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Clustering of related individuals in a population of the Australian lizard, *Egernia frerei*

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Abstract

Stable social aggregations are rarely recorded in lizards, but have now been reported from several species in the Australian scincid genus *Egernia*. Most of those examples come from species using rock crevice refuges that are relatively easy to observe. But for many other *Egernia* species that occupy different habitats and are more secretive, it is hard to gather the observational data needed to deduce their social structure. Therefore, we used genotypes at six polymorphic microsatellite DNA loci of 229 individuals of *Egernia frerei*, trapped in 22 sampling sites over 3500 ha of eucalypt forest on Fraser Island, Australia. Each sampling site contained 15 trap locations in a 100 × 50 m grid. We estimated relatedness among pairs of individuals and found that relatedness was higher within than between sites. Relatedness of females within sites was higher than relatedness of males, and was higher than relatedness between males and females. Within sites we found that juvenile lizards were highly related to other juveniles and to adults trapped at the same location, or at adjacent locations, but relatedness decreased with increasing trap separation. We interpreted the results as suggesting high natal philopatry among juvenile lizards and adult females. This result is consistent with stable family group structure previously reported in rock dwelling *Egernia* species, and suggests that social behaviour in this genus is not habitat driven.

Keywords: Australia, *Egernia*, lizards, philopatry, relatedness, social group

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Introduction

Philopatry should be favoured in social vertebrates because of the advantages derived from cooperation among kin (Lambin *et al*. 2001). Thus, in species where behaviour is difficult to observe, a pattern of nonrandom association among related individuals in a population might be a first indicator of cohesive social aggregations. Queller & Goodnight (1989) described a technique to estimate relatedness among pairs of individuals with known genotypes at highly variable microsatellite loci. This technique has clarified many studies of kin-related behaviour and allowed the identification of genetic parents, siblings, and other levels of relatedness that could previously only be inferred from behavioural observations.

Inferences about social behaviour based on observation alone can be misleading even in well-studied species. For example, genetic analysis has showed that extra-pair fertilization is common among socially monogamous birds (Birkhead & Møller 1992). Other recent studies that have used genetic analysis to clarify observations of social behaviour have demonstrated that immigrants into cooperative breeding groups of crows were actually related to group members (Baglione *et al*. 2003). In another example, banner-tailed kangaroo rats were found to make normally unobserved reproductive forays over several home ranges, reducing the incidence of mating with closely related neighbours (Winters & Waser 2003). Thus, social interactions that would not be suspected from visual observation can be inferred from genetic data. In particular, genetic analysis can provide important clues about social structure in populations.

Studies of social systems in lizards have lagged behind those of other vertebrate groups, because of the secretive

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nature of many lizard species, and because many lizard species spend much of their active time basking and little time in social activity. Some species with obvious visual displays among agamid and iguanid lizard groups have polygynous mating systems, with dominant males defending territories that might contain home ranges of one or more females (Fox *et al*. 2003). The social and mating systems of the many more secretive lizard species have remained elusive, although some recent observational studies have suggested alternative social structures. For example, long-term monogamous partnerships have been reported in the sleepy lizard, *Tiliqua rugosa* (Bull 1988, 2000; Bull *et al*. 1998) and the chameleon, *Chamaeleo hoehnelii* (Toxopeus *et al*. 1988). Long-term stable aggregations have been reported in the gidgee skink, *Egernia stokesii* (Duffield & Bull 2002), and the land mullet, *Egernia major* (Klingenböck *et al*. 2000; Osterwalder *et al*. 2004).

As in other taxa, the advent of techniques to characterize genotypes at variable microsatellite loci, and to estimate relatedness among individuals, has allowed new opportunities to explore social behaviour in lizards. Debate about the evolution of social behaviour has been dominated by examples from mammals and birds. Examples from lizards should provide a fresh phylogenetic perspective to these questions, but the first step is to characterize the social systems among lizard species.

