & Dugatkin 1996; Van Oers *et al.* 2008). Alternatively, in species such as *Egernia*, where pairs are relatively stable, it may be a combination of male and female phenotype that influences the level of extra-pair paternity within a female's litter (see Van Oers *et al.* 2008). This is particularly likely if individuals assortatively mate and aggressive males paired to aggressive females spend relatively less time with their social partner and more time pursuing extra-pair copulations, increasing the opportunity for more aggressive females to undertake extra-pair copulations (Wingfield 1984; Raouf *et al.* 1997; Rosvall 2008; Van Oers *et al.* 2008).

Overall, our results suggest that paternity acquisition in females covaries with their consistent aggressive phenotype, independent of the effects of mating opportunity.

In contrast to the idea that females respond flexibly according to current social environments with regard to multiple mating and the pursuit/acceptance of extra-pair copulations (see Jennions & Petrie 2000 for a review), our study suggests that a deeper understanding of mating systems may result from an explicit focus on individual-level female (and male) behavioural phenotypes and their relationship with key reproductive strategies. Understanding how variation in correlated suites of phenotypic traits result in variation in fitness is a central concept in evolutionary biology. Clearly, our study suggests that understanding the costs and benefits of female promiscuity, along with covariation between promiscuity and other fitness-related behavioural traits (some of them not necessarily related to mating contexts), should contribute heavily towards our understanding of the evolution of mating systems across a wider range of taxa.

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