Group Structure and Stability in Social Aggregations of White's Skink, *Egernia whitii*

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Abstract

Most lizards display relatively simple social systems, but more complex and stable social aggregations appear to be common in one lineage of Australian skinks, the Egernia Group. Previous studies on this lineage have focused on species inhabiting crevices in large and disjunct rocky outcrops. Here, we describe the social organization of White's skink, *Egernia whitii*, a burrowing species that inhabits rocky habitats in south-eastern Australia. We examined social group size, composition and stability over two field seasons using a capture-mark-recapture study, behavioral observations and genetic analyses. Twenty-four social groups, each comprising two to six individuals, were present at our study site, with 75% of lizards belonging to a social grouping. A higher proportion of adults than juveniles were part of a group, while more adult females belonged to a group than adult males. Groups generally comprised a single adult pair or an adult pair with juveniles. However, groups comprising one male with multiple females and multiple individuals of both sexes also were present. Groups were highly stable throughout the study, although individual group members were observed singly on half of all observations. Paternity analysis using four microsatellite loci revealed that juveniles within groups were closely related to adults in the group, with 38% living in groups with both parents and 71% in groups with at least one parent. Our data demonstrate the presence of complex sociality in a burrowing *Egernia* species and, together with previous studies, suggest that stable social organization is widespread across different habitats and phylogenetic groupings within the Egernia Group.

Introduction

Animals display a diverse array of social systems, ranging from solitary individuals (e.g. Wcislo & Danforth 1997; Admusu et al. 2004), temporary resource-based aggregations (e.g. Graves & Duvall 1995), socially cohesive and cooperative aggregations (e.g. Goossens et al. 1998; Cockburn 2003), to highly social or eusocial colonies (e.g. Jarvis et al. 1994; Duffy et al. 2000). In particular, social systems involving cohesive and temporally stable social aggregations have arisen independently in many vertebrate taxa. For example, in many birds and mammals, offspring delay dispersal to remain within their natal territory with their parents, resulting in highly related and generally cooperative social aggregations (Hatchwell & Komdeur 2000; Krause & Ruxton 2002).

Reptiles, and lizards in particular, have generally been neglected in studies examining the evolution of sociality because they have traditionally been considered to display relatively simple social systems (i.e. lacking large aggregations and/or stable group structures; Brattstrom 1974; Fox et al. 2003). While present evidence indicates that this is true for the majority of lizard species, several species are known

to form short-term aggregations associated with reproduction or thermoregulation (reviewed in Graves & Duvall 1995; Elfstrom & Zucker 1999). However, research over the past decade has increasingly revealed instances of more stable social aggregations in lizards. For instance, short-term studies and anecdotal data indicate isolated instances of species with long-term pair bonds and 'stable' family groups within several phylogenetically independent lineages of lizards (e.g. agamids, Panov & Zykova 1993; chameleons, Toxopeus et al. 1988; cordylids, Mouton et al. 1999; iguanids, Lemos-Espinal et al. 1997a; tropidurids, Halloy & Halloy 1997; xenosaurids, Lemos-Espinal et al. 1997b). In contrast to these relatively scattered and isolated origins of complex sociality, long-term social aggregations involving closely related individuals appear to be widespread within one lineage of Australian scincid lizards, the Egernia Group (reviewed in Chapple 2003).

The Egernia Group comprises approx. 50 species and four genera of large viviparous skinks (*Corucia*, *Cyclodomorphus*, *Egernia* and *Tiliqua*; Greer 1989). Although little is known about the social organization of *Corucia* and *Cyclodomorphus* (reviewed in Gardner 1999), detailed studies have demonstrated that the sleepy lizard (*Tiliqua rugosa*) forms monogamous pairings during the breeding season (reviewed in Bull 2000). However, the genus *Egernia* has attracted most of the attention because it comprises 32 species that range in social complexity from those that are primarily solitary through to species with highly complex social aggregations (Chapple 2003). Behavioral field studies have indicated that *Egernia kingii* (Masters & Shine 2003), *Egernia modesta* (Milton 1987) and *Egernia major* (Osterwalder et al. 2004) live in stable aggregations, while the presence of closely related individuals in aggregations of *Egernia frerei* has recently been inferred solely on the basis of genetic data (Fuller et al. 2005). However, more significantly, long-term behavioral field investigations that have incorporated molecular studies have revealed that several species live in stable (>5 yr) social groups comprising highly related individuals, indicating the presence of family groups (*Egernia cunninghami*, Stow et al. 2001; Stow & Sunnucks 2004a,b; *Egernia saxatilis*, O'Connor & Shine 2003; *Egernia stokesii*, Gardner et al. 2001; Duffield & Bull 2002; *Egernia striolata*, Bonnett 1999).