Of particular interest in this debate is the Australian scincid genus, *Egernia*, in which 23 of the 30 described species have been reported, largely from anecdotes, to form social aggregations (Gardner 2000; Chapple 2003). Why has group dwelling become the predominant social structure in this taxon, while it is apparently uncommon among most other lizard species? An independent molecular phylogeny (Donnellan, personal communication) shows that the genus *Egernia* is a speciose clade with both social and nonsocial species, which is nested within related and predominantly nonsocial scincid lizard taxa. Within this context, questions about the origin of sociality in this taxon can be addressed and related to the hypotheses derived for other taxonomic groups.

A preliminary step is the rigorous assessment of the social structures in a representative sample of species. Genetic analyses of three rock-crevice-dwelling species, *E. stokesii* (Gardner *et al*. 2001, 2002), *Egernia saxatilis* (O'Connor & Shine 2003), and *Egernia cunninghami* (Stow *et al*. 2001; Stow & Sunnucks 2004) have shown stable social groups containing monogamous breeding partners with one or more cohorts of their offspring. In the species that occupy rock crevices, social behaviour may have evolved from a shortage of suitable refuges for dispersing juveniles (Duffield & Bull 2002). For other species, particularly those occupying other habitat types, such as the sand burrowers, the social structure has been described mainly from anecdotes and from incidental observations that individuals are sometimes found together (Chapple 2003). For five species, including *Egernia frerei*, there are no recorded observations to indicate if they do or do not aggregate.

E. frerei, the major skink, is a large scincid lizard (snout-to-vent length *c*. 180 mm) distributed along coastal areas of northeast Australia and in southern New Guinea, occupying well-watered forested country or seasonally dry woodland (Cogger 1992; Wilson & Swan 2003). Little is known of its behaviour except that it shelters in hollow logs, cavities of root systems in fallen trees, or in burrows under large rocks (Wilson & Knowles 1988). The present study considers a population on the large sand island, Fraser Island, where *E. frerei* refuges in burrow systems, possibly dug by native rats, or under fallen logs (Cooper 2002; Murray, personal observation). On this island, live young of *E. frerei* are born in January, but there are no records of the timing of any dispersal phase.

For secretive species like *E. frerei*, it is hard to make the non-destructive long-term observations needed to describe social structure. In this study we used genetic analyses instead to make inferences about the social structure of one population of this species.

Methods

Study site

The study was conducted in a 3500-ha area of dry sclerophyll forest, dominated by mixed eucalypt trees (Stanton 1979) on the southeastern section of Fraser Island, within 15 km of the township of Eurong (25°31′S, 153°09′E). We chose 22 sampling sites, each a 50 m × 100 m block at least 50 m from any road or walking track, and an average 680 m (range 220–1200 m) from any other sampling site. All sites were situated on a southerly aspect on similar aged dune systems, but had experienced fire regimes of varying frequency and recency (last fire 1.5–7 years ago). The most northern site and most southern site were within 15.5 km of each other.

At each sampling site, 15 trap locations were established in three rows of five locations per row, each 25 m apart, making a 50 m × 100 m trapping grid. Diagonally adjacent trap locations in the grid were 35.5 m apart. At each trap location, two adjacent Elliot traps were baited with a mixture of peanut butter, rolled oats, and honey, making a total of 30 traps per site.

Traps were opened during daylight hours for a total of 22 days in November 2002 (10 days) and February 2003 (12 days). The sampling times spanned the spring and summer when lizards are likely to be most active, and when any dispersal is most likely to have occurred. Adult lizards were sexed by eversion of the hemipenes in males in February, but not all adults were tested by this method in the November sample. Snout-to-vent length (SVL) was measured, and a blood sample was taken from the caudal vein for DNA analysis. Each lizard was marked by a unique toe clip and the toe clips were also retained as backup for DNA analysis. From SVL histograms, four age-size categories were determined: adults (> 155 mm), subadults (115–155 mm), juveniles from spring/summer 2002 (85–115 mm), and newborns from spring/summer 2003 (< 85 mm). Newborn lizards were only recorded in the February sampling.

