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ECOLOGY, LIFE-HISTORY, AND BEHAVIOR IN THE AUSTRALIAN SCINCID GENUS *EGERNIA*, WITH COMMENTS ON THE EVOLUTION OF COMPLEX SOCIALITY IN LIZARDS

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Abstract: Squamate reptiles generally have been ignored in the search for a unified theory for the evolution of sociality due to the perception that they exhibit little social behavior beyond territoriality and dominance hierarchies and display polygynous mating systems. However a growing body of research has revealed unsuspected levels of social complexity and diversity in mating systems within the squamate lineage, particularly among the members of the Australian Scincid genus *Egernia*. Several species of *Egernia* are amongst the most highly social of all squamate reptiles, exhibiting stable social aggregations and high levels of long-term social and genetic monogamy. Social complexity is widespread within the *Egernia* genus, with reports of social aggregations in 23 of the 30 described species. The purpose of this review was to examine the potential for the *Egernia* genus as a model system for study of the evolution of sociality and monogamy within squamate reptiles.

Current evidence indicates there is substantial variability in social complexity both within and between species, with social organization covering the spectrum from solitary to highly social. Four highly social *Egernia* species are known to live in stable social aggregations consisting of closely related individuals (adults, subadults, juveniles; i.e., 'family' groups) that appear to utilize chemical cues to recognize group members (kin recognition). Enhanced vigilance against predators is one presumed benefit of group membership. Additionally, juveniles within social groupings appear to receive low levels of indirect parental care. Several *Egernia* species create scat piles that mark group territories. Three *Egernia* species exhibit long-term social and genetic monogamy and several inbreeding avoidance strategies have been documented. However, it is currently unknown whether monogamy is widespread within *Egernia*.

Egernia species occupy a broad range of habitats, although most are terrestrial, saxicolous or semi-arboreal. Several species display an attachment to a permanent home site, generally a rock crevice, burrow or tree hollow. *Egernia* species take 2–5 years to mature, live for 5–25 years, and are viviparous with litter size positively correlated with body size. Several *Egernia* species are herbivorous, with the degree of herbivory increasing with body size and during ontogeny in larger species. Most smaller species are either insectivorous or omnivorous. Species of *Egernia* have a wide range of reptilian, avian, and mammalian predators. Several larger species possess several behavioral and morphological features to prevent their extraction from rock crevices, including highly modified keeled scales and numerous defensive behaviors. Color pattern polymorphism is present in five *Egernia* species.

Potential ecological correlates of sociality and monogamy are discussed. The life-history hypothesis predicts long-lived, late-maturing species should evolve complex sociality. The habitat availability hypothesis relies on the assumption that refugia may be limited in some ecological settings, and group formation is a consequence of co-habitation of available refugia. These hypotheses are not mutually exclusive, and testable predictions are formulated and discussed. Specific future research directions are outlined to take advantage of *Egernia* as a model system for comparative research on a lineage that represents an independent origin of social organization comparable to that found in birds and mammals.

Key words: Color pattern polymorphism; *Egernia*; Habitat use; Herbivory; Life-history; Mating systems; Scincidae; Sociality.

The Australian Scincid genus *Egernia* comprises some of Australia's largest, more ubiquitous and easily identifiable lizards (Cogger, 2000; Greer, 1989). Several species of *Egernia* are among the most highly social of all squamate reptiles, and recent research has suggested that studies focused on this genus could provide a valuable contribution to our understanding of the evolution of complex sociality and monogamous mating systems in reptiles. Complex sociality appears to be widespread within the *Egernia* lineage, with anecdotal reports of social aggregations documented for 23 of the 30 currently recognised species. The size, complexity, and stability of these aggregations appear to vary noticeably both among species, and among populations of the same species, indicating diversity of social organization within the genus.

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Understandably, initial investigations of sociality in *Egernia* have focused on species that display the most apparent and complex social organizations. Although several species were generally found in small groups (adult pair and/or their offspring; *E. saxatilis*, O'Connor and Shine, 2003; *E. striolata*, Bonnett, 1999), *Egernia cunninghami* and *E. stokesii* were found to live in groups of up to 17 individuals (Duffield and Bull, 2002; Gardner et al., 2001; Stow et al., 2001; A. Stow, unpublished data). These long-term behavioral and molecular studies also demonstrated that social groupings in each of these species were stable between seasons and were comprised of closely related individuals ('family' groups). As a result of such temporal stability in group structure, adult pairs in several species (*E. cunninghami*, *E. saxatilis*, *E. stokesii*) appear to be socially monogamous, also exhibiting a high degree of genetic monogamy (Gardner et al., 2002; O'Connor and Shine, 2003; A. Stow, unpublished data). However, social organization within *Egernia* is likely to cover the spectrum from these examples of highly social species to those that remain predominately solitary throughout their lives.

Squamate reptiles have been assumed to exhibit little social behavior beyond territoriality and dominance hierarchies (e.g., Brattstrom, 1974; Stamps, 1977) and consequently reptilian examples are severely lacking in the sociality literature. The widespread incidence of complex sociality (and the diversity of social organization) within the *Egernia* genus provides a unique opportunity to study the independent evolution of sociality within a reptilian lineage. Likewise, monogamy such as that observed in *E. cunninghami*, *E. saxatilis* and *E. stokesii* (Gardner et al., 2002; O'Connor and Shine, 2003; A. Stow, unpublished data) is relatively rare in lizards, because most species exhibit polygynous mating systems (Bull, 2000). Therefore, *Egernia* also may provide insight into the independent evolution of monogamy in squamate reptiles.

The factors responsible for promoting the evolution and loss of complex sociality are an essential component in the broader search for a unified theory for the evolution of sociality within both vertebrate and invertebrate taxa (e.g., Cahan et al., 2002). Recent attempts to obtain such a unified theory have relied on cases of convergent evolution of similar social systems within phylogenetically independent lineages to search for ecological correlates related to the evolution or loss of social organization (Cahan et al., 2002), thus identifying factors important in the evolution of sociality (e.g., Crespi, 1994; Danforth, 2002; Duffy et al., 2000; Schwarz et al., 1998; Soucy and Danforth, 2002). Consequently, for each independent origin of complex sociality two vital components are required: 1) a well-resolved phylogeny to trace the evolution (and loss) of sociality within the lineage; and 2) detailed ecological, behavioral and life-history information with which to correlate to evolutionary origins and loses of complex social organization (Cahan et al., 2002; Hughes, 1998).

Although phylogenetic relationships among *Egernia* species are to date unresolved (see Evolution, Systematics and Taxonomy section), this review summarizes the ecological, behavioral and life-history information available for *Egernia* to highlight potential correlates of sociality and monogamy within the genus and present hypotheses relating to the evolution of sociality within *Egernia*. However, any synthesis presented is inevitably preliminary as the study of complex sociality and monogamy in *Egernia* is still in its infancy. Detailed study has been completed on only four species: *E. cunninghami* (Stow et al., 2001; A. Stow, unpublished data), *E. saxatilis* (O'Connor and Shine, 2003), *E. stokesii* (Duffield and Bull, 2002; Gardner et al., 2001, 2002), and *E. striolata* (Bonnett, 1999).

This review builds upon Greer's (1989) brief summary of *Egernia* ecology and behavior (as part of an overview of Australian lizards) and the work of Hutchinson (1993) and Gardner (1999). Although the review is focused primarily on social behavior and mating systems, several other interesting traits (herbivory, ontogenetic dietary shifts, burrowing, scat piling, color pattern polymorphism) within the *Egernia* genus also are examined.

EVOLUTION, SYSTEMATICS AND TAXONOMY

The evolution of *Egernia* species from an ancestral immigrant from New Guinea and its subsequent radiation across Australia has been examined in detail (Heatwole and Taylor, 1987; Horton, 1972). Horton (1972) suggested that the ancestor of *Egernia* (presumed to be

TABLE 1.—Currently recognized *Egernia* species and species groups (after Horton, 1972; Storr, 1968, 1978; Cogger et al., 1983; Cogger, 2000; Hutchinson, personal communication). Full references for the taxonomic authorities are provided in the Literature Cited.

Species group	Species	Authority	Common names
cunninghami	*cunninghami*	Gray, 1832	Cunningham's Skink
	depressa	Günther, 1875	Pygmy Spiny-tailed Skink
	hosmeri	Kinghorn, 1955	Hosmer's Skink
	stokesii	Gray, 1845	Gidgee Skink, Spiny-tailed Skink, Stoke's Egernia/Skink
kingii	*kingii*	Gray, 1838	King's Skink
striolata	*striolata*	Peters, 1870	Tree Skink
	carinata	Smith, 1939	none
	douglasi	Glauert, 1956	Kimberley Crevice Skink
	formosa	Fry, 1914	Goldfields Crevice Skink
	mcpheei	Wells and Wellington, 1984	McPhee's Egernia
	napoleonis	Gray, 1838	South-western Crevice Skink
	pilbarensis	Storr, 1978	Pilbara Crevice Skink
	saxatilis	Cogger, 1960	Black Rock Skink
luctuosa	*luctuosa*	Peters, 1866	Western Glossy Swamp Skink, Western Mourning Skink
	coventryi	Storr, 1978	Swamp Skink, (Eastern) Mourning Skink
whitii	*whitii*	Lacépède, 1804	White's Skink
	guthega	Donnellan et al., 2002	Snowy Mountains Rock Skink
	inornata	Rosén, 1905	Rosen's Desert Skink, Desert Skink, Unadorned Skink
	kintorei	Stirling and Zietz, 1893	Great Desert Skink, Kintore's Egernia/Skink
	margaretae	Storr, 1968	Centralian Ranges Rock Skink, Flinders Ranges Rock Skink, Margaret's Egernia
	modesta	Storr, 1968	Eastern Ranges Rock Skink
	montana	Donnellan et al., 2002	Tan-backed Rock Skink
	multiscutata	Mitchell and Behrndt, 1949	Heath Skink, Bull Skink, Southern Sand Skink
	pulchra	Werner, 1910	Spectacled Rock Skink, South-western Rock Skink
	slateri	Storr, 1968	Slater's Egernia/Skink, Floodplains Skink
	striata	Sternfeld, 1919	Night Skink, Striated Egernia
major	*major*	Gray, 1845	Land Mullet
	arnhemensis	Sadlier, 1990	Arnhem Land Egernia
	frerei	Günther, 1897	Major Skink
	rugosa	De Vis, 1888	Yakka Skink

Mabuya multifasciata) entered Australia from New Guinea via a Torres Strait land bridge during a period of lowered sea level during the Pliocene. The rainforests of northern Queensland may have formed a 'pool' from which populations expanded during glacial periods (Horton, 1972). Heatwole and Taylor (1987) identified a series of events, mostly related to changes in climatic conditions (glacial periods and periods of aridity) and fluctuations in sea level, that presumably lead to the diversification of *Egernia* across the continent. These events resulted in penetration of *Egernia* southward along either side of the Great Dividing range, followed by the inland expansion of the range into the Northern Territory, South Australia and Western Australia. Several periods of aridity created arid barriers, separating populations that ultimately differentiated into coastal and arid adapted forms. Horton (1972) suggested that species groups were formed from the expansion of populations from the north Queensland rainforest 'pool', while penetration into other areas resulted in the differentiation of species within these species groupings.

There are currently 30 described species in the *Egernia* genus, all endemic to Australia except *E. frerei*, which extends into New Guinea (Cogger, 2000; Donnellan et al., 2002). Six species groups are generally recognized within *Egernia* (following Horton, 1972; Storr, 1978; M. Hutchinson, personal communication; Table 1), although species within the *whitii* species group can be further classed as rock-dwelling (*E. whitii*, *E. guthega*, *E. margaretae*, *E. modesta*, *E. montana*, *E. pulchra*) or desert/coastal burrowing species (*E. inornata*, *E. kintorei*, *E. multiscutata*, *E. slateri*, *E. striata*). The species groups are based primarily on morphological characters (e.g., sharply keeled scales in the *cunninghami* group) and may not represent monophyletic groups (Gardner, 1999).

Examination of phylogenetic relationships among *Egernia* and the related genera within the *Egernia* group, *Tiliqua*, *Cyclodomorphus*, and *Corucia*, has proved problematic. A recent phylogeny of *Egernia* by Donnellan et al. (unpublished data) that included sequence data from 19 species representing all six species groups lacked strong bootstrap support for most nodes, despite the data set (approx. 3000bp) from two mitochondrial (12SrRNA, ND4) and two nuclear genes (c-mos, beta-fibrinogen intron 7). Initial indications are that the *luctuosa*, *major* and *whitii* species groupings each represent monophyletic clades. The *cunninghami*, *kingii* and *striolata* species groups appear to be paraphyletic and the morphological characters on which they are based may represent instances of convergence to a particular environment (e.g., saxicoline habitat of the *cunninghami* group).

Detailed taxonomic descriptions and distributional information for *Egernia* species contained in this review are provided in Horton (1972), Storr (1968, 1978), Cogger et al. (1983), and Cogger (2000). Two recently described species within the *whitii* species group, *E. guthega* and *E. montana* (Donnellan et al., 2002), also are included in this review. Due to doubts over the validity of several subspecies, particularly within the *whitii* group (Donnellan et al., 2002), information on subspecies will not be considered in this review (e.g., *E. pulchra pulchra* and *E. p. longicauda* information presented as *E. pulchra*).

Life History

Egernia life-history strategies are characterized by large body size, delayed maturity, and large offspring body size. Although these trends appear to be most evident in the larger *Egernia* species, the majority of these traits are also evident in the medium-sized species (Table 2). Life spans are generally long, known to exceed 5 years in all species studied. Several species live in family groups with juveniles remaining with their parents until they disperse as adults (see Sociality section). *Egernia stokesii* juveniles may remain in their natal group for up to five years until they reach maturity (Duffield and Bull, 2002), and similar patterns have been documented for *E. kingii* (Arena, 1986; Langton, 2000; R. Wooller, personal communication) and *E. cunninghami* (Barwick, 1965; A. Stow, unpublished data; Van Weenen, 1995). Although adult mortality is low, juvenile mortality in the first year is generally high (Duffield and Bull, 2002; Van Weenen, 1995; R. Wooller, personal communication). For example, Duffield and Bull (2002) reported that approximately 33% of juvenile *E. stokesii* survived their first year. Data on age at maturity and juvenile survivorship is lacking for most of the other species.

Although the *Egernia* genus contains some of Australia's largest skinks (>200 mm SVL), which generally have long life spans (>10 years), the majority of species are medium-sized (75–150 mm SVL; Table 2). These medium-sized species (e.g., *E. striolata*, *E. coventryi*, *E. whitii*, *E. modesta*) take around 2–3 years to mature (generally at about 70–85 mm SVL) and may live for up to 10 years (Table 2). Newborns of these species range from 35 to 50 mm SVL, whilst newborns of the larger species are generally around 55 to 95 mm SVL (Table 2).

