Group-living in the Australian skink, *Egernia stokesii.*

A thesis submitted for the degree of Doctor of Philosophy

by

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For Dion,
wish you were here.

Author's Declaration

I certify that this thesis does not incorporate, without acknowledgment, any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

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Elvira Jane Lanham.
May, 2001.

Abstract.

Until recently, reptiles have been thought to exhibit little more than rudimentary sociality. Males of most species studied so far are either solitary or defend territories, containing one or more females. Some species have developed complex visual displays to maintain their territory and tolerance of other males is limited to non breeding juveniles.

Much of the ideas about lizard social behaviour have come from the study of visually-orientated species such as the iguanids and agamids. Little is known about the more fossorial species, but as their behaviour receives more attention there appears to be more diversity among these taxa than first thought.

Egernia stokesii displays unusually stable, long-term group fidelity, with groups in one well studied population ranging from 2-17 individuals (Duffield and Bull, 2001). Group members share the same home range and overnighting refuges and can stay together for at least five years. Individuals within these groups spend significantly more time interacting with one another than with lizards from neighbouring groups and they are significantly more related to each other than to the rest of the population.

The question that this thesis addresses is why this unusual behaviour occurs. What are the benefits to *E. stokesii* of year round group-living when other closely related species that share the same habitat do not show this type of group fidelity.

Initially, grouping behaviour was investigated in other populations than the one from which this behaviour was first described. This was to ensure that group fidelity was not just a phenomena of one population and also to address the hypothesis that group size will vary depending on environmental conditions. A survey of four regions within the South Australian distribution of this species found groups of up to nine individuals occurred throughout the South Australian range of this lizard, and group size fluctuated depending on habitat.

The mechanisms behind the formation of these groups was then investigated by examining the possibility that grouping occurred only as a result of a limit in suitable refuge sites. Groups of different compositions were provided with opportunities to disperse by allowing them access to more crevices than there were individuals. In general, lizards still remained aggregated when compared to a random distribution, especially related juveniles.

If grouping behaviour could not just be accounted for by a lack of suitable habitat, then there should be benefits to the individual. The physical benefits of grouping to the thermal biology of the lizards were examined. Lizards formed larger aggregations at cooler temperatures and they were able to maintain a higher temperature after sunset when they were in groups, compared to when they were alone.

Antipredator advantages of grouping behaviour were also investigated. Juvenile lizards in a group came out from their shelter for longer period than those living alone. Both adults and juveniles in a group showed reduced vigilance behaviour (measured as eyes open per minute of basking time) compared to lizards living alone, although the vigilance of the group as a whole was not reduced. In fact, in a separate experiment, lizards in a group responded sooner to a potential threat than when they were by themselves.

Individual lizards derive both thermal and antipredator benefits from joining a group, but these may not be equally shared among group members. In the final data chapter of this thesis, experiments are reported that show that subordinate lizards spent more time in refuges and less time basking when they were grouped, compared to when they were alone. This suggests they were curtailing activities such as thermoregulation as a response to the presence of other lizards.

The results reported in this thesis suggest a sophisticated sociality in *E. stokesii* that has not previously been documented in lizards.

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Chapter 1

Introduction

The study of sociality has derived much of its knowledge from work on insects such as the hymenoptera (bees, ants and wasps) and from mammals such as primates, lions and highly social ground-dwelling species such as meerkats (*Suricata suricatta*) and prairie dogs.

So far, reptiles have contributed little to this field. This thesis explores some of the benefits of sociality in an Australian lizard that has been shown to exhibit unusual sociality for a reptile (Duffield and Bull, 2001).

1.1 Evolution and function of sociality in animals.

While benefits of sociality to an individual vary from one species to another, the costs of group living are universal (Alexander, 1974). Animals that live in groups must compete for resources, they also increase the likelihood of transmission of disease or parasites (eg MacRae, 1996; Davis and Brown, 2000) and they may be more conspicuous to predators (Lott, 1991 ;eg Connell, 2000). In groups there are increased opportunities for mate displacement, reproductive interference and infanticide. Also, where relatives form a group, inbreeding depression is also a risk

Yet sociality, in a variety of forms, persists among species of most taxa. A society is defined as a group of individuals belonging to the same species and organised in a cooperative manner (Wilson, 2000) The most highly developed form of sociality, termed eusociality is characterised by a reproductive division of labour, where most group members do not reproduce, there are overlapping generations and there is cooperative care of the offspring that are produced by a few breeders (Table 1-1). In this form of social organisation, the social group has non-reproductive members that can perform defensive and resource gathering tasks to enhance the fitness of offspring of the reproductive group members (Wilson, 1971).

Table 1-1 Social systems as defined by Wilson, (1971).

Degree of sociality	Cooperative care of young	Reproductive castes	Overlap between generations
Solitary/Communal	-	-	-
Quasisocial	+	-	-
Semisocial	+	+	-
Eusocial	+	+	+

Eusociality, as defined above was first established in the Hymenoptera (ants, bees & wasps). Most species within this Order have a unique form of sex determination, termed haplodiploidy, where fertilised eggs produce females and unfertilised eggs produce males. In this system, females are more related to their sisters than they are to their daughters. Over time, this has produced sterile female castes, which revolve around a central, fertile female. This type of colony was thought to represent the pinnacle of social evolution, where group members are completely reliant on other individuals either for food or reproduction (Wilson, 1975). Many researchers also assumed that this degree of sociality was unique to these insect taxa, and probably relied on the presence of haplodiploidy.

Recent studies have revealed this assumption to be untrue. In many taxa, species have evolved eusociality, quasi sociality and sub sociality several times, not necessarily gradually working their way up a line of increasing evolutionary sophistication (Crespi and Choe, 1997). This suggests that eusociality does not represent a "higher" level of evolution, but only another "strategy" to the conditions encountered by an organism (Wcislo, 1997).

A haplodiploid breeding system does not automatically obligate species to be eusocial. Two examples of haplodiploid groups that show all the known forms of sociality are the Thysanoptera, and the augochlorine sweat bees (Hymenoptera: Halictidae) Species within the Order Thysanoptera, which are all haplodiploid, display communal, subsocial and eusocial systems (reviewed Crespi and Choe, 1997).

The augocholorine sweat bees also show all possible social systems listed above, as well as containing solitary forms (Danforth and Eickwort, 1997). Solitary species such as *Augochlora pura* have singles nests, where one female excavates her own nest cavity and constructs and provisions her own cells. Females from communal species of sweat bee aggregate during brooding but do not cooperate in cell construction or provisioning. Semisocial forms such as *Megommation insigne* have reproductive division of labour among females and some evidence of cooperative provisioning. Semisociality is often a facultative alternative to solitary nesting and both forms can occur in the same species, within the same area. Alternatively, eusocial species show semisociality in the first generation (Danforth and Eickwort, 1997).

Eusociality has also been species that do not have a haplodiploid genetic system. Jarvis (1981) showed that the classical definition of eusociality could be applied to a diploid mammal, the Naked Mole rat (*Heterocephalus glaber*). She then also discovered that eusociality occurred in another bathyrid species, The Damaraland Mole-rat (*Cryptomys damarensis*) (Jarvis *et al.*, 1994).

These two remarkable subterranean mammals live in burrows in the semi-arid regions of Saharan Africa. They can only dig burrows, and therefore disperse, after rain, so opportunities for leaving the colony are limited due to the low and sporadic rainfall of the area. Groups can also burrow more efficiently and therefore locate new foraging opportunities more swiftly after rain. Due to very low dispersal rates, imbreeding is high within colonies and many females do not reproduce at all, leaving reproduction to one or two members of the colony in a similar manner to social insects (Jarvis *et al.,* 1994).

The two main problems inherent in the strict classification of social systems shown in Table 1-1 are that firstly, it is applicable to insect societies, from which it was derived, but it is rarely as useful in describing the sociality of mammals, birds, fish or reptiles, since everything else is less social when these criteria are used (Costa and Fitzgerald, 1996) (although some exceptional mammals such as the Naked and Damarland Mole-rats just described seem to fit the criteria for eusociality).

Secondly, pigeon-holing taxa into one of the definitions, assumes the form of sociality is constant within taxa and it gives researchers a pre-conceived idea of what they will find when investigating the social behaviour of a species. Having a name for something does not mean that it is necessarily well understood. In fact, understanding might be impaired rather than promoted (Wcislo, 1997).

Expanding the definitions of sociality and identifying the common features of and driving forces behind insect and mammal/bird sociality is likely to further our understanding of the fundamental questions about the evolution of social behaviour. Questions that are likely to benefit from an interspecific approach include why individuals reduce their own reproductive success to help raise other offspring and what causes animals from distantly related taxa in different environments to independently evolve the same level of sociality (Brockman, 1997).

Recent work also suggests that altruistic behaviour, characteristic of all forms of sociality (see Table 1-1) may evolve not just from the traditional explanations of kin selection and a trade off between costs and benefits of sociality, but may be influenced by indirect genetic effects (IGE's) (Wolf, *et al.,* 1998). The most common example of an IGE is that of the effect of the maternal environment on the phenotype of the offspring.

When individuals within a population mate non-randomly by inbreeding avoidance, "maternal effects" can accelerate the evolution of a rare, mutant trait such as altruism (Wade, 2000). The discovery of the effects of IGE's on the evolution of certain traits within populations may provide a better explanation for how altruism has evolved in so many different species.

Causative agents for the formation of societies over evolutionary time are difficult to determine. They can vary between single species, and even between populations of the same species (Berger, 1988). Two broad categories can be identified that contain most of the possible factors influencing the evolution of sociality. They are a) ecological constraints, where groups form due to a shortage of resources such as refuge sites, and b) philopatry, where individuals gain by being in close proximity to conspecifics (Emlen, 1994). Ecological constraints can also encompass the tendency of an animal to return to a site independent of the behaviour of conspecifics.

It may be difficult to determine the primary agent for the evolution of group-living in a species, since it may derive additional benefits from group-living or evolve additional group related behaviours after the initial development of grouping behaviour. For example, sociality may have evolved as a result of an increased patchiness of food, but animals may then derive antipredator benefits by being able to mob potential predators. Ecological constraints and philopatry need not be mutually exclusive (Emlen, 1994), but it can be useful to categorise the mechanisms of group formation into either of these two categories. Grouping behaviour that is the result of a shortage of resources would, at least intuitively, be less likely to be evolutionary stable, than that which occurred due to mutual benefits to individuals, since any environmental change, however temporary, could cause individuals to disperse.

For this thesis, group-living is defined as the year-round, frequent interaction of the same individuals within a population. Sociality is when these interacting individuals show some form of cooperation.

1.2 Ecological constraints

1.2.1 Increased population density and a shortage of resources.

Groups of animals may form as a result of increased population density or scarcity/patchiness of resources. Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) was thought to occur to facilitate defence again predation, but data collected by Childress and Herrnkind (1997) suggest that aggregation does not increase with predation intensity, and over 53% of the variation in den sharing can be accounted for by lobster density.

Lack of suitable breeding habitat has been proposed for the evolution of cooperative breeding in many species of birds, especially those that have very specific habitat requirements and are long-lived (reviewed in Ford, 1989). Territory is essential for successful breeding in these species, males must be able secure access to good nesting and foraging areas in order to be attractive to a female. In a transfer experiment conducted on the Seychelles warbler (*Acrocephalus sechellensis*), Komdeur *et al.*, (1995) found that both habitat saturation and variability in territory quality affected the decision of individuals to disperse. Where there were few opportunities to establish a new territory, juveniles stayed in natal territories.

The Florida Scrub Jay (*Aphelocoma c. coerulescens*) displays cooperative breeding, with helpers at the nest being philopatric offspring from the previous season. Florida Scrub Jays are sexually mature at about one year of age, but sometimes do not breed until four years of age (Woolfenden and Fitzpatrick, 1984). Breeding can only commence when a male secures his own territory. He does this in one of four ways. 1) mate replacement outside his natal nest. 2) "territory budding", where a male, paired with an immigrant female, inherits a portion of his natal territory. 3) through direct inheritance of the natal territory 4) rarely, a male will form a new territory between two others. The limiting factor in this species is suitable habitat. They depend on rare Florida Oak scrub, which occurs in scattered patches, producing an islandlike distribution (Woolfenden and Fitzpatrick, 1984).Thus lack of suitable habitat is a major factor constraining juveniles to stay with their parents.

1.3 Philopatry.

Lack of suitable areas to disperse to may not be the only reason for group-living. Individuals may gain benefits from joining a group, or remaining in their natal group and so do not disperse, even when suitable areas are available. This section reviews some of the advantages to joining a group.

1.3.1 Predator avoidance

Group-living can reduce predation risk for an individual in two main ways. Firstly, joining a group decreases the probability that an individual has of being eaten, even if larger groups are more conspicuous. The "dilution effect" (Hamilton, 1971) has been demonstrated in many species of fish (eg Krause and Godin, 1995), birds (Cresswell, 1994) and mammals (Roberts, 1996). An extension to the idea of reducing the probability of capture by joining a group is the "selfish herd" theory (Hamilton, 1971).

The "selfish herd" theory states that individuals will be attracted to one another as a mechanism to reduce their risk of predation. Hamilton's theory predicts that animals on the edge of a group will be more susceptible to capture than those at the centre. Sadedin and Elgar (1998) tested between the "selfish herd" and "dilution" theories by examining the differences in scanning behaviour of feeding spotted turtle doves (*Streptopelia chinensis*) at rectangular versus square feeders. When the birds fed at the rectangular feeder, then there were few individuals in the centre of the flock, compared to a more two dimensional group formation at the square feeder. They found that although scanning behaviour decreased with increasing flock size in both treatments, it declined at a significantly lower rate in the rectangular treatment (slope = -0.02), compared to the square treatment (slope = -0.05) suggesting that the geometry of the flock (ie having more birds in the centre) affects the scanning rate of the group.

Secondly, benefits can also be gained for an individual joining a group if there is either a greater probability of detecting a potential threat, or an individual group member can spend less time being vigilant and more time engaged in foraging, thermoregulating or other beneficial behaviours, without increasing its risk of being taken by a predator (Pulliam, 1973). Many studies have shown that as group size increases, individual vigilance declines. The "group size effect"(Lima, 1995), has been observed in some fish species and has been quantified for many species of mammals and birds (see (Quenette, 1990) and (Elgar, 1989) for reviews).

The most popular explanation for this effect is the "many-eyes" hypothesis (Lima, 1990). Individuals within a group can devote less time to being vigilant to potential threats without increasing their risk of being taken by a predator since others are also scanning for danger (Lima, 1995).

Essential to this hypothesis is that all members of a group are alerted to a potential threat when one or a few individuals detect the threat. This "collective detection" (Lima, 1995), is essential to the "many eyes" model otherwise the group's ability to detect a threat is compromised, and the benefit to group members is negated (Lima, 1995).

Groups of animals can also engage in aggressive defence against predators or competitors. Mobbing, where groups of animals attack a potential predator, occurs in many bird and mammal species, and appears to be a major advantage for the formation of large groups by the Fieldfare, *Turdus pilaris*. Predation on eggs and nestlings decreased with increasing colony size and mobbing was more effective in larger groups (Wiklund and Andersson, 1994). One of the main functions of helpers at the nests of Harris' Hawks (*Parabuteo unicinctus*) is the mobbing of potential nest predators (Dawson and Mannan, 1991).

Communal care, where reproductively active members of the population share the care of all the offspring in the group, is an additional benefit in forming groups for Lionesses (*Panthera leo*). Groups form primarily to protect offspring from infanticidal males (Pusey and Packer, 1994). However, lionesses will also nurse non-offspring when costs are low, such as when the infants are close kin, when the female has a small litter of her own and presumably has milk to spare, or when her own cubs are older and require less of her milk.

Slender-tailed Meerkats, (*Suricata suricatta*) are highly social mammals and group members share many aspects of the rearing of young. Specific duties include babysitting at the den, creching on foraging trips, providing prey items and allonursing, including spontaneous lactation. Such intensive communal care may be a result of the enormous fluctuations in resource availability in the semi-arid environment of the Kalahari Desert (Doolan and Macdonald, 1999).

Helpers may not just derive inclusive fitness benefits from helping at their natal nest, but they may stand to inherit the nest area from their parents. Passerine birds may cooperatively breed because there is a shortage of available territories to disperse to or they can increase their lifetime reproductive output by increasing the number of offspring that their parents produce. However, they may also be able to inherit all or part of their parents territory, eliminating the costs of dispersal all together (Woolfenden and Fitzpatrick, 1984).

Another form of cooperative breeding is lekking behaviour, an aggregation of males performing courtship displays which females attend primarily for the purpose of fertilisation (Hőglund and Alatalo, 1995). Leks are advantageous to males if resources and/or females are distributed in such a way as to be difficult to defend from other males (Deutsch, 1994). Females may also be able to gain higher quality partners (Hőglund and Alatalo, 1995).

1.4 Costs of sociality.

The most well-documented costs of sociality are an increased chance of disease and parasitism, a reduction in reproductive opportunities, and increased competition for resources.

Group-living may increase the probability of transmission of ectoparasites, since individuals come into contact with each other more often. Studies in passerine birds by Poulin (1991) found that feather mite prevalence was significantly greater in group-living Californian passerines than in solitary species. However, Poiani (1992) showed that although some sedentary Australian passerines showed the same trend, when all Australian species are examined there is no evidence that group-living does increases contagious ectoparasite load.

Migratory bird species in general have higher parasitic loads and most of the species that Poiani (1992) examined were migratory. Poulin (1991) did not distinguish between sedentary and migratory birds in his analysis. Migration may influence parasitic load as much as group size. Poiani (1992) also suggests that many Australian passerines may have been living in groups for long enough to have developed effective anti-parasitic behaviours, such as preening, control of migrants into colonies and immune responses to ectoparasites which offset increased probability of transmission.

The type of parasite can also influence whether or not social animals are more likely to be heavily infested than solitary species. Predatory parasites that can seek their hosts independently, show the opposite trend to sedentary species and are actually less prevalent when animals group, compared to when they are alone (Cote and Poulin, 1995; Wikelski, 1999).

Most studies that have examined the influence of sociality on ectoparasitism have emphasised that close social contact increases the rate of ectoparasitic transmission. This suggests that social contact should be curtailed to reduce the costs of parasite load (Mϕller *et al.*, 1998). If costs were sufficiently high, then social behaviour may be reduced in some species.

However, in some social insect species, parasitism may actually increase social behaviours, such as helping, and thereby drive the evolution of increased sociality (O'Donnell, 1997). For instance, a parasite that effectively castrates or partially castrates its host will decrease the reproductive output of infected individuals. This selects for an increase in helping behaviour (to increase inclusive fitness) which in turn increases the level of sociality of the host species (O'Donnell, 1997). Such behaviour represents an interesting paradox. Social behaviour may be costly to the host by increasing the incidence of such parasitism, but the parasitism itself increases the level of sociality.

Another paradox is that of allogrooming for ectoparasites in vertebrates. The social contact required for the removal of ectoparasites from group members increases group cohesion, thereby facilitating increased transmission of the ectoparasite. However, although allogrooming may have initially evolved for parasite removal and may still be the primary reason for allogrooming in some species (eg Perez-Perez and Vea, 2000), it appears to offer both the groomed and the groomer additional social benefits such as reduced aggression and relaxation (Aureli *et al.*, 1999). These benefits may outweigh the increase in exposure to parasites that closer social interaction creates.

A significant cost to birds and mammals of delayed dispersal can be a reduction in mating opportunities, either because there is less access to unrelated breeding partners when an animal delays dispersal from the natal nest, or because there is increased competition for the partners that are available (Emlen, 1984). For example, Blumstein and Armitage (1998), found that as the complexity of social behaviour increased within ground-dwelling sciurids, and there were larger philopatric groups, the proportion of adult females that bred decreased. There was also a decrease in litter size and sub-adults took longer to produce their first litter in socially complex species. However, these costs were offset by increased first-year offspring survival in these species (Blumstein and Armitage, 1998). This could be why complex social organisation tends to occur in species with long lives and late maturity.

Suitable breeding partners may not be the only resource that individuals that join groups must compete for. For example, Coho Salmon (*Oncorhynchus kisutch*), engaged in more risk-taking behaviour to obtain food when there were more conspecifics around, independent of the risk of predation. When resources become scarce due to increased competition, individuals in a group will take more chances to procure the food that is available (Grand and Dill, 1999).

