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Complex mating system and dispersal patterns in a social lizard, *Egernia whitii*

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Abstract

In contrast to the polygynous mating systems typically displayed by most reptilian taxa, long-term genetic monogamy appears to be widespread within a lineage of group-living Australian scincid lizards, the *Egernia* group. We have recently shown that White's skink, *Egernia whitii*, lives in small but temporally stable social aggregations. Here, we examine the mating system, spatial organization, and dispersal patterns of *E. whitii* using behavioural field studies and data from four microsatellite loci. Parentage analysis of *E. whitii* litters revealed that its mating system is characterized by both polygyny and monogamy. Polygyny was the predominant mating system but within-season social and genetic monogamy was common (36–45% of breeding pairs). The incidence of between-season monogamy in *E. whitii* was rare compared to that reported for its congeners. Low levels of multiple paternity (12% of litters) and extra-group paternity (16%) were detected. Social groups are generally comprised of closely related individuals, but breeding pairs were not more closely related compared to other potential mates. Spatial autocorrelation analyses revealed significant positive local genetic structure over 50 m, which was consistent for all age–sex classes. There was no clear and consistent evidence for sex-biased dispersal, with assignment tests (mean assignment index) and relatedness analyses suggesting female-biased dispersal, but spatial autocorrelation analyses indicating a trend for male-biased dispersal. We discuss the implication of our results in regard to the factors promoting the evolution of monogamy within the *Egernia* group.

Keywords: monogamy, philopatry, polygyny, relatedness, sex-biased dispersal, spatial autocorrelation

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Introduction

Monogamous mating systems have evolved independently on numerous occasions across a wide variety of animal taxa (Gowaty 1996; Mathews 2002; Whiteman & Cote 2004). Social monogamy, the formation of cooperative pair bonds for breeding activities, is the predominant mating system in birds (Bennett & Owens 2002), but it occurs less frequently in mammals (Komers & Brotherton 1997), fish (Whiteman & Cote 2004), and several other vertebrate and invertebrate taxa (reviewed in Mathews 2002). The advent of molecular techniques for parentage assignment has significantly enhanced our understanding of the mating systems of animal taxa, challenging several long ingrained beliefs (Hughes 1998). For example, it is now well documented that genetic monogamy (i.e. no extra-pair copulations, with the pair the sole parents of resultant offspring) occurs in less than 25% of socially monogamous bird species (Griffith *et al*. 2002).

Lizards generally display relatively simple polygynous mating systems (reviewed in Bull 2000). Several species appear to exhibit within-season social monogamy (Toxopeus *et al*. 1988; Olsson & Shine 1998), but until recently long-term genetic monogamy had not been reported in lizards. Field studies utilizing genetic techniques have now documented long-term monogamous pairings in *Tiliqua rugosa* (Bull 2000), *Egernia cunninghami* (Stow & Sunnucks 2004a), *Egernia saxatilis* (O'Connor & Shine 2003) and *Egernia stokesii* (Gardner *et al*. 2002). Importantly, all four species are members of the *Egernia* group, a monophyletic lineage of Australian skinks that comprises four genera (*Egernia*, *Tiliqua*, *Cyclodomorphus*, and *Corucia*; Greer 1989). The seemingly widespread

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incidence of genetic monogamy within this lineage of lizards provides an opportunity to test hypotheses relating to the evolution of monogamy developed in other taxa. Monogamy is predicted to occur where (i) biparental care is required to raise young (Emlen & Oring 1977; Clutton-Brock 1991), (ii) males guard single females (Parker 1974; Stamps 1983), (iii) availability of mates is low (Whiteman & Cote 2004), or (iv) females are advantaged by the presence of the male (Gowaty 1996). However, examination of the factors responsible for promoting monogamy in the *Egernia* group is simplified by the absence of direct parental care in lizards (Shine 1988), with only low levels of indirect parental care present within *Egernia* species (Chapple 2003; O'Connor & Shine 2004).

The sleepy lizard, *T. rugosa*, only forms monogamous pairings during the breeding season (Bull 2000), but the three *Egernia* species studied to date (*E. cunninghami*, *E. saxatilis*, *E. stokesii*) live in stable social aggregations comprised of highly related individuals, which are present year-round (Gardner *et al*. 2001; O'Connor & Shine 2003; Stow & Sunnucks 2004a). Consequently, mechanisms to avoid inbreeding should be expected in these group-living lizards (e.g. Pusey & Wolf 1996). Indeed, recognition of kin and group members has been demonstrated in *Egernia* (Bull *et al*. 2000, 2001) and several species appear to actively select mates that are less related compared to other potential mates (Gardner *et al*. 2001; Stow & Sunnucks 2004b). Given the high levels of genetic monogamy within *T. rugosa*, *E. cunninghami*, and *E. stokesii* (> 75%), inbreeding avoidance through multiple mating does not appear to be widespread (Bull & Cooper 1999; Gardner *et al*. 2001; Stow & Sunnucks 2004a).

Sex-biased dispersal, where individuals of one sex have a greater tendency to disperse or disperse further than members of the other more philopatric sex, is another inbreeding avoidance strategy as it acts to separate opposite-sex siblings prior to mating (Pusey & Wolf 1996). Three hypotheses exist to explain disparity in dispersal between the sexes: (i) the 'resource-competition' hypothesis (Greenwood 1980), (ii) the 'local mate competition' hypothesis (Dobson 1982; Perrin & Mazalov 2000), and (iii) the 'inbreeding avoidance' hypothesis (Pusey 1987). Each hypothesis predicts male-biased dispersal in taxa with polygynous mating systems. In contrast, in monogamous species, female-biased dispersal is anticipated under the 'resource-competition' hypothesis, with no bias expected under the other two hypotheses (reviewed in Favre *et al*. 1997). Current evidence appears to support these broad expectations with male-biased dispersal most prevalent in mammals where polygyny is the predominant mating system, while birds which are socially monogamous generally display female-biased dispersal (Greenwood 1980; Pusey 1987). The recent development of genetic techniques to infer dispersal patterns in natural populations (reviewed in Goudet *et al*. 2002; Prugnolle & De Meeus 2002; Peakall *et al*. 2003) has enabled researchers to enhance the understanding of dispersal patterns in other vertebrate groups (Austin *et al*. 2003; Taylor *et al*. 2003).

Most reptiles are polygynous and male-biased dispersal has been demonstrated in lizards in accordance with theoretical expectations (e.g. Doughty *et al*. 1994; Rassman *et al*. 1997; but see Olsson & Shine 2003). In contrast, no bias in dispersal or female-biased dispersal would be predicted in members of the *Egernia* group that possess monogamous mating systems. The absence of sex-biased dispersal in *T. rugosa* (Bull & Cooper 1999) is in accordance with this expectation, but the presence of male-biased dispersal in *E. cunninghami* (in fragmented habitats, Stow *et al*. 2001) and *E. stokesii* (Gardner *et al*. 2001) is contrary to predictions. In this study, we examine the mating system, spatial organization, and dispersal behaviour of White's skink (*Egernia whitii*) using a field study, behavioural observations, and a range of microsatellite DNA analyses to assign paternity and infer patterns of dispersal. We have recently demonstrated that *E. whitii* lives in stable social aggregations comprising two to six individuals, and adult pairs within these groups appear to be socially monogamous (Chapple 2005). Given that the group structure in *E. whitii* is similar in many respects to that reported for *E. saxatilis*, a species that displays long-term genetic monogamy (O'Connor & Shine 2003), we predicted that *E. whitii* would also display genetic monogamy.