Geographic variation in life-history characteristics has been observed in several species. *Egernia whitii*, for example, exhibits a cline in body size, morphology, and color pattern along its distributional range (Donnellan et al., 2002). Populations from northern New South Wales and southeastern Queensland take 2 years to mature (Milton, 1987) whereas Tasmanian populations take up to four years to mature (Hickman, 1960; Rawlinson, 1974). Animals from both areas appear to mature around the same size (80–85 mm SVL) therefore variation in growth rate ultimately tied to climatic conditions may be responsible for later maturity in the Tasmanian populations. Van Weenen (1995) also reported that *E. cunninghami* were smaller in size (160–180 mm SVL) on West Island off the coast of South

TABLE 2.—Life history characteristics of the *Egernia* genus. Snout–vent length (SVL) is measured in mm. Tail length is expressed as a percentage of SVL. Reference codes: 1 = Storr (1968); 2 = Storr (1978); 3 = Wilson and Knowles (1988); 4 = Swan (1990); 5 = Cogger (2000).

Species	Adult SVL	Tail length	Newborn SVL	Age at maturity	SVL at maturity	Life span	References
cunninghami							
E. cunninghami	230–250	100	57–70	5	190–200	>20	Barwick (1965), Flower (1925), Stow et al. (2001), 4, 5
E. depressa	100–115	35	54–59	–	–	–	Day (1980), 2, 5
E. hosmeri	150–180	60	66–73	3–5	–	12–24	Post (2000), 5
E. stokesii	155–190	35	65–95	5	170	10–25	Duffield and Bull (1996, 2002), Gardner (1999), 2, 3, 4, 5
kingii							
E. kingii	200–230	130	60–80	3	185–190	–	Arena (1986), Richards (1990), Wooller (personal communication), 5
striolata							
E. striolata	100–118	–	47–54	2–3	–	–	Bustard (1970), Bull and Bonnett (in press), 4, 5
E. carinata	100–105	110	–	–	–	–	2, 4, 5
E. douglasi	160–170	90–100	–	–	–	–	2, 5
E. formosa	80–105	140	–	–	–	–	2, 5
E. mcpheei	130–143	110–140	–	–	–	–	Shea et al. (2000), 4, 5
E. napoleonis	120–130	140	–	–	–	–	2, 5
E. pilbarensis	120	130–140	–	–	–	–	2, 5
E. saxatilis	110–135	–	–	–	95–100	–	G. Shea (unpublished data), 3, 4, 5
luctuosa							
E. luctuosa	120–130	175–200	–	–	–	–	2, 5
E. coventryi	100–130	150	34–41	2–3	70–75	>8	Clemann (1997), Clemann and Beardshell (1999), Douch (1994), Manning (2002), Robertson (1980), 2, 5
whitii							
E. whitii	80–110	160	40–45	2–4	80–85	>8.5	Hickman (1960), Milton (1987), Rawlinson (1974), 3, 5
E. guthega	95–110	120–130	–	–	75	–	Donnellan et al. (2002)
E. margaretae	90–105	160–190	–	–	–	–	1, 5
E. modesta	100–110	160	40–45	2	85	>5	Milton (1987), 1, 4, 5
E. montana	90–110	160	39	–	74	–	Donnellan et al. (2002)
E. multiscutata	80–95	150–170	–	–	–	–	1, 2, 5
E. pulchra	100–110	150–220	–	–	–	–	2, 3, 5
E. inornata	75–85	120–140	35	2	–	–	Daniel (1998), 1, 2, 4, 5
E. kintorei	190–200	110–130	70–80	2	165–175	–	McAlpin (2001*a*), Pearson et al. (2001), 1, 3, 5
E. slateri	85–95	115–145	–	–	–	–	1, 5
E. striata	100–110	130–140	–	–	–	–	1, 5
major							
E. major	300–330	115–120	75–80	–	250–270	11–23	Klingenbock et al. (2000), Shea (1999), 4, 5
E. arnhemensis	180	–	–	–	–	–	5
E. frerei	180–200	130	–	–	–	–	4
E. rugosa	200	100	–	–	–	–	5

TABLE 3.—Reproductive characteristics of the *Egernia* genus. Relative clutch mass (RCM) is measured as a proportion of female *post-partum* mass. Reference codes: 1 = Storr (1968); 2 = Storr (1978); 3 = Wilson and Knowles (1988); 4 = Swan (1990); 5 = Cogger (2000).

	Litter size		Reproductive cycle			
Species	Mean	Range	Mating/ovulation	Parturition	RCM	References
cunninghami						
E. cunninghami	5.8	1–8	Nov	Jan–Feb	–	Barwick (1965), Niekisch (1980), 3, 4, 5
E. depressa	2	2–3	–	–	–	Day (1980), 3
E. hosmeri	2	1–4	late August	Dec–Jan	–	Post (2000)
E. stokesii	5.08	1–8	–	Feb–March	0.20	Duffield and Bull (1996)
kingii						
E. kingii	4–6	2–8	late Nov	mid-late April	–	Arena (1986), R. Wooller (personal communication)
striolata						
E. striolata	3.3–4	2–6	–	Jan–Feb	0.26	Bull and Bonnett (in press), Bustard (1970)
E. carinata	–	–	–	–	–	No records
E. douglasi	–	–	–	–	–	No records
E. formosa	–	2–3	–	–	–	3
E. mcpheei	–	3–5	–	Jan–Feb	–	4
E. napoleonis	–	2–4	spring	–	–	Ehmann (1992), 3, 4
E. pilbarensis	–	–	–	–	–	No records
E. saxatilis	–	1–5	–	Jan–March	–	O'Connor and Shine (2003), 4
luctuosa						
E. luctuosa	–	–	–	–	–	No records
E. coventryi	2.5–3	1–6	Nov	Jan–Feb	0.37	Clemann (1997), Manning (2002), Robertson (1980)
whitii						
E. whitii	2.6–2.9	1–5	Sept–Oct	Jan–Feb	–	Bell (1997), Hickman (1960), Milton (1987), Rawlinson (1974), 4
E. guthega	3	3	late spring/ early summer	March	–	Green and Osborne (1994), Donnellan et al. (2002)
E. margaretae	–	–	–	–	–	No record
E. modesta	2.7	1–5	Sept–Oct	Jan–Feb	–	Milton (1987)
E. montana	–	4	–	mid-Feb	–	Donnellan et al. (2002)
E. multiscutata	–	1–3	–	mid-late summer	–	Victorian Natural Resources and Environment (2000)
E. pulchra	3	–	–	–	–	3
E. inornata	2.1	1–4	–	–	0.13	Pianka and Giles (1982)
E. kintorei	6	1–7	late spring/ early summer	late Dec	0.39	McAlpin (2001*a*), Pearson et al. (2001)
E. slateri	–	–	–	–	–	No record
E. striata	2.6	1–4	–	Dec–Jan	0.10	Pianka and Giles (1982)
major						
E. major	–	2–9	Oct	Feb	–	Shea (1999), 4
E. arnhemensis	–	–	–	–	–	No record
E. frerei	–	–	–	–	–	No record
E. rugosa	–	–	–	–	–	No record

Australia compared to mainland populations despite life-history traits (e.g., age to maturity, size at birth) similar to their mainland counterparts. Consequently, life-history patterns in mainland and island populations of *Egernia* may differ due to variation in climate, food availability and predator abundance.

Most *Egernia* species possess tails that are between 1 to 1.5 times their SVL, although *E. luctuosa* and *E. pulchra* may have tails up to twice their body size (Table 2). Several saxicoline species (e.g., *E. stokesii*, *E. depressa*, *E. hosmeri*) have shorter (35–60% of SVL) dorsoventrally flattened tails (Table 2) that also have utility in antipredatory behaviors (see

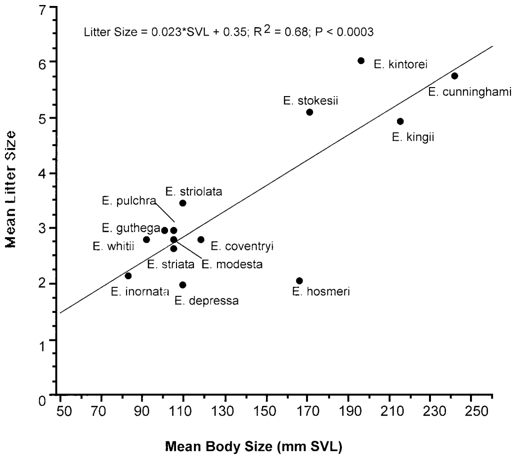

FIG. 1.—Relationship between body size (SVL; mm) and mean litter size in *Egernia*. Body size is the average of the adult SVL range shown in Table 2. References for the mean litter sizes of each species are shown in Table 3. The results of the regression analysis and significance level are shown.

Predation and Defense section). In *E. kintorei* the tail may be an important source of energy reserves; the tail base of several individuals was swollen with fat stores during good seasons (McAlpin, 2001*a*).

REPRODUCTION

Generalizations about the reproductive ecology of *Egernia* is somewhat impeded by the absence of detailed data for some species (Table 3) and a well-resolved phylogeny. However, sufficient data is available to summarize the major trends within the genus. All *Egernia* species are viviparous (Greer, 1989) and the three species that have been studied (*E. cunninghami*, *E. striolata* and *E. whitii*) possess relatively simple Type 1 placentas (Weekes, 1935). These species are not thought to be closely related, and the Type 1 placenta may be symplesiomorphic in *Egernia*.

Litter size varies both among species (from 1 to 9) and within individual species (Table 3). Several patterns in reproductive ecology are evident in *Egernia*. There appears to be a significant relationship between body size and fecundity in *Egernia*, with larger species having larger mean litter sizes (Fig. 1, Table 3). Most species appear to conform to the general size-fecundity relationship in *Egernia* except for *E. hosmeri* (Fig. 1, Table 3). This anomaly may be due to mean litter size being derived from a limited number of breeding females in a captive population of *E. hosmeri* (Post,

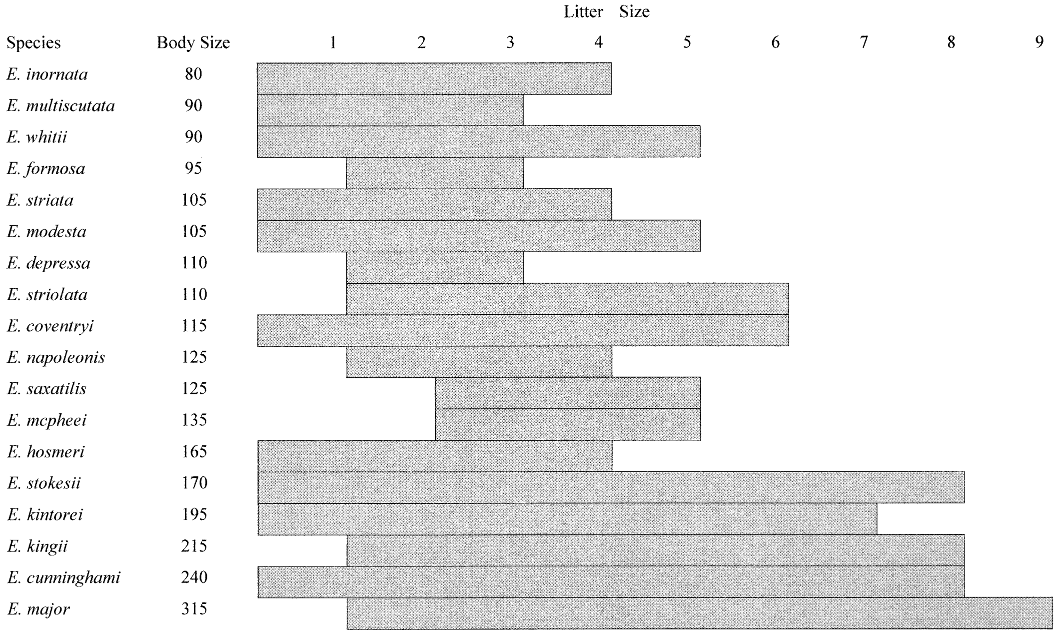

FIG. 2.—Variability in litter size in relation to body size in *Egernia*. Body size is the average of the adult SVL range shown in Table 2. References for the litter size range of each species are shown in Table 3.

2000). The range of litter sizes reported for each species is also rather variable, generally increasing with relation to body size (Fig. 2, Table 3). Although the slope of the size-fecundity relationship may be influenced by phylogeny (Harvey and Pagel, 1991), it remains clear that within *Egernia*, both mean litter size and variation in litter size increase with body size.

Offspring sex ratio at birth was found to be 1:1 in *E. modesta* and *E. whitii*, and a positive relationship between maternal size and litter size was also documented within each species (Milton, 1987). In *E. striolata*, larger mothers (SVL) also have been found to produce larger litters in *E. striolata*, in addition to heavier litter masses (both total litter mass and RCM; Bull and Bonnett, in press). Consequently, the relationship between maternal size and litter size is predicted to occur in several other *Egernia* species. However, there may be a trade-off between litter size and offspring size as *E. stokesii* juveniles from larger litters were generally found to be smaller (partial correlation between juvenile SVL and litter size corrected for maternal mass and SVL, $r = -0.44$, $P = 0.038$; Duffield and Bull, 1996).

Reproductive cycles vary somewhat among *Egernia* species; however, in the majority of species parturition generally occurs near the end of summer or the beginning of autumn, with one litter produced per season (Greer, 1989; Table 3). Duffield and Bull (1996) reported that a quarter of *E. stokesii* they collected failed to produce a litter; therefore, females of some species may not produce litters each year. There is one report that *E. inornata* produced two litters in a season (Pianka and Giles, 1982). Post (2000) also provided some evidence that some species of *Egernia* are capable of producing multiple litters in a season with the report of a captive *E. hosmeri* producing two litters in a season. However, detailed field studies examining the prevalence of multiple litters within *Egernia* species are lacking.