1.5 Phylogenetic inertia and causation.

Early work on social organisation adhered strictly to the adaptionist paradigm. That is, that there must be some benefit or reduced cost in the formation of groups and that social organisation will "adapt" to changes in availability of resources by changing group size or level of sociality. In many taxa the benefits are clear, but in others determining the relative input between ecological constraints and the benefits of grouping is difficult. Some species appear to maintain social organisation that are not best suited to the environment (Berger, 1988).

Phylogenetic inertia is the maintenance of an ancestral trait although its adaptive significance is no longer applicable. Sociality could be the subject of phylogenetic inertia if a population did not change its group size or social organisation to best utilise its current environment. For example, although Yellow Mongooses *(Cynictis penicillata)* have a similar diet to the group-foraging Meerkats (*Suricata suricatta*) and Bat-Eared Foxes *(Otocyon megalotis)*, they still forage in a sub optimal group size for the clumped distribution of their main prey item, termites (Nel and Kok, 1999).

The macaques are the most geographically widespread and socially diverse primate genus. Although ecological and climatic conditions may have altered several times during their evolution, phylogeny predicted 75% of the variability in social organisation among species in this genus (Thierry, *et al.*, 2000). This suggests a high level of phylogenetic inertia in the evolution of social behaviours such as nepotism and reduced aggression among the 16 macaque species that Thierry, *et al.*, (2000) examined.

Variable levels of social organisation among populations of the same species under different conditions would constitute evidence against a significant role of phylogenetic inertia. For instance, Illinois populations of the Prairie Vole (*Microtus ochrogaster*) are monogamous, there is little evidence of sexual dimorphism and philopatric offspring engage in alloparenting of their younger siblings. However, Kansas populations of the same species are not monogamous, are sexually dimorphic and show little alloparental care. Differences in the level of resource availability between the two regions may explain the variability in social organisation between the two populations (Roberts *et al.*, 1998).

1.6 Social organisation in reptiles

1.6.1 In General

Reptiles have largely been ignored in reviews of sociality (eg Gadagkar, 1994; Hughes, 1998) for exceptions see Wilson, (2000) and Brattstrom, (1974). Early researchers concluded that reptiles lacked behavioural complexity, had difficulty learning (taking 50+ trials to learn the way to food in a Y maze) and were generally pretty stupid. Some of these studies were performed at sub-optimal temperatures for the animal, so effectively may have been studies in reptilian metabolic inactivity (Brattstrom, 1974). Consequently, reptiles were considered behaviourally and socially inferior to other vertebrates.

The most well-documented social system described in lizards has been territoriality. Territoriality can incorporate the defence of a home range or the exclusion of others from favoured resources such as refuging and basking sites. Typical territoriality in lizards involves a dominant male defending an area containing food, basking and refuging sites, and sometimes, also females (Stamps, 1977).

Home site defence, where a dominant male patrols and protects his whole home range often occurs in visually-orientated, sit-and-wait foragers that use elevated positions within their home range to display to potential intruders (Stamps, 1977). Iguanids are amongst the most well-studied group and most of them show home site defence (Stamps, 1977). Many species of agamid also exhibit spacing and territorial behaviour to iguanids (Stamps, 1977). For example, Peninsula Dragons (*Ctenophorus fionni*) defend small home ranges that include one or two females using an unusual hind limb push up display to deter intruding males (Johnston, 1997).

Territory size is strongly linked to the mating system of many lizard species. In small species, male lizards can defend territories that overlap with the small home ranges of many females. This often results in a polygynous mating system (Stamps, 1983a). Males of larger species that occupy large home ranges, find defending an area big enough for several females too costly. Instead, males of large species tend to defend a single female against rivals, home ranges tend to overlap and monogamy is more common (Stamps, 1983a).

Territoriality breaks down in many species in captivity, or when densities increase in the field to create crowded conditions. Lizards in these conditions usually form despotic hierarchies with the largest and most aggressive male dominating the others in the group (Stamps, 1977; eg Torr and Shine, 1994).

Aggregation can be just the result of synchrony of response to the same cues. All turtles must nest on land, although their feeding grounds might be thousands of kilometres from suitable nesting sites. In many species females exhibit an "en masse" response to environmental cues to nest, although social contact between them may not occur at all (Ehrenfeld, 1979). In some turtles, nesting occurs in a single night in the same area. For instance, 40,000 *Lepidochelys kempii* females have been reported nesting on the same mile of beach, on the same night, near Tamailipas, Mexico (Wilbur and Moran, 1988).

Social aggregations are rarely reported among reptiles. When grouping occurs, it usually has a seasonal basis - individuals come together to breed and disperse immediately afterwards. Birthing rookeries in viperid snakes are one example. Gravid snakes occupy distinct areas from non-gravid animals, usually in areas containing better thermoregulatory sites (Graves and Duvall, 1995). Aggregation itself may increase the ability to thermoregulate and increased thermoregulation seems to aid gestation, with females of many species increasing their body temperature when gravid (Schwarzkopf and Shine, 1991).

The Western Whip Snake (*Hierophis viridiflavus*) forms aggregations of gravid females in June each year. These aggregations contain no males or non-gravid females, and the same snakes return to the same site year after year (Capula and Luiselli, 1995). Female Green Iguanas (*Iguana iguana*) nesting together gain antipredator benefits for their clutch because their burrows are deeper and more complex than if they nest singly. Complex burrows make access to neonates by predators more difficult (Rand and Dugan, 1983).

Temperate zone reptiles form large inactive aggregations during colder months, some species also bask and are active on sunny days during winter (Ruby, 1977), while species such as the Red-sided Garter Snake (*Thamnophis sirtalis parietalis*) forms inactive aggregations of thousands of individuals during the colder months (reviewed in Gregory, *et al.*, 1987).

Aggregation also occurs in some species during the mating season. Lekking behaviour, (where males congregate in an area visited by females) occurs in many species of birds and mammals (Widemo and Owens, 1999). It was considered too high a level of sociality for reptiles until Wikelski *et al.*, (1996) showed its existence in Marine Iguanas (*Amblyrhynchus cristatus*). Females of this species are more aggregated during the breeding season and during that time are attracted to the clustered territories of males (called leks). (Wikelski *et al.*, 1996).

Marine Iguanas of the Galapagas Islands also aggregate in sleeping piles during the afternoon and evening, outside of the breeding season. Dee Boersma (1982) found that individuals in the centre of larger piles of lizards on Fernandina Island maintained higher body temperatures than lone lizards, or those on the edge of the pile. However, Wikelski, (1999) studied aggregation in the same species on Genovesa Island and found that a reduction in mobile tick load was the main benefit of grouping and that body temperatures of alone and grouped lizards did not differ during the cooling down period between 1730-2130 hrs. This discrepancy may be due to the difference in size of lizards on each of the islands. Lizards on Genovesa are up to 7 times smaller than those on Fernandina Island. This could mean that they do not receive the same thermal benefits as the larger lizards due to greater surface to volume ratios (Wilkelski, 1999).

Adders (*Vipera berus*) are highly philopatric both within and between years, with very low dispersal rates, even when conspecific populations are less than 500 metres away. Even in large areas of suitable habitat, snakes remain with their natal population (Madsen and Shine, 1992).There is intense competition among brothers for the limited mating opportunities that this philopatry produces. As a result, Adders in Smygehuk Sweden, have a highly skewed sex ratio, with females producing significantly more daughters than sons. Daughters do not directly compete with each other for mates as brothers do (Madsen and Shine, 1992). Therefore selection favours the production of female offspring. Aggregation in this species contributes to a sex ratio significantly different to the normal 50/50 ratio (Madsen and Shine, 1992).

There has been little published data on long term group fidelity in reptiles. Two species of lizard show large aggregations of lizards that appear to be more than just seasonal . Mouton *et al.*, (1999) reported groups of up to 30 individuals under one rock in the Armadillo Lizard, *Cordylus cataphractus.* Lemos-Espinal *et al.,* (1997) found groups of up to nine individuals together in *Sceloporus mucronatus mucronatus.* Both studies differ from overwintering aggregations that have been reported previously because large groups were found during the summer months, suggesting that these aggregations have more than just a thermal function. Groups usually contained one adult of both sexes and then sub adults and juveniles. Some groups also contained other adults of both sexes, so groups could be more complex than family groups.

Visually-orientated, diurnal lizards have been assumed to exhibit more complex social behaviour than other reptile species (Brattstrom, 1974), possibly because researchers are more aware of visual signals like enhanced colour, dewlap extension, head bob and push-up displays. However, recent research on other species has shown them to exhibit more complexity than previously thought (Schwenk, 1995). Fossorial taxa such as scincids are showing a diversity of social systems previously unrecorded in the more intensively studied iguanid and agamid families. The notion that other taxa lack behavioural complexity, may not be a biological reality but just the result of fewer studies on these taxa (Torr and Shine, 1996).

Skinks show highly developed responses to chemical stimuli and can differentiate between their own and other species, between sexes and sometimes between individuals using just chemical signals (reviewed in Cooper, 1994). For example, *Tiliqua scincoides*, a large, long-lived skink, common throughout southern Australia, directed significantly more tongue flicks to the odours of a conspecific than to either a control or to its own odour (Graves and Halpern, 1991). Skinks may use their highly developed chemoreception to locate mates and identify familiar lizards in future encounters which may reduce aggression.

Social and genetic monogamy have been reported for very few lizard species (Bull, 2000), but has been extensively studied in the skink, *Tiliqua rugosa.* This large, long-lived lizard is common throughout much of southern Australia. It is solitary throughout much of the year, but pairs up in spring for 6-8 weeks, mates and then separates again well before the female gives birth in March of the following year (Bull, 1988). Extra pair fertilisations occurring infrequently (only 14% of offspring were fathered by a male that was not the female's regular partner) and lizards show long –term pair fidelity across years (Bull *et al.,* 1998).

Unlike most monogamous birds and mammals, *T. rugosa* shows no parental care of offspring. They do however have a low reproductive output (mean of 2 offspring per female per year) which has been correlated with monogamy in mammals (Kleiman, 1977). Several hypotheses for both the prolonged pairing in one season, and for the tendency to choose the same partner in successive seasons, are currently being explored (eg How and Bull, unpublished data). One benefit for females of pairing within a season, is that male *T. rugosa* are more vigilant when paired than when not, and are more vigilant than their partner (Bull and Pamula, 1998). Males may pair with females to prime them for reproduction, protect them from other males or because they have proven to be fecund in the past.

The Tasmanian Snow Skink, *Niveoscincus microlepidotus* also exhibits behavioural monogamy, with pairs remaining together for an average of 29 days and as long as 84 days. Males use chemical cues to identify females, and will follow the trail of their partner, rather than an unfamiliar female. (Olsson and Shine, 1998).

Overwintering aggregations have been recorded in the Scincidae, although the social significance of these aggregations has not received much attention (Greer, 1989). *Lampropholis guichenoti* forms groups during winter, and it is suggested that other species within this genus do also (Swan, 1988). Several species of the *Eumeces* genus also form aggregations during winter and before the breeding season (Duvall, *et al.*, 1980). Scott and Sheldahl (1937) in Duvall, *et al.*, (1980) reported a winter aggregation of 52 *Eumeces septentrionalis* individuals in a "...football-sized wad". *Eumeces fasciatus* also occurs in winter aggregations and Duvall, *et al.*, (1980) suggest that they may use pheromones to locate conspecifics and form these aggregations.

Skinks, like other lizards, rarely show maternal care (Shine, 1988). However, it has been reported in some species, including members of the *Eumeces* genus. Females of both *Eumeces fasciatus and Eumeces laticeps* brood their eggs and will retrieve and continue to brood their own eggs and eggs of congeneric species, if they are experimentally removed (Vitt and Cooper, 1989). In *Eumeces okadae* brooding has been shown to increase hatching success by more than 10 times that of unbrooded eggs (Hasegawa, 1985) . Post hatching association between mothers and offspring has not been observed for any species in this genus (Vitt and Cooper, 1989).

Communal egg laying also occurs in several Australian skink species and is associated with species that live in the southern parts of Australia where winters are cold. Large aggregations of eggs representing the efforts of many females can be found in both *Lampropholis* and *Saproscincus* genera. All the eggs in a nest are laid within hours of each other, meaning that females respond to the same nesting cues at the same time. (reviewed in Greer, 1989). Other genera that exhibit communal egg-laying include *Carlia tetradactyla* (Porter, 1993) and *Morethia adelaidensis* (Greer, 1989).

Long-term group fidelity and associated social behaviour has not been reported within the Scincidae, although anecdotal reports of large aggregations within the *Egernia* genus suggest that such social organisation could exist.

1.6.2 Sociality in the *Egernia* genus

Large, long-lived, herbivorous skinks such as many in the *Egernia* genus are likely to exhibit more diversity in their social behaviour than the smaller, insectivorous and visually orientated species that have received more attention so far. Many *Egernia* species show similar characteristics to members of the Iguana genus, which have shown unusual complexity of social behaviour for a reptile, including lekking (Wikelski *et al.,* 1996), social grouping of juveniles (Burghardt, 1977; Burghardt and Rand, 1985) and the formation of sleeping aggregations (Dee Boersma, 1982; Wikelski, 1999). They have the fossorial nature of the Scincidae, meaning not only has much of their social behaviour remained unstudied, but they lack many of the visual displays that are used in other species for intraspecific communication and so must rely on less obvious forms of communication such as chemoreception and subtle postures.

Several species in the Australian skink genus *Egernia* have been reported to live in communal aggregations, sometimes interpreted as family groups (Hutchinson, 1993) The *Egernia* genus is widely distributed throughout Australia with one species in New Guinea. It comprises 28 species of medium to large lizards. All species are viviparous and most are diurnal (Cogger, 2000).

The phylogeny of the *Egernia* genus has not been fully explored, but based on morphological characters, it is divided into six main subgroups. They are the *cunnighami, striolata, luctuosa, whitii, kingii* and *major* groups (Gardner,

(Table 1-2). The *cunninghami* group, which is composed of all the spiny-tailed members of the genus includes *E. cunninghami, E. hosmeri, E. stokesii and E. depressa*. All these lizards have been found by various researchers in colonies of up to 17 individuals (Gardner, 1999), usually interpreted as family groups. As well as all possessing a spiny tail that does not detach, all these species live in crevices in rocky outcrops or in loose, scree habitat.

Most members of the *striolata* group also exhibit grouping tendencies (Table 1-2). *E. saxatilis* and its close relative *E. striolata* are found throughout the year in pairs or small groups. The most common group size is two, with one adult of both sexes. Groups containing an adult female and her offspring are also commonly observed (D.O'Connor – pers. comm; Bonnett,1999).

In *E. striolata*, genetic analysis has shown that groups vary in their degree of relatedness to each other (Bonnett, 1999). Some groups seem to associate closely with relatives, while others share crevices with lizards that are no more related than what would be expected by chance. *E. striolata* associate with other individuals directly, but they also seem to "time share" their crevices, with different lizards spending time in a particular crevice at different times of the day. *E. striolata* shows home site fidelity and some tendency toward natal philopatry (Bonnett, 1999), but they lack the large group sizes and strong tendency to aggregate that has been recorded in the *cunninghami* group (Gardner, 1999) (Table 1-2).

Table 1-2 Summary of *Egernia* sociality. Observations are presented in the current taxonomic groupings (adapted from (Gardner, 1999)).

Taxa	Sociality type	Summary of text	Reference
Cunninghami *cunninghami*	"family" groups -groups of young (<1 yr old	"adults of both sexes, sub-adult and young…form aggregations of varying complexity."	Barwick (1965) See also van Weenen (1995).
hosmeri	"family" groups	"in colonies of two to nine individuals"	Stammer (1976) in Shea (1995)
stokesii	"family" groups	"Sometimes as many as four to five individuals will be found turning over a single stone" Groups of 2-17 individuals that are more related to each other than to the rest of the population	Alexander (1922) Duffield and Bull (2001)
depressa	" family" groups	"The female gives birth to two live young… this is preceded by her actively chasing out any inhabitants of the home crevice".	Ehmann and Tyler (1995)
kingii *kingii*	"family" groups	Eg "juveniles coexist with parents until they reach sexual maturity at approx. 3 years of age"	Pers. comm. Phil Areana, Jaqui Richards and Garry Connell
Striolata			
striolata	Winter aggregation Pairs "family" groups	"four adult specimens together…consisting of two males and two females" "Male and female pairs observed in same arboreal and rocky crevices" "on smaller trees, it is usually solitary, but a colony of eight has been found on a large, old Red River Gum".	Swan (1988) Bonnett (1999) Ehmann and Tyler (1995)
saxatilis	"family" groups pairs	Males and female adults, immatures and juveniles in same retreat; male and female paires sometimes with one or more immatures Adult pairs consisting of a male and female, juveniles usually avoid adult crevices, probably due to high incidence of infanticide in this species	Pers. comm Mark Hutchinson Pers.comm Dave O'Connor
mcpheei			
carinata	colonies (?)	"it occurs disjointed and isolated, in colonies and populations"	Ehmann and Tyler (1995)
napoleonis			
formosa			
douglasi	"family" groups	"shelters in deep rock and wood crevices where it lives in small, localised colonies and groups"	
pilbarensis (?)			
luctuosa			
coventryi			

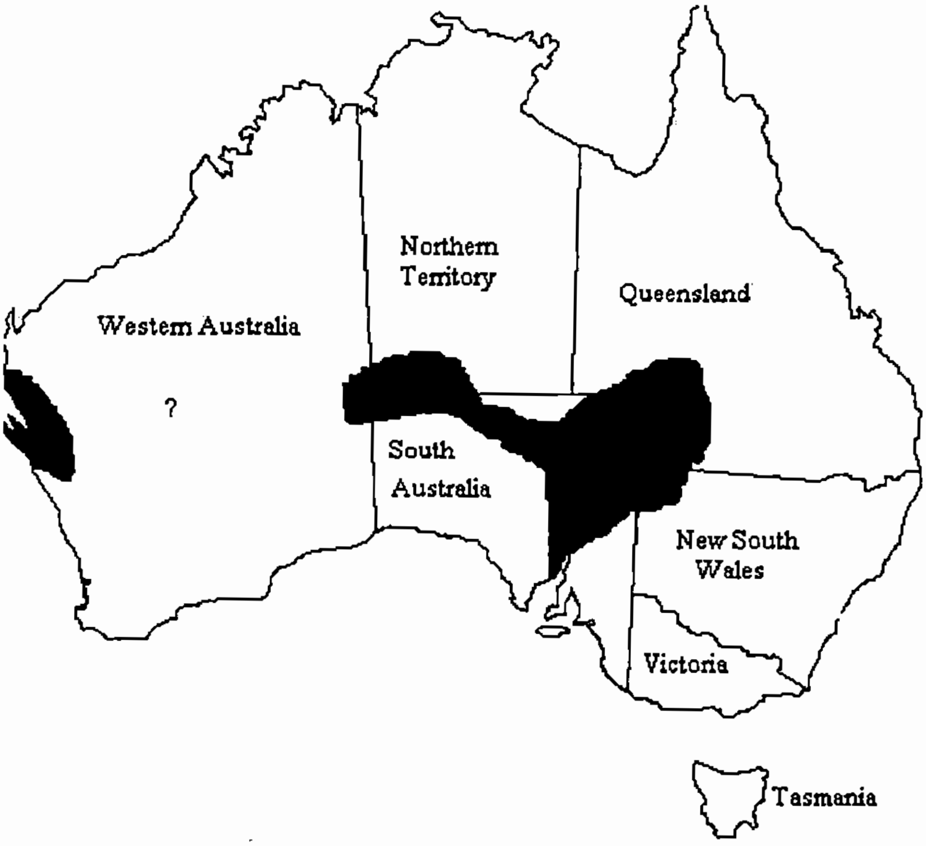
luctuosa			
whitii			
whitii	pair bonds and "family" groups	"adults coexist as breeding pairs sharing the same retreat" and "young stay with their parents until the next litter is born when they are displaced"	Milton (1987) (see also Hickman 1960; Rawlingson 1974; Swan 1988)
multiscutata	"family" groups	"The lizards are communal, several often sharing a warren"	Coventry and Robertson (1980)
modesta	pair bonds and "family" groups	"adults coexist as breeding pairs sharing the same retreat" and "young stay with their parents until the next litter is born when they are displaced" also "the same pair of adult may remain together for up to 3 years"	Milton (1987)
pulchra			
margaretae	pairs	males and female pairs observed in same retreat	pers. comm. Mark Hutchinson
inornata	solitary solitary with delayed dispersal of juvenile	"Generally thought to be solitary.." "female with juvenile for a little while"	Webber (1978) pers. comm. Steve M^c^Alpin
slateri	"family" groups	"this species tends to inhabit communal burrow systems which tend to be grouped into colonies in suitable habitat"	Ehmann and Tyler (1995)
striata	solitary and single adult "family" groups Pairs	"Juveniles of striata may remain in their mother's burrow for some time as evidenced by excavating fairly large burrows…juveniles in the same burrow system with an adult" "Two adults commonly occupy the same burrow system…it is not known if these pairs are of the same or opposite sex"	Pianka and Giles (1982) Henzell (1972)
kintorei	"family" groups pairs and "family" groups	"A burrowing species in which large and complex burrow system may be occupied by family groups". "Two adults commonly occupy the same burrow system, the members… being of opposite sex" and "One burrow at Aileron contained seven individuals"	Cogger (2000) Henzell (1972)
major			
major	pairs and "family" groups	"land mullets shelter, often as a small colony… they bask often as a group before foraging independently".	Ehmann and Tyler (1995)
frerei			
arnhemensis			
rugosa	colonies(?)	"it tends to occur in discrete colonies within its range"	Ehmann and Tyler (1995)

1.7 The study animal – *Egernia stokesii.*

1.7.1 Distribution.

Egernia stokesii occurs throughout much of central and southern Australia (Figure 1-1) (Cogger, 2000). They also occur on several islands off the coast of Western Australia including Houtman's Abrolhos where Alexander (1922), first recorded that they were found in groups (Table 1-2).