Although anecdotal reports suggest that some degree of sociality exists in at least 17 species (Chapple 2003), substantial diversity in social organization is evident within *Egernia*. Current evidence suggests

that at least two species (*Egernia coventryi*, *Egernia inornata*) live a primarily solitary existence (Daniel 1998; Chapple 2003), while the social system of a further four species is unknown (Chapple 2003). Even though only a small proportion of 'social' species have been studied intensively it is already clear that group structure varies substantially between species (Chapple 2003). Group structure and the level of sociality also have been shown to vary considerably among populations of *E. cunninghami* (Barwick 1965; Van Weenen 1995; Stow & Sunnucks 2004a) and between populations of *E. striolata* living in different habitats (e.g. rock outcrops vs. tree stumps; Bustard 1970; Bonnett 1999). It is such intrageneric diversity in sociality that makes the Egernia Group an ideal lineage in which to examine a phylogenetically independent origin of complex social behavior and identify the ecological factors promoting sociality (Chapple 2003).

To date most research attention has been focused on several highly social saxicolous species that inhabit large rock crevices in disjunct rock outcrops (*E. cunninghami*, *E. saxatilis*, *E. stokesii*; see Chapple 2003). Recent phylogenetic evidence indicates that these three species are part of the same subclade within the genus (of four subclades; Chapple 2003; S. Donnellan & M. Hutchinson, unpublished data). In contrast, comparatively less is known about the social organization of other members of the genus that predominately use burrows or hollow logs as permanent retreat sites (Chapple 2003). In this paper, we use behavioral field studies in combination with molecular analyses to describe the social organization of White's Skink, *Egernia whitii*, a predominately burrowing species that lives in rocky habitats (Chapple 2003). Anecdotal evidence from previous short-term studies of populations of *E. whitii* in Tasmania (Hickman 1960; Bruyn 1994; Girardi 1996) and Queensland (Milton 1987) have suggested that it lives in small family groups comprising an adult pair and their offspring.

Color pattern polymorphism (discrete and under genetic control) is present within *E. whitii* with patterned and plain-back (lacking dorsal pattern) individuals occurring in varying relative frequencies throughout its distribution (described in detail in Milton 1987, 1990; Donnellan et al. 2002; Chapple 2003). Interestingly, further anecdotal reports have suggested that *E. whitii* may preferentially form social groupings with individuals of the same color morph (Milton 1987). Our main aim in this study was to characterize the group structure and stability of *E. whitii* social aggregations. In addition, we

sought to examine whether color pattern polymorphism influenced social organization in *E. whitii* as suggested by Milton (1987).

Methods

Study Species

Egernia whitii is a medium-sized scincid lizard [95-mm snout-vent length (SVL)] distributed among a variety of habitats in southeastern Australia (Chapple 2003). It occurs across a wide altitudinal range from sea level to 1600 m, encompassing coastal heaths, grasslands, woodlands, and dry sclerophyll forests (Cogger 2000; Wilson & Swan 2003). *Egernia whitii* is generally found in close association with rock outcrops where it excavates deep and complex burrows under or at the base of rocks and shrub vegetation (Chapple 2003; Wilson & Swan 2003). These lizards concentrate the majority of their basking and foraging activities within close proximity of a permanent shelter site (e.g. rock crevice or burrow; Greer 1989; Chapple 2003). *Egernia whitii* is an opportunistic forager that is primarily insectivorous (reviewed in Chapple 2003). It is viviparous with mating occurring in Sep. to Oct. (spring) and one to five offspring born in late Jan. to Feb. (late summer; Hickman 1960; Milton 1987).