Materials and methods

Study species

Egernia whitii is a medium-sized viviparous skink [snout-vent length (SVL) 95 mm] that occurs in grasslands, woodlands, and dry sclerophyll forests throughout south-eastern Australia (Wilson & Swan 2003). It typically lives in close association with rocky habitats where it utilizes crevices, exfoliating rock slabs, and burrows as retreat sites (Wilson & Swan 2003). Such rock crevices and burrow systems are used as permanent retreat sites, with lizards concentrating the majority of their basking and foraging activities within proximity to these retreat sites (Chapple 2003). Mating occurs in spring (September to October) and one to five offspring are produced in late summer (January to February) (Chapple 2003).

Field methods

The study was conducted at a 150 × 150 m site adjacent to Westermans Hut (35°53′S, 148°58′E) near Grassy Creek in Namadgi National Park in the Australian Capital Territory. The study area, described in detail in Chapple (2005), is located at an altitude of 1250 m above sea level (a.s.l.) and

predominately consists of open grassland interspersed with small patches of remnant semialpine woodland.

We conducted the study over two field seasons (2001–2002, 2002–2003) between October and March, the active season for *E. whitii*. Lizards at the site were caught by noosing, 'mealworming', or by hand. Measurements of SVL and other standard morphometric measurements (±0.1 mm) were taken upon initial capture, with each lizard toe-clipped. The tip of each individual's tail (*c.* 1 cm) was removed and stored in 70% ethanol for later genetic analysis. Sex was determined via eversion of hemipenes in males, and female reproductive status was assessed by abdominal palpation. All individuals at the site during the first season were recaught and remeasured in the second season. Our capture–mark–recapture (CMR) data indicated that virtually all lizards (except two juveniles) at the site were caught during the study.

Approximately 40 single-day surveys were conducted during the study. Fieldwork commenced just prior to the emergence of lizards in the morning and continued until lizards returned to their retreat site in the early evening. Our field methods are described in detail in Chapple (2005). Briefly, upon arrival at the study area, all rock crevices and burrow entrances at the site were visually inspected for lizards. Following these initial surveys, behavioural observations were conducted for the remainder of the day to document interactions between lizards. Every time a lizard was caught or observed, a GPS reading (Garmin GPS 12XL) was taken of its location, enabling the position of each lizard to be plotted onto a map of the field site. The geographical distance between lizards was calculated using GENALEX version 5.1 (Peakall & Smouse 2001). Using a combination of this spatial data and our behavioural observation data, we determined the structure and composition of 24 social groupings at the site (details in Chapple 2005).

At our site, *E. whitii* attains sexual maturity at around 75 mm SVL (D. Chapple unpublished). Consequently, it was possible to classify all lizards at the site as adult male (AM), adult female (AF) or juvenile (J). In the first season, there were 111 resident lizards at the site (36 AM, 37 AF, 38 J), while there were 108 resident lizards during the second season (35 AM, 35 AF, 38 J). Pregnant females at the site in late January of each season were caught and brought into the laboratory prior parturition, where they were housed individually in plastic containers [350 mm (L) × 250 mm (W) × 140 mm (H)] in a room maintained at 18 °C. Retreat sites were provided and heat tape (set at 35 °C) positioned under one half of the container enabled lizards to maintain their preferred temperatures for 14 h each day. Lizards were provided food (mealworms, crickets) and water *ad libitum*. Females gave birth within 3 weeks after being brought into the laboratory. Newborns were measured (±0.1 mm), toe-clipped and their tail tip (*c.* 1 cm) removed for genetic analysis. Females and their youngs were returned to the site of maternal capture once parturition was complete. Virtually the entire 2002 and 2003 cohorts were born in the laboratory. Two pregnant females could not be caught in January 2002. Seven females that were pregnant during the second season could not be caught in late January 2003 when major bushfires in the National Park restricted access to the study area for 3 weeks.

Microsatellite genotyping

DNA was extracted from tail tip samples using a modified hexadecyltrimethyl ammonium bromide (CTAB) protocol. All individuals at the study site, including laboratory-born offspring, were genotyped for four tetranucleotide microsatellite loci: *EST1*, *EST2*, *EST4*, *EST12* (Gardner *et al*. 1999). In *E. whitii*, these loci are unlinked, conform to the expectations of Hardy–Weinberg equilibrium (HWE), and are highly variable and informative with 20, 20, 14 and 21 alleles, respectively (Chapple 2005). Microsatellite analysis was performed as in Chapple (2005). Loci were labelled with fluorescent dyes: *EST1* (NED), *EST2* (NED), *EST4* (PET) and *EST12* (6-FAM). All loci were amplified in separate reactions. The products of *EST1* and *EST12* mixed and run together, as were the products of *EST2* and *EST4*. Mixed amplification products were run on an ABI 3100 automated DNA sequencer. Genescan 500 LIZ size standard (Applied Biosystems) was run with each sample to enable accurate sizing of alleles and comparison between runs. Results were analysed with GENEMAPPER version 3.0 software (Applied Biosystems).

Parentage assignment

We used the program CERVUS 2.0 (Marshall *et al*. 1998) to assign paternity to all offspring born in the laboratory where the mother was known. The following simulation parameters were used: 10 000 cycles, 100% of candidate parents sampled, 100% of loci typed and a genotyping error rate of 1% (calculated in CERVUS from our data). CERVUS was primarily used to determine genotypic mismatches between offspring and candidate parents, rather than a way to assign paternity strictly on the basis of log-likelihood ratio scores (LOD score).

We used the 'one-parent-known' option in CERVUS to assign paternity. All adult males at the site were included as candidate fathers. To avoid possible errors caused by inaccurate age determination, we included all males whose SVLs were 70–75 mm. We accepted paternity assignment where the candidate had the highest LOD score and was the only candidate with no mismatches (94 of 119 assignments, 79%). Where two or more candidate males had no mismatches, we excluded males that were never seen in close proximity to the female if the other male was the female's social partner (determined from long-term behavioural

observations) or had fathered other offspring in the litter (18 of 119 assignments, 15%). In each instance, one candidate male was always either the social partner or had been assigned as the father of other offspring in the litter using the first criteria. We generally considered the father to be unknown and unsampled if all candidate fathers had one or more mismatches (16 newborns). We assigned paternity to males that had one mismatch when it was one of the two most likely fathers based on LOD scores and were either the social partner of the female or had fathered other offspring in the litter (seven of 119 assignments, 6%). Such mismatches could be the result of the high level of mutation in these loci (Gardner *et al*. 2000), although in the majority of cases the mismatch was at *EST1* (five instances), which has a low frequency of null alleles (Chapple & Keogh, submitted).

Relatedness estimation

We used the program RELATEDNESS 5.08 (Goodnight & Queller 1998) to estimate pairwise and average relatedness. This program calculates the Queller & Goodnight (1989) index of relatedness (*R*). Standard errors of *R* estimates were obtained by jackknifing over the four loci (Goodnight & Queller 1998). The average relatedness of the various age–sex classes, both within and among social groups, were compared by jackknifing over the unpaired *R* difference using RELATEDNESS. Separate analyses were conducted for each season. To assess the power of our data to identify close relatives we examined the distribution of pairwise *R* for known relatives. The average pairwise *R* for laboratory-born full siblings identified from parentage analysis ($N = 162$, 0.487 ± 0.017) closely matched theoretical expectations.