Several species of *Egernia* may take several days to complete parturition of their litter. Duffield and Bull (1996) found that *E. stokesii* produced their litter over an average of 2.8 days, although the time to complete parturition ranged from 1 to 12 days (mean litter size 5.08). The duration of parturition in *E. stokesii* was constant between years and was not related to litter size, litter mass, or maternal SVL (Duffield and Bull, 1996). Such prolonged parturition was also observed in *E. striolata* (1–7 days, mean litter size 3.29; Bull and Bonnett, in press), *E. coventryi* (2–3 days, mean litter size 5.25; Manning, 2002) and *E. whitii* (1–10 days, mean litter size 2.55; D. Chapple, unpublished data). The incidence and significance of prolonged parturition in *Egernia* is unknown. Litter sizes in *Egernia* are similar to many other similar sized viviparous scincid genera (Greer, 1989); therefore, increased energetic expenditure during birth due to litter size is an unlikely cause. Indeed, individuals of several species have been observed to produce their entire litter in a single day, evidence that they are not necessarily restricted by energetic constraints during parturition (Duffield and Bull, 1996; Bull and Bonnett, in press). It is plausible that staggering production of the litter may act to gradually assimilate new individuals into the social group, reducing aggression by other adults in the social group and lowering risk to the entire litter. Such a strategy could be important considering that several species of *Egernia* are extremely aggressive towards unfamiliar individuals, particularly juveniles (see Kin Recognition and Social Cohesion section). However, the significance of staggering parturition in *Egernia* clearly warrants further investigation.

Birthing behaviour in *Egernia* has been observed rarely. Hickman (1960) observed *E. whitii* giving birth in cavities under rocks or in holes in the ground. These refugia presumably protected the mother and her offspring during parturition. Post (2000) observed *E. hosmeri* females positioning themselves so that their vents were clear of the ground during parturition and panting with open mouths prior to giving birth to each neonate. Data available for several *Egernia* species suggests that both parental care and infanticide can occur immediately following parturition. Post (2000) noted that *E. hosmeri* mothers and juveniles ate the foetal membranes immediately after birth; one female was seen to eat the yolk of a recently born, but underdeveloped, neonate that was still alive. In *E. stokesii*, mothers consumed the yolk sac and birth membranes of their offspring and assisted them out of their embryonic sac (Lanham and Bull, 2000). Such assistance could be interpreted as a form of direct parental care. Infanticide also has been observed in *E. stokesii* soon after birth (Lanham and Bull, 2000). Lanham and Bull (2000) reported that an *E. stokesii* female ate her third born neonate while it was still alive, even though it appeared fully developed and healthy. Interestingly, the female exhibited no further signs of aggression to the remaining six offspring in her litter (Lanham and Bull, 2000).

Very little is known about the male reproductive cycle in *Egernia* with information limited to studies on *E. whitii* (Bell, 1997; Milton, 1987), *E. modesta* (Milton, 1987) and *E. cunninghami* (Barwick, 1965). In *E. modesta* and *E. whitii* testes remained flaccid throughout the winter with testes becoming distended during the mating season in September and October (Bell, 1997; Milton, 1987). Sperm was detected in the vas deferens from October to January (Milton, 1987), and testes regressed from November to March (Bell, 1997). Barwick (1965) found size of testes in *E. cunninghami* did not fluctuate substantially throughout the year. Testis mass gradually increased during hibernation until peak sperm production in late October and November, then gradually decreased until March (Barwick, 1965).

Mating System and Monogamy

Detailed information about the mating system of *Egernia* species is available for a few species. Early anecdotal reports indicated that *E. inornata* mated with the same partner several times on one day or over several days, suggesting monogamy (Webber, 1978). However, the recent analysis of DNA microsatellites for *Egernia* (Cooper et al., 1997; Gardner et al., 1999; Stow, 2002) has enhanced our knowledge of the mating system of several species, in particular *E. stokesii*, *E. cunninghami* and *E. saxatilis*. The mating systems of these three species are characterised by high levels of both social and genetic monogamy.

Monogamy both within and between seasons appears to be a common mating strategy in *E. stokesii*. Gardner et al. (2002) found that in 16 laboratory born litters, 75% of litters were fathered by a single male parent and no male contributed to more than one litter. This result indicates that there is a high degree of within season genetic monogamy in *E. stokesii*. In a five-year field study utilizing DNA microsatellites, Gardner et al. (2002) found that most *E. stokesii* females also maintained the same male breeding partner for successive cohorts, several for the entire duration of the study. The majority of *E. stokesii* juveniles (88.6%) were found to occur in social groups consisting of both their parents (Gardner et al., 2002). A high proportion of both males (88.9%) and females (63.9%) were found to have multiple cohorts of offspring only with the same breeding partner (Gardner et al., 2002).

Egernia cunninghami also exhibits a high degree of mate fidelity both within and between breeding seasons (A. Stow, unpublished data). O'Connor and Shine (2003) recently reported that long-term monogamy is evident in *E. saxatilis*. Social aggregations in *E. saxatilis* were comprised primarily of a single breeding pair (83% of social groups with at least one adult present) and up to three cohorts of their full-sibling offspring (O'Connor and Shine, 2003). Despite the presence of long-term behavioral monogamy, genetic analysis (DNA microsatellites) revealed multiple paternity in 20% of litters with two or more offspring (O'Connor and Shine, 2003). The rate of extra-group paternity in *E. saxatilis*, was 7%, indicating that extra-pair mates are usually from the same social grouping (O'Connor and Shine, 2003). These studies suggest monogamous mating systems are present in several *Egernia* species. However, studies to date have focused on three large and highly social species and it is currently unknown whether species that display less complex sociality also exhibit long-term monogamy. As long-term social and genetic monogamy also occurs in the related genus *Tiliqua* (Bull, 2000), the *Egernia* lineage may be an ideal system in which to examine the evolution of monogamous mating systems.

Egernia stokesii and *E. cunninghami* live in long-term stable social groupings that consist of highly related individuals (see Sociality section), and interestingly, there appears to be several behavioral mechanisms to avoid inbreeding (Gardner et al., 2001; Stow et al., 2001; A. Stow, unpublished data). Members of breeding pairs are significantly less related to

TABLE 4.—Habitat preferences and burrowing in species of *Egernia*. Adapted from Greer (1989).

Species	Habitat			Burrowing	Reference
	Saxicolous	Terrestrial	Semi-arboreal		
cunninghami					
E. cunninghami	X			No	Barwick (1965), Cogger (2000)
E. depressa	X		X	No	Storr (1978), Cogger (2000)
E. hosmeri	X			No	Cogger (2000)
E. stokesii	X		X	No	Cogger (2000), Duffield and Bull (2002)
kingii					
E. kingii		X		Yes	Bush et al. (1995), Wilson and Knowles (1988)
striolata					
E. striolata	X		X	No	Bonnett (1999), Bustard (1970), Hutchinson (1993)
E. carinata	X		X	No	Cogger (2000), Wilson and Knowles (1988)
E. douglasi	X			No	Wilson and Knowles (1988)
E. formosa	X		X	No	Cogger (2000), Wilson and Knowles (1988)
E. mcpheei	X		X	No	Swan (1990)
E. napoleonis	X		X	No	Bush et al. (1995), Swan (1995), Wilson and Knowles (1988)
E. pilbarensis	X			No	Cogger (2000), Wilson and Knowles (1988)
E. saxatilis	X		X	No	Cogger (1960), Smales (1981), Swan (1990)
luctuosa					
E. luctuosa		X		?	Bush et al. (1995), Wilson and Knowles (1988)
E. coventryi		X		Yes	Clemann (1997, 2001), Robertson (1980)
whitii					
E. whitii	X	X		Yes	Cogger (2000), Hickman (1960), Milton and Hughes (1986)
E. guthega	X	X		Yes	Donnellan et al. (2002)
E. margaretae	X	X		Yes	Cogger (2000), New South Wales National Parks and Wildlife Service (2000), Wilson and Knowles (1988)
E. modesta	X	X		Yes	Milton and Hughes (1986), Wilson and Knowles (1988)
E. montana	X	X		Yes	Donnellan et al. (2002)
E. multiscutata		X		Yes	Cogger (2000), Coventry and Robertson (1980), Ford (1963), Hudson et al. (1981)
E. pulchra	X	X		Yes	Bush et al. (1995), Ford (1963, 1965), Wilson and Knowles (1988)
E. inornata		X		Yes	Pianka and Giles (1982), Webber (1978, 1979)
E. kintorei		X		Yes	McAlpin (2001*a*), Pearson et al. (2001), Wilson and Knowles (1988)
E. slateri		X		Yes	Horner (1991), Wilson and Knowles (1988)
E. striata		X		Yes	Pianka and Giles (1982)
major					
E. major		X		Yes	Klingenbock et al. (2000), Swan (1990), Wilson and Knowles (1988)
E. arnhemensis	X			?	Horner (1991)
E. frerei		X		Yes	Swan (1990), Wilson and Knowles (1988)
E. rugosa		X		Yes	Cogger (2000), Wilson and Knowles (1988)

each other than to other potential mates within the same social group (Gardner et al., 2001; A. Stow, unpublished data). This results in low average relatedness among breeding pairs and indicates that these *Egernia* species avoiding breeding with close relatives (Gardner et al., 2001; A. Stow, unpublished data). Genetic studies indicated that although both sexes exhibit natal philopatry, female group members are generally more related than male group members, suggesting sex-biased dispersal (Gardner et al., 2001; Stow et al., 2001). Although there are indications that male-biased dispersal occurs in *E. stokesii* and *E.*

cunninghami, there is currently no available behavioral data on the dispersal patterns of each sex. Consequently, at least two of the four potential inbreeding avoidance mechanisms exist in *Egernia*: 1) kin recognition and the ability to selectively breed with unrelated individuals (see also Kin Recognition and Social Cohesion section); and 2) kin-biased dispersal (reviewed in Pusey and Wolf, 1996). Interestingly, promiscuity, another potential inbreeding avoidance strategy (Pusey and Wolf, 1996) does not appear to be widespread in the species studied to date with each exhibiting high levels of genetic monogamy.

Habitat, Activity, and Thermoregulation

Habitat preferences in *Egernia* are diverse and varied, with at least one species (sometimes in low densities) found in most terrestrial areas and habitats in Australia (Greer, 1989). Although each species can be defined as terrestrial, saxicolous or semi-arboreal (Table 4), *Egernia* are found in variety of habitats including rainforest (*E. major*, *E. frerei*), woodlands (*E. striolata*, *E. whitii*), coastal dunes (*E. multiscutata*, *E. whitii*), alpine meadows and woodland (*E. guthega*, *E. montana*, *E. whitii*), arid sand plains (*E. kintorei*, *E. slateri*, *E. inornata*) and saltmarshes (*E. coventryi*, *E. luctuosa*) (Donnellan et al., 2002; Greer, 1989). Winter hibernation is evident in most *Egernia* species, especially in cooler and alpine environments. The majority of species are diurnal, exhibiting peaks in activity during the morning and late afternoon. However, some species including *E. kintorei*, *E. striata* and *E. inornata* are crepuscular to nocturnal, although their activity patterns are flexible depending on the environmental conditions (Pianka and Giles, 1982). *Egernia striata* appears adapted for foraging at night as it has an elliptic eye, a characteristic trait of nocturnal species (Cogger, 2000). However, Pearson et al. (2001) found that although *E. kintorei* has a circular pupil under normal daylight conditions, the pupil contracts to a vertically elliptical form when a strong torch is shone in the eye. Such a trait may also allow *E. kintorei* to successfully forage at night.

Egernia generally exhibits a strong attachment to a permanent home site (e.g., rock crevice, hollow log, tree stump, or burrow; Greer, 1989). Animals rely on these home sites for short and long-term shelter and the majority of their activities are focused around their retreat site (Greer, 1989).

Egernia stokesii, *E. depressa*, *E. hosmeri* and *E. cunninghami* are large diurnal lizards that are saxicolous (Table 4), sheltering within crevices in large rocky outcrops (Barwick, 1965; Stammer, 1976; Van Weenen, 1995). Occasionally, hollow logs and semi-arboreal habitats are used as shelter sites (Cogger, 2000; Stammer, 1976; Storr, 1978; Swan, 1990; Wilson and Knowles, 1988; Table 4). Longer-term studies on habitat use have only been completed for *E. stokesii* and *E. cunninghami*. In *E. stokesii*, members of the same social group generally bask in close proximity and occasionally on top of each other (Duffield and Bull, 2002; Lanham, 2001). Individuals of the same social group share a common crevice refuge and are generally observed within a core set of crevices within the group's home range (80% of observations; Duffield and Bull, 2002). Each social group has between 2–11 crevices, of which 1–7 are core crevices (Duffield and Bull, 2002). The home range overlap between social groups is relatively small (14.1%) and dispersal in and out *E. stokesii* populations is generally low (Duffield and Bull, 2002).

The habitat use and activity of *E. cunninghami* has been examined in two populations, one near Canberra (Barwick, 1965) and the other on West Island off the coast of South Australia (Van Weenen, 1995). On West Island, lizards occupy small overlapping home ranges (8–36 m^2, mean 15 m^2) with lizard density negatively correlated to home range size (Van Weenen, 1995). As a result, overall density of *E. cunninghami* on West Island (368 adults/subadults per ha; Van Weenen, 1995) was substantially higher than that found by Barwick (1965) in a population in Canberra (82 per ha). However, large social aggregations were still observed in both populations. Dispersal in each population was apparently limited (about 20 m), with the longest recorded movement being 70 m in the Canberra population (Barwick, 1965; Van Weenen, 1995). Around Canberra *E. cunninghami* hibernates from April to September, remaining inactive and not feeding during this period (Barwick, 1965).

Egernia kingii is terrestrial (Table 4) and is found in coastal regions of south-western Western Australia and offshore islands (Arena, 1986; Bush et al., 1995; Humphreys, 1990). Although it generally occurs in low densities on the mainland it is present on offshore islands in extremely high densities (800–950 per ha) with very small and overlapping home ranges (Arena, 1986; Langton, 2000; R. Wooller, personal communication). *Egernia kingii* generally foraged close to coastal dune areas but seldom ventured far from the rocky areas it used for refuge (Bush et al., 1995). Arena (1986) suggested low predation on adults and an abundance of food was responsible for the high densities of *E. kingii* observed on many offshore islands. *Egernia kingii* sheltered in rock crevices or burrows (Bush et al., 1995; Langton, 2000; Wilson and Knowles, 1988). It appears to have a strong attachment to its home site and displaced individuals are capable of navigating their way home (Langton, 2000). Mechanisms responsible for the navigational abilities of *E. kingii* are currently unknown. As in *Tiliqua rugosa* (sleepy lizard) (Zuri and Bull, 2000*a*,*b*), individuals may use visual rather than chemical cues to assess their spatial orientation in relation to their home site.

Although *E. pilbarensis* and *E. douglasi* appear confined to rocky areas (Cogger, 2000; Wilson and Knowles, 1988), several other species (*E. carinata*, *E. formosa*, *E. mcpheei*, *E. napoleonis*, *E. saxatilis*, *E. striolata*) appear to be semi-arboreal (hollow logs, tree stumps) or use rock outcrops depending on the local availability of each habitat (Cogger, 2000; Hutchinson, 1993; Swan, 1990; Wilson and Knowles, 1988; Table 4). *Egernia striolata* and *E. saxatilis*, for example, live in rock outcrops or on tree stumps in various parts of their range depending on the availability of each habitat (Bonnett, 1999; Bustard, 1970; Hutchinson, 1993; Smales, 1981; Swan, 1990; Wilson and Knowles, 1988). Such geographic variation in the structural habitat of *E. striolata* may also influence its degree of sociality (see Sociality section).