Figure 1-1 Distribution of Egernia stokesii (after Cogger, 2000).



1.7.2 Ecology and life history

E. stokesii reaches maturity at 5-6 years of age at which time it attains an average SVL(snout-vent length) of 19cm (Greer, 1989; Duffield and Bull, 2001). It normally produces 2-8 live young in February or March of most years (Duffield and Bull, 1996), although clutches of one and up to nine neonates have been observed (pers. obs).

E. stokesii lives for at least 10 yrs (Greer, 1989), with one captive specimen estimated to be 25 yrs old (Swan, 1990). Adult mortality is low (estimated to be approximately 3% by Duffield and Bull, (2001)). Juvenile mortality in the first year is at least 40%, but once animals attain the age of 4 yrs, mortality decreases to the same level as for adults (Duffield and Bull, 2001).

Although previously reported as primarily insectivorous (Ehmann, 1992), Duffield and Bull (1998) found that diet changes with development, juveniles take around half of their total calorific intake from insects, while adults are almost exclusively herbivorous. *E. stokesii* stores fat in its tail as do other closely related lizards such as *Tiliqua rugosa.* This is probably an adaptation to seasonal food availability (Pough, 1973).

E. stokesii occupies a diverse range of habitats. In the southern tip of its range, on the Eyre Peninsula of South Australia it inhabits extensive corridors under shale rock just above the shoreline. Here it ventures into the intertidal zone, possibly to increase its foraging opportunities when terrestrial resources are restricted (G. Johnston - pers comm). In Western Queensland, it has not been found in rocky outcrops as it has in much of the rest of its range, but rather occupies the hollows of old growth gidgee trees (*Acacia georgina*) (from where one of its common names, the Gidgee Skink is derived). In these populations, up to four adult lizards have been found occupying the same branch of a gidgee tree, with population densities estimated to be up to 20 lizards per hectare (S.McAlpin, pers comm).

Detailed studies of the biology of these populations have not been published, work so far has concentrated on the South Australian populations which are restricted to rocky outcrops (Cogger, 2000) and man made structures such as woodpiles and metal heaps (pers. obs). In rock outcrops, it occupies both horizontal and vertical rock crevices, sometimes several metres into the rock.

Populations of *E. stokesii* in South Australia are often associated with the plant *Enchylena tomentosa* (Duffield, pers comm). This species of salt bush is common throughout the *E. stokesii* home range. The bush produces berries throughout much of the year, which are a major component of the diet of the *E. stokesii* (Duffield and Bull, 1998).

E. stokesii is host to several ectoparasites. They include two species of tick *Amblyomma vikkiri* (Acari:Ixodidae) (Keirans *et al.*, 1996) and *Amblyomma limbatum* (Stein, 1999). A phlebotomine sand fly, *Australophlebotomus dycii* has also been found feeding on the blood of *E. stokesii.* Six species of blood parasite have been found to infect South Australian populations of *E. stokesii*, although most occur at low levels of infection in the lizards (Stein, 1999).

At normal levels of infection, neither ticks nor blood parasites seem to adversely affect the health of *E. stokesii*. However, when levels are experimentally elevated, juvenile *E. stokesii* with high tick loads fed more often but gained weight at a slower rate than their uninfected counterparts (Main, 1998).

1.7.3 Previous research on the social behaviour of *Egernia stokesii*

Investigations into the social organisation of *E. stokesii* initially began in 1993, as part of an honours project (Duffield, 1993). A population inhabiting an isolated rock outcrop called Camel Hill near Hawker, in the Flinders Ranges of South Australia, was found to have individuals in quite large groups, that shared crevices and home ranges in a way that seemed unusual for lizards (Duffield, 1993). Much of the initial study on the social organisation of *E. stokesii* concentrated on several populations of lizards around the Hawker area, in the southern Flinders Ranges.

Later, in a more comprehensive study (reported in Duffield and Bull, 2001), members of this population were found to remain in stable groups of up to 17 individuals, which shared rock crevice refuges and home ranges. Average home range size for an individual lizard was 446m^2 lizards at the Camel Hill site. Groups occupied a mean area of 864 m^2. Home ranges were not aggressively defended against neighbouring groups, but lizards spent significantly more time interacting with their own group members than animals in neighbouring groups (Duffield and Bull, 2001). Group members spend much of their time basking together on rocks near the crevice entrance, and are sometimes preyed upon by raptorial birds while basking (Duffield pers comm). Other potential predators include elapids such as brownsnakes (*Pseudonaja textilis*) and possibly the rare Krefts tiger snake (*Notechis ater*).

The social organisation of *E. stokesii* differs from all published data on aggregation behaviour in lizards in the year-round stability of the groups found. Of the 77 adults monitored over the five years of study, 56 lizards (72.7% of the adult population) remained in the same group for three or more years and 45 lizards (58.4% of the adult population) were in the same group for more than four years. In this isolated rocky outcrop, only one lizard was recorded dispersing off the outcrop, and voluntary group changes were rare (Duffield and Bull, 2001).

Groups consisted of up to 11 adults, and usually contained one or two adults of each sex (Duffield and Bull, 2001). *E. stokesii* has a monogamous mating system with 75% of litters having only one father (Gardner, 1999). Usually this male was from the female's own group, although females sometimes bred with males from a neighbouring group. Multiple paternity within a litter was uncommon and males were never found to father more than one litter in a season (Gardner, 1999). Most young (88.6%) had parents from within the same group, while adult lizards that contributed to two successive cohorts usually mated with the same partner in successive years (Gardner, 1999).

Of the 17 groups of lizards analysed from the Camel Hill site, relatedness for both sexes was significantly greater within groups than among them. Females were significantly more related to females within their group than males were to other males within their group. These data suggest that natal philopatry is common to both sexes, but when dispersal occurs, it is normally the males that disperse (Gardner, 1999).

Nearly 95% of juveniles that were recorded on the hill were found in the same group as their mother. Of the 31 juveniles born on the hill during the 5 yrs of observation, 30 of them stayed in the same group that they were born in. Juveniles remain in their natal group for up to 5 yrs, they do not reproduce until at least this age in the field (Duffield and Bull, 2001),but have produced young at four yrs of age in outside pens in captivity (pers obs).

Main and Bull (1995) found that juvenile *E. stokesii* were not only able to differentiate between their mother and an unfamiliar female, but they also chose to spend more time in contact with her, than the unfamiliar female. Mothers were also shown to be able to recognise their own offspring, and also chose to spend more time in contact with their own offspring.

Despite an apparent preference to be near their own offspring, maternal care has rarely been observed in *E. stokesii*. Females will sometimes assist neonates by consuming the embryonic sac if the baby is having trouble removing it, whereas normally the neonate would remove and eat the sac itself. Conversely, females have occasionally been observed to selectively devour their own offspring, although the reason for this is not known (Lanham and Bull, 2000) (see appendix 2).

Allogrooming, where one group member inspects and removes ectoparasites from another, is an important part of social living in many mammals (eg in primates (Di-Bitetti, 1997) and in impala (Mooring and Hart, 1997)). This behaviour has been attributed to maintaining social relationships in chimpanzees (eg Baker and Aureli, 2000) and/or reducing ectoparasite infection in White-Crowned Mangabeys (*Cercocebus torquatus lunulatus*) (Perez-Perez and Vea, 2000).

Griffin (unpublished data) found that *E. stokesii* living in groups with the same number of ticks attached as those living alone showed no difference in the rate of tick detachment and she found no evidence that other group members removed ticks. Allogrooming is a social behaviour that has not been shown to occur in *E. stokesii.*

To maintain a stable social group, members must be able to recognise each other and distinguish between group members and intruders. Bull *et al.*,(2000a) found that *E. stokesii* showed a stronger response (measured by both tongue flicks and time in contact) to both scats and body secretions from non group members compared to group members. The mean number of tongue flicks directed at the body secretions of a non-group member was 6.1 (SEM=1.1) compared to only 3.2 (SEM=0.5) for lizards from their own group. Further experiments showed that familiarity was more important than relatedness in determining how lizards would respond to the stimulus (Bull *et al.*, 2000a).

Physical manifestation of aggression is rare in *E. stokesii.* When lizards are caught by hand in the field they rarely open their mouths or attempt to bite the handler (Duffield, 1993; pers. obs). Only one instance of the death of a lizard as a result of intraspecific aggression has been recorded in the field. A juvenile lizard was found dead in the population at Camel Hill with numerous bite marks to its body, possibly caused by an adult Gidgee Skink (Duffield and Bull, 2001).

Intragroup aggression can occur if siblings that are kept as a group in captivity approaching sexual maturity are not separated. This is generally easily prevented by putting lizards of this age in unrelated groups (pers obs). This may be the time that dispersal would occur in the field, and the aggression that has been observed in such groups is an attempt to displace related animals and avoid inbreeding.

The only other instance of aggression observed was when an unrelated neonate was introduced into a group containing a female and her newborns. The female immediately seized the head of the unfamiliar lizard in her mouth and it had to be extricated from her jaws before its head was crushed. Several similar introductions had been made with other females without incident. These females accepted the unfamiliar juvenile as if it was one of their own, showing no signs of aggression. The cause of the aggression by this one female is unknown (pers.obs).

Scat piling, where lizards defecate in the same area and create conspicuous "latrines" is a common feature of the behaviour of many species within the *Egernia* genus (Greer, 1989). Large "latrines" can be found underneath the active crevices of *E. stokesii*. These seem not to be used as a chemical signal, but rather are just the result of the tendency in *Egernia* species to remain close to their crevices, especially during morning basking.

Lizards were first tested to see if they responded differently to the scats from familiar (other group members) versus unfamiliar lizards. Experiments were then conducted to see if lizards would avoid or be attracted to refuges with scats from themselves or other group members outside. They showed elevated tongue flick rates to the scats from unfamiliar lizards, but showed no preference for or avoidance of refuges with other lizard's scats outside them (Griffin, unpublished data). This suggests that although lizards can recognise the scats of individual lizards, they do not avoid refuges because of scat-piling.

In many lizards, latrines are located a distance from home crevices, presumably to avoid advertisement to predators, this does not seem to have diminished this behaviour in *E. stokesii*. Latrines occur in the large, closely related skink, *E. kintorei*. Ehmann, (1992) has speculated that this behaviour is actually designed to attract insects. This hypothesis has not been tested for scat piling in *E. stokesii*.

Egernia striolata, a smaller relative of *E. stokesii*, commonly shares the same habitat. Although the two species have not been observed to share the same crevice, they have been observed in adjacent crevices. In Queensland, where *E. stokesii* occurs in trees, *E. striolata* is often found in the same tree, but not the same branch (S.McAlpin, pers comm). The relationship and interactions between these two species has not been specifically examined, but it would be interesting because *E. striolata* shows grouping tendencies, but is less gregarious than *E. stokesii*, smaller, and much more aggressive (Bonnett, 1999: pers.obs).

This thesis aims to examine the unusual social organisation of *E. stokesii* and determine if some of the benefits of group-living that have been proposed for social birds and mammals apply to *E. stokesii.*

The first aim of this project is to examine the spatial distribution of animals in populations other than the one on Camel Hill in the Flinders Ranges for which social aggregation has been shown (Duffield and Bull, 2001). Such a survey would determine if group-living occurred in other populations, or was confined to only one population.

The second aim is to determine if grouping behaviour occurs only as a result of a shortage of suitable crevices. If lizards still choose to aggregate with the availability of excess crevices, this would suggest that grouping confers advantages to individual lizards.

The third aim is to examine two possible benefits of group-living (enhanced thermoregulation and predator detection).

Finally, group structure will be investigated. The behaviour of lizards living alone and in a group will be compared and the behaviour of dominant and subordinate lizards within a group will also be examined.

This study will expand on the limited knowledge of grouping behaviour in lizards by experimentally examining possible benefits of this behaviour. If the grouping behaviour that has been demonstrated in this species previously, can be shown to be a result of mutual attraction among individuals then this behaviour could be classed as true sociality (Wilson, 2000). True sociality has not been demonstrated in a lizard species to date.

Chapter 2

2 General Methods

2.1 Collection and transport.

Lizards were collected from within the South Australian distribution of *E. stokesii* (see Chapter 1). Most of the lizards used in experiments for this thesis were the offspring of females collected in January, 1996. Lizards were collected from several sites within four regions of South Australia (Table 2-1). Lizards were occasionally caught in Elliot traps, but more often had to be prised out from the rock crevices that they had wedged themselves into (Figure 2-1). Some lizards found in the Woomera area (Table 2-1) were collected from metal or woodpiles, rather than rock crevices. Further information on group composition of lizards caught is detailed in Chapter 4.

After collection, lizards were transported in plastic containers with air holes, or in muslin bags. They were taken to the Animal Care Unit at Flinders University of South Australia, usually within a few days of capture. All procedures used in handling and maintaining lizards and all experiments were approved by the Flinders University Animal Welfare Committee. Lizard colonies were inspected fortnightly by an independent vet to ensure health and well being.

Figure 2-1 The most often used method of capturing lizards was by gently prising them out of rock crevices.

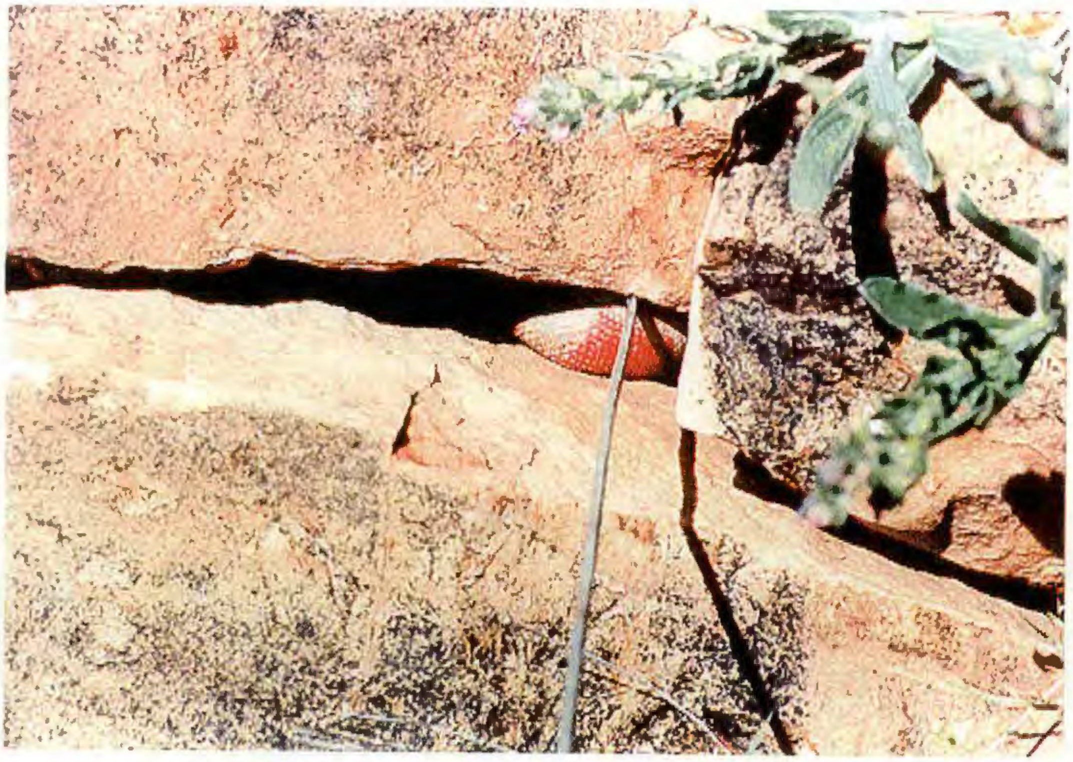


Table 2-1 Regions where lizards were captured.

Location	**GPS**	**Number of lizards captured & brought back to Flinders**
Hawker area	29°54"31.7s, 136°11"07.2e	30
Whyalla area	33°02s,137°35e	40
Woomera area	36°08"8.9s, 139°38"39.6e	25
Gawler Ranges	32°52s, 136°49e	10

2.2 *Sexing of lizards*

E. stokesii shows little or no sexual dimorphism and, as in species such as *Tiliqua scincoides* sex can only be reliably determined by laparotomy (Graves and Halpern, 1991) or ultrasound. The sex of a lizard could be presumed by probing for hemipenes when the lizard was warm and active. It was only possible to probe for hemipenes after the age of 3 yrs. Juveniles and sub adults used in this study could not be reliably sexed.

2.3 Lizard Husbandry.

Lizards were housed in three different types of enclosures: aquariums (35.5cm x 30cm x 60cm), indoor pits (72cm x 69cm x 42cm) or outside, semi-natural enclosures (Small pens: 3m x 1.4m with 77cm walls. Large pens:3.05m x 3.0m with 54cm walls) (Figure 2-2). Lizards were only kept inside, in aquariums for a few weeks after collection, and to give birth. They were then either transferred to outside enclosures or indoor pits where they were held between experiments. All experiments except those in Chapter 8 were performed in outside pens. The experiments for Chapter 8 were performed in indoor pits with windows above them to provide natural light.

Figure 2-2 Typical outside, semi-natural holding enclosure.

2.3.1 Feeding

Lizards were fed twice weekly all year when they were inside, and twice weekly when outside if ambient temperature exceeded 23 °C. They were provided with water ad libutum in a shallow dish.

Most lizards were kept outside all year, even during the winter months, although experiments were not conducted during that time. Lizards were provided with shelter from the rain, but were not fed from May – September of each year of the study. On sunny days during that time, lizards would come out and bask and their scats contained evidence that they had been eating grasses and insects. Lizards usually lost between 2-5% of their body weight during winter. They quickly regained this once regular feeding recommenced.

E. stokesii is omnivorous, with vegetation making up most of an adults diet (Chapter 1). While being held in captivity the lizards' diet consisted of fruit (usually pears, apples and watermelon) and vegetables (usually peas, broccoli and parsley) with eggshells for calcium and commercial reptile supplement added. In the outside pits, this food also attracted flying insects that the lizards would occasionally take. Most pens also contained a small amount of grass that was sometimes eaten by the lizards.

2.3.2 Marking of lizards

Field-caught lizards were toe clipped immediately upon capture for identification purposes. Lizards born in captivity were toe-clipped a few days after birth. Lizards were also paint marked for identification from videotape. Water-soluble, non-toxic commercial model paint ("Gunze sangyo aqueous hobby color") in pink and white was used to contrast with the substrate. This made individual lizards easy to identify on video and was used to mark individuals from all groups, where video analysis was used to examine behaviour. In case this may have increased conspicuousness to predators, outside pens were covered with chicken wire to prevent access by potential predators.

At the conclusion of these experiments, all animals were returned to the same sites in the field that they were collected from, as part of a re-introduction experiment conducted in conjunction with the Department of Environment and Natural Resources, South Australia.