Choice of breeding partners

We examined the degree of relatedness between *E. whitii* breeding pairs at the site. The pairwise *R* matrix from RELATEDNESS was used to compare the relatedness between actual breeding pairs to (i) all other potential opposite sex partners at the site, and (ii) all potential opposite sex partners within a 20-m radius. Two-sample randomization tests were performed to test for a difference in mean relatedness using RUNDOM 2.0 (Jadwiszczak 2003). We completed the analysis with 10 000 permutations to obtain exact *P* values. For instances where there were less than two potential partners within a 20-m radius, we used the average relatedness to the nearest two neighbours (generally within 30 m). Potential breeding partners were strictly classified as individuals over 75 mm SVL. Where individuals had more than one breeding partner during a season we used their average relatedness to all actual mates. Consequently, we analysed each sex separately.

Spatial structure

To examine the spatial genetic structure of lizards present at the site in each season we employed the powerful multilocus spatial autocorrelation (SA) techniques developed by Smouse & Peakall (1999) and Peakall *et al*. (2003). Genetic distance was calculated in GENALEX version 5.1 (Peakall & Smouse 2001) as described in Peakall *et al*. (1995) and Smouse & Peakall (1999). For our data, we found that the genetic distance calculated in GENALEX was highly correlated with Queller & Goodnight's (1989) *R* (Mantel test: Rxy = 0.832). We were primarily interested in detecting positive autocorrelation at shorter distances, which is predicted under models of restricted dispersal. SA analyses were conducted in GENALEX, which calculates an autocorrelation coefficient (*r*) for predefined distance classes. Tests for significance are performed through 1000 random permutations. GENALEX also calculates the 95% confidence intervals for estimates of *r* via bootstrapping (1000 bootstraps). It is possible to calculate *r* across multiple populations (Peakall *et al*. 2003) enabling us to treat the 2001/2002 and 2002/2003 data as separate populations to obtain an overall estimate of *r* (called *rc*) and spatial genetic structure for *E. whitii* at our study site. SA tests enable visualization of the spatial relationship through correlograms (plot of *r* as a function of distance). Where positive spatial genetic distance is observed, the first *x*-intercept provides an indication of the extent of nonrandom genetic structure (Peakall *et al*. 2003). We examined SA of *E. whitii* using two distance classes: 5 m and 10 m. Because the selection of distance class strongly influences the ability to detect the true extent of genetic structure, we also conducted a multiple distance class analysis (*Multiple Dclass*) as outlined in Peakall *et al*. (2003). This approach calculates *r* at increasing distance-class sizes, with the distance class where *r* is no longer significant considered to provide an estimate of the true extent of positive spatial genetic structure.

Tests of sex-biased dispersal

Given the limited direct observation of dispersal during our CMR study (Chapple & Keogh submitted) and the well-documented problems commonly encountered during such studies (e.g. Koenig *et al*. 1996), we conducted four indirect tests for sex-biased dispersal: (i) relatedness between individuals; (ii) spatial autocorrelation; (iii) mean assignment index; and (iv) variance of assignment index. The relatedness estimates (*R*) were used to test hypotheses regarding differential dispersal between the sexes. If sex-biased dispersal is present in *E. whitii*, we would expect that the average relatedness of the dispersing sex would be lower than the mean relatedness of the nondispersing sex (e.g. Prugnolle & De Meeus 2002). We completed separate SA analyses for each sex as outlined previously in order to determine whether the pattern of positive autocorrelation

was consistent for males and females (e.g. Peakall *et al*. 2003).

Sex-biased dispersal was also examined using assignment indices (Favre *et al*. 1997; Mossman & Waser 1999). The assignment index calculates the probability that a particular genotype should be present in the population from which it was sampled, after correction for population differences (Favre *et al*. 1997; Goudet *et al*. 2002; Prugnolle & De Meeus 2002). The corrected assignment indices (*AIc*) are distributed around a mean of zero, and since recent immigrants tend to have lower *AIc* values compared to residents, the dispersing sex is predicted to exhibit a lower mean *AIc* compared to the more philopatric sex (Favre *et al*. 1997). Likewise, the dispersing sex should display greater variance in *AIc* because it should comprise of both resident (positive values) and immigrant (negative values) individuals (Favre *et al*. 1997). We used FSTAT 2.9.3 (Goudet 2001) to calculate individual *AIc* values. The significance of sex-specific differences in the mean and variance of *AIc* was determined using a randomization method in FSTAT (10 000 permutations). The Grassy Creek site consists of two rock outcrops separated by 15–20 m, with each treated as separate populations in the FSTAT analyses.

Results

Parentage assignment

In the 2001/2002 season the 32 pregnant females that were brought into the laboratory to give birth produced 80 offspring, while in the 2002/2003 season, 22 females gave birth to a total of 55 offspring. We were able to assign paternity to 119 of the 135 (88%) offspring born in the laboratory. This was largely a consequence of the father(s) of four entire litters (total 14 offspring) being unsampled during the first season. Presumably the father(s) of these litters either died or dispersed from the site before the commencement of the study in late 2001. Although it is possible that one or more adult males remained unsampled during the study, this is unlikely because we never observed unmarked adult males during our CMR study and paternity was assigned to all but one juvenile in the second season.

Mating system

Assignment of paternity to laboratory-born offspring enabled breeding pairs at the site to be identified and the mating system of *Egernia whitii* to be inferred (Table 1). Our discussion is limited to the 50 litters produced in the laboratory, excluding the four litters where paternity could not be assigned. Seven litters were comprised of only one offspring, with multiple paternity detected in five of the 43 litters (11.6%) comprising two or more newborns. Although litter size in *E. whitii* was relatively small (1–4 offspring), multiple paternity was detected in four litters with two offspring and one litter with three offspring. Instances of multiple paternity never involved more than two males. For individuals where parentage was assigned, within each season males generally had more partners compared to females (Table 2). Extra-group paternity was detected in eight litters (16%) during the study (Table 1).

Both monogamy and polygyny were evident in *E. whitii* (Table 1). In the first season, 10 litters (35.7%) were the result of pairs that were socially and genetically monogamous, while 13 litters (46.4%) were the product of polygynous pairings where the resident male fathered the entire litter of all females within its social group. A further three litters (10.7%) resulted from extra-group paternity where the extra-group male fathered some or all of the litter. The final two litters were the result of a male who fathered the entire litter of his social partner as well as an extra-group female (7.2%). In the 2002/2003 season there were 10 (45.4%) monogamous pairs, six litters (27.3%) produced from within-group polygyny, four litters (18.2%) the result of complete or partial extra-group paternity, and two (9.1%) produced by a male who fathered the entire litter of his social partner and an extra-group female.

Breeding pairs in five groups (A, G, J, N, O) were monogamous in both seasons, while 15 groups failed to exhibit monogamy in both seasons (Table 1). Group Q comprised only of juveniles and three groups (E, K, L) were not present in both seasons (Chapple 2005). Polygynous social groupings were generally not stable in composition between seasons, with males typically mating with most of the resident females within the group (Table 1). Within-season monogamy was detected in 14 breeding pairs during the study (Table 1). Of these pairings, two comprised groups that only formed in the second season, while one breeding pair was present only in the first season with the female not seen at the site in the second season. The resident female in group N formed a monogamous pairing with a different male each season (Table 1). Long-term monogamy appears to be relatively rare with only five of the remaining 10 breeding pairs exhibiting monogamy in both seasons. Consequently, *E. whitii* displays a mixture of mating systems, exhibiting both social and genetic monogamy and polygyny.