Egernia coventryi and *E. luctuosa* are terrestrial species (Table 4) and obligate dwellers of densely vegetated wetlands, including both freshwater and saltmarsh habitats (Bush et al., 1995; Clemann, 1997; Robertson, 1980; Schulz, 1985; Smales, 1981; Wilson and Knowles, 1988). *Egernia coventryi* occurs predominately in coastal areas in southeastern Australia with relatively few inland populations (Clemann, 2000, 2001), while *E. luctuosa* occurs in southwest Western Australia (Wilson and Knowles, 1988). Both are secretive skinks that seldom venture far from cover or vegetation and both will enter the water (swimming or diving) when pursued (Clemann, 1997; Wilson and Knowles, 1988). *Egernia coventryi* was once considered nocturnal; however, Robertson (1980) demonstrated it is a diurnal heliothermic species. Although it overwinters in logs, it is generally active from early September to May when ambient temperatures exceed about 18° C (Clemann, 2000, 2001; Schulz, 1985). It frequently basks on fallen timber, litter and flood wreck, typically occurring and foraging in and adjacent to dense hydrophilic sedge and tussock vegetation (Clemann, 1997, 2000, 2001; Robertson, 1980; Smales, 1981). It shelters in burrows (see Burrow Use and Retreat Site section), beneath rocks and logs, or in the base of tussocks and sedges (Clemann, 1997; Robertson, 1980; Schulz, 1985). One report estimated a core activity range of 10 to 35 m^2 around its burrow and juvenile dispersal up to 200 m (Robertson, 1980). *Egernia coventryi* is an aggressive species that will chase conspecifics from its territory (Clemann, 1997, 2000). It may occupy the same burrow for several days, but will utilize any burrow to facilitate escape from predators (Clemann, 1997). *Egernia coventryi* lives in areas that are regularly flooded and it appears unlikely that lizards remain in burrows that have been inundated with water (Clemann, 1997). This potential lack of stability in its habitat may be one explanation for why it appears to have no permanent group structure (see Sociality section).

Several species of *Egernia* appear to be obligate burrowers (Table 4): *E. multiscutata* (Coventry and Robertson, 1980; Hudson et al., 1981), *E. inornata* (Daniel, 1998; Pianka and Giles, 1982; Webber, 1978, 1979), *E. slateri* (Wilson and Knowles, 1988), *E. striata* (Pianka and Giles, 1982) and *E. kintorei* (McAlpin, 2001*a*). However, several other species are facultative burrowers in suitable habitats and saxicolous in others: *E. whitii* (Hickman, 1960; Milton, 1987), *E. modesta* (Milton, 1987), *E.*

margaretae (New South Wales National Parks and Wildlife Service, 2000). The obligate burrowers tend to be restricted to arid and semi-arid areas of central Australia, generally in sandy and gravely habitats (McAlpin, 2001*a*; Pianka and Giles, 1982). However, *E. multiscutata* lives in coastal dunes and open heathlands (also semi-arid sandy areas) close to rocky habitats (Cogger, 2000; Coventry and Robertson, 1980). These species appear to have relatively large activity ranges, which may reflect adaptation to their arid and semi-arid environments (Henzell, 1972). The remaining species (*E. whitii*, *E. montana*, *E. guthega*, *E. modesta*, *E. pulchra*, *E. margaretae*) are usually associated with rocky habitats located in woodland, heathland and forests, inhabiting crevices and burrows at the base of rocks and logs (Donnellan et al., 2002; Ford, 1963; Wilson and Knowles, 1988).

Egernia whitii occurs in a wide range of vegetation types including eucalypt dominated open-forest, sandy coastal areas, woodland, tussock grassland and open heathland (Donnellan et al., 2002). However, it also co-occurs with *E. guthega* and *E. montana* in alpine areas of NSW and Victoria (Donnellan et al., 2002). *Egernia montana* is found in open areas. Its ecology is very much linked to the granite boulders, slabs, or rock screes (Donnellan et al., 2002). It occurs in a wide range of vegetation including tall open-forest, woodland, and heathland (Donnellan et al., 2002). In the north of its range *E. montana* is generally found in montane and subalpine conditions above 1400 m; however, in more southern locations it occurs in taller eucalypt forest down to 900 m (Donnellan et al., 2002). *Egernia guthega* has not been recorded in habitats below 1600 m and may occur at elevations as high as 1940 m (Donnellan et al., 2002). It prefers areas with rock or sub-surface boulders hidden beneath soil or thick vegetation such as granite rock outcrops and boulder fields (Donnellan et al., 2002). It occurs in a range of vegetation types including snow-gum, woodland with grassy or shrubby understoreys, dry tussock grassland, and tall and short heath (Donnellan et al., 2002).

Egernia frerei, *E. rugosa*, and *E. major* are terrestrial, diurnal, secretive species (Table 4) that are generally found in ecotonal forest in rainforest and wet/dry sclerophyll forest areas (Cogger, 2000; Klingenbock et al., 2000; Wilson and Knowles, 1988). These species commonly use large fallen logs for shelter, and bask in clearings and other sunny areas (Klingenbock et al., 2000; Swan, 1990). The large body size of *E. major* facilitates slow heating and cooling rates, allowing retention of high body temperatures as they forage in cool forest areas (Klingenbock et al., 2000). *Egernia rugosa* are only occasionally found in rocky areas (Swanson, 1976); whereas, *E. arnhemensis* appears to be predominately saxicolous (Horner, 1991). *Egernia arnhemensis* lives in closed forests where it prefers thickly vegetated rocky gorges with numerous deep crevices (Horner, 1991). It is generally active between late afternoon and late evening (Horner, 1991).

Egernia species are considered to be posturing heliotherms, modifying their postural orientation to adjust to the rate of heat gain and seeking shade to reduce body temperatures (Johnson, 1977). Body temperature is generally higher in species that inhabit warmer drier areas than those that live in wetter cooler areas (Greer, 1989). It has been suggested that species such as *E. inornata*, *E. slateri*, *E. kintorei* and *E. striata* are able to exist in the arid zone primarily due to their use of burrows (Henzell, 1972; Webber, 1978, 1979). Their burrows act to reduce temperature oscillations and provide a stable environment (Henzell, 1972). Relative humidity is generally high within the burrows of these species, which acts to reduce water loss (Henzell, 1972). These species have been observed to bask at the burrow entrance, utilizing several postures where only portions of their body are outside the burrow. It has been suggested that this behavior, combined with the orientation of the burrow entrance, may affect body temperature and therefore have a thermoregulatory function (Pianka and Giles, 1982; Webber, 1978, 1979). When temperature become excessive, the burrow also provides these species with refuge from full exposure to the sun (Daniel, 1998; Henzell, 1972).

Egernia cunninghami is one of the few *Egernia* species where thermoregulatory behavior has been investigated. Fraser (1985*a*) investigated sexual and temporal variation in heating and cooling rates. Heating rate was consistently faster than the rate of cooling, and may facilitate maintaining high body temperatures while foraging in shade. Although the rate of heat gain was similar between the sexes, males tended to have slower cooling rates than females (Fraser, 1985*a*). Seasonal variation in heating and cooling rate was found to exist, with both rates generally faster during the activity period than in winter (Fraser, 1985*a*). This result indicated thermoregulatory behavior may be modified during winter hibernation.

Burrow Use and Retreat Sites

Burrowing and the utilization of an excavated burrow are probably primitive traits in Lygosomine skinks, and such traits appear widespread in *Egernia* (Greer, 1989; Table 4). Several species (e.g., *E. whitii*, *E. striata*, *E. inornata*) create burrow systems with escape hatches that stop just below the surface to facilitate rapid escape (Greer, 1989). *Egernia inornata* and *E. striata* have also been observed to seal off the entrances to their burrow system during winter hibernation (Henzell, 1972; Pianka and Giles, 1982). The complexity of burrow systems varies considerably between species and geographically between conspecific populations (Greer, 1989). Burrowing has not been documented for several *Egernia* species (Table 4).

Egernia coventryi constructs its own burrows or uses those of yabbies and crabs; the structure of these burrow systems is currently unknown (Clemann, 1997). *Egernia kingii* readily uses burrows formed by fairy penguins and shearwaters (Bush et al., 1995; Richards, 1990; Wilson and Knowles, 1988). It may use several burrows during the year with the occupied burrow easily identified by the presence of a scat pile at its basking site near the burrow entrance (Ehmann, 1992). *Egernia major*, *E. frerei* and *E. rugosa* have been observed to construct burrows beneath fallen logs or within vegetation (Ehmann, 1992; Swan, 1990; Wilson and Knowles, 1988).

Burrow systems appear more elaborate in *E. whitii*, *E. guthega*, *E. margaretae*, *E. modesta*, *E. montana*, *E. multiscutata*, *E. pulchra*, *E. inornata*, *E. kintorei*, *E. slateri* and *E. striata* (Table 4). All these species are active burrowers, with many constructing complex burrow systems with interconnecting tunnels and several entrances. Several species, for example *E. multiscutata* (Wilson and Knowles, 1988), *E. inornata* (Daniel, 1998; Pianka and Giles, 1982; Webber, 1978, 1979) and *E. kintorei* (Pearson et al., 2001), are generally only found by locating their burrow systems. Short descriptions of burrows have been reported for *E. pulchra*, *E. slateri*, *E. margaretae*, *E. montana* and *E. guthega*. *Egernia pulchra* excavates extensive burrow systems in sandy soils under and between partially buried rocks (Ehmann, 1992) while *E. margaretae* digs long burrows (about 80 cm) into rock crevices or at the base of rocks and boulders (Henzell, 1972; New South Wales National Parks and Wildlife Service, 2000). *Egernia slateri* constructs multi-entranced burrow networks at the base of shrubs and tussocks (Henzell, 1972; Wilson and Knowles, 1988). *Egernia guthega* and *E. montana* construct deep burrow networks beneath rocks (Donnellan et al., 2002). *Egernia guthega* generally digs into the decomposing granite and humus beneath boulders and shrubs, with both the soil and winter snow cover providing good insulation in its harsh alpine environment (Donnellan et al., 2002).

More detailed burrow descriptions are available for *E. whitii* (Hickman, 1960), *E. multiscutata* (Coventry and Robertson, 1980; Ford, 1963; Hudson et al., 1981), *E. inornata* (Pianka and Giles, 1982; Webber, 1978, 1979), *E. striata* (Pianka and Giles, 1982), and *E. kintorei* (McAlpin, 2001*a*). *Egernia kintorei* constructs large burrows in sand ridges and flats to a depth of over 1 m and up to 10 m in diameter (McAlpin, 2001*a*). The burrow may start simply with a single tunnel and one entrance. New tunnels are added progressively over about two years, leading to the formation of a complex burrow system with 5–10 entrances and a network of interconnected tunnels 5–6 m across (McAlpin, 2001*a*). *Egernia whitii* is capable of actively excavating burrows under rocks and logs or in tree roots and cracks in the soil (Hickman, 1960; D. Chapple, personal observation). Burrows typically have at least two openings, possibly to facilitate ventilation and easy escape when pursued by predators (Hickman, 1960). *Egernia multiscutata* constructs multi-entranced burrows at the base of small shrubs, generally located on the northern slopes of dunes close to the summit (Coventry and Robertson, 1980; Ford, 1963; Hudson et al., 1981). Burrows have 2–10 entrances located some distance apart with burrow entrances superficially resembling rabbit warrens (Henzell, 1972; Hudson et al., 1981). Plant roots may act to stabilize the burrow systems which can cover 2 m^2 and be up to 60 cm deep (Coventry and Robertson, 1980; Hudson et al., 1981).

Egernia inornata is an accomplished digger that constructs its own burrow system (Daniel, 1998; Pianka and Giles, 1982; Webber, 1978, 1979). Although *E. inornata* burrows are generally simple, increased burrow complexity has been reported in some populations (Daniel, 1998; Greer, 1989). Pianka and Giles (1982) reported that *E. inornata* burrows were simple U-shaped tubes, located about 30 cm below the surface. They found one entrance was generally open, the sole entrance to the burrow, with the other stopping just below the surface to act as an escape hatch in an emergency (Pianka and Giles, 1982). Daniel (1998) found that *E. inornata* burrows in the Middleback Ranges, South Australia, were more complex. Burrows were clustered within open scrubland habitats. Each burrow had between one and nine entrances, with the complexity of each burrow increasing over time. However, in most *E. inornata* populations, individuals appear to be constantly constructing and moving between burrows (Daniel, 1998). Daniel (1998) also observed frequent movements among burrows (mean distance moved 70 ± 20 m per month). Lizards occupied several burrows over a period of a few days (Daniel, 1998; Webber, 1978, 1979), with most burrows unoccupied at any one time (Daniel, 1998). The entrance to the burrow was usually at the base of vegetation (generally *Triodia* shrubs), fallen timber, or rocks and generally faced north to northwest (Daniel, 1998; Pianka and Giles, 1982; Webber, 1978). Sand removed during the construction of the burrow was usually smoothed near the burrow entrance, presumably to conceal its location (Pianka and Giles, 1982).

Egernia striata constructs complex burrow systems with interconnected tunnels and openings as far as 1 m apart (Pianka and Giles, 1982). The burrow is generally deep and may resemble a rabbit warren (Pianka and Giles, 1982). Most of the sand excavated during construction is piled into a large mound near the south to southwest facing main entrance, with the mound acting as a lookout or basking platform (Pianka and Giles, 1982).

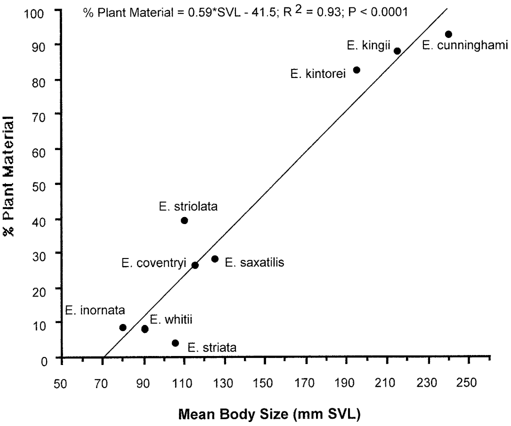

Fig. 3.—Relationship between body size (SVL; mm) and percentage plant material in the diet for *Egernia* species. Body size is the average of the adult SVL range shown in Table 2. Refer to Table 5 for diet references for each species. The results of the regression analysis and significance level are shown.