Microsatellite DNA

DNA was extracted from blood stored on FTA paper according to the processing method for nucleated erythrocytes given in Burgoyne *et al*. (1994). For those individuals from which blood was not obtained, DNA was extracted from toe clips stored in 70% ethanol using the salt extraction methodology of Miller *et al*. (1988).

Individuals were genotyped for six microsatellite loci: four tetranucleotide loci $(AAAG)_n$ developed from *Egernia stokesii* (*Est1*, *Est2*, *Est4*, *Est9*, Gardner *et al*. 1999) and two dinucleotide loci $(CA)_n$ (*Tr5.21*) and $(TC)_n(CA)_n$ (*Tr5.20*) cloned from *Tiliqua rugosa* (Cooper *et al*. 1997). Polymerase chain reaction (PCR) amplification was performed according to conditions outlined in Gardner *et al*. (2000). Negative controls (only sterile water and PCR reagents) were included in each PCR run. Following verification of PCR amplification (visualized using agarose gels stained with ethidium bromide), PCR products of all six loci were mixed together in equal proportions and run on standard microsatellite gels on an Applied Biosystems 377 automated sequencer. Fluorescent labelling of the loci was as follows: *Est1*-HEX, *Est2*-FAM, *Est4*-HEX, *Est9*-TET, *Tr5.20*-TET, *Tr5.21*-HEX. A standard ladder sample marked with GS2500ROX (ABI) fluorescent dye was run with each sample, allowing accurate sizing of alleles and comparison between gels. Results were analysed with GENESCAN software (Applied Biosystems).

Relatedness estimation and other estimators

The CERVUS program version 2.0 (Marshall *et al*. 1998) was used to estimate the probability of null alleles at each locus and to provide allele frequency and heterozygosity data.

Loci were examined for nonconformation to Hardy–Weinberg equilibrium (HWE) and for pairwise tests of linkage disequilibrium (LD) between loci using GENEPOP version 3.3 (Raymond & Rousset 1995). Probabilities of significance were computed through the Markov chain method (Guo & Thompson 1992) using 100 batches and 1000 iterations per batch as implemented in GENEPOP. Levels of significance were Bonferroni corrected for multiple tests (Rice 1989).

Pairwise relatedness and average relatedness were estimated using the program RELATEDNESS 5.04 (Goodnight & Queller 1998). This program calculates an index of relatedness (*R*), a relative measure that is calibrated by the frequency of alleles and number of individuals in a population of interest. In this study, relatedness values were calculated with respect to allele frequencies derived from the entire sample (229) of genotyped lizards. Standard errors of *R* estimates were obtained by jackknifing over the six loci (Queller & Goodnight 1989). The relatedness estimates for various age and sex classes, within and among the 22 sites, were compared by jackknifing over the unpaired *R* difference using RELATEDNESS. The significance of the difference between any two relatedness values was calculated using a jackknife resampling technique (over loci) followed by a standard *t*-table routine [robust to deviations from normality (Zar 1974)]. When comparing among sites data were weighted by site to adjust for potential biases resulting from different numbers of individuals at each site.

Results

The lizards sampled

Over the 22 trapping days there were 272 lizard captures (87 in November; 185 in February), with an average 12.4 captures per day (range 4–38). Of 229 individual lizards, the sample included 154 adults, 43 subadults, 16 juveniles and 16 newborns. It was possible to sex 112 adults and subadults, of which 48 were males and 64 were females.

Of the 43 recaptures, 29 (67.4%) were lizards that had been first caught in November and then recaptured in February, and 28 of those were adult or subadult lizards. Of the recaptures between trips, 22 (75.9%) were captured at the same trap location, while 26 (89.7%) were at the same or an adjacent trap location within the same site. No individual lizard was trapped at more than one site. Individual sites yielded an average 10.4 different captured lizards (range 5–22) with 15 sites having eight or more different lizards sampled.