Choice of breeding partners

Although several breeding pairs were closely related, our data indicate that breeding pairs at the site generally were not more closely related to each other compared to other potential breeding partners (Table 3). In particular, the adult male in group B was highly related (pairwise *R* around 0.5) to both adult females in his group. Several other males (three in each season) and females (five in first season, four in second season) had average *R* values close to that expected for half-siblings (i.e. > 0.2; Range 0.209–0.353).

Table 1 Summary of breeding pairs and the mating system of *Egernia whitii* at the Grassy Creek field site. Group I is not included as the resident female could not be caught in either season while pregnant. Group Q has been excluded as it was comprised entirely of juveniles. Mating system codes: M, monogamous; P, polygynous; MP, multiple paternity; EGC, extra-group paternity; ?, unknown

	Within-group adults						
Group	Males	Females	Female parents	Male parents	Offspring	Year of birth	Mating system
A	1	1	140	138	3	2002	M
					3	2003	M
B	1	2	40	64	4	2002	P
				43*	3	2003	P, EGC(Group C)
			55	64	3	2002	P
					3	2003	P
C	1	1	42	43	3	2002	M
					3	2003	P, EGC(Group B)
D	1	2	44	unknown	4	2002	?
				66	3	2003	P
			45	unknown	3	2002	?
				66	3	2003	P
E	1	1	51	49	2	2002	M
F	1	1	52	50, 136†	2	2003	MP, EGC(solitary)
G	1	1	137	139	1	2002	M
					2	2003	M
H	1	2	57	56	3	2002	P
				56	2	2003	P
			128		1	2002	P
				56, unknown	2	2003	P, MP
J	1	1	125	124	3	2002	M
					3	2003	M
K	1	1	58	154	2	2003	M
L	1	1	134	123	1	2003	M
M	1	1	61	131, unknown	3	2002	MP
				131	3	2003	M
N	2‡	1	133	53	3	2002	M
				153	3	2003	M
O	2	2	54§	59	3	2002	M
			156	151	2	2002	M
					2	2003	M
P	1	2¶	80§	145	2	2002	P
R	1	1	90	91*	3	2002	EGC(Group S)
				141	3	2003	M
S	1	1	86§	91	2	2002	P, EGC(Group R)
T	1	1	77	78	2	2002	M
				78, 96	2	2003	P, MP(Group U)
U	2	4**	85	97	3	2002	P
			101	96	3	2002	M
			152††	unknown	3	2002	?
				97	2	2003	P
			164	96, 97	2	2003	P(Group T), MP
V	1	3	83§	82	2	2002	P
			84	82	4	2002	P
					3	2003	P
			144§	82	1	2002	P
			142‡‡	82	2	2002	P, EGC(solitary)
W	2‡·§§	4§§	71	94	1	2002	P
			76	unknown	4	2002	?
			81	94	2	2002	P
			93	94	3	2002	P
				102	3	2003	M
X	1	2	73§	72	1	2002	P
			75§	97*	1	2002	P, EGC(Group U)

*Paternity of the entire litter from an extra-group male. †Multiple paternity involving a solitary adult male. ‡A different adult male was present in the group each season. §Female was pregnant in the second season, but was not caught due to restricted access to the NP during bushfires. ¶The second female in group P could not be caught in either season while pregnant. **Only two adult females were present in the group each season. ††Female was solitary in the first season, joining group U in the second season. ‡‡SB142 was a solitary female whose entire litter in the first season was fathered by SB82. §§·Refer to Chapple (2005) for details of group changes between seasons.

Table 2 Number of breeding partners for male and female *Egernia whitii* in each season

	2001/2002			2002/2003		
Sex	*N*	Mean ± SE	Range	*N*	Mean ± SE	Range
Male	19	1.47 ± 0.19	1–4	20	1.25 ± 0.10	1–2
Female	28	1.04 ± 0.04	1–2	22	1.18 ± 0.08	1–2

Although males in the first season were more closely related to other potential mates at the site ($P = 0.028$), there was no significant difference in average *R* compared to potential mates within 20 m ($P = 0.125$). In the first season, females were more related to all other potential mates at the site ($P = 0.044$) and those within a 20-m radius ($P = 0.034$), although these results were not significant when females from group B were excluded ($P = 0.184$ and 0.131, respectively). Breeding pairs in the second season were not more closely related compared to all other potential mates or those within close proximity ($P > 0.133$ in all cases).

Relatedness among E. whitii *at the study site*

The average relatedness (*R*) of all lizards at the site in each season, as well as the average relatedness among each age-sex class is shown in Table 4. Relatedness among males was significantly higher than that among females at the site ($P < 0.01$ in both seasons). Likewise, the average relatedness among adult males was greater than that evident among adult females ($P < 0.02$ in both seasons). Adults of both sexes (AM, AF, all adults) were more closely related compared to the average relatedness among juveniles ($P < 0.029$ in all cases), except for adult females in the first season ($P = 0.536$).

Relatedness within social groups

The high average relatedness (*R*) of individuals within the same social group indicates that *E. whitii* lives in groups comprising closely related individuals (Table 5). In both seasons, the average relatedness among individuals within the same group was significantly greater than that among lizards in different social groups ($P < 0.001$; Table 5). This trend was consistent for adults ($P < 0.004$), adult males ($P = 0.015$ in first season, $P = 0.056$ in second season), adult females ($P < 0.002$), juveniles ($P < 0.02$), males ($P < 0.001$) and females ($P < 0.002$). However, the average within-group relatedness did not significantly differ between each age-sex class ($P > 0.309$ in all cases), except that adults in groups were less closely related compared to juveniles in 2001/2002 ($P = 0.003$) and adult females were more closely related to each other compared to juveniles in 2002/2003 ($P = 0.004$).

Table 4 Average relatedness (*R*) among *Egernia whitii* at the Grassy Creek site in each season. Standard errors (SE) jackknifed over loci

	2001/2002			2002/2003		
	N	Ave. *R*	SE	*N*	Ave. *R*	SE
Overall	111	0.0083	0.0014	108	0.0053	0.0011
Males	53	0.0180	0.0045	52	0.0144	0.0038
Females	58	0.0060	0.0037	56	0.0033	0.0046
All adults	73	0.0076	0.0015	70	0.0051	0.0021
Adult males	36	0.0238	0.0079	35	0.0182	0.0069
Adult females	37	0.0045	0.0053	35	0.0047	0.0045
Juveniles	38	0.0026	0.0023	38	−0.0035	0.0017

Spatial structure

A significant relationship was detected between geographical and genetic distance for *E. whitii* at the Grassy Creek site. Results of the spatial autocorrelation analyses did not differ substantially between seasons therefore we only present the combined results from both seasons (Fig. 1). Except for the 140 m distance class where only 18 pairwise comparisons were possible, the minimum number of pairwise comparisons for other distance classes was 125. Positive spatial genetic structure was evident in *E. whitii* over shorter distances. At the 5 m distance class *rc* values were positive and significant at 5 m, 10 m, and 15 m, with an *x*-intercept of 55 m (Fig. 1A). At the larger distance class of 10 m, *rc* values were positive and significant at 10 m, 30 m and 40 m, but not at 20 m, with and *x*-intercept of 53 m (Fig. 1B).