Study Site and 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 is located at an elevation of 1250 m a.s.l. and consists predominately of open grassland interspersed with small patches of remnant semi-alpine woodland. *Egernia whitii* was abundant at the site, with both the patterned and plain-back color morph present within the population. Small granite outcrops are widely distributed across the study site creating ample retreat sites for *E. whitii* in the form of rock outcrops and loose surface rocks. *Egernia whitii* were always found in close association with these rocky habitats, generally favoring microhabitats in open grassland areas that provided plentiful basking opportunities. All lizards at the site excavated complex burrow systems at the base or beneath rocks, with the larger burrow systems extending over several meters with multiple entrances. Burrows were used as daily retreat sites and during winter hibernation. The site is bordered on one side by a small creek (approx.

5-m wide), which separates the site from a nearby rock outcrop (approx. 40 m) comprising suitable habitat. On the other three sides the study area is surrounded by open grassland unsuitable for *E. whitii*, with approx. 150 m to the nearest rock outcrop.

The study was conducted over two field seasons (2001/2002 and 2002/2003) during the active period for *E. whitii* (Oct. to Mar.). Although the site was visited regularly over the entire season (approx. 40 single day surveys with 9 d between surveys on average), fieldwork was most intense during Oct. and late Dec. to early Feb. Lizards at the site were caught by noosing, by hand or 'mealworming'. Mealworming involves tying a mealworm to a piece of string and placing it in front of the lizard. When the lizard grabs the mealworm it is lifted into the air and placed into a collection bucket. Measurements of SVL and other standard morphometric measurements (±0.1 mm) were taken upon initial capture of each lizard and every individual was toe-clipped and given a non-toxic paint mark. The tip of the tail (approx. 1 cm) was removed and stored in 70% ethanol for genetic analysis. The sex of each individual was determined via eversion of hemipenes in males and the color morph of each individual (patterned or plain-back) was recorded. Handling time was minimized (<10 min) and lizards were always returned to the exact site of capture. All individuals caught during the first season were recaught and remeasured during the second season. During subsequent surveys animals that had sloughed their skin and shed their paint mark were recaptured, identified using their unique toe-clip, and the paint mark reapplied. Only two lizards (both juveniles) that were observed during the study were not able to be caught.

During each survey, fieldwork was conducted from just prior to the emergence of lizards until lizards returned to their retreat site in the early evening. The timing of emergence and retreat was dependent both on temperature, weather conditions, and season. On fine days emergence was generally within 1 h of sunrise, but was often delayed on days of cool or inclement weather. Upon arrival at the study area all rock crevices and burrow entrances at the site were visually inspected for lizards. The large size of many rocks at the site precluded rock turning during these morning surveys, although many smaller rocks were carefully lifted to search for sheltering lizards. Rocks were only turned once per survey to limit disturbance to the lizards at the site. During these initial surveys lizards were considered to be together if they were found in the same burrow

system, rock crevice or retreat site, under the same rock or within 1 m of each other.

Following these surveys, behavioral observations were conducted for the remainder of the day. In order to provide reference points for behavioral observations the entire field site was divided into 30 × 30-m quadrants that were marked with wooden stakes. All known *E. whitii* retreat sites (i.e. burrow entrances, rock crevices) were marked with paint to facilitate easy visual reference during behavioral observations. A GPS reading (Garmin GPS 12XL, Garmin International Inc., Olathe, Kansas, USA) of the location of each retreat site was taken in order to produce a map of the field site. GPS readings were accurate to within 3–4 m, with the location of marked retreat sites verified manually with a compass and tape measure during the initial stages of the study. Behavioral observations involved visually surveying all known rock crevices, burrow entrances and basking sites and recording the location and activity of lizards at the site. If an individual was sighted more than 2 m away from a paint marked retreat site, a GPS reading was taken of its location. The presence of other lizards within 1 m of the focal lizard was recorded along with any relevant behavioral interactions between these individuals. The location of each lizard was only recorded once per day to ensure that each behavioral observation was independent.