Genotypes

Within the sample, the six microsatellite loci had a mean of 14.2 alleles per locus and an average heterozygosity of 0.66 (SE 0.22) (Table 1). Considering only adults lizards, five loci conformed to the expectations of HWE. Only locus *Est2* deviated significantly ($P < 0.001$) as a result of an excess of homozygote genotypes, suggesting either null alleles or short allele dominance. Using CERVUS, we estimated a frequency of 0.08 for null alleles at this locus, a low frequency confirmed by the absence of any null allele homozygotes in the sample. Given the high polymorphic information from this locus we retained it in our analyses. No significant LD was detected ($P > 0.01$ in all cases) among any pair of loci.

Table 1 Number of alleles observed in the *n* individual *Egernia frerei* sampled, and observed and expected heterozygosity for the six microsatellite loci

Locus	No. of alleles	*n*	Heterozygosity Observed	Heterozygosity Expected
Est1	30	225	0.804	0.935
Est2	18	229	0.764	0.912
Est4	4	225	0.280	0.261
Est9	20	228	0.803	0.904
Tr5.20	6	229	0.489	0.485
Tr5.21	7	224	0.799	0.754

Table 2 Average relatedness (*R*) among *n* lizards for all sampling sites

	Average *R*	SE (jackknifed over loci)	*n*
All lizards	0.0100	0.0061	229
Adult females	0.0110	0.0159	59
Adult males	0.0269	0.0217	42
Young (subadults + juveniles + newborns)	0.0276	0.0176	76

Values for adult females and adult males are derived just from the 185 total lizards sampled in February, when sexes could be reliably determined. Other values come from the 229 total lizards sampled over both trips.

Relatedness estimates

Table 2 shows the average relatedness (*R*) among groups of lizards over all sampling sites combined. Data from the February trip, when sexes were determined, showed no significant effect of age or sex class over the total study area. Relatedness among adult females was not significantly different from relatedness among adult males ($P = 0.18$), or from relatedness among younger lizards ($P = 0.12$) and relatedness among adult males did not differ significantly from relatedness among younger lizards ($P = 0.95$).

Table 3 shows the average *R* among groups of lizards from within each site. The overall average relatedness among lizards sampled from the same site was significantly greater than among lizards sampled from different sites, whether considering all lizards ($P < 0.0001$), adults and subadults ($P < 0.0001$), adults ($P = 0.0009$), subadults, juveniles and newborns ($P = 0.0002$), or juveniles and newborns ($P = 0.0004$). The average relatedness of adult females from within the same site was significantly greater than that among adult females from different sites ($P = 0.0021$), while there was no significant difference among adult males within and among sites ($P = 0.4909$).

Among the 15 sites where there were eight or more lizards sampled, there were 54 trap locations where more than one individual lizard was trapped. From this sample, the average relatedness of lizards captured at a single trap location was 0.1500 (SE = 0.0388). The data were partitioned into pairwise comparisons of relatedness between young, adults and young, and adults trapped within the same trap, adjacent traps (25–35.5 m apart), and distant traps within the same site (50–110 m apart). Results from this analysis revealed that young lizards were more related to other young and to adults captured at the same trap or an adjacent trap, than to lizards trapped greater distances apart within a site (Fig. 1).

When all adults were combined, they did not show similar spatial patterns of relatedness (Fig. 1). However, when adult males and females were considered separately (Fig. 2), relatedness among pairs of females from the same trap location was higher than that of females from adjacent or distant traps within sites. Relatedness among pairs of males within a site was lower than that of females, and was not related to how far apart they were captured (Fig. 2).