Table 3 Relatedness between *Egernia whitii* breeding pairs and potential mates at the Grassy Creek site

			Breeding pairs			
Season	Sex	*N*	*R* ± SE	Range	Potential partners *R* ± SE	Potential partners within 20 m *R* ± SE
2001/2002	Male	19	0.087 ± 0.041	−0.160–0.549	−0.008 ± 0.010	0.011 ± 0.025
	Female	28	0.082 ± 0.041	−0.244–0.598	−0.004 ± 0.007	−0.019 ± 0.024
2002/2003	Male	20	0.024 ± 0.041	−0.244–0.499	−0.019 ± 0.006	0.022 ± 0.030
	Female	22	0.050 ± 0.042	−0.244–0.499	−0.015 ± 0.005	0.019 ± 0.023

Table 5 Average relatedness (*R*) among *Egernia whitii* individuals present within social groups at the Grassy Creek site during the 2001/2002 and 2002/2003 seasons. Standard errors (SE) jackknifed over loci are shown in parentheses. Twelve groups were stable in composition between seasons. Groups K and L were only present in the second season. NA indicates that this comparison was not available

Group	Year	All	Adults	AM	AF	J	Males	Females
A	Both	0.391 (0.034)	0.139 (0.231)	NA	NA	0.253 (0.253)	0.676 (0.195)	0.516 (0.065)
B	01/02	0.603 (0.092)	0.551 (0.014)	NA	0.543 (0.063)	0.689 (0.152)	NA	0.638 (0.099)
	02/03	0.662 (0.110)	0.551 (0.014)	NA	0.543 (0.063)	NA	NA	0.682 (0.076)
C	01/02	0.492 (0.170)	0.247 (0.250)	NA	NA	NA	NA	0.550 (0.125)
	02/03	0.278 (0.128)	0.247 (0.250)	NA	NA	0.111 (0.151)	0.106 (0.146)	0.550 (0.125)
D	Both	0.075 (0.085)	0.075 (0.085)	NA	0.400 (0.041)	NA	NA	0.400 (0.041)
E	01/02	0.198 (0.043)	−0.008 (0.15)	NA	NA	0.409 (0.251)	0.433 (0.017)	−0.053 (0.07)
	02/03	0.437 (0.015)	NA	NA	NA	NA	0.433 (0.017)	NA
F	01/02	0.278 (0.017)	−0.119 (0.02)	NA	NA	NA	NA	0.443 (0.016)
	02/03	−0.161 (0.03)	−0.131 (0.03)	NA	NA	NA	NA	−0.171 (0.02)
G	Both	−0.05 (0.151)	−0.048 (0.15)	NA	NA	NA	NA	NA
H	Both	0.306 (0.066)	0.410 (0.079)	NA	0.656 (0.074)	0.096 (0.106)	NA	0.345 (0.064)
I	01/02	0.377 (0.164)	0.170 (0.190)	NA	NA	NA	0.253 (0.195)	NA
	02/03	0.141 (0.073)	0.173 (0.193)	NA	NA	NA	0.253 (0.195)	−0.174 (0.03)
J	Both	0.117 (0.062)	−0.040 (0.14)	NA	NA	NA	0.411 (0.016)	NA
K	02/03	−0.025 (0.18)	−0.025 (0.18)	NA	NA	NA	NA	NA
L	02/03	0.062 (0.199)	0.062 (0.199)	NA	NA	NA	NA	NA
M	Both	−0.058 (0.18)	−0.058 (0.18)	NA	NA	NA	NA	NA
N	01/02	0.185 (0.060)	−0.062 (0.13)	NA	NA	NA	0.476 (0.091)	NA
	02/03	0.224 (0.075)	0.240 (0.151)	NA	NA	NA	0.331 (0.197)	NA
O	Both	0.060 (0.050)	0.060 (0.050)	0.051 (0.188)	0.413 (0.011)	NA	0.051 (0.188)	0.413 (0.011)
P	Both	0.029 (0.039)	0.029 (0.039)	NA	0.071 (0.162)	NA	NA	0.071 (0.162)
Q	01/02	0.391 (0.338)	NA	NA	NA	0.391 (0.338)	NA	0.391 (0.338)
	02/03	0.199 (0.035)	NA	NA	NA	0.199 (0.035)	NA	0.199 (0.035)
R	Both	−0.183 (0.04)	−0.183 (0.04)	NA	NA	NA	NA	NA
S	Both	0.195 (0.187)	0.195 (0.188)	NA	NA	NA	NA	NA
T	Both	0.141 (0.225)	0.141 (0.225)	NA	NA	NA	NA	NA
U	01/02	0.111 (0.041)	0.134 (0.072)	0.649 (0.267)	−0.182 (0.07)	− 0.07 (0.067)	0.116 (0.080)	0.030 (0.030)
	02/03	0.202 (0.051)	0.202 (0.051)	0.648 (0.269)	−0.160 (0.07)	NA	0.648 (0.269)	−0.160 (0.07)
V	01/02	0.256 (0.073)	0.205 (0.077)	NA	0.546 (0.128)	NA	0.535 (0.134)	0.546 (0.128)
	02/03	0.127 (0.044)	0.205 (0.077)	NA	0.546 (0.128)	NA	0.056 (0.147)	0.546 (0.128)
W	01/02	0.169 (0.098)	0.169 (0.098)	0.663 (0.209)	0.043 (0.042)	NA	0.663 (0.209)	0.044 (0.042)
	02/03	0.007 (0.051)	0.007 (0.051)	–0.187 (0.04)	0.099 (0.058)	NA	–0.187 (0.04)	0.099 (0.058)
X	Both	0.532 (0.188)	0.532 (0.188)	NA	0.594 (0.125)	NA	NA	0.594 (0.125)
01/02 within-group		0.221 (0.032)	0.117 (0.029)	0.422 (0.160)	0.352 (0.067)	0.321 (0.062)	0.390 (0.051)	0.376 (0.073)
between-group		−0.001 (0.002)	0.004 (0.002)	0.016 (0.005)	−0.001 (0.006)	−0.020 (0.007)	0.009 (0.008)	−0.002 (0.006)
02/03 within-group		0.162 (0.021)	0.117 (0.031)	0.217 (0.130)	0.352 (0.065)	0.132 (0.069)	0.323 (0.042)	0.298 (0.044)
between-group		−0.001 (0.001)	0.002 (0.002)	0.020 (0.007)	−0.003 (0.006)	−0.026 (0.005)	0.012 (0.006)	−0.001 (0.006)

At both size classes there is a gradual decline in *rc* values after about 50 m, with values becoming negative with increasing geographical distance (Fig. 1A, B). Figure 2A shows the overall genetic correlation *rc* for *E. whitii* at the site for increasing size classes. Values were generally high and significant between 5 and 10 m, with *rc* rapidly declining (but remaining significant) until the distance class of 100 m (Fig. 2A). This pattern of local positive spatial genetic structure was consistent between the sexes and for each age-sex class (Fig. 2A, C). Females exhibited a trend for stronger local positive structure over 10 m compared to males (Fig. 2B), as did adult females in relation to adult males (Fig. 2C), but neither difference was significant (error bars overlap). However, *rc* declined more rapidly in females and adult females compared to males between the 20 m and 50 m distance classes (Fig. 2B, C). Juveniles also displayed positive genetic structure up to 100 m compared to only 50 m in adults of either sex (Fig. 2C).