Foraging Behavior and Diet

The majority of skinks generally feed opportunistically on a diet of insects and other invertebrates (Brown, 1991; Pough, 1973). Members of the *Egernia* genus exhibit some atypical patterns in relation to their diet and foraging behavior. The proportion of plant material in the diet increases with body size for 9 species ranging from small species (e.g., *E. striata*, 4.6%; *E. whitii*, 8.4%; *E. inornata*, 9%) to medium-sized species (*E. coventryi*, 26.7%; *E. saxatilis*, 28.6%; *E. striolata*, 39.7%) to the largest species (*E. kintorei*, 82.5%; *E. kingii*, 88%; *E. cunninghami*, 92.8%) (Arena, 1986; Brown, 1983, 1991; Clemann, 1997; Pianka, 1986; Pianka and Giles, 1982; Richards, 1990; Fig. 3; excludes scat data). Although this evidence suggests herbivory is related to body size in *Egernia*, the evolution of herbivory in the genus will be better addressed with information on diet in more species, along with a well-resolved phylogeny. A recent analysis by Cooper and Vitt (2002) did take phylogeny into account, and confirmed the generality of the relationship between large body size and herbivory across all lizard taxa. Cooper and Vitt (2002) found that substantial plant consumption favors the evolution of large body

TABLE 5.—Foraging behavior and diet for species of *Egernia*. In most instances data presented is from studies (scat analysis, gut contents) where substantial diet analysis has been completed. Anecdotal reports or captive diets have not been included in the table.

Species	Type			Ontogenetic shift	Reference
	Insectivory	Omnivory	Herbivory		
cunninghami					
E. cunninghami		Juvenile	Adult	Yes	Barwick (1965), Brown (1991), Pollock (1989), Van Weenen (1995)
E. hosmeri			Adult	?	Shea (1995)
E. stokesii		Juvenile	Adult	Yes	Duffield and Bull (1998)
kingii					
E. kingii		Juvenile	Adult	Yes	Arena (1986), Richards (1990)
striolata					
E. striolata		X		No	Bustard (1970), Swan (1990)
E. napoleonis		X		?	Bush et al. (1995), Swan (1995)
E. saxatilis		X		No	Brown (1991)
luctuosa					
E. coventryi	Juvenile	Adult		Yes	Clemann (1997), Douch (1994), Robertson (1980), Schulz (1992)
whitii					
E. whitii	X			No	Brown (1991), Hickman (1960)
E. inornata	X			?	Pianka and Giles (1982), Webber (1978)
E. kintorei		X		?	McAlpin (2001*a*)
E. striata	X			?	Pianka and Giles (1982)
major					
E. major		X		?	Schulz and Eyre (1997), Shea (1999)
E. frerei		X		?	Swan (1995)

size in lizard taxa, most likely as the result of energetic considerations (sensu Pough, 1973). It is likely the same general pattern would hold within *Egernia*.

Although omnivory and herbivory have evolved numerous times in Iguania, Scleroglossa, and Scincomorpha (including Scincidae; Cooper and Vitt, 2002), only between 0.8 to 2.0% of extant species are herbivorous (using the criterion of >90% plant volume in the diet; Cooper and Vitt, 2002; Pough, 1973). Consequently, the large number of *Egernia* species that are herbivorous (Table 5) is unusual. Cooper and Vitt (2002) found herbivorous lizards tended to be folivorous and possessed adaptations for processing leaves, including dentition for cutting and reducing leaves, elongated intestines, colic valves that slow passage of food, and intestinal flora that digest cellulose. Indeed, many of these traits are found in *E. cunninghami* and *E. kingii* (Carron, 1975; Pollock, 1989; Richards, 1990). Omnivorous lizards generally lack such specializations and tend to feed more on easily digestable fruits, flowers and seeds that are usually highly nutritious and seasonally abundant (Cooper and Vitt, 2002). Omnivorous *Egernia* species also tend to include such items in their diet when available (Table 5).

Ontogenetic shifts in diet from insectivory to herbivory have been demonstrated in Iguanids, Skinks, Lacertids, Tropidurids, Phrynosomatids and Corytophanids (Cooper and Vitt, 2002; Pough, 1973). Such ontogenetic shifts in dietary preferences are evident in the large *Egernia*, *E. cunninghami*, *E. kingii* and *E. stokesii* (Table 5). Although juvenile *E. cunninghami* can survive on a strictly herbivorous diet they prefer invertebrates and grow faster when they are predominately insectivorous (Pollock, 1989). Richards (1990) demonstrated an ontogenetic change in the morphology of the digestive tract of *E. kingii*, but in *E. cunninghami* and *E. kingii* the digestive efficiencies of adults and juveniles on a diet of plant material were both high (~70–80%) and did not appear to differ between age classes (Pollock, 1989; Richards, 1990). Although *E. cunninghami* and *E. kingii* were predominantly herbivorous they still consumed invertebrate prey opportunistically as adults (Arena, 1986; Brown, 1991; Richards, 1990; Van Weenen, 1995). This may act to increase the nutritional value of their diet, as adult *E. cunninghami* fed on insectivorous diets had a significant increase in digestive efficiency (Shine, 1971). *Egernia* therefore appear to exhibit some degree of dietary plasticity, which may be beneficial if the availability of insects and plant material fluctuates seasonally (e.g., Barwick, 1965; Duffield and Bull, 1998; Pollock, 1989).

Although herbivorous as adults, *Egernia cunninghami*, *E. stokesii* and *E. kingii* include Coleopterans as the major prey item when invertebrate material is consumed (Brown, 1991; Pollock, 1989; Shea, 1995). *Egernia kingii* was also reported to feed on small lizards and seabird eggs (Arena, 1986; Meathrel and Klomp, 1990; Wooller and Dunlop, 1990). Egg predation by *E. kingii* on the eggs of little penguins (*Eudyptula minor*) and sliver gulls (*Larus novaehollandiae*) may have a substantial impact on the reproductive success of these two species (Meathrel and Klomp, 1990; Wooller and Dunlop, 1990). Silver gulls and little penguins have prolonged breeding seasons of 8 and 6 months respectively, and seabird eggs provide *E. kingii* with a constant food source (Meathrel and Klomp, 1990; Wooller and Dunlop, 1990). This may also explain high population densities of these lizards on some of these islands (Arena, 1986; Langton, 2000). In an exclusion experiment Wooller and Dunlop (1990) reported 20% silver gull egg mortality in areas where *E. kingii* were excluded compared to 56% egg mortality in control areas where *E. kingii* had access, suggesting significant egg predation. Although an important dietary component, seabird eggs accounted for only a small proportion of each individual's diet; 88% of the diet of *E. kingii* consisted of plant material (Arena, 1986; Richards, 1990; R. Wooller, personal communication; Table 5).

Omnivory is the predominant dietary pattern in *E. coventryi*, *E. striolata*, *E. napoleonis* and *E. saxatilis*, with *E. coventryi* exhibiting a subtle ontogenetic shift from insectivory to omnivory (Table 5; Clemann, 1997). *Egernia striolata* and *E. saxatilis* appear to consume large and hard-bodied prey items, consisting predominantly of coleopterans, ants, grasshoppers, and cockroaches (Bustard, 1970; Brown, 1991). *Egernia coventryi* also feeds on spiders, flying insects, aquatic invertebrates, and small skinks (Clemann, 1997; Douch, 1994; Robertson, 1980; Schulz, 1992).

Egernia whitii, *E. inornata*, and *E. striata* are predominately insectivorous, but some plant material is consumed. The larger *E. kintorei* is omnivorous (Table 5). Plant material in these species, when present, generally consists of seeds, flowers and some fruits (Hickman, 1960; McAlpin, 2001*a*; Pianka and Giles, 1982). The arthropods consumed were mostly ants and termites in *E. inornata*, *E. striata* and *E. kintorei* (McAlpin, 2001*a*; Pianka and Giles, 1982); however, *E. whitii* also includes coleopterans, hemipterans, and arachnids in the diet (Brown, 1991; Hickman, 1960). *Egernia whitii* also includes a high proportion of hard-bodied prey items in the diet (Brown, 1991) and was observed to attack its prey head first and rub prey items against rocks (Hickman, 1960). The desert burrowing species *E. inornata* and *E. kintorei* were observed catching prey opportunistically as they passed their burrow entrances (Daniel, 1998; Pianka and Giles, 1982; Webber, 1978). *Egernia striata* and *E. kintorei* may forage actively at night venturing away from their burrows (McAlpin, 2001*a*; Pianka and Giles, 1982). *Egernia major* and *E. frerei* appear to be omnivorous despite their large body size (Table 5). Shea (1999) described a high frequency of fungi and nocturnal invertebrates in the diet of *E. major*, and anecdotal reports include snails, fungus and fruits (Schulz and Eyre, 1997; Swan, 1990).

PREDATION AND DEFENSE

Birds, snakes, and mammals are the major predators of *Egernia*. A wide variety of predators have been documented preying upon *Egernia*, including introduced cats and foxes (Table 6). Several species of *Egernia* (including *E. whitii*, *E. napoleonis*, *E. pulchra* and *E. inornata*) have been observed fleeing into their burrow or crevice when threatened by predators (Bush et al., 1995; Ford, 1965; Hutchinson, 1993; Webber, 1978; D. Chapple, personal observation). McAlpin (2001*a*) observed foxes and cats waiting near burrow entrances to attack *E. kintorei* as they emerged

TABLE 6.—Documented predation on *Egernia*. Predation records include observations of predation events and diet studies of predator species.

Species	Predator			Reference
	Scientific name	Common name	Introduced	
cunninghami				
E. cunninghami	*Pseudechis porphyriacus*	Red-bellied Black Snake	No	Shine (1977), Shine (1987*a*)
	Hoplocephalus bungaroides	Broad-headed Snake	No	J. Webb and R. Shine (personal communication)
E. stokesii	*Pseudonaja textilis*	Eastern Brown Snake	No	G. Duffield (unpublished data cited in Gardner, 1999)
	Suta suta	Myall or Curl Snake	No	Shine (1988*b*)
	Falco cenchroides?	Kestrel	No	G. Duffield (unpublished data cited in Gardner, 1999)
	Vulpes vulpes	Fox	Yes	G. Duffield (unpublished data cited in Gardner, 1999)
	Felis catus	Feral Cat	Yes	G. Duffield (unpublished data cited in Gardner, 1999)
striolata				
E. striolata	*Furina* [*Glyphodon*] *dunmali*	Dunmall's Snake	No	Shine (1981)
	Felis catus	Feral Cat	Yes	Molsher et al. (1999)
E. napoleonis	*Morelia spilota variegata*	Carpet Python	No	Shine and Slip (1990)
E. saxatilis	*Austrelaps ramsayi*	Highland Copperhead	No	Shine (1987*b*)
	Dasyurus maculatus	Tiger Quoll	No	Belcher (1995)
luctuosa				
E. coventryi	*Falco berigora*	Brown Falcon	No	P. McDonald (unpublished data)
	Vulpes vulpes	Fox	Yes	Taylor (1994)
whitii				
E. whitii	*Austrelaps ramsayi*	Highland Copperhead	No	Shine (1987*b*)
E. guthega	*Austrelaps ramsayi*	Highland Copperhead	No	Donnellan et al. (2002)
	Falco cenchroides	Kestrel	No	Donnellan et al. (2002)
E. margaretae	*Notechis ater*	Black Tiger Snake	No	Shine (1987*c*)
E. multiscutata	*Notechis ater*	Black Tiger Snake	No	Schwaner (1985)
E. kintorei	*Vulpes vulpes*	Fox	Yes	McAlpin (2001*a*)
	Felis catus	Feral Cat	Yes	McAlpin (2001*a*)
	Dasycercus cristicauda	Mulgara (Dasyuridae)	No	McAlpin (2001*a*)
major				
E. major	*Pseudechis porphyriacus*	Red-bellied Black Snake	No	Shine (1987*a*)

from their burrows. Foxes and cats may also employ this strategy against other species (e.g., *E. inornata*, *E. slateri*, *E. kintorei*, *E. multiscutata*) where individuals can be located by the presence of burrows. The continual movement between burrows by *E. inornata* may represent a mechanism to prevent this attack strategy by predators (Daniel, 1998).

Several species of *Egernia* have keeled scales, and there appears to be a relationship between the degree of keeling and the place of refuge (Cogger, 1960; Greer, 1989). In general, the more heavily keeled species (e.g., *E. cunninghami*, *E. stokesii*, *E. hosmeri* and *E. depressa*) tend to shelter in rock crevices or hollow logs, while the lightly keeled species (e.g., *E. saxatilis*, *E. striolata*, *E. major*) are saxicolous or semi-arboreal and shelter under exfoliating bark (Cogger, 2000; Greer, 1989). The smooth scaled species (e.g., *E. whitii*, *E. inornata*, *E. coventryi*) generally live in burrows or small rock crevices (Cogger, 2000; Greer, 1989).

The saxicoline species *E. cunninghami*, *E. stokesii*, *E. hosmeri* and *E. depressa* possess heavily keeled scales that have utility in several defensive behaviors to prevent their extraction from rock crevices and hollows (Greer, 1989; Cogger, 2000). The animal positions itself in the crevice generally facing away from the predator with its limbs pressed tightly against the body (Greer, 1989). Arching of the back or inflation of the lungs (e.g., *E. depressa*; Horner, 1991) acts to press the body against the crevice wall with the short, flat and extremely spiky tail pressed against the substrate (Greer, 1989). Any force exerted to extricate the lizard will cause the keels and tail spikes to dig into the sides of the retreat, making it more difficult to remove them (Greer, 1989). Similar defensive behaviors to prevent extraction from rock crevices have been reported for other saxicoline lizard taxa (Cooper et al., 2000), suggesting the evolution of such defensive behaviors is related to rocky habitats that these lizards inhabit. For species such as *E. cunninghami*, *E. stokesii*, *E. hosmeri* and *E. depressa* that seldom venture far from their crevice, this defensive mechanism appears to be extremely effective. *Egernia stokesii*, *E. depressa* and *E. hosmeri* possess short tails with heavily keeled scales that may further assist in such defensive behaviors. The ability to autotomize the tail has been lost in *E. stokesii* and *E. depressa* (Greer, 1989; Hutchinson, 1993), and the modified tail morphology and associated defensive behaviors in rocky environments may be adaptations to deter predation.

Background matching in some *Egernia* species may act to reduce detection by predators, particularly visually oriented predators such as birds. Barwick (1965) suggested the color pattern of *E. cunninghami* closely matches its background, and similar suggestions have been noted for *E. stokesii* (Gardner, 1999). Fraser (1985*b*) demonstrated that *E. cunninghami* closely matches its background (within 3–4% in the visible spectrum). Finally, Milton (1990) provided evidence that differential detection of pattern morphs by visually oriented predators may occur in certain habitats.