Table 3 Average relatedness among lizards from within each site and among lizards from different sites

	Within site Average *R*	Within site SE (jackknifed over loci)	Within site *n*	Between site Average *R*	Between site SE (jackknifed over loci)	Between site *n*
All lizards	0.0766	0.0142	229	0.0070	0.0059	229
Adults & subadults	0.0664	0.0148	197	0.0022	0.0059	197
Adults	0.0579	0.0207	153	−0.0015	0.0014	153
Young (subadults, juveniles & newborns)	0.1143	0.0297	73	0.0233	0.0174	76
Juveniles & newborns	0.2109	0.0636	23	0.0317	0.0307	32
Adult females	0.1142	0.0484	55	0.0073	0.0161	59
Adult males	0.0419	0.0477	35	0.0263	0.0228	42

Values are derived as for Table 2.

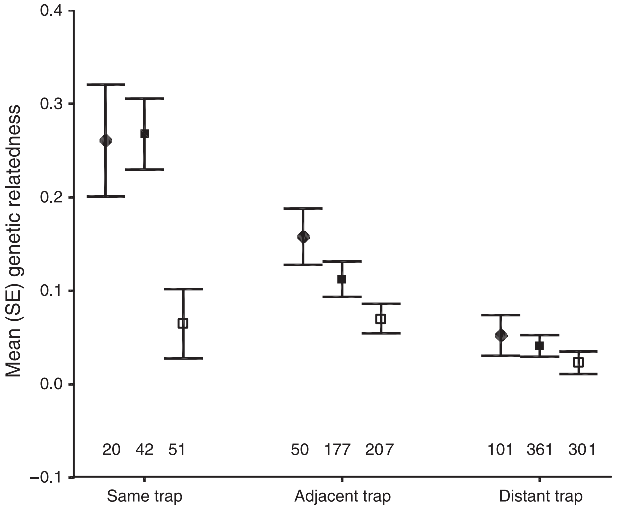

Fig. 1 Mean relatedness (±1 SE) between all pairs of young (closed circles), adults and young (closed squares), and adults (open squares) trapped within the same trap location, adjacent traps (25–35.5 m apart) and distant traps (50–110 m apart) within the same site. Number of pairs indicated along *x*-axis.

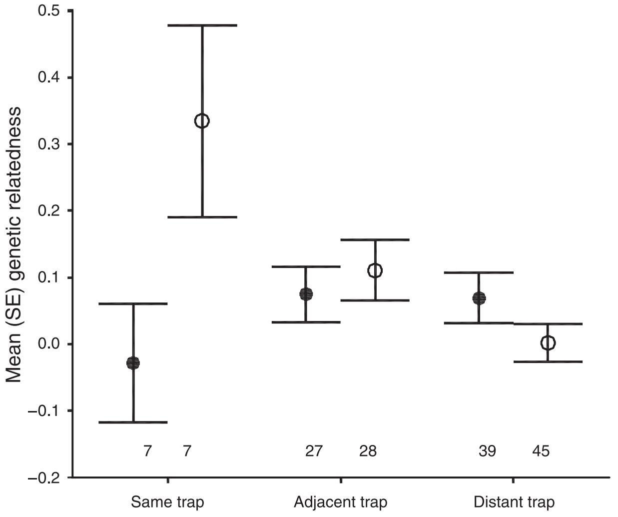

Fig. 2 Mean relatedness (±1 SE) between all pairs of adult males closed circles) and adults females (open circles) trapped within the same trap location, adjacent traps (25–35.5 m apart) and distant traps (50–110 m apart) within the same site. Number of pairs indicated along *x*-axis.

Discussion

Three sets of data from this study suggested that individuals of *Egernia frerei* show site fidelity. (i) Recaptures were usually at the same or adjacent trap locations over a 3-month period, suggesting little short-term dispersal. (ii) There was significantly higher relatedness within sites than among sites, for all categories of lizards except adult males. Lizards were more closely related to each other when they were found in closer proximity. (iii) Within sampling sites, levels of relatedness declined with distance between trap locations. This was a particularly strong trend among pairs of young lizards (from newborns to subadults), among pairs of adults and young, and among adult females.