Sex-biased dispersal

There is no unequivocal evidence for sex-biased dispersal in *E. whitii*. Although (i) higher average relatedness (*R*) among males (all males and AM) compared to among females (all females and AF; Table 4) and (ii) females having a lower mean assignment index (*AIc*) compared to males (difference only significant in first season; Table 6) are suggestive of female-biased dispersal, the spatial autocorre-

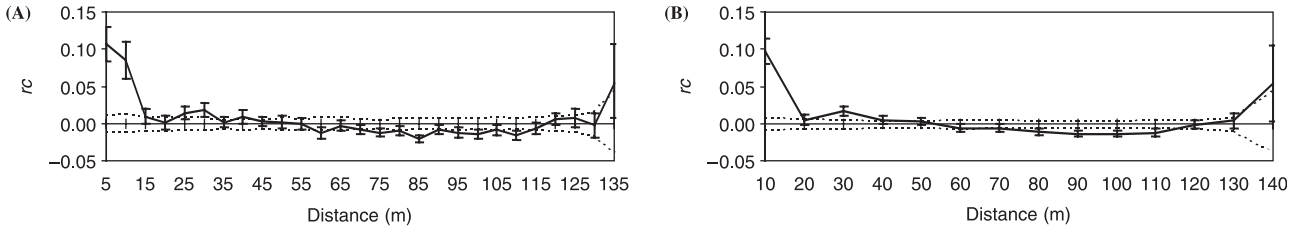

Fig. 1 Correlogram displaying the combined genetic correlation (*rc*) over both seasons for *E. whitii* at the Grassy Creek site as a function of distance. Dashed lines represent 95% confidence intervals about the null hypothesis of a random distribution of genotypes. Ninety-five percent (95%) confidence error bars about *rc* were determined by bootstrapping. Two distance classes are shown: (A) autocorrelation for distance classes of 5 m; and (B) autocorrelation for distance classes of 10 m. The maximum pairwise geographical distance was 135 m.

lation analyses revealed females exhibited a nonsignificant trend (95% CI bars overlap) for more local spatial genetic structure at 5 m and 10 m, with *rc* values declining rapidly after 20 m (Fig. 2B, C). This latter trend is consistent with a slight male-bias in dispersal. The lack of sex-specific differences in variance of *AIc* further supports the conclusion that no clear sex-bias dispersal patterns are evident in *E. whitii*, suggesting that both sexes are philopatric to some degree.

Discussion

Mating system

The combination of our extensive behavioural association data Chapple (2005) and our genetic data have provided significant insight into the mating system of *Egernia whitii*. Our data indicate that the mating system of *E. whitii* is characterized by both polygyny and monogamy. While polygyny was the most common mating strategy, within-season monogamous pairings accounted for a considerable proportion of litters produced in both seasons (35.7% and 45.4%). The composition of the majority of social groups at the site was stable between seasons, particularly for adult pairings Chapple (2005), but social and genetic monogamy was detected in both seasons for only five breeding pairs. This is in stark contrast to the situation present in the other members of the *Egernia* group where long-term genetic monogamy characterizes their mating systems (*Tiliqua rugosa*, Bull 2000; *Egernia cunninghami*, Stow & Sunnucks 2004a; *Egernia saxatilis*, O'Connor & Shine 2003;

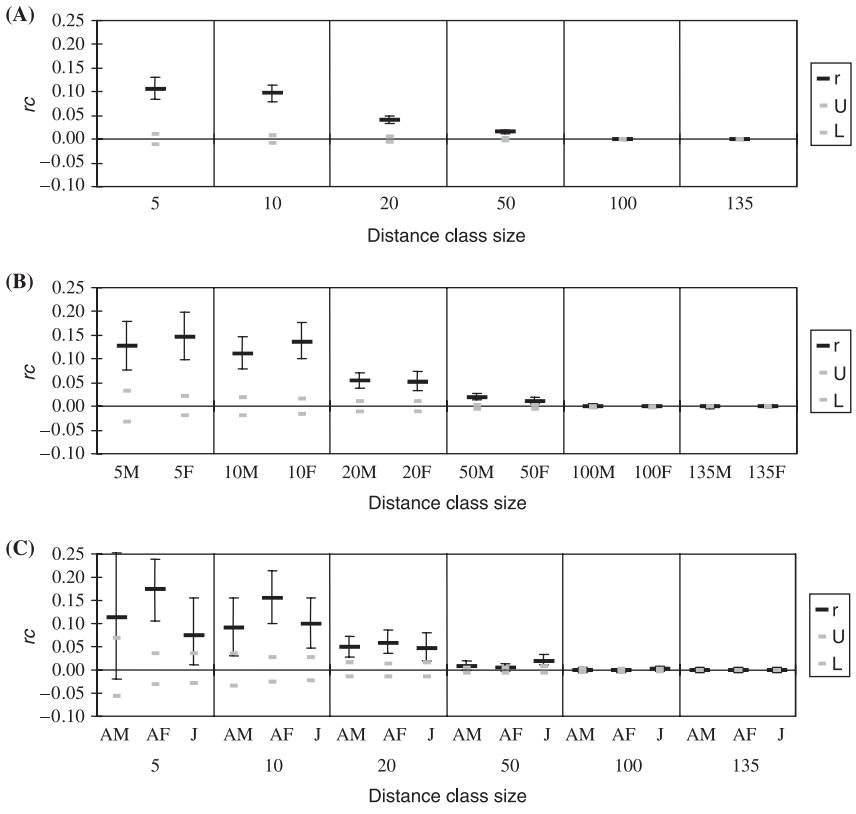

Fig. 2 Combined genetic correlation *rc* for *E. whitii* across both seasons for increasing distance class sizes. The grey bars indicate the 95% confidence intervals [Upper (U) and Lower (L)] about the null hypothesis of a random distribution of genotypes. Ninety-five percent (95%) confidence error bars around *rc* were determined via bootstrapping. (A) All individuals. (B) Comparison of males vs. females. (C) Comparison of adult males (AM) vs. adult females (AF) and juveniles (J). Note that the minimum number of pairwise comparisons is 28, except for AM at the 5-m distance class where there are only nine pairwise comparisons.

Year		*N* (M:F)	Mean *AIc*			Variance *AIc*		
			Male	Female	*P*	Male	Female	*P*
2001/2002	Overall	53:58	0.51497	−0.47058	0.0269	4.98250	5.40738	0.7598
	Adults	36:37	0.65263	−0.63499	0.0206	4.99170	5.37974	0.8273
2002/2003	Overall	52:56	0.39401	−0.36586	0.0804	4.25815	5.50758	0.4110
	Adults	35:35	0.36860	−0.36860	0. 1832	4.54637	5.43206	0.6502

Table 6 Results of mean assignment index (mean *AIc*) and variance of assignment index (variance *AIc*) tests for sex-biased dispersal for *Egernia whitii* at the Grassy Creek field site. Assignment indices were calculated in FSTAT 2.9.3 (Goudet 2001), with significance (*P*; two-tailed) assessed using randomization (10 000 permutations)

Egernia stokesii, Gardner *et al*. 2002). *E. whitii* exhibits social group structure that is comparable with other *Egernia* species, but its mating system appears to differ substantially.