COLOR PATTERN POLYMORPHISM

Color pattern polymorphism occurs in five *Egernia* species (Table 7). *Egernia modesta* was listed as being polymorphic by Donnellan et al. (2002); however, recent examination of museum material has indicated that this species lacks distinct color morphs (D. Chapple, unpublished data). Three general morph types occur in *Egernia*: patterned, plain-back (lacking dorsal pattern) and patternless (lacking dorsal and lateral patterns) (Donnellan et al., 2002; Henzell, 1972; Milton, 1990). Most species only exhibit two of the three possible morphs, although all are present in *E. whitii* and *E. margaretae* (Donnellan et al., 2002; D. Chapple, unpublished data) Apart from pattern and coloration, each morph is morphologically indistinguishable (Donnellan et al., 2002; Milton et al., 1983; Milton, 1990). The genetic basis for color pattern polymorphism in *Egernia* is currently unknown, although the majority of color and pattern polymorphisms have simple Mendelian inheritance (e.g., Hoffman and Blouin, 2000).

TABLE 7.—*Egernia* species that exhibit color pattern polymorphism.

Species	Most common morph	Reference
whitii		
E. whitii	Patterned	Donnellan et al. (2002), Milton (1987, 1990)
E. margaretae	Patternless	Donnellan et al. (2002), Henzell (1972), Horner (1991)
E. montana	Plain-back	Donnellan et al. (2002)
E. multiscutata	Patterned	Donnellan et al. (2002), Hudson et al. (1981)
E. pulchra	Patterned	Ford (1963), Wilson and Knowles (1988)

The occurrence and relative abundance of each morph varies among populations (Table 7). Although both morphs of *E. multiscutata* occur sympatrically in South Australia (S. Bellamy, personal communication), only the patterned form is present in the Victorian population (Victorian Natural Resources and Environment, 2000). The frequency of the plain-back morph varies geographically in *E. whitii* (Storr, 1968). There is a high incidence of the plain-back morph on Kangaroo island, while only the patterned form of *E. whitii* is found in Tasmania (Donnellan et al., 2002). Henzell (1972) found the relative frequency of the plain-backed morph of *E. whitii* varied from 0–30%, although the variation in morph frequency could not be consistently correlated with any environmental factors. Milton (1990), examining museum specimens, showed that the relative abundance of *E. whitii* plain-back morphs decreased with increasing latitude (i.e., from north to south; Queensland: 0.26, N = 131; New South Wales: 0.21, N = 541; Victoria: 0.10, N = 828), suggesting that some ecological or environmental factor linked with latitude might be responsible for maintaining color pattern polymorphism in this species.

Morphological, reproductive, ecological, and genetic variation between the patterned and plain-backed color morphs has only been examined in *E. whitii* (Donnellan et al., 2002; Henzell, 1972; Milton et al., 1983; Milton and Hughes, 1986; Milton 1987, 1990). Milton (1987) showed the life history traits and reproductive ecology of each *E. whitii* morph were similar. Female *E. whitii* generally produced litters of same color morph as themselves (Henzell, 1972; Milton, 1987). However, litters consisting of offspring of each color morph regularly occurred, although such instances were more common in plain-back females (Milton, 1987). Female-biased sex ratio was reported in a population for patterned, but not plain-back, morphs (Milton, 1987). Despite earlier suggestions that plain-backed morphs may prefer more open habitats compared to patterned individuals (Milton and Hughes, 1986), *E. whitii* morphs did not differ in habitat use (D. Milton, unpublished data).

There are conflicting reports about the level of interbreeding between *E. whitii* morphs. Milton (1990), using allozyme data, reported non-random mating between each color morph in Queensland, with each morph preferentially mating with a partner of the same morph. However, Donnellan et al. (2002) found no evidence of genetic differentiation or assortative mating between the two morphs (patterned, plain-back) on Kangaroo Island. Donnellan et al. (2002) raised the possibility that the finding in Queensland (Milton 1990) could be the consequence of population substructuring in a widespread sample rather than evidence for assortative mating. Alternatively, the conflicting results could be related to different patterns of association between *E. whitii* individuals in each population. Milton (1987) found that *E. whitii* in Queensland populations formed social groups consisting almost exclusively of individuals of the same color morph. Such a situation could result in a pattern similar to assortative mating between color morphs. The absence of assortative mating on Kangaroo Island may be related to a high incidence of mixed-morph social groups. Mixed-morph groups were common in New South Wales and Victoria, and *E. whitii* individuals apparently did not segregate on the basis of their color pattern (D. Chapple, personal observation).

The similarity in the characteristics of color pattern in the five polymorphic *Egernia* species (Table 7) might suggest that polymorphism has only originated once within the monophyletic *whitii* species group (see Evolution, Systematics and Taxonomy section). Color pattern polymorphism is more prevalent within the rock-dwelling species (4 of the 6 species) within the species group compared to the obligate burrowing species (1 of the 5 species) (Table 7). Assuming that polymorphism is the ancestral state within the *whitii* species group, color polymorphisms have been lost secondarily in the majority of obligate burrowing species. Alternatively, if color pattern polymorphism is not the ancestral condition, then polymorphism may have evolved more frequently in rock-dwelling species that live in more mesic or coastal habitats compared to the semi-arid and arid desert burrowing species. Consequently, ecological and environmental factors may be correlated with the evolution or loss of color pattern polymorphism in *Egernia*; however, the evolution of polymorphism will be better addressed with a well-resolved phylogeny.

SOCIALITY

Although complex social organization is rare in squamate reptiles, complex sociality is apparently widespread within the genus *Egernia*. In most species of *Egernia*, social aggregations are observed any time of year, and have been described as families or colonies (Gardner, 1999; Greer, 1989; Hutchinson, 1993). Social aggregations have been reported in 23 of the 30 described species of *Egernia* (Table 8). The level of sociality is currently unknown for five species, hence the actual incidence of social groups in the genus may be higher. The only *Egernia* species considered to be solitary are *E. inornata* and *E. coventryi*.

In many instances the evidence for social aggregations in *Egernia* is circumstantial, with no indication of the degree of complexity of aggregations (Table 8). Long-term studies demonstrated that *E. stokesii* (Duffield and Bull, 2002; Gardner et al., 2001, 2002), *E. cunninghami* (Barwick, 1965; Stow et al., 2001; A. Stow, unpublished data), *E. saxatilis* (O'Connor and Shine, 2003) and *E. striolata* (Bonnett, 1999) exhibited stable social groups

Table 8.—Summary of *Egernia* sociality. Detailed summaries are provided in the text. Adapted from Gardner (1999).

Species	Sociality type	Group size	Study type			Reference
			Anecdotal	Short-term	Long-term	
cunninghami						
E. cunninghami	family group	2–26			X	Barwick (1965), Stow et al. (2001), A. Stow (unpublished data)
E. depressa	family group	–	X			Ehmann (1992), Horner (1991), Swanson (1976)
E. hosmeri	family group	2–9	X			Stammer (1976), Swanson (1976)
E. stokesii	stable family group	2–17			X	Duffield and Bull (2002), Gardner et al. (2001), Lanham (2001)
kingii						
E. kingii	family group	–	X	X		Arena (1986), Humphreys (1990), Richards (1990)
striolata						
E. striolata	solitary/small group	1–3			X	Bustard (1970)
	pairs/subadult groups	≤10		X		Bonnett (1999)
	family groups	–	X			Ehmann (1992), Swanson (1976)
E. carinata	colonies	–	X			Ehmann (1992)
E. douglasi	family group	–	X			Ehmann (1992)
E. formosa	no record					
E. mcpheei	family group	5–18	X			R. Hobson (personal communication)
E. napoleonis	family group	–	X			Bush et al. (1995)
E. pilbarensis	no record					
E. saxatilis	family group	2–14			X	O'Connor and Shine (2003)
luctuosa						
E. luctuosa	no record					
E. coventryi	solitary	1	X	X		Taylor (1994, 1995), N. Clemann (personal communication)
whitii						
E. whitii	family group	2–6		X		Bruyn (1994), Hickman (1960), Milton (1987)
E. guthega	colonies	–	X			Donnellan et al. (2002)
E. margaretae	pairs	2	X			Hutchinson (personal communication cited in Gardner, 1999)
E. modesta	family group	2–6		X		Milton (1987)
E. montana	colonies	–	X			Donnellan et al. (2002)
E. multiscutata	family group	–	X			Coventry and Robertson (1980), Hudson et al. (1981)
E. pulchra	family group	–	X			Ford (1963)
E. inornata	solitary	1		X		Daniel (1998)
E. kintorei	family group	2–10	X			Henzell (1972), McAlpin (2001*a*), Pearson et al. (2001)
E. slateri	family group	–	X			Ehmann (1992)
E. striata	pairs	2	X			Henzell (1972)
	family group	–	X			Pianka and Giles (1982), S. McAlpin (personal communication cited in Lanham 2001)
major						
E. major	family group	–	X	X		Ehmann (1992), Klingenbock et al. (2000)
E. arnhemensis	no record					
E. frerei	no record					
E. rugosa	colonies	–	X			Ehmann (1992), Swanson (1976)

comprised of closely related individuals. Shorter-term studies confirmed *E. whitii* (Milton, 1987), *E. modesta* (Milton, 1987) and *E. major* (Klingenbock et al., 2000) were consistently found in social groups but did not provide information about their stability or level of relatedness among group members.

The degree of sociality varies both within and among species (Greer, 1989) (Table 8). Intraspecific variation in sociality may be associated with habitat structure, at least in some species. Bustard (1970), working on a population of *E. striolata* in northern New South Wales where this species lives on tree stumps, reported it was only rarely found in groups. However, in South Australia *E. striolata* is a rock-dweller and commonly occurs in social aggregations comprised of closely related individuals (Bonnett, 1999). Lanham (2001) reported sociality was widespread in South Australian populations of *E. stokesii* (70% of all lizards collected were in groups), but group size varied among habitats. Although habitat features may be associated with sociality, questions remain as to the cause of the association. There is no hard evidence that lack of suitable refuges promotes sociality. Several species of *Egernia* apparently form groups even when suitable habitat is not limiting. Individuals of *E. striolata*, for example, remained in close contact and shared crevices even when their preferred habitat (rock crevices) was plentiful (Bonnett, 1999). Group members also remained in contact away from crevice refuges (Bonnett, 1999).

Temporal variation in sociality is also known to occur in *Egernia*. In *E. kintorei* burrow occupancy, group size, and composition were dynamic (McAlpin, 2001*a*). Likewise, O'Connor and Shine (2003) found that although 72% of *E. saxatilis* could be assigned to a social group, the majority of individuals spent a considerable amount of time on their own. Individuals of a family only spent 33% of their time in close proximity to other members of the group (O'Connor and Shine, 2003).

Group size varies among populations of *E. cunninghami*. Barwick (1965) found social aggregations of *E. cunninghami* near Canberra were comprised 2–17 individuals with around 83% of all individuals found in groups. In northern New South Wales group size varied from 2 to 26, although average group size was 8 (A. Stow, unpublished data). Group size was lower (2–9) with fewer animals found in groups (65%) on West Island off the coast of South Australia (Van Weenen, 1995).

Genetic evidence exists for stable, complex, social aggregations in *E. cunninghami*, *E. stokesi*, *E. saxatilis*, and *E. striolata*. Individual *E. cunninghami* in social aggregations were closely related and represented extended family groupings (Stow et al., 2001; A. Stow, unpublished data). Successive litters may remain with their parents for several years, resulting in formation of long-term stable social aggregations comprising a single breeding pair and variously aged juveniles and subadults (Barwick, 1965; A. Stow, unpublished data; Van Weenen, 1995).

Genetic evidence showed stable social aggregations of *E. stokesii* consisted of a breeding pair, their offspring from two or more cohorts, and other closely related individuals (Gardner et al., 2001). Social aggregations were made up of 2–17 individuals with 2–8 permanent members, although some animals were floaters, not belonging to any group (Duffield and Bull, 2002). *Egernia stokesii* groups were generally stable and occupied the same crevice, with individuals basking in close proximity and utilizing the same scat pile (Duffield and Bull, 2002). Duffield and Bull (2002) found most adults (73%) were permanent members of a social group for at least three years and 58% for more than four years. Most adults (73%) remained in the group in which they were first recorded for at least five years, suggesting *E. stokesii* aggregations are extremely stable (Duffield and Bull, 2002).

O'Connor and Shine (2003) examined the social behavior of *Egernia saxatilis* in a three-year study that combined behavioral observations and genetic analysis of relatedness using DNA microsatellites. Group size in *E. saxatilis* ranged from 2–14, with an average of 4.42 individuals per social group (O'Connor and Shine, 2003). The most commonly observed social grouping consisted of an adult breeding pair and in many instances one or more of their offspring (O'Connor and Shine, 2003). Thus, 'nuclear' family structure appears to be evident in *E. saxatilis* (O'Connor and Shine, 2003). The majority of *E. saxatilis* (72%) could be assigned to a social group, and such aggregations were found to be stable between years

(O'Connor and Shine, 2003). In social groups consisting of more than one adult, a single adult pair was generally observed (83% of groups; O'Connor and Shine, 2003). O'Connor and Shine (2003) reported that most juveniles (85%) lived in social groups, 65% in a group with at least one parent and 39% in a group with both parents.

In South Australia, groups of up to 10 *E. striolata* were observed, with groups generally sharing crevice refuges (Bonnett, 1999). However, the tendency to aggregate appeared dependent on both age and sex (Bonnett, 1999). Adults primarily used crevices used by only one or two animals, although females were more likely to be solitary than males (Bonnett, 1999). In contrast, subadults were more likely to use crevices where two or more lizards had been recorded (Bonnett, 1999). Individuals using a common crevice were found to be more related than expected by random associations (Bonnett, 1999).

O'Connor and Shine (2003) summarized the following similarities between the social systems of *E. cunninghami*, *E. stokesii*, *E. striolata* and *E. saxatilis*: 1) all live in social groupings; 2) groupings consist of closely related individuals; and 3) such groupings appear to be temporally stable, persisting for more than one year. However, several aspects of social organization clearly differ between these species. *Egernia stokesii* and *E. cunninghami* are the most social *Egernia* species, existing in large extended 'family' groupings for multiple seasons. Group members of these two species are commonly found in close proximity, basking together and sharing retreat sites (Barwick, 1965; A. Stow, unpublished data; Duffield and Bull, 2002). Few individuals were observed on their own (*E. stokesii* 30%, Lanham, 2001; *E. cunninghami* 21%, Barwick, 1965). *Egernia saxatilis* live in smaller groups (or 'nuclear' families). Although individuals remain in the group territory, they tend to use different areas within the group range at any one time (O'Connor and Shine, 2003). Sociality in *E. striolata* appears more flexible with related individuals sharing rock crevices and home ranges (Bonnett, 1999). However, social organization in *E. striolata* is similar in many respects to that observed in *E. saxatilis*, in that group members are not always found in close proximity (Bonnett, 1999). Consequently, although these four *Egernia* species exhibit the most complex social organizations within all squamate reptiles, considerable variation in social complexity exists among them.