2.4 Experimental methods

2.4.1 Video taping of behaviour.

Video recording of experiments was done using a Sony Video 8 Handycam camera attached to a Sony Time Lapse 24 video cassette recorder (SVT-100P). Standard VHS videotapes were used to record behaviour for all experiments, as normal behaviour was inhibited in the presence of an observer. For many experiments, the lizards were watched from a distance in a concealed position while recording was occurring. This was done using a TV monitor attached to the camera. Specific experimental designs are detailed in the methods section of each chapter.

Chapter 3

3 Ethogram

3.1 Introduction

Studies of reptilian social behaviour are becoming more common, as the diversity of social structure and behavioural displays of this group are being recognised . Lizards have been shown to exhibit long term monogamy (Bull, 2000), lekking behaviour (Wikelski *et al.*, 1996) and recognition of individuals (Olsson, 1994a). As a pre-requisite to the interpretation of such behaviour, a knowledge of the behavioural repertoire of a species is important (Torr and Shine, 1994).

This chapter contains observations on all behaviours that have been recorded in *Egernia stokesii* during the course of this study. This includes material from videotapes of experiments in both inside and outside pits, and field observations. Possible functions for each behaviour are noted, but were not experimentally tested. Statistical analysis was not performed on any of the behaviours listed in this chapter. However, some of the behaviours identified and described here were statistically analysed in Chapter 8 to examine differences in behaviour between grouped and alone lizards, and between dominant and subordinate group members (Chapter 8).

Emphasis is placed on behaviours that have possible social functions, although ordinary behaviours such as moving and drinking are also included. Where possible, comparisons are made to similar behaviours reported in other skink species.

3.2 Methods

Data were collected on the behavioural repertoire of *E. stokesii* both in the field and in captivity. Most of the observations were made from video playback taken in outside pens as part of experiments which are reported in the rest of this thesis. Observations of lizards in semi-natural enclosures may represent an adequate compromise between the possible artefacts in behaviour in an artificial indoor environment, and the difficulty of observing all aspects of behaviour in the field (Greenberg, 1977). Some observations were also carried out while collecting the lizards from the field.

3.3 Results and Discussion- Ethogram for Egernia stokesii.

In general, *E. stokesii* engaged in social interactions often during periods of observation, especially while basking. There was no one particular behaviour that seemed to be strikingly different to the behaviours reported for other scincid lizards but the level of social interaction appeared greater than that reported in ethograms of other scincids (eg Torr and Shine, 1994).

3.3.1 Behaviours exhibited while the lizard is still

Lizards spent much of the observation time lying still. Either in, or just outside their refuge.

<u>Adpress</u> – Lizards flatten their body against the substrate, sometime raising one or more limbs off the substrate. Associated with both thermoregulatory and antipredator behaviour. Lizards will adpress their bodies against the substrate in the morning at the beginning of a basking session, or if a threat is suddenly upon them and there is little chance of escape. Head is usually on the substrate.

<u>Alert</u> – Lizard lies still, but with head raised off the substrate. The head is often raised and <u>tilted</u> toward the source of a stimulus of interest.

<u>Basking</u> – Lizard lies still, perpendicular to the heat source. Lizards spend a significant proportion (up to 85% of their time out of their refuge) basking. Body is not flattened against the substrate as it is when <u>adpressed.</u> Head can be on the substrate or slightly raised.

<u>Eyes closed</u>- The bottom lid is brought up to cover the eye. *E. stokesii* exhibits both synchronous eye closures (SEC) and asynchronous eye closure (SEC) (where one eye closes while the other remains open). Eye closure (either SEC and ASEC) was used as an assay of reduced vigilance in Chapter 7. *Sceloporus occidentalis* was the first reptile to have its asynchronous eye closure quantified (Mathews and Amlaner, 2000). ASEC in *S. occidentalis* is also identified as the closure of one eye while the other remains open. Mathews and Amlaner, (2000) found that ASEC was associated with the same elevated postures of the lizard as those associated with SEC. They also found that ASEC was not associated with an increase in arousal latencies, (usually associated with sleep) suggesting that ASEC is not a form of behavioural sleep in this lizard.

Egernia species have a primitive eye with a fully movable, but opaque lower eyelid that lacks the spectacle that many Australian pygopodids and some geckos possess

(Greer, 1989). *E. stokesiis'* eyes are likely to behave like free evaporating surfaces (Mautz, 1982). In arid conditions eye closure may be useful in reducing moisture loss in basking lizards (Kavanau, 1997).

Lizards were never observed to tongue flick while their eyes were closed, suggesting that they were not chemically assaying the environment when their eyes were closed.

3.3.2 Behaviours used by *E. stokesii* to evade capture

There were several behaviours used by *E. stokesii* to evade capture. Some of these may have been used to avoid predation by predators.

Bloating - This behaviour occurred when an attempt was made to extricate a lizard from a crevice. The lizard wedges itself, head first into the crevice then expands itself, presumably by holding air in its lungs, so it becomes very difficult to move the lizard. Lizards can hold this position for up to 20 minutes (pers. obs).

Freezing - If lizards were more than approximately one metre away from an observer, they would sometimes remain completely still, although they would be focused on the observer as they approached. Sudden movements, and getting within approximately 50 cm would usually mean they would move quickly towards a refuge. Freezing has been observed in other species as an antipredator behaviour. *Anolis cristatellus* remains immobile when first exposed to a potential predator, the Puerto Rican snake, (*Alsophis portoricensis*) (Leal and Rodriguez-Robles ,1995). This may be a low cost, but effective strategy, since Leal and Rodriguez-Robles (1995) found that *Alsophis portoricensis* only attacked *Anolis cristatellus* after it began to move.

Gaping – Mouth open, tongue extruded, accompanied by a hissing sound. Only observed during and after capture. Probably associated with defence. This behaviour, though common in other lizards during capture, (eg Sleepy Lizards (D.Burzacott, pers comm) and Blue Spiny lizards, *Sceloporus cyanogenys* (Greenberg, 1977)) was rarely observed in *E. stokesii*. It was seen only in one female from the Billa Kallina area (see Chapter 4) and their offspring.

Head tilt – similar to "head cock" as observed in the Blue Spiny Lizard (*Sceloperus cyanogenys)* by Greenberg (1977). Lizard tilts its head sideways, presumably so the eye closest to a stimulus can look upwards.

Head turn – animal looks to the side, moves its entire head, so both eyes can look either left or right similar function to head tilt. In *E. stokesii* head tilts or turns us are usually directed at a sudden sound or movement and may be associated with vigilance to a threat or to the movements of conspecifics. The number of head tilts/turns was used as one assay of vigilance in Chapter 7.

Moving – Seems to be either fast run stop, fast run stop, or slow walk (around crevices and basking sites) *E. stokesii* can run quickly if required to (up to 1.5 m/s – pers. obs), however they often seem to prefer to move in a run-stop-run mode, possibly due to their physiology, most lizards have low aerobic capacity (Bennett, 1982).

3.3.3 Intraspecific interactions

Social interactions are likely to be an important part of the behavioural repertoire of *E. stokesii* given that it lives in stable, year-round aggregations (Chapter 1).

Biting – occurs infrequently, usually lizards are bitten on the head, neck or base of tail. Biting is usually associated with lungeing chasing and tail and body twitching. *E. stokesii* has never been observed to open its mouth as a threat before biting. Biting can occur without a pre-cursor such as chasing or lungeing, a lizard will just reach over with its head and grab part of another lizard's body in its mouth.

Chasing – one lizard chases another, occurs especially with introduction of a new lizard into a group or in crowded conditions. A near-mature male has been observed chasing the same aged female, possibly as a pre-copulatory scenario.

Conspecific body licking - *E. stokesii* will often repeatedly tongue flick an unfamiliar lizard under the eyes and around the mouth and vent when it is first introduced into a group. This seems to be a way for the lizards to explore the body secretions, possibly pheromones, of a new individual. Occasionally biting or chasing follows this initial interaction, but overt aggression is rare. Generally, a new lizard that was introduced into a group in captivity was readily accepted by the rest of the group.

Sceloporus occidentalis, the Western Fence lizard also tongue flicks around the eyes of unfamiliar lizards, especially when the intruder is male. Duvall (1982) suggests that this behaviour might occur in *S. occidentalis* because there is at least one exocrine gland in the area and this may be what the lizards are searching for when they tongue flick.

Face wiping on substrate – A lizard wipes the same spots on the face that other lizards tongue flick (see conspecific body licking) on a basking rock or crevice area. In *Sceloporus* occidentalis this behaviour may be a way of leaving chemical deposits as a signal to conspecifics and may also spread secretions from an exocrine gland located in the rictus oris area of the face (Duvall, 1982).

Lungeing – lizard lunges at another lizard, usually toward its head or base of tail. Often followed by biting. Occurs infrequently.

Mass escape - Lizards basking in a group will suddenly flee to a refuge, with one individual leading. The others seem to only be responding to the flight of that individual, rather than what they themselves have seen. Mouton *et al.,* (1999) documented a similar response in *Cordylus cataphractus* while examining the grouping behaviour of that species.

Piggyback basking – This behaviour involves one lizard lying on top of another, and may extend to short periods of the lizard on the bottom carrying the other for short distances. This behaviour usually occurs while lizards are basking, and is particularly common among juveniles (see Chapter 8). A similar behaviour, termed a "lie-on" was reported in *Lampropholis guichenoti* by Torr and Shine (1994). Instances of the "lie-on" occurred infrequently in their study, whereas in *E. stokesii* it occurs during most basking sessions involving groups of animals (Chapter 8).

Tail and body twitching – often associated with chasing, and biting. Lizard moves tail in a stereotyped slow motion way from side to side. Body twitching is similar, although the muscles throughout the body are contracted and released, producing a wave-like motion that extends down the body. Sometimes the lizard coils its body into a sort of S shape before the contraction.

Carlia rostralis, a small skink from the wet tropics of Queensland exhibits a similar behaviour that appears to be associated with copulation. This jerky, exaggerated movement was performed by a male before he attempted to bite the flank of a female and initiate copulation (Whittier, 1993). This behaviour may serve a similar function in *E. stokesii*, although a successful copulation was never observed after this behaviour, but it may be that it is a pre-cursor, and copulation took place after the period of observation.

Jerky, exaggerated movements have also been observed in *L. guichenoti*. Torr and Shine (1994) termed this behaviour "strobe-motion" and suggested that it was a social behaviour, usually performed by males and responded to by females, associated with the assertion of dominance. They also suggest that a pheromone could be produced during this display, as females that were not watching the displaying male, still responded to it. It may be that "strobe-motion" is also associated with mating behaviour in *L. guichenoti.*

3.3.4 Other behaviours

Defecating – Lizard lifts its tail and expels faeces.

Digging – usually at the entrance to a crevice or a wall. Forelegs are used one at a time to dig the substrate. Lizards have been known to tunnel from one pen to another, often through more than 10cm of sand.

Drinking – Lizard extrudes it tongue into a water source, either a bowl of water, or water from the substrate after rain. *E. stokesii* will lick water from substrate in preference to taking water from a bowl.

Open mouth –mouth open for at least one second – possibly aids heat loss. Has been observed in captive lizards. May be associated with heat dissipation (Carpenter and Ferguson, 1977).Unlike gaping, lizards do not open their mouth all the way, and do not hiss. The mouth is usually only open for 1-4 seconds and is not directed at anything.

Scratching – This behaviour was observed on only two occasions, both occurred in outdoor pits. The lizard lifted its hind leg and used it to scratch just behind its ear, in a similar manner to the way in which a scratches for fleas. The tympanum and surrounding area is a common place for the accumulation of mites and ticks, this behaviour may be a way of dislodging parasites, although on both occasions that this behaviour was observed there were no discernible parasites on the lizards.

Wall climbing – Occurs most often in small pens, or indoor enclosures (see Chapter 8). Lizard attempts to climb the pen wall, and will try to dig into the wall with its claws, sometime they just stand up against the wall, without moving.

Rock climbing – The same as wall climbing but done up against rocks or other substrates, may occur as lizards are trying to climb or could be some kind of thermoregulatory posture, in response to the changing position of the sun.

Yawn – Mouth wide open for less than one second. Lizard fully extends its mouth but does not hiss, as in gaping.

In general, *E. stokesii* displays a similar array of behaviours to other skink species for which ethograms have been published. Torr and Shine (1994) described their surprise at the low number of social interactions performed by the Garden Skink, *Lampropholis guichenoti*, a small scincid lizard found on the east coast of Australia. Although hard to compare without quantitative data on the rate of interactions for either species, *E. stokesii* seem to differ from *L. guichenoti* in the level of interactions with conspecifics. Torr and Shine (1994) report that *L. guichenoti* appear to almost ignore other lizards, and rarely respond to them.

E. stokesii spend at least a proportion of most basking sessions involved in piggyback basking, and exhibit a collective response (termed a mass escape) to the fleeing of any member of the group. They will also spend much of their inactive time in a crevice or refuge with another lizard, even when other refuges are available (Chapter 5).

Aggressive behaviour was rarely observed in *E. stokesii*. Biting and chasing occurred occasionally when a new lizard was introduced into a group and was seen directed at a familiar group member on a couple of occasions. These behaviours could represent aggression toward intruders and pre-copulatory behaviour. Scarring has been recorded on adult lizards infrequently, and usually appears to be the result of a previous tick infestation rather than of a conspecific attack.

One behaviour that has not been recorded in *E. stokesii* that might be expected is allogrooming, where a conspecific grooms and bites at the skin of another. Torr and Shine (1994), noted this behaviour in *L. guichenoti* which appears to display far fewer social interactions than *E. stokesii*. A benefit of living in large, stable aggregations could be that other lizards are able to remove ectoparasites, but this behaviour has not been observed, even when specifically tested for by Griffin (unpublished data) (see Chapter 1).

E. stokesii maintains low levels of aggressive behaviour even in quite large groups or in crowded conditions. E. stokesii exhibits behaviours that suggest that both visual (eg body twitching) and chemical (eg tongueflicking) communication is important.

Chapter 4

4 Geographic variation in group size

4.1 Introduction.

Much of this thesis is concerned with comparing the behaviour of lizards that are grouped or alone to determine the possible advantages that grouping behaviour confers for *E. stokesii.* If this behaviour provides important benefits to the lizards and is not just occurring due to a shortage of suitable habitat, then it should persist in different microhabitats throughout the range that this lizard occupies. However, if it only occurs due to limited refuges at some sites then more continuous habitat, more abundant refuge or food resources should produce a reduction in the proportion of lizards that are found in a group and the mean group size.

E. stokesii occupies a diverse range of habitats throughout its range (shown in Chapter 1). Throughout most of the southern part of this range they usually occur in crevices in rocky outcrops (Cogger, 2000; Chapter 1). However, in these areas they can also be found in piles of railway sleepers, metal heaps and even retaining walls (pers. obs). In western Queensland, there are few suitable rocky outcrops, but the hollows in old growth gidgee trees (*Acacia georgina*) are used instead of rock crevices for shelter (see Chapter 1 for a full description). Even in areas where *Egernia stokesii* is only found in rocky outcrops, the quality of the habitat can vary, depending on the rock type and distribution.

These variations in habitat may produce differences in conditions and access to resources for lizards, which may affect their grouping behaviour. Studies in mammals suggest that larger groups form when resources are patchy or unpredictable (Pulliam and Caraco, 1984). For instance, colonies of Common Mole-Rats *Cryptomys h. hottentotus* at an arid site were significantly more stable than those in mesic sites. Dispersal was four times lower at the mesic site than at the arid site, although population density at the mesic site was more than ten times that of the arid site (Spinks *et al.*, 2000). Since both food and new social groups are more patchy at the arid site, the costs of dispersal are higher (Spinks *et al.*, 2000). This study suggests that Common Mole-Rats can adjust their social behaviour depending on environmental conditions.

Groups of up to 17 individuals have been found to occur in Flinders Ranges populations of *E. stokesii*, but group size and composition may vary from this in other areas, depending on habitat or climatic conditions. To examine the group structure among different populations, group size and structure was recorded from a sample of *E. stokesii* from four different regions in South Australia.

Intraspecific geographic variation in phenotype is common in many species of Australian lizards (Qualls and Shine, 1998) and seems to reflect both inherent genetic variability and environmentally induced effects. Geographic variation has been shown to occur in morphological and life history traits including body size (Baird *et al.*, 1997), growth rate (Niewiarowski, 1994) & reproductive output (Forsman and Shine, 1995). In *Saiphos equalis*, a scincid lizard occurring along the east coast of New South Wales, the reproductive mode varies throughout the lizards' distribution. In high-elevation sites, the skinks are viviparous whereas the coastal lizards produce incompletely developed embryos inside partially calcified eggshells. The Sydney form represents an evolutionary intermediate between "normal" oviparity and viviparity. The difference in reproductive mode between the populations is probably a result of cooler conditions at the high-elevation site (Smith and Shine, 1997).

Differences in behaviour among conspecific populations have been documented in other species of lizards. For instance, predator avoidance mechanisms differ intraspecifically in some species, probably as a result of differences in predation pressure between populations. For example, Blazquez *et al.*, (1997) found that populations of *Ctenosaura hemilopha* that had been released onto Cerralvo Island in the Gulf of California, allowed closer approach by a potential threat, than the same species on the mainland. This difference is probably a result of reduced predation pressure on the island (Blazquez, *et al.*, 1997).

Few studies have examined differences in grouping behaviour between populations of lizards, mostly because few lizard species are considered to exhibit anything more than rudimentary sociality (Stamps, 1977; Torr and Shine, 1994). However, Mouton *et al.*, (1999) suggest that group size may vary geographically in the group-living cordylid, *Cordylus cataphractus.*

If group size varies geographically in *E. stokesii*, then identifying the environmental differences between sites may give clues about the factors that influence the formation of groups. Also, if group size varies geographically within a species, it would suggest that grouping is not the result of phylogenetic inertia (Chapter 1) but a response to changing environmental conditions.

4.2 Methods

The data used in this analysis were collected during several field trips where lizards were being caught for other experiments either in the field or at Flinders University. Lizards were collected during the period of 17th January, 1996 to 2nd July, 1997 from four regions within the South Australian range that *E. stokesii* occupies (Figure 4-1). The climate in these four regions is summarised in Table 4-1. Collection sites and details are listed in Table 4-2.

Figure 4-1 Location of collection sites, and the broad regions where lizards were collected (red dots represent specific sites where lizards were collected, the coloured areas represent the regions sampled).

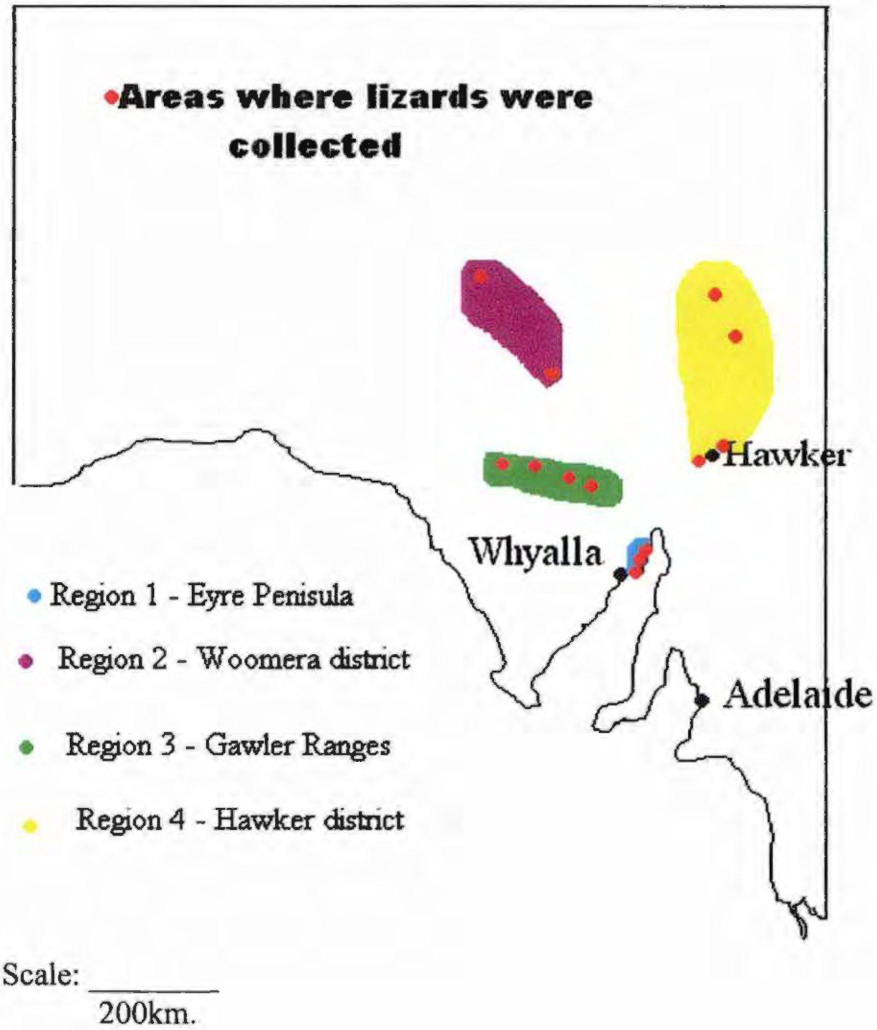


Table 4-1 Weather data from a single weather station in each of all four regions where lizards were collected (Means are from all records collected over approximately 100 years).