Despite the small litter sizes of *E. whitii* in our study (1–4 offspring), multiple paternity was detected in 11.6% of litters consisting of two or more offspring. This is similar to the level of within-litter multiple paternity reported for *T. rugosa* (19%, Bull *et al*. 1998), *E. stokesii* (25%, Gardner *et al*. 2002), *E. saxatilis* (20%, O'Connor & Shine 2003) and *E. cunninghami* (2.6%, Stow & Sunnucks 2004a). The possibility exists in *Egernia* that a higher incidence of multiple paternity might be concealed by the presence of sperm precedence or competition (e.g. Olsson & Madsen 1998), but this remains to be investigated. Similarly, the rate of extra-group paternity found in *E. whitii* (16%) is consistent with that evident in *E. saxatilis* (7%, O'Connor & Shine 2003). However, such similarities mask substantial underlying disparities in the mating system of *E. whitii*. Most notably, males that engaged in extra-group copulations generally fathered the entire litters of extra-group females, rather than contributing to a litter with multiple fathers. This may provide an explanation for the high proportion of *E. whitii* juveniles at the study site that live in aggregations with only one parent Chapple (2005). The composition of social groupings at the study site also influenced the mating system of *E. whitii*. Six social groups consisted of a single AM with two or more AF (Table 1). In such groups polygyny was the predominant reproductive strategy, with males generally fathering the entire litters of all resident females. Although such polygynous social groups have been reported in *E. saxatilis* (O'Connor & Shine 2003) and *E. stokesii* (Gardner *et al*. 2002), they occur extremely rare.

The tendency for adult male *E. whitii* to mate with all adult females within their social group was reflected in our data indicating that males have more partners within a season compared to females (Table 2). This may partly explain why *E. whitii* did not appear to actively select mates that were more unrelated compared to other potential mates within close proximity. Previous reports that *T. rugosa* (Bull & Cooper 1999), *E. cunninghami* (Stow & Sunnucks 2004b) and *E. stokesii* (Gardner *et al*. 2001) preferentially chose mates which are more distantly related compared to other potential mates within the same group or home range have generally been interpreted as an inbreeding avoidance mechanism (e.g. Pusey & Wolf 1996). The capacity for many *Egernia* species to recognize close relatives and group members presumably facilitates such inbreeding avoidance (Bull *et al*. 2000, 2001). Intriguingly, such kin-recognition abilities have the capacity to drastically alter predictions regarding sex-biased dispersal and may promote a male-bias (Lehmann & Perrin 2003), potentially explaining the presence of male-biased dispersal in *E. cunninghami* (in fragmented habitats) and *E. stokesii* (Gardner *et al*. 2001; Stow *et al*. 2001).

Levels of within-group relatedness observed in *E. whitii* appear to be comparable to that documented in *E. stokesii* (Gardner *et al*. 2001) and *E. cunninghami* (Stow *et al*. 2001) aggregations. Consequently, *E. whitii* might have been expected to choose breeding partners that were less related than other potential mates (e.g. Gardner *et al*. 2001; Stow & Sunnucks 2004b). However, excluding the breeding pairs within group B, mating pairs were not found to be more related compared to other potential mates. Indeed, most of the breeding pairs (78% with pairwise $R < 0.2$) were less related than that expected for half-siblings (i.e. 0.25). In lizards, inbreeding resulting from mating between siblings might be evidenced via high incidences of malformed offspring (e.g. Olsson *et al*. 1996). Apart from one juvenile that was stillborn, birth deformities were not evident in the 135 *E. whitii* offspring born in the laboratory. Consequently, the avoidance of mating with close relatives may be sufficient to enable *E. whitii* to avoid inbreeding.

We identified several factors that may restrict the occurrence of monogamy within *E. whitii*. Mate guarding has been implicated as playing an important role in promoting monogamy in *T. rugosa*, with males potentially constrained from engaging in polygyny because of an inability to defend multiple females (Bull 2000). However, in our study male *E. whitii* appeared to have little difficulty mating with the majority of females within their social group. Mate guarding is also unlikely in *E. whitii* as social groups are present year round, with all members seemingly cooperating to defend the group territory Chapple (2005). Female *E. whitii*, as in other *Egernia* species, appear to gain benefits from prolonged pairings with males (e.g. Gowaty 1996), which may provide some explanation for the existence of

several monogamous pairings at our study site. For instance, *E. whitii* in groups might benefit from enhanced vigilance against predators Chapple (2005). In addition, the availability of mates (e.g. Whiteman & Cote 2004) did not appear to be a restricting factor in *E. whitii* as there was an even adult sex ratio at our study site Chapple (2005). Virtually all males that were assigned paternity were resident within a social group, and females were more likely to be part of a group than males (97% versus 76%; Chapple (2005)), so solitary males might experience restricted access to females. These factors may explain the presence of both polygyny and monogamy in *E. whitii*.

Our study indicates that a diverse range of mating systems might exist within members of the *Egernia* group. Although there has only been detailed examination of the mating system of five species, three distinct mating systems already are evident: (i) combination of polygyny and within-season monogamy (*E. whitii*, present study); (ii) long-term genetically monogamous pairings during the breeding season (*T. rugosa*, Bull 2000); and (iii) long-term genetic monogamy within temporally stable social aggregations (*E. stokesii*, Gardner *et al*. 2002; *E. saxatilis*, O'Connor & Shine 2003; *E. cunninghami*, Stow & Sunnucks 2004a). Such diversity in mating systems within the *Egernia* group provides exciting opportunities to examine the putative factors responsible for promoting monogamy in the absence of biparental care.

Spatial structure and dispersal patterns

Two lines of evidence support our previous conclusions Chapple (2005) that *E. whitii* social aggregations are comprised of closely related individuals. First, individuals within groups were significantly more closely related compared to individuals from other social groups (Table 5). Second, our spatial autocorrelation analyses revealed significant positive autocorrelation for distances up to 50 m (Figs 1 and 2), indicating restricted dispersal over shorter distances. Our data relating the composition of *E. whitii* social groups demonstrates that individuals of both sexes sometimes remain within their natal group for substantial periods of time Chapple (2005). However, the absence of significant discrepancies in the variance of *AIc* values between the sexes indicates that both sexes disperse to some degree (e.g. Mossman & Waser 1999).

Our analyses were unable to reveal any clear and consistent patterns of sex-biased dispersal in *E. whitii*. The mean *AIc* test (only first season) and relatedness estimates suggested female-biased dispersal, the spatial autocorrelation analyses indicated a slight trend for male-biased dispersal, while the variance *AIc* test failed to detect any significant sex-specific differences. Taken together, these results indicate that there is no unambiguous evidence for sex-biased dispersal in *E. whitii*. Perhaps this is not surprising considering that we documented both polygyny (conducive to a male-bias) and monogamy (conducive to a female-bias) in this species. Consequently, it is plausible that the lack of consistent patterns with regard to sex-biased dispersal is the result of two mating systems (with opposing dispersal outcomes) co-occurring in *E. whitii*.

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References

Austin JD, Davila JE, Lougheed SC, Boag PT (2003) Genetic evidence for female-biased dispersal in the bullfrog, *Rana catesbeiana* (Ranidae). *Molecular Ecology*, **12**, 3165–3172.

Bennett PM, Owens IPF (2002) *Evolutionary Ecology of Birds*. Oxford University Press, Oxford.

Bull CM (2000) Monogamy in lizards. *Behavioural Processes*, **51**, 7–20.

Bull CM, Cooper SJB (1999) Relatedness and avoidance of inbreeding in the lizard, *Tiliqua rugosa*. *Behavioral Ecology and Sociobiology*, **46**, 367–372.

Bull CM, Cooper SJB, Baghurst BC (1998) Social monogamy and extra-pair fertilization in an Australian lizard, *Tiliqua rugosa*. *Behavioral Ecology and Sociobiology*, **44**, 63–72.

Bull CM, Griffin CL, Bonnett M, Gardner MG, Cooper JB (2001) Discrimination between related and unrelated individuals in the Australian lizard *Egernia striolata*. *Behavioral Ecology and Sociobiology*, **50**, 173–179.

Bull CM, Griffin CL, Lanham EJ, Johnston GR (2000) Recognition of pheromones from group members in a gregarious lizard, *Egernia stokesii*. *Journal of Herpetology*, **34**, 92–99.