Our understanding of the potential benefits of social groupings in *Egernia* is limited. Lanham (2001) suggested social aggregation in *E. stokesii* might benefit thermoregulation and predator detection. *Egernia stokesii* in larger groups maintained higher body temperatures after sunset (Lanham, 2001). Individual vigilance of *E. stokesii* group members was reduced compared to solitary individuals, although the overall vigilance of the entire group was equivalent to that of a solitary animal (Lanham, 2001). *Egernia stokesii* appeared able to warn other group members about potential threats as entire groups retreated into their crevices simultaneously (Gardner, 1999; Lanham, 2001). Social aggregations appear to have defensive benefits as both *E. stokesii* and *E. cunninghami* were able to detect approaching predators earlier when they were in groups compared to when they were alone (Eifler, 2001; Lanham, 2001).

Tolerance of juveniles in social groups may represent a form of indirect parental care (Shine, 1988*a*), particularly in species where aggression may result in serious injury or death. Such indirect parental care has only been examined in detail in *E. saxatilis*, a species highly aggressive towards conspecifics (D. O'Connor, unpublished data). Adult *E. saxatilis* were as aggressive towards subadults and neonates as towards other adults (D. O'Connor, unpublished data). However, adult females were less aggressive towards their own offspring than to unrelated offspring (D. O'Connor, unpublished data). Adult *E. saxatilis* were less aggressive towards juveniles when their mother was present, suggesting that close proximity to their mother conferred benefits to juveniles (D. O'Connor, unpublished data). There is also evidence to suggest that juveniles in territory holding family groups spent more time basking compared to juveniles in subordinate family groups (D. O'Connor, unpublished data). Consequently, it appears beneficial for juvenile *E. saxatilis* to belong to a social group, particularly a family group. Thus, indirect parental care may encourage aggregations of closely related individuals to occur in *E. saxatilis* rather than simply groupings of unrelated individuals (O'Connor and Shine, 2003; D. O'Connor, unpublished data).

Anecdotal evidence for complex sociality is available for other *Egernia* species (Table 8). *Egernia hosmeri* and *E. depressa* form social aggregations consisting of adults and juveniles (interpreted as family groups), within rock crevices or hollow logs (Ehmann, 1992; Horner, 1991; Stammer, 1976; Swanson, 1976). *Egernia kingii* occurred in groups of 2–3 adults and some subadults and juveniles that remained within the group until they reached maturity (Arena, 1986; Humphreys, 1990; Richards, 1990). Social aggregations have been reported for *E. carinata*, *E. mcpheei*, *E. napoleonis* and *E. douglasi* (Table 8). *Egernia carinata*, *E. napoleonis* and *E. douglasi* apparently formed localized colonies in rock crevices and hollow logs (Bush et al., 1995; Ehmann, 1992). *Egernia mcpheei* were found in large aggregations (5–18 individuals) containing adults and juveniles, under exfoliating basalt and in old hut stumps (R. Hobson, personal communication).

Social aggregations have not been reported in *E. luctuosa* or *E. coventryi* (Table 8). Although *E. coventryi* were observed basking close together (~30 cm), this species is known to be extremely aggressive and conspecifics will kill each other in high densities in captivity (i.e., >2–3 in 2 m diameter enclosure; Taylor, 1994, 1995; N. Clemann, personal communication). Consequently, *E. coventryi* is currently regarded as a solitary species (Table 8). No records are available for the level of sociality in *E. frerei* or *E. arnhemensis*, although both *E. major* and *E. rugosa* form small colonies (Ehmann, 1992; Swanson, 1976).

Although delayed dispersal may occur in *E. inornata* (Daniel, 1998; Webber, 1978) this species is generally considered to be solitary. Male and female *E. margaretae* pairs have been observed using the same retreat (Hutchinson, personal communication cited in Gardner, 1999), but the group structure is currently unknown. Evidence for social aggregations in *E. pulchra* (Ford, 1963), *E. slateri* (Ehmann, 1992), *E. multiscutata* (Coventry and Robertson, 1980; Hudson et al., 1981) and *E. striata* (Henzell, 1972; Pianka and Giles, 1982) comes from the observation that several individuals, generally adult pairs and juveniles, were found in the same burrow system. In *E. kintorei* group size may be large (2–10) with juveniles from the current and previous year found in the same burrow as their parents (Cogger, 2000; Henzell, 1972; McAlpin 2001*a*; Pearson et al., 2001). *Egernia whitii* and *E. modesta* generally live in groups containing 2–6 individuals consisting of a breeding pair and their offspring, which remain in the group for about one year when they are displaced by the next litter (Bruyn, 1994; Hickman, 1960; Milton, 1987). Associations between breeding pairs in these two species may last up to three years (Milton, 1987).

Kin Recognition and Social Cohesion

Group and kin recognition based on chemical cues has been demonstrated in several *Egernia* species. *Egernia stokesii* discriminated between chemical cues of group and non-group members (Bull et al., 2000), while self-recognition was reported for *E. inornata* and *E. striolata* (Bull et al., 1999*a*). Reciprocal mother-offspring recognition was demonstrated in *E. stokesii* (Main and Bull, 1996), while *E. striolata* was able to discriminate, using chemical cues, between unfamiliar lizards based on their degree of relatedness (Bull et al., 2001). Group or kin recognition appears to have an important function in *E. striolata* as individuals were shown to alter their behavior in the presence of unrelated individuals (Bull et al., 2001). *Egernia whitii* killed unrelated offspring placed with them (Bruyn, 1994) and therefore kin recognition may play an important role in group formation and cohesion. However, the exact mechanism for kin recognition in *Egernia* is unclear as evidence exists for both familiarity (*E. stokesii* group recognition, Bull et al., 2000) and genetic ('true') kin recognition (*E. stokesii* mother/offspring recognition, Main and Bull, 1996; *E. striolata*, Bull et al., 2001).

Aggressive interactions have been observed between group members in several species of *Egernia*. Adult *E. hosmeri* have been observed attacking newborns, inflicting serious injury, and adult males can also be extremely aggressive towards each other (Post, 2000). Intense aggression was observed between *E. whitii* individuals despite the presence of social groups in this species (Bruyn, 1994; Girardi, 1996; Hutchinson, 1993; D. Chapple,

TABLE 9.—Published references to scat piling in the *Egernia* genus.

Species	Scat piler	Reference
cunninghami		
E. cunninghami	Yes	Barwick (1965)
E. hosmeri	Yes	Post (2000), Stammer (1976)
E. stokesii	Yes	Duffield and Bull (1998), Gardner (1999)
kingii		
E. kingii	Yes	Ehmann (1992)
striolata		
E. striolata	Yes	Bull et al. (1999*a,b*), Bustard (1970)
luctuosa		
E. coventryi	Yes	Clemann (1997), Douch (1994)
whitii		
E. whitii	Yes	Hickman (1960), Swan (1990)
E. inornata	Yes (underground)	Hutchinson (1993)
	No	Bull et al. (1999*a*), Webber (1978)
E. kintorei	Yes	McAlpin (2001*a*), Pearson et al. (2001)
E. slateri	Yes	Ehmann (1992)
major		
E. rugosa	Yes	Ehmann (1992), Wilson and Knowles (1988)

personal observation). However, aggressive encounters were less frequent in groups of closely related individuals (Bruyn, 1994). Early suggestions that social hierarchies exist within *Egernia* aggregations (Barwick, 1965) have found support from recent investigations. Lanham (2001) found the benefits of sociality were not equally shared amongst *E. stokesii* group members. Subordinate individuals were less active and spent less time basking when in a group. Male *E. kingii* were observed fighting during the breeding season, and in captivity they establish dominance hierarchies with bouts of aggression (Arena, 1986). Likewise, male *E. whitii* form dominance hierarchies in captivity. Data from an endocrine study suggested subordinate males experienced higher stress than dominant ones (Bell, 1997). Clearly, the mechanisms through which *Egernia* maintain their social structure and causes of variation in sociality are poorly understood and warrant further investigation.

Scat Piling

Many species of *Egernia* exhibit a tendency to repeatedly defecate at the same site, creating prominent 'latrines' or scat piles near their crevice or burrow (Greer, 1989). The incidence of scat piling was previously believed to be restricted to six species of *Egernia* (Greer, 1989); however, scat piling has now been observed in 11 species (Table 9). Scat piling occurs in many species of mammal and the production of latrines are believed to serve a variety of social functions such as territory marking (e.g., Roper et al., 1993; Sneddon, 1991). However, apart from *Egernia*, there is no evidence to suggest that any species of squamate reptile utilizes scat piles as a social marker in a similar manner to mammals (Bull et al., 1999*a*).

Scat piles are located near the entrance to a permanent home site, generally a crevice or burrow. Regular defecation at the one site by all group members results in the formation of a large scat pile (>50 scats, 1–3 m^2; *E. cunninghami*, Barwick, 1965; *E. kintorei*, McAlpin, 2001*a*) and in some instances, particularly for rare or secretive species, scat piles indicate the presence of the species in the area (e.g., *E. rugosa*, Wilson and Knowles, 1988). Although the large size of scat piles and their proximity to the permanent home site may advertise their presence to potential predators, it has been suggested that scat piles serve some important function in *Egernia*.

The simplest explanation for the occurrence of scat piles is that they are found at the favored morning basking site where the lizard first reaches temperatures adequate to induce defecation, and scat piles accumulate passively (Bull et al., 1999*a*; Greer, 1989). However,

TABLE 10.—Conservation status of species of *Egernia* that have been listed Nationally or in any State. Recovery plans that are currently in place are indicated. Codes for Australian States are: VIC = Victoria; SA = South Australia; WA = Western Australia; NSW = New South Wales.

	Conservation status					
Species	Crit. endangered	Endangered	Vulnerable	Threatened	Rare/extinction likely	Recovery plan
cunninghami						
E. cunninghami			SA			–
E. stokesii aethiops					WA	–
badia					WA	–
luctuosa						
E. coventryi		SA	VIC			VIC
whitii						
E. margaretae		NSW				NSW
E. multiscutata	VIC					VIC
E. inornata				VIC		–
E. kintorei		SA/National				National
E. slateri		SA/National				–
major						
E. rugosa			QLD			–

defecation may occur more than once each day (morning and afternoon) with lizards travelling to the same site to defecate (e.g., *E. whitii*, Hickman, 1960). Therefore, the 'active' formation of scat piles suggests scat piling serves some purpose. Ehmann (1992) suggested scat piles might act to attract insects close to the home site, which lizards could presumably feed upon opportunistically, but there is no evidence favoring this hypothesis. Scat piling may instead serve some social function in species of *Egernia* that exhibit complex sociality.

There is some evidence scat piles mark the territory of a social group (e.g., Barwick, 1965; Swan, 1990). *Egernia striolata* (Table 9) discriminated between chemical cues in its own scats from those in the scats of unfamiliar lizards (Bull et al., 1999*a*). These signals were unrelated to diet (Bull et al., 1999*a*). *Egernia stokesii* (Table 9) also discriminated between group and non-group members using chemical cues contained in scats (Bull et al., 2000). *Egernia inornata*, a species that lacks complex sociality but does make scat piles near burrow entrances (Table 9), is apparently unable to discriminate between chemical cues from scat (Bull et al., 1999*a*). These studies support the view that scats serve some social function. Bull et al. (1999*b*) demonstrated that *E. striolata* use chemical cues rather than visual or tactile cues to discriminate between scats. Evidence suggests chemical cues consist of a complex combination of chemical signals (Bull et al., 1999*b*). Consequently, scats may contain individual signals that indicate residency of an individual or social group, although lizards may not necessarily avoid areas with such signals (e.g., *E. stokesii*, C. Griffin, unpublished data). Because scat signals deteriorate with time (Bull et al., 1999*a*), scat piling may be necessary to renew the signal and retain its social function.

Sociality in Other Lizard Taxa

Numerous species of squamates form aggregations generally associated with reproduction (reviewed by Graves and Duvall, 1995) or thermoregulation (e.g., winter aggregations; Congdon et al., 1979; Elfstrom and Zucker, 1999). For example, some Australian skinks (e.g., *Lampropholis guichenoti*) form hibernation aggregations of up to 50 individuals (Pengilley, 1972; Powell et al., 1977; Rawlinson, 1974). Although these species display a degree of sociality, none could be classified as exhibiting stable social aggregations. Lemos-Espinal et al. (1997*a*) reported the iguanid *Sceloporus mucronatus mucronatus* forms stable groups of up to nine individuals, with most groups consisting of a single male and female pair. Female-juvenile pairs or groups living within rock crevices were documented in *Xenosaurus newmanorum* in Mexico (Lemos-Espinal et al., 1997*b*). In South

America, females of *Liolaemus huacahuasicus* (Tropiduridae) remained with their offspring and shared the same area for up to two years (Halloy and Halloy, 1997). Occasionally, a male may be present and contribute to the defense of the territory (Halloy and Halloy, 1997). The agamid, *Stellio caucasius*, was reported to occur in stable social aggregations consisting of a single male, one or more females, juveniles and subadults (Panov and Zykova, 1993).

Complex sociality (i.e., stable aggregations) therefore appears to have evolved multiple times in a diverse array of lizard lineages. The most well studied is the armadillo lizard, *Cordylus cataphractus*, in South Africa (Mouton et al., 1999). Most *C. cataphractus* (85%) were found in social aggregations. These lizards have been observed to occur in large groups with up to 30 individuals. Although smaller groups (<9) usually only have a single male, larger groups can consist of more than one male. All members of a group were observed to retreat simultaneously to refuge when threatened (Mouton et al., 1999), a trait also observed in *E. cunninghami* and *E. stokesii*. Four related species, *C. peersi*, *C. macropholis*, *C. cordylus* and *C. giganteus*, also exhibit some degree of complex sociality, but not to the same extent as *C. cataphractus* (Branch, 1975, 1988; Mouton et al., 1999).

Conservation Status

Nine *Egernia* species are currently recognized by state or national legislation as being threatened, vulnerable or endangered, and recovery plans are in place for four of these species (Table 10). *Egernia cunninghami*, *E. stokesii*, *E. margaretae*, *E. multiscutata* and *E. inornata* are listed under state legislation due to the rare occurrence of outlier or disjunct populations within a particular state (Table 10). However, each of these species has widespread distributions elsewhere in Australia and therefore the species itself is not of significant conservation concern. *Egernia coventryi*, *E. kintorei*, *E. slateri* and *E. rugosa*, however, are rare, endangered or threatened throughout their distribution and therefore represent a more substantial conservation concern (Table 10).