Both of the trends in relatedness suggest natal philopatry leading to aggregations of related individuals. The results were consistent with successive cohorts of young staying together within the home range of their parents. This very fine scale of genetic differentiation among groups of related lizards has also been reported in *Egernia stokesii* where genetically distinct groups occur within 25 m of each other (Gardner *et al*. 2001).

The data also suggest sex-biased dispersal, with females remaining with relatives even as adults. Males are more likely to disperse than females, because males within a site and within a trap location tend to be less closely related to each other than females are.

While these results do not in themselves indicate any level of social organization, kin competition should select for enhanced dispersal unless it was balanced by some advantage from collaboration among kin (Perrin & Goudet 2001). Some advantages of group living, such as enhanced vigilance and indirect protection of juveniles against possible predators, have already been demonstrated in *E. stokesii* (Lanham & Bull 2004) and *Egernia saxatilis* (O'Connor & Shine 2004). Other potential benefits for animals that live in small social groups include access to food and refuge resources for juveniles in the parental territory, and the opportunity for subadults to inherit the territory (Komdeur & Hatchwell 1999). Individuals in stable groups may take less time to locate a partner (Rasa 1997), and may share parental care of young (Heinsohn *et al*. 2000). Lizards in social groups may reduce heat loss by close contact (Elfström & Zucker 1999) and cooperate in ecto-parasite removal (Wikelski 1999).

Cohesion among related individuals has been suggested as a basis for social group formation in other *Egernia* species that form stable aggregations. *Egernia stokesii* respond differently to signals from group members and nongroup members (Bull *et al*. 2000), and *Egernia striolata* increase their levels of aggression to more distantly related intruder lizards (Bull *et al*. 2001). None of these aspects of social structuring have yet been investigated in *E. frerei*, but the apparent family group associations suggest a social structure and possible collaboration within groups in this population.

In summary, results of the present study are consistent with natal philopatry, and with low dispersal of young lizards up to the subadult stage for males, and up to adult stages for females. Age to maturity is unknown for *E. frerei*, but of *E. stokesii*, a smaller species, can take up to 5 years (Duffield & Bull 2002). This suggests that family groups in *E. frerei* will be stable over multiple years. Reduced relatedness among adults suggests some dispersal after maturity, and the higher relatedness of females than of males within a site, suggests that the dispersal may also be male-biased.

Previous detailed studies of the social systems in *Egernia* species have focused on rock-crevice-dwelling species (*E. stokesii*, Gardner *et al*. 2001, 2002; *E. cunninghami*, Stow *et al*. 2001; Stow & Sunnucks 2004; *E. saxatilis*, O'Connor & Shine 2003). All of these species have been found to live in long-term stable social aggregations and exhibit high levels of genetic monogamy. Those species are also probably part of a separate lineage within the genus *Egernia* from the lineage containing *E. frerei* (Donnellan, personal communication). For the other *Egernia* species, and specifically for species in other habitat types, our understanding of social behaviour has been largely based on anecdotal accounts of individuals discovered together (Chapple 2003).

One hypothesis for the evolution of social group structure in *Egernia* is that specific habitat types, such as rock outcrops, have favoured group living more than other habitats. This study provides the first strong evidence that a nonsaxicoline species of *Egernia*, *E. frerei*, also lives in aggregations of highly related individuals, and suggests that social living in *Egernia* is not restricted to a single habitat type.

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Susan Fuller has interests in molecular ecology and contributed the microsatellite DNA analysis while she held a postdoctornal position at Flinders University. Mike Bull works on the behavioural ecology of Australian lizards. Kris Murray did the field sampling as a research assistant, and Ricky-John Spencer was conducting a broader investigation into the impact of fire on the Fraser Island fauna, including these lizards.