Chapple DG (2003) Ecology, life history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs*, **17**, 145–180.

Chapple DG (2005) Evolutionary ecology and molecular phylogenetics of the *Egernia whitii* (Lacertilia: Scincidae) species group. PhD Thesis. Australian National Univesity, Canberra, Australia.

Clutton-Brock T (1991) *The Evolution of Parental Care*. Princeton University Press, Princeton, New Jersey.

Dobson FS (1982) Competition for mates and predominant male dispersal in mammals. *Animal Behaviour*, **30**, 1183–1192.

Doughty P, Sinervo B, Burghardt GM (1994) Sex-biased dispersal in a polygynous lizard, *Uta stansburiana*. *Animal Behaviour*, **47**, 227–229.

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 214–223.

Favre L, Balloux F, Goudet J, Perrin N (1997) Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **264**, 127–132.

Gardner MG, Bull CM, Cooper SJB (2002) High levels of genetic monogamy in the group-living Australian lizard, *Egernia stokesii*. *Molecular Ecology*, **11**, 1787–1794.

Gardner MG, Bull CM, Cooper SJB, Duffield GA (2000) Microsatellite mutations in litters of the Australian lizard *Egernia stokesii*. *Journal of Evolutionary Biology*, **13**, 541–550.

Gardner MG, Bull CM, Cooper SJB, Duffield GA (2001) Genetic evidence for a family structure in stable social aggregations of the Australian lizard *Egernia stokesii*. *Molecular Ecology*, **10**, 175–183.

Gardner MG, Cooper SJB, Bull CM, Grant WN (1999) Isolation of microsatellite loci from a social lizard, *Egernia stokesii*, using a modified enrichment procedure. *Journal of Heredity*, **90**, 301–304.

Goodnight KF, Queller DC (1998) *RELATEDNESS 5.08*. Available at http://www.gsoftnet.us/GSoft.html.

Goudet J (2001) *FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3)*. Available at http://www.unil.ch/izea/softwares/fstat.html.

Goudet J, Perrin N, Waser P (2002) Tests for sex-biased dispersal using biparentally inherited genetic markers. *Molecular Ecology*, **11**, 1103–1114.

Gowaty PA (1996) Battle of the sexes and origins of monogamy. In: *Partnerships in Birds: The Study of Monogamy* (ed. Black JM), pp. 21–52. Oxford University Press, Oxford.

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.

Greer AE (1989) *The Biology and Evolution of Australian Lizards*. Surrey Beatty and Sons, Sydney.

Griffith SC, Owens IPF, Thuman KA (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, **11**, 2195–2212.

Hughes C (1998) Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology*, **79**, 383–399.

Jadwiszczak P (2003) *RUNDOM Projects 2.0 LITE*. Available at http://pjadw.tripod.com.

Koenig WD, Van Vuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution*, **11**, 514–517.

Komers PE, Brotherton PNM (1997) Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **264**, 1261–1270.

Lehmann L, Perrin N (2003) Inbreeding avoidance through kin recognition: choosy females boost male dispersal. *American Naturalist*, **162**, 638–652.

Marshall TC, Slate J, Kruuk L, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, **7**, 639–655.

Mathews LM (2002) Territorial cooperation and social monogamy: factors affecting intersexual behaviours in pair-living snapping shrimp. *Animal Behaviour*, **63**, 767–777.

Mossman CA, Waser PM (1999) Genetic detection of sex-biased dispersal. *Molecular Ecology*, **8**, 1063–1067.

O'Connor D, Shine R (2003) Lizards in 'nuclear families': a novel reptilian social system in *Egernia saxatilis* (Scincidae). *Molecular Ecology*, **12**, 743–752.

O'Connor D, Shine R (2004) Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). *Animal Behaviour*, **68**, 1361–1369.

Olsson M, Gullberg A, Tegelstrom H (1996) Malformed offspring, sibling matings, and selection against inbreeding in the sand lizard (*Lacerta agilis*). *Journal of Evolutionary Biology*, **9**, 229–242.

Olsson M, Madsen T (1998) Sexual selection and sperm competition in reptiles. In: *Sperm Competition and Sexual Selection* (eds Birkhead TR, Moller AP), pp. 503–577. Academic Press, Cambridge.

Olsson M, Shine R (1998) Chemosensory mate recognition may facilitate prolonged mate guarding by male snow skinks, *Niveoscincus microlepidotus*. *Behavioral Ecology and Sociobiology*, **43**, 359–363.

Olsson M, Shine R (2003) Female-biased natal and breeding dispersal in an alpine lizard, *Niveoscincus microlepidotus*. *Biological Journal of the Linnean Society*, **79**, 277–283.

Parker GA (1974) Courtship persistence and female guarding as male time investment strategies. *Behaviour*, **48**, 157–184.

Peakall R, Ruibal M, Lindemayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution*, **57**, 1182–1195.

Peakall R, Smouse PE (2001) *GENALEX Version 5: genetic analysis in Excel. Population genetic software for teaching and research*. Australian National University, Canberra. Available at http://www.anu.edu.au/BoZo/GenAlEx.

Peakall R, Smouse PE, Huff DR (1995) Evolutionary implications of allozyme and RAPD variation in diploid populations of diocecious Buffalograss *Buchloe dactyloides*. *Molecular Ecology*, **4**, 135–147.

Perrin N, Mazalov V (2000) Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist*, **155**, 116–127.

Prugnolle F, De Meeus T (2002) Inferring sex-biased dispersal from population genetic tools: a review. *Heredity*, **88**, 161–165.

Pusey A (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution*, **2**, 295–299.

Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends in Ecology and Evolution*, **11**, 201–206.

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.

Rassman K, Tautz D, Trillmich F, Gliddon C (1997) The microevolution of the Galapagos marine iguana *Amblyrhynchus cristatus* assessed by nuclear and mitochondrial genetic analyses. *Molecular Ecology*, **6**, 437–452.

Shine R (1988) Parental Care in Reptiles. In: *Biology of the Reptilia* (eds Gans C, Huey RB), pp. 275–329. Alan R. Liss, New York.

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. *Heredity*, **82**, 561–573.

Stamps JA (1983) Sexual selection, sexual dimorphism, and territoriality. In: *Lizard Ecology: Studies of a Model Organism* (eds Huey RB, Pianka ER, Schoener TW), pp. 169–204. Harvard University Press, Cambridge.

Stow AJ, Sunnucks P (2004a) High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology*, **13**, 419–430.

Stow AJ, Sunnucks P (2004b) Inbreeding avoidance in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology*, **13**, 443–447.

Stow AJ, Sunnucks P, Briscoe DA, Gardner MG (2001) The impact of habitat fragmentation on dispersal of Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. *Molecular Ecology*, **10**, 867–878.

Taylor MI, Morley JI, Rico C, Balshine S (2003) Evidence for genetic monogamy and female-biased dispersal in the biparental care mouthbrooding cichlid *Eretmodus cyanostictus* from Lake Tanganyika. *Molecular Ecology*, **12**, 3173–3177.

Toxopeus AG, Kruijt JP, Hillenius D (1988) Pair-bonding in chameleons. *Naturwissenschaften*, **75**, 268–269.

Whiteman EA, Cote IM (2004) Monogamy in marine fishes. *Biological Reviews*, **79**, 351–375.

Wilson S, Swan G (2003) *A Complete Guide to Reptiles of Australia*. Reed New Holland, Sydney.

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