Region	**Mean yearly rainfall (mm)**	**Mean maximum air temperature (°C)**	**Mean minimum air temperature (°C)**
Whyalla area (1)	276.1	29.8	2.2
Woomera area (2)	246.6	34.2	5.8
Gawler Ranges (3)	312.3	33.0	3.7
Hawker (4)	190.2	33.6	3.7

When a lizard was captured, its snout vent length, body mass, sex (not always possible to determine, see Chapter 1) and the position of the site were recorded as well as the number of lizards within a 50 cm radius of it. All lizards this close were considered to be within the same group. In many cases, the lizards were in the same crevice.

Search effort was not standardised across regions, but each location was searched for a minimum of 20 person hrs and a maximum of 160 hrs.

4.3 Results.

4.3.1 Group composition.

During the survey period, 136 lizards were collected (Table 4-2). Adults were considered to be lizards of 100mm SVL or more, sub-adults were 70 –100 mm, and juveniles were under 70 mm. Of the 136 lizards collected, 95 (70%) were found in groups (at least one lizard within 50cm of it) The maximum group size was 9 individuals, this group consisted of 5 adults, 3 juveniles (estimated age 1 yr or less) and a sub-adult (approximately 3-4 yrs old) This group was found in the Black Point area, north-east of Whyalla, SA (Region 1), in June, 1997 (Table 4-2: Table 4-3).

Table 4-2 Summary of groups found in geographical survey (A = Adult, us = unknown sex, SA= Sub adult, J =Juvenile, F= Female, M = Male). Position was taken with a hand held GPS for all locations except those in the Whyalla region where the position of the nearest town (Whyalla) is given. Numbers in brackets in the Region column represent the number given to that region in future analysis in this chapter.

Location	**position**	**Region**	**Date**	**Season**	**Habitat type**	**No. of lizards caught**	**Group structure**
Black Point	33s02, 137e35	Whyalla (1)	26/5/97	Autumn	scree	12	**2 singles** (2 us A's) **1 pair** (2 us A) **2 fours** (1 x 1 us A, 1 us SA, 2 J) (1 x 2 us A, 2 J)
Black Point	33s02, 137e35	Whyalla	14/6/97	Winter	scree	18	**1 single** (1 us A) **1 x three** (1 us A, 2 us SA) **1 x five** (3 us A, 1 F A, 1 J) **1x nine** (5 us A, 1 us SA, 3 J)
Black Point	33s02, 137e35	Whyalla	15/6/97	Winter	scree	10	**3 singles** (2 us A, 1 us SA) **1 pair** (2 us A) **1 x five** (1 us A, 1 us SA, 3 J)
Fitzgerald Bay	33s02, 137e35	Whyalla	31/10/96	Spring	scree	9	**2 singles** (1 F A, 1 M A) **1 x three** (1 F A, 1 M A, 1 F SA) **1 x four** (2 F A, 1 M A, 1 F SA)
Fitzgerald Bay	33s02, 137e35	Whyalla	11/12/96	Summer	scree	1	**1 single** (1 F A)
Fitzgerald Bay	33s02, 137e35	Whyalla	26/11/96	Summer	scree	3	**3 singles** (2 us A, 1 us SA)
Fitzgerald Bay	33s02, 137e35	Whyalla	1/04/97	Autumn	scree	3	**1 single** (1 us A) **1 pair** (2 us A)
Point Lowly	33s02, 137e35	Whyalla	2/04/97	Autumn	scree	8	**6 singles** (6 us A) **1 pair** (2 us A)
Point Lowly	33s02, 137e35	Whyalla	2/5/97	Autumn	scree	3	**3 singles** (3 us A)
Point Lowly	33s02, 137e35	Whyalla	2/7/97	Winter	scree	4	**2 singles** (1 us A, 1 us SA) **1 pair** (2 us A)

Table 4.2 continued....

Location	**position**	**Region**	**Date**	**Season**	**Habitat type**	**No. of lizards caught**	**Group structure** **(*not captured)**
Billa Kallina	31°24”31.8 s, 136°57’19.8 e	Woomera (2)	18/1/96	Summer	Wood & metal piles	8	**2 fours** (1 F A, 2 M A, 1 us A) (1 F A, 1 M A, 1 us A, 1 us SA)
Island Lagoon	36°08”8.9 s, 139°38”39.6 e	Woomera	17/1/96	Summer	scree	12	**1 pair** (2 M A) **2 x five** (2 F A, 2 M A, 1 us A), (2 F A, 3 us SA)
Island Lagoon	36°08”8.9 s, 139°38”39.6 e	Woomera	29/12/96	Summer	scree	5	**1 single** (1 us A) **1 x four** (2 us A, 1 F SA, 1 us SA)
Lincoln Gap	32.38s, 135.52 e	Gawler Ranges (3)	6/4/97	Autumn	Rock outcrops	4	**2 pairs** (2x2 us A)
Nonning	32°52s, 136°49e	Gawler Ranges	28/1/97	Summer	Rock outcrops	1	**1 single** (1 us A)
Wartaka	32.38s, 135.52 e	Gawler Ranges	23/1/97	Summer	Rock outcrops	7	**1 single** (1 us A) **3 pairs** (2 x us A) (1 x 1 us A, 1 us SA)
Yardea	32.38s, 135.52 e	Gawler Ranges	29/1/97	Summer	Rock outcrops	7	**1 single** (1 us A) **3 pairs**(3x2 us A)
Hawker	29°54”31.7 s, 136°11”07.2 e	Hawker (4)	20/1/96	Summer	Rock outcrops	10	**7 singles** (5 F A, 1 M A, 1 us SA) **2 pairs** (1 F A, 1 unknown*) (1 F A, 1 M A)
Hawker	29°54”31.7 s, 136°11”07.2 e	Hawker	5/2/96	Summer	Rock outcrops	1	**1 single** (1 us A)
Lyndhurst	30.6s, 138.42 e	Hawker	2/1/97	Summer	Rock outcrops	2	**2 singles** (2 us A)
Nooltana Creek	29°54”31.7 s, 136°11”07.2 e	Hawker	4/2/97	Summer	Rock outcrops	2	**1 pair** (2 us A)
Partacoona	29°54”31.7 s, 136°11”07.2 e	Hawker	21/1/97	Summer	Rock outcrops	6	**3 singles** (2 F A, 1 uk A) **2 pairs** (1 F A, 1 J*) (1 F A, 1 M A)

The most common group size found in the survey was the pair (26.5 % of lizards were found with one other conspecific). When sex could be determined, these pairs were usually a male and female adult. On many occasions, sex could not be determined (Table 4-2). One pair found at Partacoona, consisted of a female and a juvenile. A female and a sub adult were found together in Hawker, Another pair, also located at Hawker, contained two adult males (Table 4-2).

Although singles and pairs were the most common group sizes, 43.3% of animals collected were found in groups of four or more individuals (Table 4-3).

Table 4-3 Percentage and numbers of lizards in each group size for each region.

Group size

Region	**1**		**2**		**3**		**4**		**5**		**9**	
	no.	**%**	**no.**	**%**	**no.**	**%**	**no.**	**%**	**no.**	**%**	**no.**	**%**
Whyalla area (1)	24	17.6	10	7.4	6	4.4	12	8.8	10	7.4	9	6.6
Woomera area (2)	1	0.73	2	1.5	-	-	12	8.8	10	7.4	-	-
Gawler Ranges (3)	3	2.2	16	11.8	-	-	-	-	-	-	-	-
Hawker area (4)	13	9.6	8	5.9	-	-	-	-	-	-	-	-
Total	41	30.1	36	26.5	6	4.4	24	17.6	20	14.7	9	6.6

4.3.2 Seasonal trends.

4.3.2.1 Seasonal variation in group size.

Groups of lizards were collected in different seasons over an 18 month period. Before analysing the effect of region on group size, the mean group size for all four seasons was compared (Figure 4-2). Data were positively skewed and could not be transformed to fit the assumptions of parametric analysis, so a Kruskal Wallis non parametric test was used. There was no significant difference between seasons in the mean group size found, even when Spring which contributed only four groups to the analysis was excluded (Table 4-4).

However, not all regions were sampled in every season, so to account for any seasonal bias in the results, all seasons were analysed first, then for summer only to look for differences in group size among regions, since all regions were sampled during summer (Table 4-2).

Figure 4-2 Mean group size for each season that lizards were collected (note that n = number of groups found, not individual lizards).

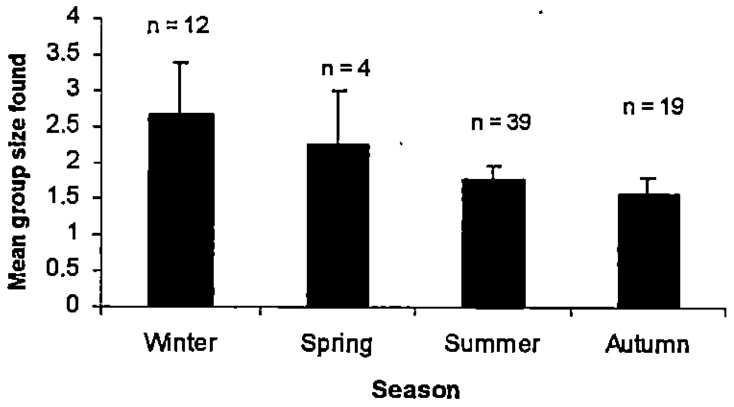


Table 4-4 Summary of non parametric Kruskal Wallis test for comparing means between multiple groups for the effect of season on mean group size of lizards collected.

Analysis	**df**	**Kruskal Wallis statistic (X^2)**	**P value**
Comparing all seasons	3	1.75	0.63
Excluding spring	2	1.43	0.49

4.3.3 Comparison of groups across regions.

4.3.3.1 Proportion of lizards found in groups across the four regions.

The variability among regions in the proportion of lizards caught alone or grouped was first examined (Table 4-5). When analysed together, the regions differed significantly in the proportion of alone versus grouped lizards (Table 4-6). Two groups emerged from the analysis, regions 2 and 3 (Woomera and Gawler Ranges), and 1 and 4 (Whyalla and Hawker). There were no differences between regions within these groups. However, if regions 2 & 3 are combined, then 40/44 (90.9%) of lizards were found in groups. This differed significantly from combined totals for regions 1 & 4 where only 55/92 (59.8%) of lizards were found in groups (Table 4-6).

Table 4-5 Summary of percentage of lizards found alone and in groups in all regions.

Region	Alone		Grouped		Of total	
	No.	%	No.	%	No.	%
Whyalla (1)	24	33.8	47	66.2	71	52.2
Woomera area (2)	1	4.0	24	96.0	25	18.4
Gawler Ranges (3)	3	15.8	16	84.2	19	14.0
Hawker area (4)	13	61.9	8	38.1	21	15.4
Total	41	30.1	95	69.9	136	100

Table 4-6 Summary of Chi-square tests for H_0: The proportion of grouped and alone lizards is independent of region.

Regions tested	X^2 test statistic	df	X^2 critical	Decision	Significance
1,2,3,4	17.27	3	7.82	Reject	p<0.00*
2 vs 3	0.74	1	3.84	Accept	0.25<p<0.5
1 vs 4	1.89	1	3.84	Accept	0.1<p<0.25
2&3 vs 1&4	13.68	1	3.84	Reject	p<0.00*

4.3.3.2 Differences among regions in mean group size.

Mean group size differed significantly among regions (Figure 4-3:Table 4-7). Region 2 (Woomera area) had a mean group size of 3.7 individuals, while the mean group size for Hawker area was only 1.3. Single lizards were included in this analysis.

Although there was no significant difference among seasons in group sizes found, the summer data were analysed to check that the differences in mean group size that were found among regions for all seasons still held when only summer data were tested (Table 4-7). The results obtained for comparing group size among regions, for summer only, were the same as the results for all seasons, that is, Woomera had a significantly higher group size than the other regions.

Figure 4-3 Mean group size in each of the four regions where sampling took place (analysis in Table 4-7) (n= number of groups found).

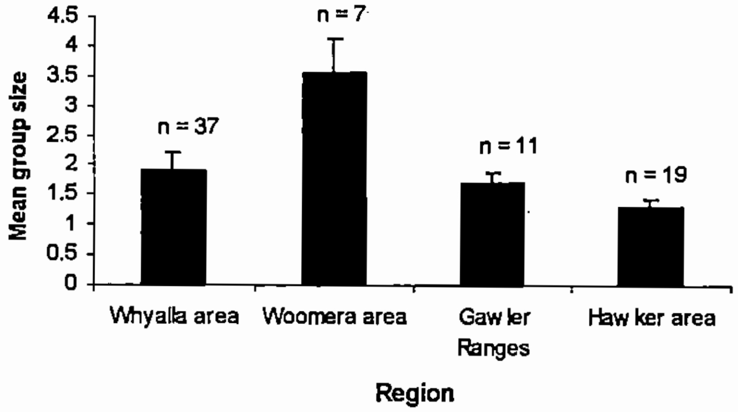


Table 4-7 Summary of results for non-parametric analysis on the differences in mean group size among regions (* denotes significance at the 5% level).

Analysis	**df**	**F statistic**	**P value**
All data – testing among 4 regions	3,70	4.93	0.00*
Summer only - testing among regions	3, 35	17.13	0.00*

Mean group size was greatest in the two regions (Woomera and Whyalla) where lizards were found in scree habitat (Figure 4-5b), rather than in solid rock crevices (Figure 4-5c).

Table 4-8 Results of post hoc tests on mean group size among regions for all seasons and for summer only (* denotes significance at the 5% level).

Region vs	**Region**	**Mean difference for all seasons**	**Standard error**	**P value**	**Mean difference for summer only**	**Standard error**	**P value**
1	2	-1.65	0.55	0.02*	-2.57	0.47	0.00*
	3	0.19	0.46	1.00	-0.67	0.45	0.90
	4	0.60	0.38	0.68	-0.32	0.41	1.00
2	1	1.65	0.55	0.02*	2.57	0.47	0.00*
	3	1.84	0.65	0.03*	1.90	0.38	0.00*
	4	2.26	0.59	0.00*	2.26	0.33	0.00*
3	1	-0.19	0.46	1.00	0.67	0.45	0.90
	2	-1.84	0.65	0.03*	-1.90	0.38	0.00*
	4	0.41	0.51	1.00	0.35	0.30	1.00
4	1	-0.60	0.38	0.68	0.32	0.41	1.00
	2	-2.26	0.59	0.00*	-2.25	0.33	0.00*
	3	-0.41	0.51	1.00	-0.35	0.30	1.00

Figure 4-5b Example of "scree" habitat (Black Point, Eyre Peninsula).

Figure 4-5c Example of typical rocky outcrop with crevices (Midgee Rocks, Eyre Peninsula).

4.3.3.3 Comparison of group size among regions when singles were removed from the analysis.

When singles were removed from the analysis and only groups (more than one individual) were used to compare group size among regions, regions 1 & 2 (Whyalla and Woomera areas) had a significantly higher mean group size than Regions 3 & 4 (Gawler Ranges and Hawker area). However, Whyalla did not differ from Woomera and Gawler Ranges was no different to Hawker area in mean group size of lizards (Table 4-9: Figure 4-4).

Due to the lack of variability in group size found at Hawker and the Gawler Ranges, a non parametric alternative to a one way ANOVA (Kruskal Wallis test) was used to analyse these data (Table 4-9).

Figure 4-4 Mean group size for each region when singles were removed from the analysis. (Note that the only group size found in the Gawler Ranges and at Hawker, where only pairs were found so the S.E.M for those regions was 0).

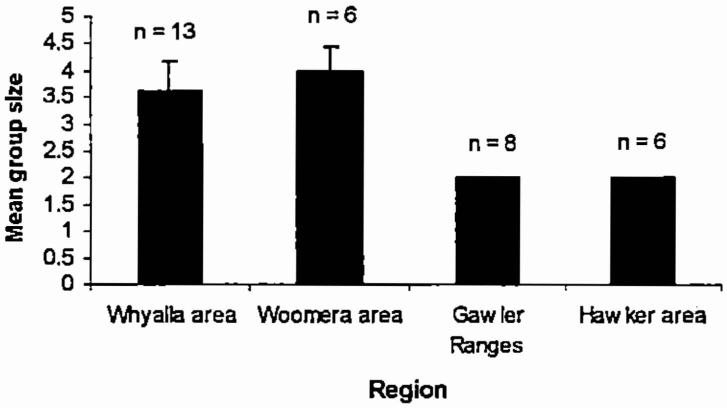


Table 4-9 Summary of results of analysis of differences in group size among regions when only groups of two or more were analysed.

Comparison	Analysis	Test statistic	df	P value
All regions	Kruskal-Wallis test	15.28	3	0.00*
Whyalla and Woomera	Mann-Whitney U test	1.00 (Z score)	1	0.37
Gawler Ranges and Hawker area	Mann-Whitney U test	0.00	1	1.00
Whyalla/Woomera combined vs Gawler Ranges/Hawker combined	Mann-Whitney U test	3.00	1	0.00*

4.4 Discussion:

Just under 70% of lizards collected in this study were found in groups. Pairs were most common, but 43% of lizards were found in groups of three or more. This suggests that grouping behaviour as shown in several populations in the Flinders Ranges around Hawker, also occurs throughout much of *E.stokesii's* range in South Australia.

Mean group size and proportion of lizards found in groups differed among regions, with the Whyalla and Woomera areas having the greatest mean group size, range of group sizes and proportion of lizards in groups. These two areas also differed from the other two in the type of habitat that *E. stokesii* was found in. In Hawker and the Gawler Ranges, lizards were usually found to inhabit deep crevices in large, granite rocks. In both the Woomera and Whyalla areas, lizards were mostly found in "scree" habitat or in piles of wood or rocks. The observed difference in group size could be explained by a difference in the difficulty of sampling each habitat.

Lizards in deep crevices may be more difficult to extract and may be obscured from the biologist. Lizards under loose rocks in the scree habitat may be easier to locate. They also dig extensive tunnels underneath the loose rock surface, which they then run to as soon as they are exposed. They seem to know exactly where these tunnels are which suggests they are part of the lizards home range, but they may run into neighbouring home ranges and quite separate groups or individuals may become mixed during attempts at capture.

Alternatively, scree may represent a "poorer" quality habitat, especially thermally. Crevices in scree can reach up to 45 °C in summer and as low as 0°C during winter (Lanham and Johnston unpublished data). Deeper crevices in the Hawker area appear to offer a more thermally stable environment. Grouping may help individuals regulate their body temperature, in cooler months (see Chapter 6), but may not be as important in summer. It could be that groups space themselves out more in this type of habitat in summer.

The Woomera region, which had the highest mean group size also had both the highest mean maximum and highest mean minimum air temperature (Table 4-1) and the second lowest rainfall, of the regions sampled. Whyalla, which had the highest rang of group sizes and the second highest mean group size had the lowest values for mean maximum and mean minimum temperature of the regions sampled. So, although temperature and rainfall was not quantitatively correlated, it does seem that they are not strongly influencing mean group size in this case. Habitat type may be more important.

This survey shows that grouping behaviour in *E. stokesii* is not just a phenomenon of one isolated population. Although the sort of long term records that have illustrated the group structure and stability at Camel Hill, Hawker (Chapter 1) could not be collected for these other populations in the time available, what is clear is that individual *E. stokesii* still group together in other areas of the lizards' range, and may aggregate in even larger numbers in other habitats, such as scree. Further work could examine more closely the costs and benefits of living in different habitats and the effects of these on grouping behaviour.