The GPS locality data recorded for each lizard during field surveys was converted to Universal Transverse Mercator (UTM) projections using the program Waypoint+ v1.7.17 (Hildebrand 1998) to obtain X,Y coordinates for the spatial location of each lizard during the study period. This enabled the location of each lizard over the course of the study to be plotted onto a map of the field site. The geographic distance between lizards or between individual observations was calculated using GenAlEx v5.1 (Peakall & Smouse 2001). This spatial data was used in combination with the survey and behavioral observation data to determine the social groupings present at the study site. Individuals were considered to be part of the same social grouping if they were found on three or more occasions during the study to be: (1) sharing the same burrow system, rock crevice or retreat site; (2) basking in close proximity (i.e. within 1 m); or (3) using the same retreat or basking sites (within a season).

Egernia whitii at the Grassy Creek field site reach sexual maturity at approx. 75-mm SVL (Chapple 2005). Consequently, it was possible to classify all lizards at the site as adult male (AM), adult female

(AF) or juvenile (J). We also were able to assign all juveniles at the study site to a particular cohort (2000, 2001, 2002 or 2003). Based on the analysis of SVL histograms and capture-mark-recapture data, *E. whitii* at the site generally reach sexual maturity during their third season, with first (55- to 65-mm SVL) and second-year juveniles (65- to 75-mm SVL) exhibiting clear differences in body size (Chapple 2005). Assignment of juveniles to the 2002 and 2003 cohorts was straightforward as almost all pregnant females at the site in late Jan. each season were caught and brought into the laboratory to give birth (details in Chapple & Keogh 2005). Parturition commenced in all females within 2 wk of arrival in the laboratory. Neonates born in the laboratory were measured ($\pm$0.1 mm), toe-clipped and their tail tip removed (approx. 1 cm) for genetic analysis. Females and their neonates were returned to the site of maternal capture within 5 d of the completion of parturition. Offspring born in the laboratory and released back at the study site were not considered as group members or site residents unless they were recaptured at the study site the following season. All nonparametric statistical analyses relating to group structure were conducting using SPSS Version 11.0 (Chicago, IL, USA).

Genetic Methods

Our genetic methods are described in detail in Chapple & Keogh (2005), but are briefly outlined here. All individuals at the study site were genotyped for four tetranucleotide microsatellite loci (Gardner et al. 1999) that are highly variable and informative in *E. whitii*: EST1, EST2, EST4, EST12 (Table 1). All offspring born in the laboratory also were genotyped for these four microsatellite loci. Results were analysed with GeneMapper v3.0 software (Applied Biosystems, Foster City, California, USA). Parentage

Table 1: Summary information for the four microsatellite loci used in the study

Locus	No. of alleles	Size range (bp)	H_O	H_E
EST1	20	226–314	0.787	0.928
EST2	20	188–280	0.969	0.923
EST4	14	123–179	0.858	0.874
EST12	21	276–374	0.890	0.933

H_O, observed heterozygosity; H_E, expected heterozygosity.
The information shown is based on the lizards (n = 127) caught at the field site and excludes offspring that were born in the laboratory. No significant deviations from Hardy–Weinberg equilibrium were found for any of the four loci.

was assigned to juveniles present at the site using CERVUS 2.0 (Marshall et al. 1998). As offspring born in the laboratory had known maternity, we assigned paternity to these newborns using the 'one parent known' option in CERVUS (Chapple & Keogh 2005). Parentage could be assigned to 119 of the 135 offspring (88%) born in the laboratory (Chapple & Keogh 2005). Both parents could be assigned to 17 of the 49 juveniles (34.7%) that were not born in the laboratory, while at least one parent could be assigned to a further 15 juveniles (30.6%; nine fathers and six mothers). For instances where parentage could not be assigned for juveniles living in groups, it was assumed that their parent(s) were not present at the site.

Results

Summary of Capture-Mark-Recapture Study

A total of 138 lizards were caught at the field site during the study. In the 2001/2002 season 118 animals were caught at the site [39 AM, 39 AF, and 40 J (21M, 19F)], while 111 E. whitii were present at the site in 2002/2003 [38 AM, 39 AF, 34 J (15 M, 19 F)]. Individuals with the patterned color morph (101, 85.6% in first season; 93, 83.8% in second season) were more common than those with the plain-back color morph (17, 14.4%; 18, 16.2%) in both seasons. The composition of lizards within the study area remained relatively stable between seasons with 91 lizards from the first season (77%) also present at the site during the second season (35 AM, 33 AF, and 23 J). Nine previously unmarked lizards, mostly juveniles (1 AM, 1 AF, and 7 J), were found at the site during the second season and had presumably dispersed into the study area. Eleven of the 75 offspring (14.7%) that were born in the laboratory in late Jan. to Feb. 2002 and released back at site were recaptured during the 2002/2003 season. The majority of lizards at the site appeared to exhibit a high degree of site fidelity, with many individuals not observed more than 2–3 m away from their permanent retreat-site (burrow systems at the base of rocks) for the entire duration of the study.