The desert burrowing species *E. slateri* and *E. kintorei* are both listed nationally as endangered (Table 10). Both species have been recorded from only a few populations and population estimates for *E. slateri* (200–300) and *E. kintorei* (6250) are extremely low, with recent range reductions for both species (McAlpin, 2001*a*; Environment Australia, 2001). Both species have declined in a similar manner to many medium sized mammals (30–1500 g; Burbridge and McKenzie, 1989) in central Australia during the past 100 years. However, similar declines have not been observed in *E. inornata* and *E. striata*, which both have widespread distributions in central Australia and share similar patterns of life-history and habitat use with *E. kintorei* and *E. slateri*. The introduction of exotic predators and competing herbivores, alteration of fire regimes and the reduction in traditional aboriginal hunting have been suggested as possible cause of the decline of *E. slateri* and *E. kintorei* (McAlpin, 2001*a,b*; Pearson et al., 2001). Foxes and cats have been observed to prey upon *E. kintorei* and rabbits have been known to displace animals from their burrows; however, their impact on these endangered species is currently unknown (McAlpin, 2001*a*).

Many species of *Egernia* live in naturally disjunct populations or have specialized habitat requirements. *Egernia coventryi* is generally restricted to coastal swamps and is therefore vulnerable to anthropogenic impacts such as the draining of natural swamps throughout its limited range (Clemann, 2000). Habitat fragmentation also may affect species that live in a wide range of habitats. *Egernia whitii* is an abundant species in eastern Australia and is commonly found in rocky outcrops, woodlands and alpine grasslands (Cogger, 2000). However, *E. whitii* appears to be vulnerable to habitat fragmentation in the box-ironbark forests in central Victoria (Mac Nally and Brown, 2001). *Egernia whitii* was found to be completely absent from all sizes of habitat fragments, but common in the surrounding reference habitats (Mac Nally and Brown, 2001). This may be a consequence of *E. whitii*'s association with rocky situations or its reliance on burrows and other permanent home retreats. However, other species such as *E. major* may benefit from some anthropogenic disturbance. *Egernia major* appears to take advantage of open clearings adjacent to forest areas and the abundance of fallen logs, although it appears to actively avoid crossing roads (Klingenbock et al., 2000).

Discussion

The *Egernia* genus is part of a monophyletic Australasian Scincid lineage, referred to as the *Egernia* group, within the *Mabuya* group that also includes the genera *Tiliqua* (7 species), *Cyclodomorphus* (9 species), and *Corucia* (1 species). These genera are divergent from their Asian and African relatives (Greer, 1989; Honda et al., 1999, 2000), and although the phylogenetic relationships between the 4 genera are still unclear (Greer, 1989; Honda et al., 1999; Donnellan et al., unpublished data), multiple shifts in mating system and sociality appear to have occurred within this clade. Anecdotal reports of complex sociality are rare in *Tiliqua*, *Cyclodomorphus* and *Corucia* (Gardner, 1999), although long-term monogamy involving annual pair bonds of 6–8 weeks during the mating season has been reported for the sleepy lizard, *Tiliqua rugosa* (reviewed in Bull, 2000).

Despite the limited number of *Egernia* species where detailed study has been completed on their social complexity (4 species) and mating system (3 species), this review highlights the potential of this genus to provide a valuable contribution to our understanding of the forces responsible for the evolution of complex sociality and monogamous mating systems. Within *Egernia*, sociality ranges from highly social to primarily solitary. This diversity in social complexity among species and populations of the same species offers exciting opportunities to relate independent origins and losses of complex sociality to the broad range of habitats that *Egernia* species inhabit and the ecological conditions they experience. Reptiles have largely been ignored in the search for a unified theory for the evolution of sociality (e.g., Alexander, 1974; Cahan et al., 2002). However, evolution of complex sociality and monogamous mating systems in reptiles, which appears to be similar to that observed in birds, mammals, and social insects, provides another data set from a distantly related lineage. Consequently, squamate reptiles, and in particular *Egernia*, appear to have much to offer in the search for the factors or ecological correlates related to the evolution or loss of complex sociality.

O'Connor and Shine (2003) suggested there are several advantages of examining the evolution of sociality and monogamy in squamate reptiles compared to the favored avian models. They propose that the phylogenetic distribution of anecdotal reports of lizard sociality suggest that: 1) the ancestral condition in lizards was non-social; and 2) complex sociality has apparently evolved independently in a variety of disparate lineages (e.g., skinks, cordylids, agamids, xerosaurids, and tropurids). In contrast, birds appear to have evolved from a common monogamous ancestor (Temrin and Sillen-Tullberg, 1994), and therefore may be unable to provide explanations about the origins of monogamy. O'Connor and Shine (2003) further pointed out that direct parental care may have been a major selective force in the evolution of sociality and monogamy in both birds (e.g., Lack, 1968; Moller, 1986; Wittenberger and Tilson, 1980) and mammals (e.g., Gubernick and Teferi, 2000). However, the virtual absence of parental care in squamate reptiles (reviewed in Shine, 1988*a*) simplifies the investigation of putative costs and benefits of social aggregations and suggests that squamate reptiles are an ideal lineage with which to examine the evolution of monogamy and complex sociality.

Evolution of Complex Sociality in Egernia

There have been numerous attempts across a wide variety of vertebrate and invertebrate taxa to identify the ecological correlates of origins and losses of social complexity (e.g., Danforth, 2002; Duffy et al., 2000; Jarvis and Bennett, 1993; Thorne, 1997). Despite the lack of a well-resolved phylogeny for *Egernia*, discussion of potential correlates of complex sociality and co-evolved combinations of traits is possible. Detailed studies on the social complexity of four species of *Egernia* yielded several hypotheses for the conditions that may have promoted aggregation and subsequent complex sociality in *Egernia*. The proposed hypotheses for the evolution of sociality, not mutually exclusive, fall into two broad categories: 1) habitat availability; and 2) life-history strategy (i.e., life-span and age at maturity).

Hypotheses about the influence of habitat availability on social complexity were proposed by Duffield and Bull (2002), and O'Connor and Shine (2003). *Egernia stokesii*, *E. cunninghami*, *E. saxatilis* and *E. striolata* (in South Australia) all live in rocky outcrops, which may be isolated from other such rocky outcrops. For *E. stokesii* at least, such outcrops may contain dense and stable populations (Duffield and Bull, 2002). If all potential crevice refuges are occupied within the outcrop, the only options are to disperse to another outcrop or share crevices (Duffield and Bull, 2002). Because dispersal distances in *E. cunninghami* and *E. stokesii* are generally low (Barwick, 1965; Duffield and Bull, 2002; Stow et al., 2001), tolerance of crevice sharing may result. Consequently, appropriate behavioral adaptations for group living may evolve in populations where large aggregations occur in shared crevices (Duffield and Bull, 2002). This hypothesis also has been invoked to explain the presence of social aggregations in *Cordylus cataphractus* (Mouton et al., 1999). O'Connor and Shine (2003) further suggested that crevice size may influence the size of resultant social groups. *Egernia stokesii* and *E. cunninghami* inhabit large crevices in rock outcrops that are able to accommodate a considerable number of individuals. However, *E. saxatilis* occupies smaller crevices in loose surface rocks, which may prevent the formation of such large aggregations (O'Connor and Shine, 2003). The habitat availability hypothesis predicts that higher levels of social complexity should evolve where habitat is limited. Importantly, it may be possible to test this hypothesis by comparing social complexity between populations of the same species that use different habitats (e.g., *E. striolata*, *E. saxatilis*).

The second category of hypotheses relate to life-history characteristics (e.g., life-span, age at maturity) and were suggested based on studies of *E. stokesii* social aggregations (Duffield and Bull, 2002), but may be extended to species such as *E. cunninghami* and *E. saxatilis*. In *E. stokesii* individuals are generally long-lived, taking up to 5–6 years to reach maturity and persisting as adults for 6 years or more (Duffield and Bull, 2002; Table 2). However, longevity in this species may be substantially longer than 12 years (up to 25 years) due to low adult and subadult mortality (Duffield and Bull, 2002; Table 2). Consequently, social relationships may develop among conspecifics sharing rock crevices (Duffield and Bull, 2002). Since *E. stokesii* mature late, adults may tolerate the presence of closely related juveniles and subadults because they pose no threat to their reproduction or present any inbreeding risk (Duffield and Bull, 2002). Furthermore, an adult could increase its offspring survival by allowing shared use of parental crevices and providing it with increased group vigilance against predators (Duffield and Bull, 2002; Lanham, 2001). The central prediction of this life-history hypothesis is that late-maturing, long-lived species should exhibit larger social aggregations. It will be possible to test this prediction with information on more *Egernia* species; however, exciting possibilities exist to compare group size and complexity in species such as *E. whitii* that exhibit geographic variation in age at maturity and other life-history traits. Support for these hypotheses also will support the studies on birds and mammals that have indicated that social groups have evolved in relation to saturated habitat, high survival, and delayed juvenile dispersal (Arnold and Owens, 1998, 1999; Emlen and Oring, 1977).

Although the assumption, particularly in squamates, is intuitive that social lineages were derived from solitary forms, the reverse also may have occurred. Indeed, recent studies have indicated that complex sociality can be lost, and derived species are secondarily solitary (e.g., Danforth, 2002; Wcislo and Danforth, 1997). I suggest studies of *Egernia* also offer the possibility to examine correlates of the secondary loss of complex sociality, because some species (e.g., *E. inornata*) or populations (e.g., tree dwelling *E. striolata*) of *Egernia* will probably be shown to be derived from social ancestors. Examination of factors that lead to the evolutionary loss of complex sociality should provide interesting insights into factors that lead to the evolution and maintenance of sociality (Wcislo and Danforth, 1997). Consequently, studies on solitary *Egernia* species such as *E. inornata* and *E. coventryi* may provide much insight into the ecological correlates of sociality in the genus.

Emlen (1994), relying mostly on avian examples, suggested family groups may evolve either from benefits associated with philopatry or habitat constraints (see above). Parental care is a central component of family groups in mammals, birds and social insects. A small degree of parental care can be considered to exist in *Egernia*, although it may be indirect or simply a consequence of group living. Several examples of parental care have been described in *Egernia*: 1) mother assisting young out of embryonic membranes; 2) reduced aggression towards and tolerance of juveniles within social groups; and 3) the associated benefits of group membership such as enhanced vigilance. Although the limited parental care in *Egernia* may increase offspring survival, at this time is hard to argue that benefits of philopatry would promote the evolution of complex sociality in *Egernia*. Rather such benefits may have evolved secondarily in the presence of stable social aggregations (e.g., Emlen, 1994).

Evolution of Monogamy in Egernia

Monogamy is rarely reported in lizards, although within season monogamy occurs in several species as a result of territoriality or mate guarding (reviewed in Bull, 2000). Long-term monogamy has been reported for *E. stokesii*, *E. cunninghami*, *E. saxatilis* and *Tiliqua rugosa*, and has been examined thoroughly in the latter species (Bull, 2000). Despite the extensive behavioral evidence for social monogamy in each species, genetic analyses revealed the incidence of extra-pair copulations. Research on birds have highlighted that social monogamy does not always imply genetic monogamy (Black, 1996; Petrie and Kempenaers, 1998). Over 90% of birds are considered socially monogamous (Ford, 1983; Lack, 1968; Moller, 1986), for example, but genetic monogamy has been found in only 10–25% of all birds studied (Griffith et al., 2002; Hasselquist and Sherman, 2001). In comparison, the level of extra-pair paternity in lizards (20% *E. saxatilis*, O'Connor and Shine, 2003; 25% *E. stokesii*, Gardner et al., 2002; 19% *Tiliqua rugosa*, Bull et al., 1998) compares favorably with passerine birds (23%, Hasselquuist and Sherman, 2001).

The evolution of monogamy in animal taxa is generally associated with the presence of stable social groups (e.g., Wittenberger and Tilson, 1980), therefore many of the factors responsible for the evolution of complex sociality also may be related to the evolution of monogamy. Long-term monogamy and complex sociality both occur in the three *Egernia* species studied to date (*E. cunninghami*, *E. saxatilis*, *E. stokesii*) and may be a consequence of breeding adults within stable social groups consistently pairing with the same partner each season (see below). However, monogamy occurs without long-term stable group structure in the closely related sleepy lizard, *Tiliqua rugosa* (reviewed in Bull, 2000). The majority of explanations for the evolution of monogamy developed using birds also involve reference to parental care (e.g., Wittenberger and Tilson, 1980; reviewed in Bull, 2000). However, monogamy has evolved repeatedly in a broad range of invertebrate and vertebrate taxa, and in the majority of instances in the absence of bi-parental care (reviewed in Matthews, 2002). Consequently, *Egernia* and the related genera *Tiliqua* provide an opportunity to examine the evolution of monogamy in the absence of direct parental care.

FUTURE RESEARCH

To take advantage of the potential of the *Egernia* lineage as a reptilian model system for the study of the evolution of complex social organization and monogamy, and to examine putative ecological and environmental correlates of sociality in any comparative framework, research on *Egernia* is needed in several areas of natural history, behavioral ecology, and systematics.

Evidence for social aggregations in the majority of *Egernia* species is primarily anecdotal, and information is needed on the diversity of social organization within the genus, particularly species with less complex social organization. Studies of costs and benefits of group living (e.g., thermoregulation, vigilance, parasite load, inbreeding) in different ecological contexts offer much scope for a variety of studies, and would shed light on conditions favoring sociality. Several *Egernia* species inhabit a wide variety of ecological environments across their range, for example, and comparison of mating systems and social complexity among populations with disparate habitat use would potentially provide the most useful insight into the ecological correlates of sociality in *Egernia*. Specifically, experiments designed to test the habitat availability hypothesis may shed light upon the costs and benefits of sociality in *Egernia*.

Mechanisms responsible for group formation and subsequent maintenance and social cohesion have yet to be adequately identified. Social groups in the four species studied to date consist of closely related individuals, and chemical cues are presumably used to maintain social groupings. Understanding the extent of kin recognition across the *Egernia* genus and whether chemical discrimination between individuals is based on familiarity or genetic kin recognition is important because this information would allow assessment of the role of kin recognition in facilitating group formation.

In addition to information on natural history of the species, it is clear that a well-resolved phylogeny for *Egernia* and the closely allied genera (*Tiliqua*, *Cyclodomorphus* and *Corucia*) is needed to clarify the systematics and taxonomy of the lineage. Once a phylogeny is available, traits presumably linked to complex sociality and monogamy can be examined in a phylogenetic context (Harvey and Pagel, 1991) in order to disentangle the roles of evolutionary history and local ecological processes, that together have resulted in the complex variation of social organization apparent within the genus *Egernia*.

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