The fact that group size seems to change depending on regional, and therefore environmental differences suggests that grouping in *E. stokesii* is not a result of phylogenetic inertia. If *E. stokesii* had retained grouping behaviour as an ancestral trait, then the group size plasticity observed in this survey would not be expected. The fact that there are regional differences suggests that group size is plastic and changes with environmental change. These results also suggest that there are definite costs and benefits associated with grouping in this species, since group size is not uniform across the species range.

Chapter 5

5 Do ecological constraints determine aggregation?

5.1 *Introduction*

Previous research has already shown that *E. stokesii* live in stable year round groups of up to 17 individuals that remain together for up to 5 yrs (Duffield and Bull, 2001) (reviewed in Chapter 1).

In large, rock-dwelling species such as *E. stokesii*, the need for suitable crevices does not diminish during the year. Many members of the Egernia genus have been shown to exhibit unique fidelity to a small area, usually consisting of one or more shelter and basking sites. This fidelity is year round in *E. stokesii* (Greer, 1989; Duffield and Bull, 2001). The home site provides protection from predation and aids thermoregulation during winter and summer (reviewed in Chapter 1).

Aggregation may occur as a result of a shortage of suitable home sites, if there are no suitable crevices available away from the natal area, juveniles may defer dispersal and remain with their parents, even after sexual maturity. Adult lizards may have had to modify their behaviour to tolerate group living if opportunities to disperse are limited. Alternatively, lizards may benefit from proximity to conspecifics (Stamps, 1988). Such benefits could include enhanced thermoregulation, increased ability to detect and escape predators (Chapter 6 & 7), and enhanced mating success (Stamps, 1988).

Although ecological constraints and philopatry need not be mutually exclusive, the relative importance of each may be important, and may vary among species (Graves and Duvall, 1995). If the only reason for the gregariousness of *E. stokesii* is a shortage of suitable crevices, then juveniles should disperse when there are other suitable crevices available.

E. stokesii have been found to occur in groups that are more related than the average for the rest of the population, suggesting that groups consist of family members and probably form due to delayed dispersal by some (probably mostly female) juveniles (Gardner, 1999; reviewed in Chapter 1). However, many groups also contain adults (both male and female) that are unrelated to the main breeding pair or any of the offspring within the group. Taken together, this suggests that juvenile *E. stokesii* should remain aggregated, even when opportunities for dispersal are available, but that related individuals should aggregate more than unrelated individuals. In this chapter, the hypothesis that lizards aggregate only as a result of a shortage of suitable crevices is investigated.

Most studies of reptile groupings have used the term aggregation loosely, preferring subjective definitions such as "....a concentration of (individuals) in a relatively small area such that the density in the aggregation contrasts sharply with that in the surrounding area" (Gregory *et al.*, 1987). Since there are so many variables likely to affect aggregation, especially across species, and when the factors influencing aggregation are important, a more objective indication of aggregation may be necessary.

Mathematical models of aggregation have been devised and used in other taxa in objective tests for departures from random spacing. Examples of such methods include Lloyds index of patchiness (Lloyd, 1967), the negative binomial distribution and the maximum likelihood methods (Krebs, 1989).

However, these models assume that the data being analysed are continuous, ie that the organisms under consideration can be found anywhere within a pre-determined area. This is not true of the possible distribution of overnighting positions for populations of *E. stokesii*. While they may spend periods of time outside of their crevice during the day, they will always seek out a refuge when threatened and for overnighting. Therefore, if their distribution was examined on a spatial scale, they would always be found to be aggregated because their preferred habitat, rock outcrops, and even crevices within those rocky outcrops, are patchily distributed. Even on a smaller scale, in an experimental setting, lizards will only be found overnighting in a crevice or shelter. This means the data collected will be discrete, rather than continuous (Zar, 1994).

A specific model for the experimental arenas that were used, and for the hypotheses being investigated was written in S plus, with the assistance of Dr Natalie Dowling. This model needed to be able to analyse discrete data and still determine if the distribution of lizards differed from what would be expected if lizards selected crevices at random. Initially, traditional measures of aggregation were used, and these showed that lizards were highly aggregated, all the time. They all made the assumption that an animal had equal probability of being found in an position within the space of the pen. This assumption was not met in the case of *E. stokesii.*

Three different, but related experiments were carried out over four years (1995-1999) to investigate aggregative behaviour in the presence of excess crevices.

5.2 Experiment 1 – Family grouping behaviour.

5.2.1 Methods

Four gravid females were collected from Hawker, South Australia in January and early February, 1995 and brought back to Flinders University. They were housed inside in aquaria under 12:12 photoperiod until they gave birth in late February and early March.

After spending the winter in aquaria inside (see Chapter 2 General Methods), both the females and their offspring (three females with five offspring and one with four) were transferred to four semi-natural outdoor enclosures in October, 1995. These pens measured 3m x 1.4m and were bounded by 77cm high metal walls and enclosed with chicken wire to stop potential predators from gaining access to the lizards. Experiment 1 was carried out between 20th October, 1995 –2nd March, 1996. Lizards were fed twice per week when ambient temperature was above 23 degrees (as described in Chapter 2).

In each pen, there were four piles of besser (cinder) blocks. Each pile consisted of three blocks, two large (39cm x 19cm x 14cm), and one small (39cm x 19cm x 9cm). The three blocks were arranged to create three crevices. The small block was laid across the two large blocks that were positioned vertically(Figure 5-1). For this experiment, the hollows in the small blocks formed 2 crevices, while the gap between the two large bricks formed a vertical crevice with a gradually decreasing width (Figure 5-2). Four of these piles made up the twelve crevices available to the lizards. Aside from this, pens contained one or two small bushes that provided some shade during the day and attracted insects to the pens which the lizards, especially the juveniles (Duffield and Bull, 1998) would take.

Figure 5-1 Diagram of crevice pile. Three crevices were available to the lizards, two small ones in the top block, and one vertical crevice between the bottom blocks.

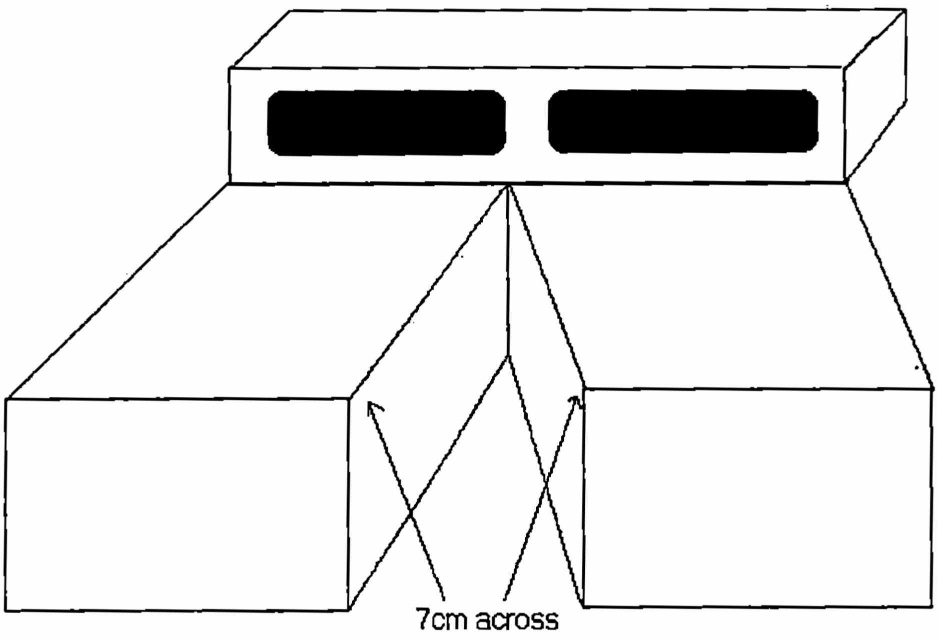
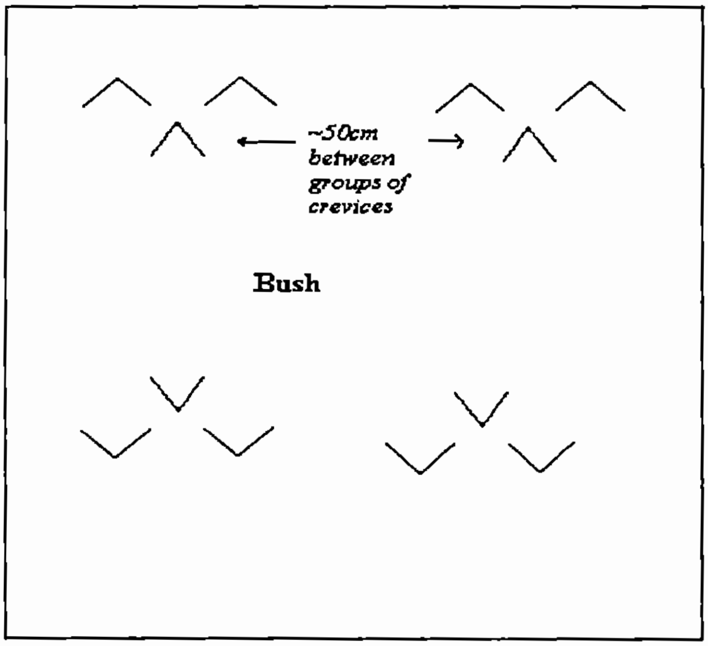


Figure 5-2 Schematic diagram of pen set up (< denotes crevices).



At 8am each morning of the experiment, the position of each lizard was recorded. Recordings were made for 40 days over a four-month period. Observations were discarded if a lizard from another pen dug into the experimental pen or a lizard from the experimental pen escaped into another pen. Lizards were only considered aggregated if they were in the same crevice, not if they were in adjacent crevices or the same crevice pile. Up to five lizards have been observed together in a vertical crevice of the same dimensions as in this experiment. One adult and up to 5 juveniles have been found in the smaller, horizontal crevices.

5.2.1.1 Analysis

Aggregation was assessed in a number of different ways. The primary method of analysis utilised a program written in an S+ program function (see appendix 1 for commands) that simulated the random selection of crevices by different numbers of lizards (3-6, depending on the experiment). This simulation produced a distribution of the lizards' position if they were choosing sites independently of each other. This simulation was run 100 times. If the real lizards were found in aggregations more often than the random simulations, it would suggest some active clustering.

In each simulation run, the number of random selections made by the computer was the same as the number of times overnighting position was recorded in each pen. The frequency of the following distributions was then calculated by the computer from its random sample. All the possible distributions for up to 5 lizards are listed below. Figure 5-2 illustrates all the possible combinations for a group of five lizards. All possible levels of aggregation for a group of six lizards are listed in Appendix 1.

Single- All lizards in separate crevices
One twin – number of occurrences of two lizards together, and the remainder of the group in separate crevices.
Triplet - frequency of occurrences of three lizards in one crevice and remainder in separate crevices

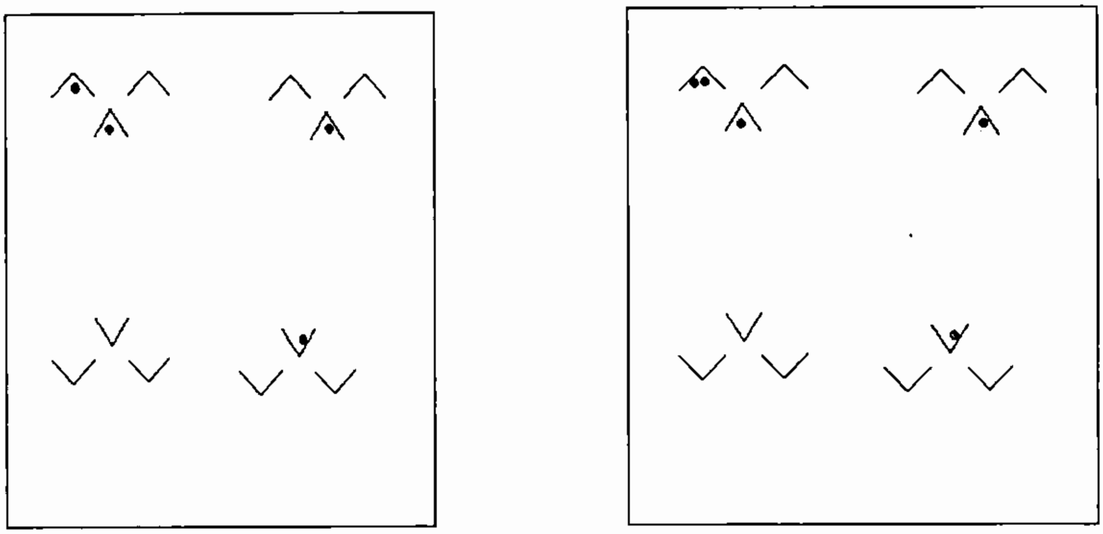
Two twins – values only for 4 or more lizards – lizards in two lots of pairs

Quad - values only for 4 or more lizards – four lizards all in the same crevice

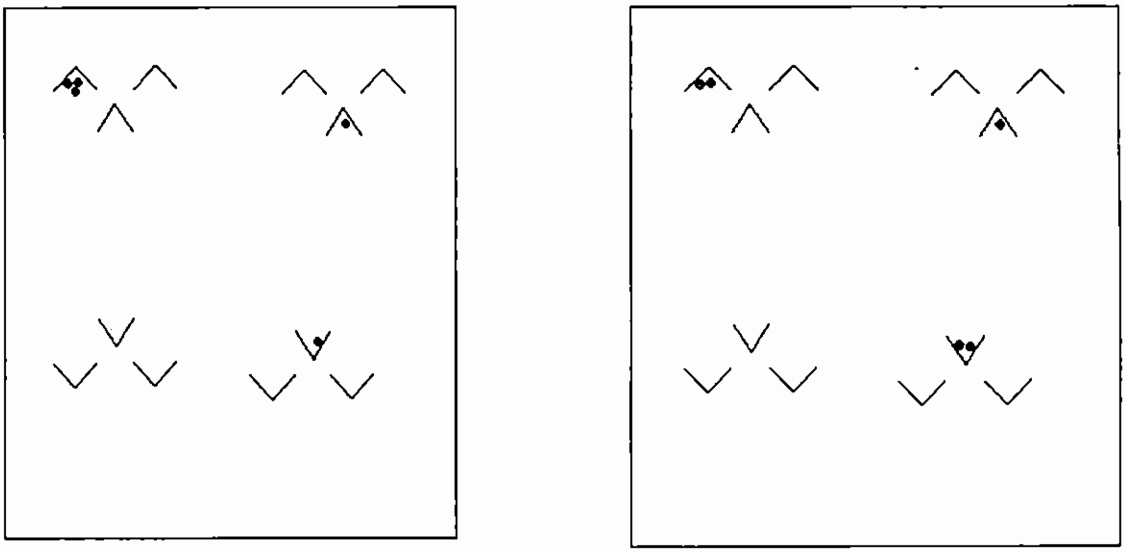
Triptwin- values only for 5 or more lizards- lizards in one triplet and one pair

Quin - values only for 5 or more lizards – five lizards all in the same crevice

Figure 5-3 All possible distributions for a pen of five lizards. The names given to each distribution are also shown.

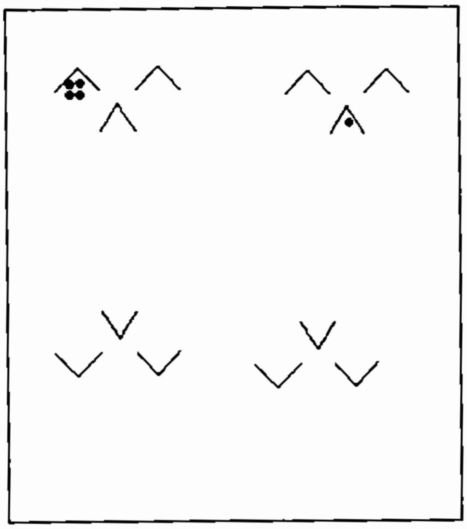


"Single" **"One twin"**

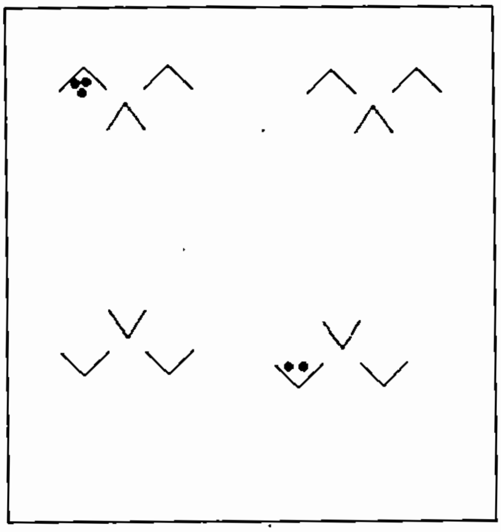


"Trip" (triplet) **"Two twins"**

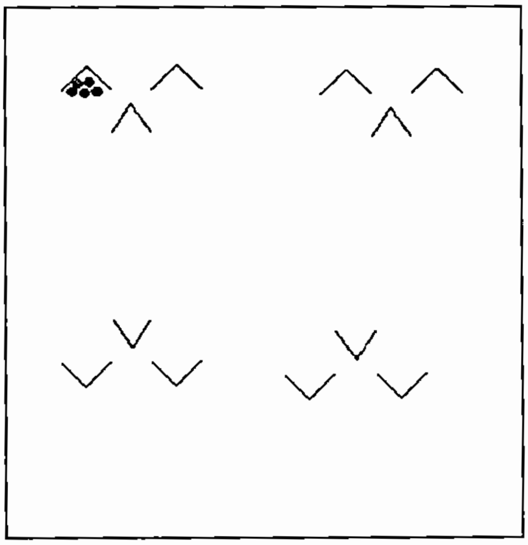
"Quad" (Quadruple)



"Triptwin" (atriplet + a twin)



"Quin" (quintuplet)



The experimental distribution (the frequency of each type of aggregation which was actually found over n days of observations) was then compared to the random model. For example, if the position of a group of 3 lizards was monitored over a period of 30 days, they may have been in separate crevices on 10 days out of that 30, found as a pair and a single on 15 occasions and all in the one crevice 5 times. Their distribution would look like this:-
Single – 10
Twin - 15
Trip – 5.

The empirical experimental distribution was compared to the random model. A count was made of how many of the 100 randomly generated distributions were more aggregated than the real data. To be more aggregated there had to be fewer singles and the same or higher level of the highest aggregation (all lizards in one crevice).

If more than 5% of the randomly generated distributions were more aggregated than the experimental distribution, the conclusion was that the level of aggregation observed could have occurred by chance and not as a result of the lizards choosing to aggregate. The value obtained was the equivalent of a p value in a standard statistical test (Zar, 1996) and the cut off for significance was defined as 5%, the same as a normal statistical test. If there were fewer than 5 aggregated cases in the 100 random simulations, then the experimental distribution was significantly different from what would happen by chance, and that the lizards were not choosing crevices independently. This would suggest active aggregation.

Two simulations were run for the random model. The first involved assuming that each lizard had an equal probability of choosing each of the twelve crevices. Theoretically, on the first day of the experiment each crevice should have the same probability of being chosen as an overnighting site for a lizard. Each day after that, the crevices were cleaned to remove residue which may influence the lizards' choice. A new observation of positions was only made if daytime maximum temperatures exceeded 22 °C meaning lizards would be active and therefore be able to make a new, independent choice about their overnighting position. However, after examining the experimental distribution, it was clear that this was not the case, and in fact lizards were favouring certain crevices and avoiding others. This showed that even pens with very different distributions were considered by the model to all be aggregated. This may occur as a result of aggregation by the lizards, or because individuals preferred certain crevices for their physical benefits. It seemed that aggregation may have been overestimated, in the same way that had been occurring with using more conventional methods of aggregation analysis.

The second simulation applied a weighting to each crevice. The weighting was calculated by first counting the number of times each crevice was chosen by an *individual* lizard over the observation period, regardless of whether it was with another lizard in that crevice or not. This value for each crevice was then divided by the total number of observations (so for example, for a pen with 3 lizards that had 30 days of data recorded, the total number of observations would be = 3 x 30 = 90 possible crevice positions). This gave a weighting for each crevice, and these were used by the computer to generate the random weighted distribution. This meant that "favourite crevices", where lizards were commonly found, had high weightings, while those that were never used by the lizards were effectively excluded from the model, receiving a weighting of zero. All experiments in this chapter were analysed in the same way, using both weighted and unweighted models.