Social Group Structure

We identified a total of 24 social groupings at the Grassy Creek site during the study (Table 2). Within each season E. whitii social groupings ranged in size from 2 to 6 (Table 2). Single adult male–adult female pairs were present within seven social groupings (29.2%), with a further seven groups comprised of an adult pair and one or more juveniles (29.2%). Six social groups at the site contained a single adult male and two or more adult females (25%), three of which contained juveniles. More than one adult of both sex were present in three social groupings (12.5%). Group Q was comprised solely of juveniles (4.1%).

The relatively low frequency of plain-back color morphs at the field site impeded our ability to definitively determine whether E. whitii was forming social groupings assortatively on the basis of color morph. However, of the 24 groups at the study site, 15 of the social groups were comprised entirely of patterned individuals (62.5%), while eight groups comprised a mixture of patterned and plain-back lizards (33.3%; Table 2). Only one social group at the site comprised entirely plain-back individuals (4.2%; Table 2).

A total of 20 individuals (2 AM, 3 AF, and 15 J) that were only observed at the site on a single occasion (14.5% of 138 individuals caught at the site) were considered to be transients rather than permanent residents within the study area. These individuals were excluded from all subsequent analyses. The remaining lizards were either solitary or a member of a social group, and were considered to be site residents. These site residents were observed an average of eight times during the study. The majority of lizards at the study site lived within a social group (89 of 118 individuals, 75.4%; Table 2). A further 29 animals (24.6%) were solitary, maintaining small but stable individual home ranges (Table 2). The relative proportion of individuals within each age-sex category that belonged to a social grouping was significantly different (AM 75.7%, AF 97.4%, J 55.8%; $\chi^2 = 18.79$, df = 2, p < 0.0001). This was predominately a result of lower incidences of juveniles in social groupings; however, adult males also were less likely to belong to a social group than adult females (AM vs. AF: $\chi^2 = 7.63$, df = 1, p = 0.006).

Egernia whitii social groupings were generally stable throughout the entire study (Table 2). Twelve of the social groups (A, D, G, H, J, M, O, P, R, S, T, and X) were stable in composition throughout the two seasons. Changes in group composition in most of the remaining social groups were generally minor involving the dispersal of juveniles in or out of the group (B, C, F, I, Q, and V). Groups K and L were only formed in the second season from individuals that were solitary in the first season. Within each season, only one adult male was present within group N with the first season male replaced by

Table 2: Summary of the composition of *Egernia whitii* social groupings at the Grassy Creek study site

Group	No. lizards involved	Group size		Adult male		Adult female		Juveniles	
		Year 1	Year 2	Patterned	Plain-back	Patterned	Plain-back	Patterned	Plain
Group A	4	4	4	1		1		2	
Group B	5	5	4	1		1	1		2
Group C	4	3	4		1		1		2
Group D	3	3	3	1		1	1		
Group E	4	4	2	1		1		2	
Group F	4	3	3	1		1		2	
Group G	2	2	2	1		1			
Group H	6	6	6	1		2		2[d]	1
Group I	4	3	4	1		1		2	
Group J	3	3	3	1		1		1	
Group K	2	NA[a]	2	1		1			
Group L	2	NA[a]	2	1		1[d]			
Group M	2	2	2	1			1		
Group N	4	3	3	2[b]		1		1	
Group O	4	4	4	2		2			
Group P	3	3	3	1		2			
Group Q	4[c]	2	4					3[c]	1[d]
Group R	2	2	2		1	1			
Group S	2	2	2	1		1			
Group T	2	2	2	1		1			
Group U	7 (8)[c]	6	4	2		3	1	2[c]	
Group V	6	5	5	1		1	2	2	
Group W	7	6	5	2	1	4[e]			
Group X	3	3	3	1		2			
Subtotal	89			25	3	30	7	18[c]	6
Solitary	29			9	0	1	0	16[d]	3
Subtotal	118			34	3	31	7	34	9
Transients	20			2	0	3	0	14	1
Total	138			36	3	34	7	48	10

Several individuals at the site were considered to be solitary or transient lizards.

[a]Groups K and L were only formed during the second season. All individuals from these groups were solitary in the first season.

[b]This group only ever contained one adult male, with the adult male present within the group changing in each season.

[c]A patterned juvenile was part of group U in the first season, but switched to group Q in the second season.

[d]The individual was a juvenile in the first season but matured to become an adult (i.e. >75-mm snout-vent length) in the second season.

[e]A patterned female within this group moved out to become solitary in the second season.

another male in the second season. The remaining three social groups (E, U, and W) were relatively less stable with multiple changes in group composition, involving the interchange of both adults and juveniles between seasons. Despite the presence of stable social aggregations within *E. whitii*, not all group members were always seen together at the same time and indeed several individuals spent considerable amounts of time on their own within the group home range. However, the average proportion of observations in which individuals were seen together with other group members (AM 48.7%, AF 50.2%, J 45.7%, and overall 48.7%) did not significantly differ between each sex-age class ($\chi^2 = 0.84$, df = 2, p = 0.656).

Twelve of the social groups at the site contained juveniles and parentage analysis revealed that juveniles were generally closely related to the adults within the group (Table 3). Excluding group Q, which consisted entirely of juveniles, the remaining 21 from a total of 25 juveniles (84%) that were part of a social group, lived within a group with at least one adult of each sex. Eight juveniles (38.1% of 21 juveniles) lived in a social group with both their parents, seven in a group with at least one parent (33.3%) and six juveniles (28.6%) lived in social groups without either parent present (Table 3). Consequently, 15 juveniles lived in a social group with at least one of their parents (71.4%). Although Group C contained juveniles from two successive

Table 3: Relatedness between juveniles and adults within social groups based on cervus parentage analysis

Group	Adult male	Adult female	Juvenile	Year juveniles were born	Both parents in social group	Mother only in social group	Father only in social group	Neither parent in social group
Group A	1	1	2	2002	2			
Group B	1	2	2	2001	2			
Group C	1	1	2	2001	1			
				2002				1
Group E	1	1	2	2001			2	
Group F	1	1	2	2001	1			
				2002				1
Group H	1	2	3	2001		2		1
Group I	1	1	2	2001				1
				2002		1		
Group J	1	1	1	2001			1	
Group N	2	1	1	2001			1	
Group Q	0	0	4	2000				1
				2001				2
				2002				1
Group U	2	4	2	2001	1			1
Group V	1	3	2	2001	1			
				2002				1

Only those social groups that contained juveniles are shown. The method for assigning juveniles to a particular cohort is described in the text. As group Q contained only juveniles these data were excluded from the analyses outlined in the text. Each social group at the site also produced numerous offspring in each season that did not remain within their natal group (i.e. dispersed or died).

cohorts simultaneously, all remaining groups only had juveniles from a single cohort in any given season (Table 3).

Discussion

Our results confirm previous anecdotal observations (Hickman 1960; Milton 1987; Bruyn 1994; Girardi 1996) that *E. whitii* lives in stable social groups, consistently primarily of either adult pairs or adult pairs with juveniles. Juveniles were generally closely related to the adults within these social aggregations, with 71% living in a social group with at least one parent (38% both parents and 33% one parent). The proportion of juveniles found living with at least one parent is lower than what has previously been documented for *E. cunninghami* (92%; Stow & Sunnucks 2004a), *E. stokesii* (87%; Gardner et al. 2001) and *E. saxatilis* (96%, 69% with both parents and 27% with one; O'Connor & Shine 2003). Such high levels of relatedness among adults and juveniles within social groups is believed to be the result of the long-term monogamous pairings which are formed in these species (Gardner et al. 2002; O'Connor & Shine 2003; Stow & Sunnucks 2004a). The high proportion of *E. whitii* juveniles living in groups with only one parent or without either parent suggests that either juveniles disperse into unrelated social groupings or that a different mating system

exists in *E. whitii*. We examine the level of genetic relatedness within social groups, the mating system and dispersal patterns in detail elsewhere, but monogamy, polygyny and extra-group paternity all appear to be common in *E. whitii* at the Grassy Creek site (Chapple & Keogh 2005).