This was likely to underestimate aggregation, since preferred crevices are likely to emerge when aggregation is occurring as well as if individuals are just favouring certain crevices. However, when aggregation was shown with this model, it was likely to be reliable (ie a low chance of a Type I statistical error). This weighted analysis provided a very conservative estimate of the level of aggregation in these experiments.

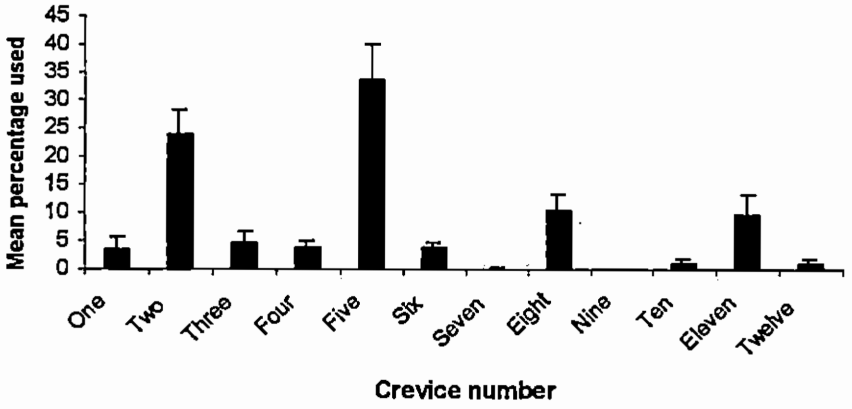
Aggregation was also examined by looking at the percentage of times when all lizards in the pen were found in the same crevice. This provided a quantitative evaluation of the difference in aggregation between treatments.

5.2.2 Results. – Experiment 1.

5.2.2.1 Crevice Preference.

There were two types of crevices in the experimental design, vertical and horizontal, since *E. stokesii* are found in both in the field (see Chapter1). During the study, lizards preferred the vertical crevice to the two horizontal ones within each block of crevices (Mann-Whitney U non-parametric test: vertical versus horizontal crevices. $U_{16,32}$=29.5, p=0.00). There was no significant difference between their preference for either north or south facing crevices (Mann-Whitney U: $U_{24,24}$=287.5, p=0.99) (Figure 5-4). This crevice favouritism was incorporated into the model generated for each pen.

Figure 5-4 Mean percentage use of each crevice for all four pens (Vertical crevices were two, five, eight & eleven) (North facing crevices were 1,2,3 and 10, 11, 12).



5.2.2.2 Aggregation.

Only four related groups were looked at for this initial study. Each group consisted of a mother and either four or five or her offspring. Each animal had at least two crevices to itself. However, a group (at least one group of two lizards in the same crevice,) was found in nearly every pen on each observation day (Table 5-1). Lizards appeared to favour certain crevices, especially the large, vertical crevices (Figure 5-4). This was taken into account in the weighted computer model.

When compared to the unweighted random distribution, all pens were significantly aggregated. When crevices were weighted according to preference by the lizards, then aggregation was found in two of the pens (Table 5-2).

The proportion of observations of lizards all in one crevice was tested to see if it could be used as an indicator of overall aggregation for future experiments. A Pearson rank correlation was used to compare the percentage of observations with lizards all in the same crevice (the highest degree of aggregation) with the probability of aggregation, as determined by comparison with the computer-generated, random weighted model.

"Quins" and "sextets" were correlated with overall aggregation (Pearsons rank correlation: -0.95, p = 0.048) as defined by the computer model. Not surprisingly, those pens deemed aggregated had a higher proportion of lizards all together (mean =10 %) than those considered not to aggregated by the computer (mean = 1.85 %) (Table 5-2). Both aggregation and the percent of observations of lizards all in one crevice was used to compare between treatments in later experiments.

Table 5-1 Percentage of observations of each distribution (a diagram of each distribution is shown in Figure 5-3)

Distribution	Pen 1	Pen 2	Pen 3	Pen 4
Single	2.5	0	0	0
One Twin	17.5	0	19.2	2.8
Triplet	7.5	3.7	23.1	8.3
Two twins	15.0	25.9	19.2	33.3
Quad	7.5	14.8	19.2	2.8
Triptwin	15.0	25.9	7.7	27.8
Quin	12.5	3.7	11.5	11.1
Two triplets	2.5	3.7	-	2.8
Quadtwin	5.0	18.5	-	11.1
Three twins	5.0	0	-	0
Sextets	10.0	3.7	-	0

Table 5-2 Summary of results of Experiment 1. Pens consisted of a female and either four or five of her offspring.

Pen (no. of nights of observation)	Number of lizards	Aggregated? (random model)	p value	Aggregated? (weighted model)	p value	Percentage of observations with lizards all in one crevice	Percentage of observations of a group (at least 2 lizards in one crevice)
1 (40)	6	Yes	0	Yes	0	10 %	97.5 %
2 (27)	6	Yes	0	No	0.11	3.7 %	96%
3 (26)	5	Yes	0	Yes	0	10%	100%
4 (36)	6	Yes	0	No	0.83	0%	100%

5.3 Experiment 2- Effect of relatedness

5.3.1 Methods.

Part a – 1996.

Experiment 2 – 1st part 24th March, 1996 – 3rd May, 1996. Nine groups of three juveniles, either unrelated, related or related with their mother.

A further nine gravid females were collected from the field in January 1996. (see Chapter 2) After being brought back to Flinders University, they were housed inside in aquaria under a 12:12 photoperiod until they gave birth in late February and early March. In late March, six groups of three juveniles alone and three groups of three juveniles with their mother were transferred to the same semi-natural outdoor enclosures used in Experiment 1. These pens contained four piles of cinder blocks which each contained three crevices (12 crevices in total per pen, in the same configuration as Experiment 1).

Three different combinations of juveniles were used:

1) Three unrelated juveniles alone
2) Three related juveniles alone
3) Three related juveniles with their mother

Each treatment had three replicates. A fourth possible treatment, that of three unrelated juveniles with an unrelated female was avoided as it posed some risk to the animals. Although sightings are rare, one observation was made of an unrelated, unfamiliar neonate that had been introduced into an area with an adult female with offspring. The adult female attacked the neonate taking its to head in her mouth. This treatment was avoided so as not to risk this situation occurring during the experiment.

Observations were made of the overnighting position of each lizard for up to 30 days during the period of 24th March, 1996 to 3rd May, 1996. Observations were made either after dark(1800-2030 hrs) or in the early morning (before 10 00 hrs and before lizards had emerged from their overnighting crevice). Notes on the prevailing weather conditions were made, but temperature was not taken.

Part 2 – 1998 30th March, 1998 – 13th May, 1998.

In 1998, the experiment was replicated but only two of the three treatments were used, treatment 1 (unrelated juveniles alone) and treatment 2 (related juveniles alone) with four replicates of each. Relatedness seemed to be more important in determining level of aggregation than the presence of an the juveniles' mother, so more replicates were sort of related and unrelated juveniles. Juveniles were aged between 3- 8 weeks old, having been born in February or March 1998.

The overnight position for each lizard in each pen was recorded in the same way as Part 1, for up to 21 days from 30th March, 1998 – 13th May, 1998. In addition to the information recorded in part 1, shaded temperature was also noted at this time, using a thermometer that was permanently located in a shaded part of an unoccupied pen.

5.3.2 Results – Experiment 2.

Smaller group sizes and larger numbers of replicates were used in 1996 and 1998, compared to the preliminary study in 1995. Relatedness was also tested as a possible factor in aggregation of *E. stokesii*. Table 5-4 summarises the results for the two years. Only the positions of the juveniles were used in the analysis for pens that also contained their mother, so they could be compared directly to pens that only contained juveniles. Note that aggregation occurred more frequently in 1996 than 1998, but this was not significantly different. To illustrate with an example, Figure

5-5 shows all the data that were obtained for one pen in 1996. Empirical data were compared to expected values from the weighted and unweighted models (Figure 5-6). Note that certain crevices were preferred, as shown by a high percentage of usage. In the example shown, crevice 11 was preferred, and used by the lizards 29 % of the time (Figure 5-6). This means that the weighted model for this pen, would select crevice 11, on average, 29% of the time when generating a random distribution.

For both years, all groups were found to be aggregated if all 12 crevices in each pen had an equal probability of being occupied by a lizard (equally weighted model). However, the differences between the weighted and unweighted models shows that a confounding factor in this analysis is that certain crevices are preferred and some were not used at all by any lizard in the pen (Figure 5-6).

Table 5-4 Summary of results for Experiment 2. Treatment: 1= unrelated juveniles without mum, 2 = related juveniles without mum, 3 = related juveniles with mum. "p" is for the weighted model and is equivalent to the p value in standard statistical tests, here it is the number of occurrences of values that have the same or fewer singles than the experimental values and the same or more values for the number of lizards all in one crevice (triplets).

Year	Pen	Treatment	Related?	Aggregated? (equal weighting)	Aggregated? (weighted model)	p	Singles (% in brackets)	Twins (% in brackets)	Triplets (% in brackets)
1996	S1	1	No	Yes	Yes	.00	5 (17.9)	19 (67.9)	4 (14.3)
1996	S7	1	No	Yes	No	.21	7 (22.6)	18 (58.0)	6 (19.4)
1996	N2	1	No	Yes	Yes	.00	1 (3.5)	22 (78.6)	5 (17.9)
1998	N5	1	No	Yes	No	.13	9 (42.9)	5 (23.8)	6 (28.6)
1998	N2	1	No	Yes	No	.26	5 (23.8)	14 (66.7)	2 (9.5)
1998	S1	1	No	Yes	No	.11	3 (14.3)	12 (57.1)	6 (28.6)
1998	N8	1	No	Yes	No	.28	1 (5.0)	18 (90.0)	1 (5.0)
1996	S8	2	Yes	Yes	Yes	.00	1 (3.4)	16 (55.2)	12 (41.4)
1996	N1	2	Yes	Yes	Yes	.00	2 (9.1)	15 (68.2)	5 (22.7)
1996	N7	2	Yes	Yes	Yes	.00	4 (14.8)	11(40.8)	12 (44.4)
1998	N1	2	Yes	Yes	No	.13	4 (19.0)	13 (62.0)	4 (19.0)
1998	N6	2	Yes	Yes	Yes	.01	3 (14.3)	10 (47.6)	8 (38.1)
1998	N7	2	Yes	Yes	No	.98	7 (35.0)	11 (55.0)	2 (10.0)
1998	S2	2	Yes	Yes	No	.14	4 (19.1)	10 (47.6)	7 (33.3)
1996	S6	3	Yes	Yes	Yes	.00	8 (27.6)	16 (55.2)	5 (17.2)
1996	S2	3	Yes	Yes	No	0.40	2 (7.1)	22 (78.6)	4 (14.3)
1996	N8	3	Yes	Yes	Yes	.00	3 (10.0)	19 (63.3)	8 (26.7)

Figure 5-5 Example of the data that were obtained from the model compared to the empirical data. Distribution of four lizards in twelve crevices over 29 observations for Pen S6, 1996. Treatment was related juveniles with mum. Experimental, random and random with weightings for favoured crevices are shown (see legend).

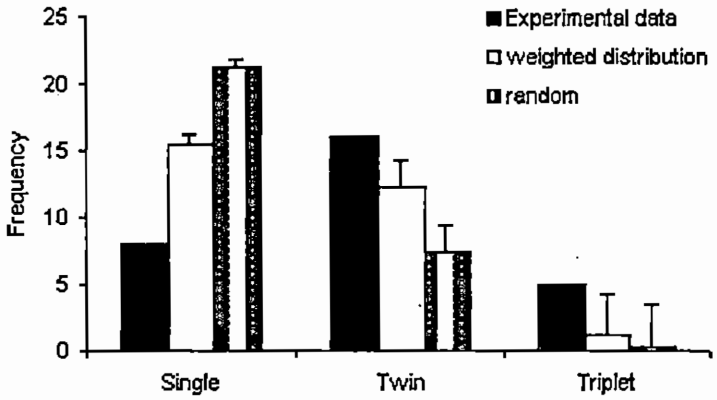
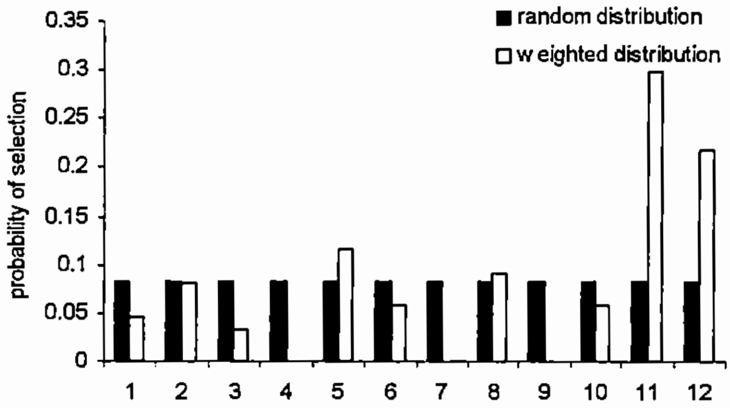


Figure 5-6 Weighting for the two different random simulations. Weightings were taken from the experimental data collected for each pen, they are compared here to the equally weighted, completely random model (data are from the same example as above) (same pen as Figure 5-5)



5.3.2.1 *Effect of treatment and year on aggregation.*

When compared to the unweighted random model, all pens were significantly aggregated for both years.

However, when compared to the weighted model, the 1996 experiment had a significantly higher proportion (77.8%) of aggregated groups than the 1998 one (12.5%) (Chi square analysis: $X^2 = 4.87$, $0.025<p<0.05$) (Table 5-4). There was a higher proportion of related groups (6/9) in 1996, compared to 1998 (4/8). Relatedness did not affect aggregation for 1996 (Chi square analysis: $X^2 = 2.0$, $0.10<p<0.25$). A Chi-square could not be performed on 1998 data because expected values were too low for the tests' assumptions.

5.3.2.2 *Effect of treatment on groups found (Part A – 1996).*

Data were initially analysed separately for each year of the study, because there was no third treatment in 1998. Data for both years were only combined for testing between related and unrelated treatments.

Lizards all in one crevice – triplets.

The proportion of observations where lizards were all found in one crevice (called a triplet) was not significantly different between treatments (Table 5-5). Unrelated juveniles were found all in one crevice on the least number of occasions (mean = 17.1%) while related juveniles were found in triplets on average, in 39% of observations. However, related juveniles in groups with their mother were only found in triplets for an average of 19.5% of observations Figure 5-7).

Proportion of observations when a group was found.

The proportion of observations when there was some form of aggregation (either two or three lizards in one crevice) was also examined. This included all observations except those where lizards were found alone, in separate crevices. The proportion of groups observed was not significantly different between treatments, values were all relatively high, with groups found in over 80% of observations for all treatments (Figure 5-7 and Table 5-4).

Figure 5-7 Mean proportion of observations with all lizards in the same crevice (triplet), and for lizards found in a group (either twin or triplet) for each treatment (summary of analysis in Table 5-4).

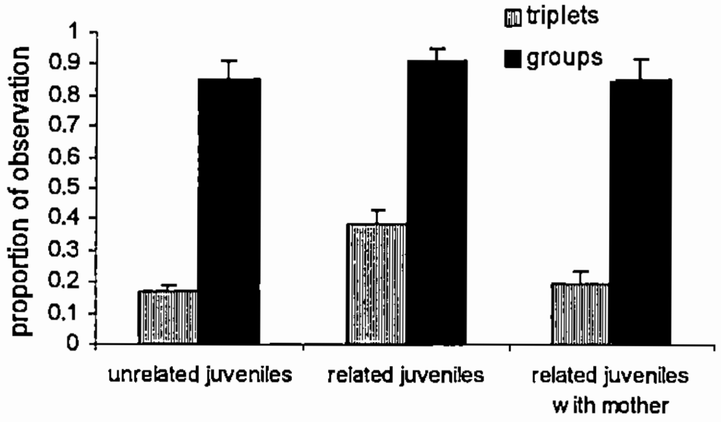


Table 5-4 Summary of statistical analysis on 1996 data (triplets are when all lizards are in the same crevice, a group is when two or more lizards share the same crevice)

Treatment	**Dependent variable**	**df**	**Analysis**	**Statistic**	**P value**
Unrelated vs related alone vs related with their mother	Prop in triplets Prop in groups	2,6 2,6	One way ANOVA	4.07 0.22	0.08 0.81
Related vs unrelated	Prop in triplets Prop in groups	7 7	Independent samples t test	1.55 0.47	0.16 0.17
Effect of mother- Related with and without their mother	Prop in triplets Prop in groups	4 4	Independent samples t test	1.02 0.47	0.34 0.66

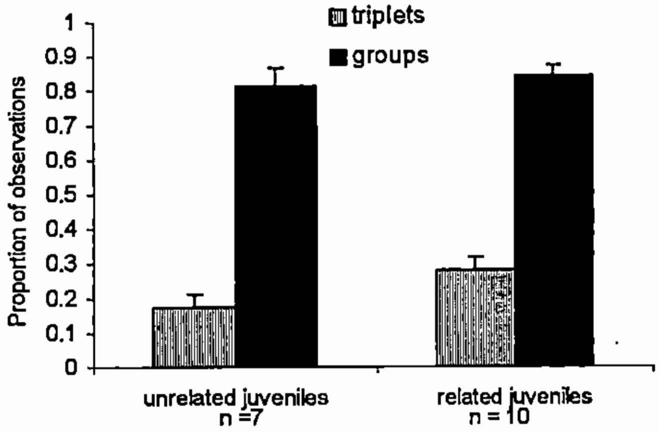
5.3.2.3 Effect of relatedness – 1996 and 1998 data combined.

Triplets.

There was no difference between years in the proportion of observations of triplets (Independent samples t test: t_{15}= 0.79, p=0.44), so data from both years were combined to test the effect of relatedness.

Related lizards in groups were found significantly more often in triplets (all together) (30% of observations) compared to only 18% for unrelated lizards (Figure 5-8).

Figure 5-8 Proportion of observations with lizards all in one crevice (triplets) and for groups for both years combined, comparing related and unrelated juveniles (Independent samples t test on arcsine transformed data: t_{15}=2.11, p=0.05*).



Groups.

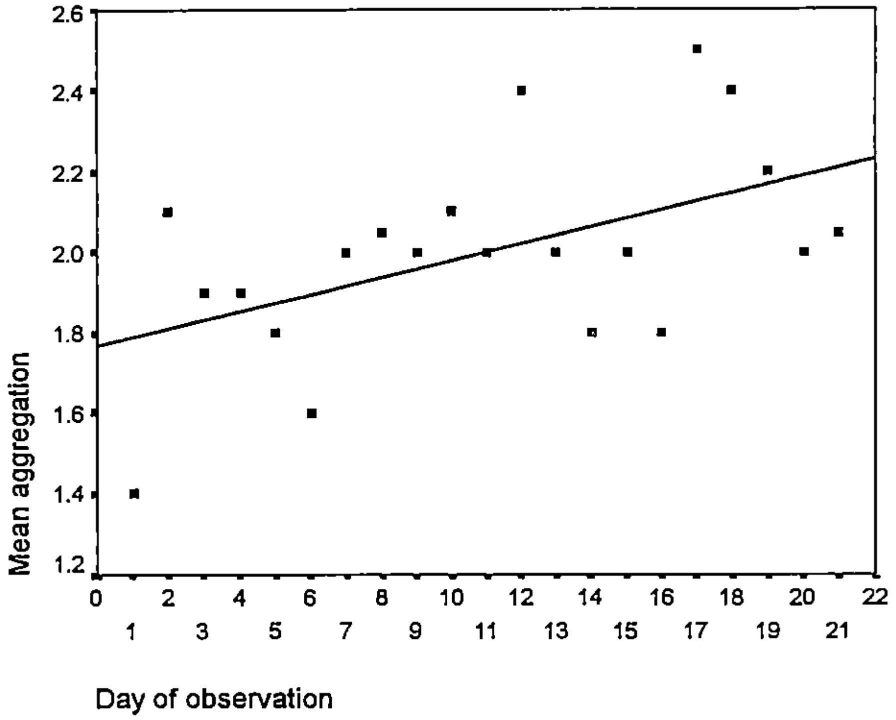
The proportion of observations of lizards in groups was not significantly different between years either (Independent samples t test: t_{15} = 1.87, p= 0.08), so data from both years were combined to analyse the effect of relatedness on the formation of groups. There was no difference between related and unrelated treatments in the proportion of observations of lizards in groups for both years combined (Independent samples t test on arcsine transformed data: t_{15}= 0.56, p= 0.59).