The social organization of *E. whitii* at our study site closely corresponds to that inferred by Milton (1987) for a population in southeast Queensland. Milton (1987) recorded the age (adult or juvenile) and sex of lizards found sheltering together while turning rocks in order to collect animals for a 5-yr life-history study. Although it is not clear whether his published data (186 observations of two or more lizards) includes multiple observations of the same individuals, it reveals similar patterns of association to that found in the present study. Milton (1987) only found adult male sheltering together on three occasions compared 63 with females and 29 with juveniles. However, as in our study, he observed that adult females were slightly more likely to be found with other adult females (11 observations). Juveniles were found frequently with both adult females (45 observations) and other juveniles (35 observations).

The most significant aspect of the study by Milton (1987) was that he only observed patterned and plain-back individuals together in two of the 186 observations, suggesting that lizards segregated into

social groups according to color morph. In contrast, in our study patterned and plain-back morphs co-occurred in a third of all social groupings, with only one group comprised entirely of plain-back individuals. Caution should be exercised in such comparisons as the relatively low incidence of plain-back individuals at our site (14.5% in present study vs. 26.7% in Milton 1987) could make it more difficult for plain-back lizards to find other plain-back lizards with which to associate. However, our anecdotal observations of other *E. whitii* populations in eastern Australia with higher relative frequencies of plain-back morphs (up to 40%) indicate that plain-back and patterned individuals are regularly observed together. As color pattern in *E. whitii* appears to display autosomal inheritance largely consistent with simple Mendelian inheritance (i.e. patterned allele dominant over recessive plain-back allele; Chapple 2005), the patterns observed by Milton (1990) may simply be the result of the aggregations comprising closely related individuals (i.e. Chapple & Keogh 2005). Consequently, a long-term behavioral and genetic study at Milton (1987) original study site would be worthwhile in the future to clarify this issue.

In the present study, *E. whitii* were found to live in small but stable social groups (2–6). Group size in *E. whitii* is considerably lower than that previously documented for *E. cunninghami* (2–27; Barwick 1965; Stow et al. 2001) and *E. stokesii* (2–17; Duffield & Bull 2002), but comparable with that recently found in *E. saxatilis* (2–14, but generally 2–6; O'Connor & Shine 2003). Lanham (2001) demonstrated considerable geographic variation in group size in *E. stokesii* between regions where it occupied rock screes and rock crevices. This is not surprising given that the space available within the retreat sites that *Egernia* inhabitation (rock crevice, burrow, and hollow log) undoubtedly limits the number of individuals that able to co-occupy them. Species of *Egernia* inhabit a wide range of habitats including woodlands, grasslands, swamps, sandy deserts, shrublands, rainforests, and coastal heathlands (Greer 1989; Chapple 2003). Consequently, both habitat structure and the size of available retreat sites may influence social group size and composition in *Egernia*. For example, larger retreat sites are required to accommodate larger social groups, and intuitively larger aggregations are potentially likely to comprise more adults and/or cohorts of juveniles and subadults.

Despite substantial differences in group composition among *Egernia* species, the proportion of individuals found to occur within social groups within each species is remarkably consistent (*E. whitii*, 75%, present study; *E. cunninghami*, 83%, Barwick 1965; *E. saxatilis*, 72%, O'Connor & Shine 2003; *E. stokesii*, 70%, Lanham 2001). In our study, we found significant differences in the likelihood of each *E. whitii* age-sex class to be part of a social group, with almost all resident adult females part of a group (97%). Adult males were less likely to be in a group (76%), while only about half of all juveniles belonged to a group (56%). Equivalent data are only available for *E. saxatilis* (O'Connor & Shine 2003) where the likelihood of adult males (43%), adult females (74%) and juveniles (85%) is considerably different from that found in *E. whitii*. Similar trends are evident in both species with females more likely to be part of a group than males, although the overall portion of adults in groups appears to be lower in *E. saxatilis*. It appears that juvenile *E. saxatilis* are more likely to belong to social groups than juvenile *E. whitii*. This is clearly reflected in the social organization of each species with *E. saxatilis* groups generally containing more juveniles, both in terms of overall number (2–12 vs. 1–4) and number of cohorts present within the group (1–3 vs. 1–2; O'Connor & Shine 2003; present study; Table 3). As age at maturity is similar for both species (Chapple 2003), such disparity suggests that *E. saxatilis* juveniles are more philopatric than *E. whitii* juveniles.

The majority of *E. whitii* social groups were stable throughout the two seasons of our study. Temporal changes in group composition were generally the result of juvenile dispersal, with the adult pair which formed the core of most groups generally constant within *E. whitii* aggregations for the duration of the study. Long-term group stability has been a hallmark of all previous studies of *E. cunninghami* (Barwick 1965; Stow & Sunnucks 2004a), *E. saxatilis* (O'Connor & Shine 2003) and *E. stokesii* (Duffield & Bull 2002). For example, the core of most *E. stokesii* social groups were generally constant across three or more consecutive field seasons (Duffield & Bull 2002). Evidence for such long-term group stability in *Egernia* is not surprising considering that most species have life spans of 10–25 yr (Chapple 2003). However, substantial differences appear to exist between each species in the amount of time that individual group members spend with other members of the group. Most group members of *E. cunninghami* and *E. stokesii* are generally observed together (Barwick 1965; Duffield & Bull 2002); however, individuals within social groups of *E. whitii* (51%) and *E. saxatilis*

(67%) appear to spend significant proportions of their time independently (O'Connor & Shine 2003; present study). On such occasions, these *E. whitii* and *E. saxatilis* individuals generally remained within the group territory, but were present in different regions of the territory at any given time.

Chapple (2003) recently suggested that the Egernia Group may represent an opportunity to test current hypotheses about the evolution and maintenance of vertebrate social systems (e.g. 'ecological constraints' hypothesis, reviewed in Arnold & Owens 1998; 'life-history' hypothesis, reviewed in Arnold & Owens 1999). However, Osterwalder et al. (2004) have correctly highlighted that the widespread incidence (i.e. phylogenetic conservatism) of more complex social systems within the Egernia Group might indicate that social organization is the product of phylogenetic inertia rather than ecological or life-history attributes of individual species. Thus, rather than broadly classifying members of the Egernia Group as solitary or 'social', categories should better reflect variability in social organization, enabling examination of the factors responsible for promoting switches in social organization. Although relatively few members of the lineage have been intensively studied four categories of social organization are already evident: (1) solitary (e.g. *E. inornata*, *E. coventryi*; Chapple 2003); (2) pair bond during breeding season (e.g. *T. rugosa*; Bull 2000); (3) stable 'nuclear' family group (e.g. *E. saxatilis*, O'Connor & Shine 2003; *E. whitii*, present study); and (4) stable extended family group (e.g. *E. cunninghami*, Barwick 1965; Stow & Sunnucks 2004a; *E. stokesii*, Gardner et al. 2001; Duffield & Bull 2002).

Given the evidence suggesting that group size and composition may be influenced by factors constraining retreat site availability recent claims that *Egernia* social organization is not related to ecology or aspects of habitat (e.g. Osterwalder et al. 2004; Fuller et al. 2005) may be premature. Our study of social organization in *E. whitii* is the first to document in detail the social system of an *Egernia* species that utilizes burrows rather than rock crevices. Recent studies have also indirectly inferred the social organization of two species (*E. major*, hollow logs in rainforests; *E. frerei*, hollow logs and burrows in *Eucalyptus* forest on a sand island) inhabiting different habitats (Osterwalder et al. 2004; Fuller et al. 2005). These studies have been invaluable as they expand our knowledge of social organization to three of the four subgroupings within the genus *Egernia* (S. Donnellan & M. Hutchinson, unpublished

data; see Chapple 2003) and provide an indication of social organization across a range of habitats. Although each study appears to indicate that 'social' species occur across a wide variety of habitats, variability in group size, and composition appears to be evident.

Acknowledgements

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