5.3.2.4 Effect of Time.

The effect of day of observation on aggregation was tested for data from 1996 and 1998 separately. Numerical values were assigned to each type of distribution within a pen. Singles (when three lizards were in 3 different crevices) received a score of "1". Twins (when there were two lizards in the same crevice and one by itself) received a score of "2" and triplets (all lizards in the one crevice) received a score of "3". Each pen on each day scored a value of 1, 2 or 3. In 1996 there was no effect of day of observation on aggregation (Friedman's non parametric test: X^2=19.35, p =0.50).

However, in 1998, day of observation significantly affected mean aggregation (Friedman's non parametric test: $X^2 = 31.86$, $p = 0.045^*$) with aggregation increasing slightly over time for both related and unrelated treatments (Figure 5-9).

Figure 5-9 Mean aggregation for related and unrelated groups combined versus day of observation for 1998.



5.3.2.5 Effect of temperature

Initially, the relationship between day of observation and temperature was tested. Figure 5-10 shows that there was no relationship between these two variables.

Only data from 1998 could be used to examine the effect of temperature on aggregation, as no temperatures were taken during 1996. The mean values for each day are shown in Figure 5-11. Aggregation showed a trend towards being inversely related to temperature, but this was not quite significant (Figure 5-11). Further investigation into the effects of temperature on aggregation is reported in Chapter 6.

Figure 5-10 Day of observation versus temperature for 1998 data (Regression analysis: R^2=0.04, $F_{1,19}$ = 0.87, p = 0.36).

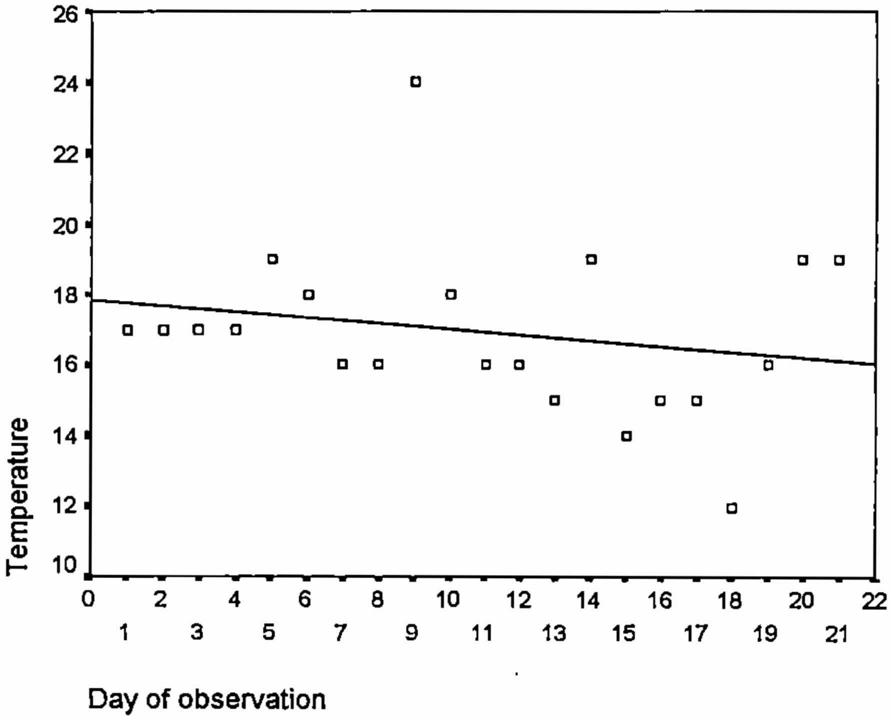
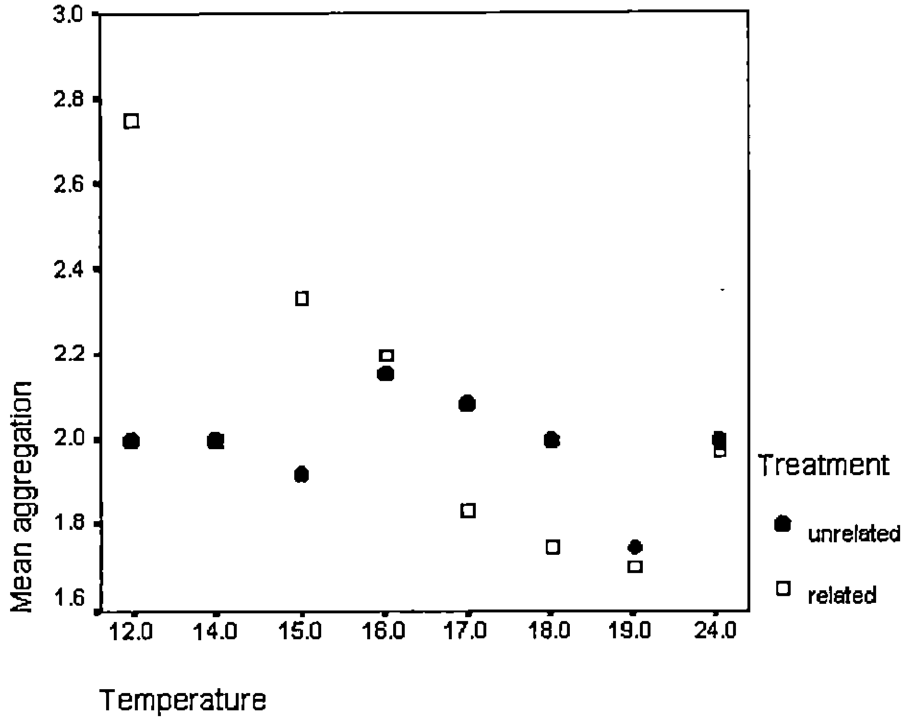


Figure 5-11 Mean aggregation against temperatures of the days when sampling took place, showing values for related and unrelated groups Experiment 2, part II (Friedman non parametric test: $X^2 = 13.1$, $p = 0.07$).



5.4 Experiment 3 Spatial manipulations.

5.4.1 Methods

After discovering that related groups were more likely to form aggregations than unrelated groups, a third set of experiments were designed to examine if this result was just an artefact of slight differences in crevice size and shape within each crevice pile, since previous experiments had used blocks that provided two types of crevice sizes.

Therefore, in 1999, the design of the experiment was altered so that each pile of besser blocks contained only one vertical crevice. Vertical crevices seemed to be preferred over horizontal ones, Larger pens were also used (3.05mx 3.0m x 0.54m). Crevice set up is shown in Figure 5-12. The same cohort of juveniles were used as in 1998, in fact four of the eight groups were the same lizards as in 1998. These juveniles were now 12-15 months old. Experiments were conducted between 25th January, 1999 -18th May, 1999. Nine groups of 3 juveniles, four related and five unrelated groups were used in the experiment. Three groups were observed over a three-week period, then they were replaced with three different groups for another three weeks, then the last three groups were used.

The three pens were set up to examine the influence of spatial scale on aggregation. One pen contained 12 crevices within an area of 9.15m^2. Another pen contained 24 crevices in the same area, while the third had 24 crevices but in double the area (18.3m^2). This experiment was not a balanced design that would allow two way ANOVA to look for impact of relatedness and spatial organisation of crevices in the same analysis.

However, this design was used to attempt to answer the following questions:

1) Does spatial scale affect the aggregation of juvenile lizards?

If aggregation occurs only due to limit in the number of suitable crevices, then by ensuring that each crevice is separate, and exactly the same, and by comparing the same number of crevices in two different –sized areas, the effect of spatial scale could be determined.

2) Does aggregation diminish with an increase in the number of crevices?

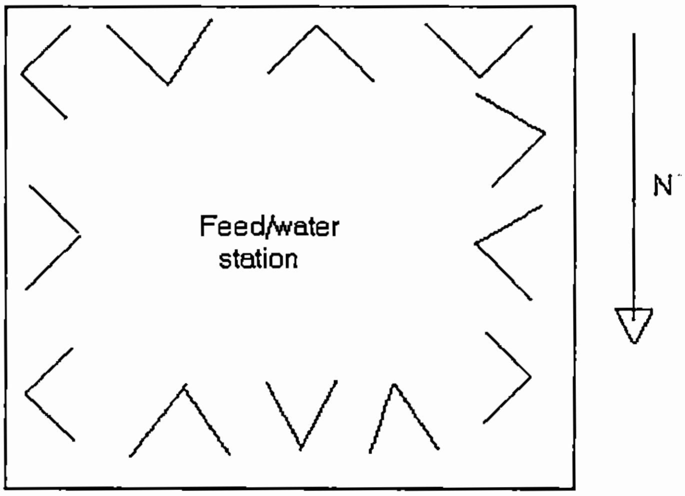
The number of crevices used in the previous experiments (12) was an arbitrary number representing excess crevices for each group size (at least two and usually three choices per lizard). However, this may not represent an excess number of crevices to each lizard, if some were unsuitable as refuges or distance from or to a neighbour was important. If lizards dispersed when the number of crevices was increased, that would suggest that 12 was not an excess.

3) Does relatedness affect the results obtained for 1) & 2)

4) Do older juveniles alter their aggregation patterns? Do the same trends from experiment 2 still occur when lizards are 18 months old and closer to sexual maturity?

The position of each lizard in each pen was recorded before 9 am each morning of the three-week experiment, along with the shade temperature. Scats were removed (as in Experiment 1 and 2, this Chapter) and blocks were also washed down to remove lizard traces. Lizards were returned to the same crevice they had overnighted in.

Figure 5-12 Diagram of pen set up for Experiment 3.



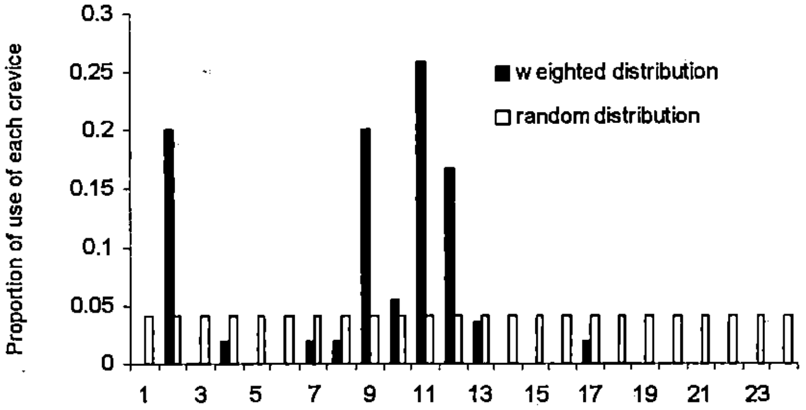
5.4.2 Results

Aggregation was still found in four out of nine groups when compared to the random model. No groups were found to be aggregated when compared to the weighted model, because that lizards were still favouring specific crevices (Figure 5-13). No groups were found with all three lizards in one crevice. This differs from the previous experiments (Table 5-5).

Table 5-5 Summary of results of Experiment 3 (No triplets where lizards are all in one crevice were found).

Pen	Related?	Number of crevices	Aggregated (unweighted)	P value (unweighted)	Aggregated (weighted model)	p value (weighted)	Proportion of singles	Proportion of twins
1a	related	24	No	0.76	No	0.99	.89	0.11
2a & 3a	unrelated	24	Yes	0	No	0.25	0.53	0.47
4a	related	12	No	0.25	No	0.81	0.63	0.37
1b	unrelated	24	No	0.20	No	0.87	0.76	0.24
2b & 3b	related	24	No	0.40	No	0.88	0.82	0.18
4b	unrelated	12	Yes	0.02	No	0.58	0.44	0.56
1c	unrelated	24	No	0.06	No	0.99	0.72	0.28
2c & 3c	related	24	Yes	0	No	0.58	0.39	0.61
4c	unrelated	12	Yes	0	No	0.72	0.28	0.72

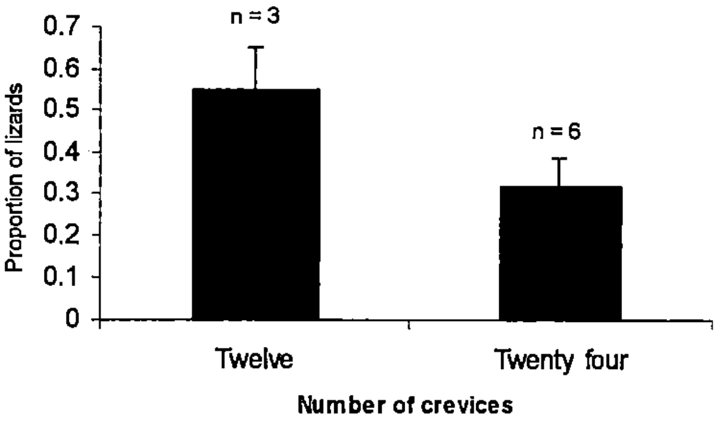
Figure 5-13 Example of the probability of use by a lizard for each crevice, with the weighted and random distributions. (Pen 1c, 24 crevices), 1999.



5.4.2.1 Effect of number of crevices and spatial scale on aggregation.

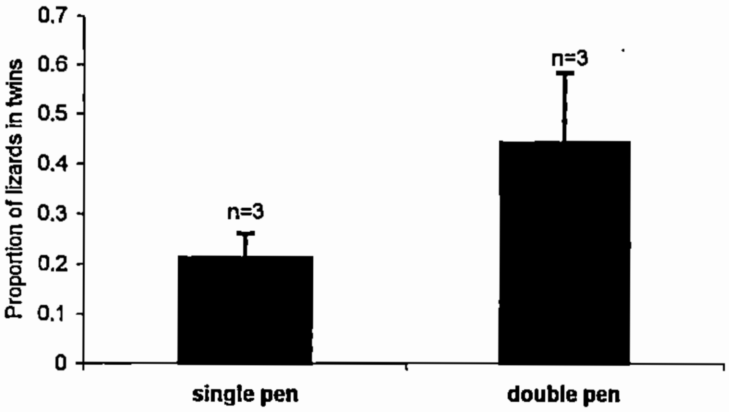
There was no significant difference in proportion of lizards found in twins between lizards housed in pens with twelve crevices) and those in pens with 24 crevices (Figure 5-14).

Figure 5-14 Proportion of lizards in twins (two in the same crevice) for pens with twelve or twenty four crevices (Independent samples t test on arcsine transformed proportions: $t_{1,7} = 1.81$, $p = 0.11$).



Lizards showed no difference in the proportion of twins between the more spaced out treatment (24 crevices in 18.3m^2) and the more cramped treatment (24 crevices in 9.15m^2).

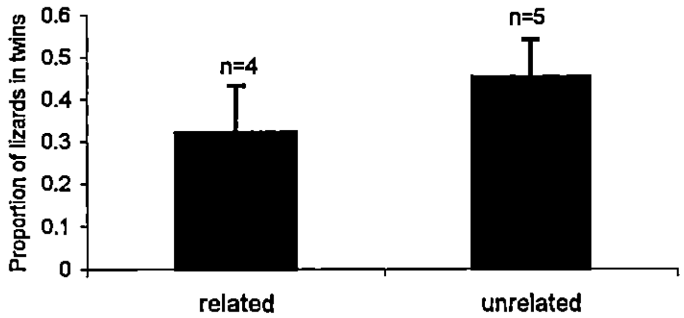
Figure 5-15 Proportion of lizards in twins for twenty four crevices in either a single pen (9.15m^2) or in a double pen (18.3m^2) (Independent samples t test on arcsine transformed data: $t_{1,7}$= 1.55, p=0.15).



5.4.3 Effect of relatedness.

There was no statistical difference found between the proportion of unrelated lizards forming twins and the proportion of related lizards in twins (Figure 5-16).

Figure 5-16 Proportion of lizards in twins for related and unrelated groups (independent samples t test on arcsine transformed proportion: $t_{1,7}$= 0.37, p= 0.15).



5.5 Discussion.

The evolution of group-living is generally explained by either a limit in resources (ecological constraints) or an advantage to an individual in staying with conspecifics (philopatry) (Emlen, 1994).

These experiments were designed to determine if aggregation was constrained by a limit in suitable crevices by providing excess crevices. A model was designed to test for aggregation firstly assuming equal liklihood of a crevice being selected by an individual lizard, and then with a weighting, based on the usage of that crevice by each lizard in the pen. The empirical distribution of lizards was then compared to what would be expected by chance. Comparison to the unweighted random model showed that lizards had a strong tendency to aggregate, even with an excess of crevices to choose from, with only a few exceptions in experiment 3, all groups were considered aggregated.

This could be because juvenile *E. stokesii* have a tendency to refuge together, or because some refuges are preferred over others, and so lizards tend to choose the same refuges. However, even if *E. stokesii* are choosing the same crevices because of inherent properties of the crevice, this result still shows an unusual tolerance of other individuals.

Other lizard species have been shown to preferentially aggregate, even when alternative refuge sites are available. Elfstrom and Zucker, (1999) compared the distribution of *Urosaurus ornatus* in artificial rock clusters to a random model and found that individuals were in contact with conspecifics more than what would be explained by chance. *U. ornatus* also used less than 20% of suitable refuging area available, suggesting that, like *E. stokesii*, individuals and aggregations are spaced non-randomly. The difference between *U. ornatus* and *E. stokesii* appears to be that groups of *E. stokesii* aggregate in shared crevices year round, not just in winter.

The tendency for lizards to prefer vertical crevices could be that these crevices had better physical properties, or it could be that lizards could cluster more easily within these crevices. This favouritism, as detected in the first experiment was why only vertical crevices were used in the third experiment.

By weighting the crevices according to preference by the lizards in the experiment, and incorporating this weighting into the model, it could be determined if lizards are choosing refuge sites independently of each other. In some cases, groups were still found to be aggregated, particularly in 1996 and in related groups of lizards. Where aggregation was not detected in the weighted analysis, it may have resulted from a strong preference to go back to the same crevices where lizards refuged together before. It is difficult to tell if this is because of the physical attributes of the refuge (for example, the aspect, temperature etc) or because of a learned association of that refuge with other lizards. Cleaning may remove odour, but does not erase spatial memory.

If pens were found to be aggregated using the weighted analysis, this emphatically proves aggregation when detected, but it cannot disprove aggregation when not detected since a preference for a few crevices may be due to association with conspecifics or it may just be the physical properties of the refuge. This model was intended to be conservative in how it determined if a particular pen was aggregated or not. The problem is it may have been too conservative and some highly aggregated pens could have been missed, just because the group chose the same crevices all the time.

Effect of relatedness.

The proportion of observations when lizards were all together was used to test for differences in aggregation between related and unrelated groups of lizards. Since this provided a quantitative measure of the level of aggregation, not just whether they were aggregated or not, as the model did. In experiment 2, related groups were more likely to be found all in the one crevice than those in unrelated groups. This provides behavioural evidence that supports genetic data that groups in the field are more related to each other than to the rest of the population, suggesting groups are mostly made up of family units and that delayed dispersal of one or both sexes is the likely mechanism for group formation (Gardner, 1999).

The fact that lizards are still choosing to share crevices with their relatives until at least eight months of age, and probably for several years, (Duffield and Bull, 2001) is unusual, since many lizard species disperse away from their natal site only weeks after birth and well before reproductive age. For example, 75% of juvenile Pygmy Blue Tongues (*Tiliqua adelaidensis*), disperse within 5 weeks of birth. The mothers of half the remaining 25% disperse during the same period of time, leaving the juvenile alone at the natal site (Milne and Bull, 2001). *Lacerta vivipara* a small (SVL = 50-70mm) lacertid occurring in Europe disperses within 10 days of birth (Lena *et al.*, 1998).

Experiment 3 was designed to test the extent of the aggregation discovered in experiment 1 and 2 by looking at older juveniles and increasing both spatial scale and number of available crevices. Only vertical crevices were used in this experiment as they had been preferred by lizards in the previous experiments. No differences were found between treatments, although no lizards were found all in one crevice in this experiment, suggesting that spatial scale and age may affect aggregation behaviour. In this experiment, there was no evidence that related groups of lizards aggregated more than unrelated ones, perhaps because they were older than the lizards used in experiment 2. This experiment could have been improved by balancing the design and by adding more replicates.

In the field, breeding pairs are less related to each other than to the average individual in the population (Gardner, 1999), suggesting lizards might be attracted to unrelated individuals when they are approaching sexual maturity. Sex differences may also begin to be important as lizards get older. Future experiments could examine the effect of ontogeny on aggregation tendency.

There was also no significant decrease in aggregation, either by increasing the number of refuges or increasing the separation between refuges. This implies that aggregation does not just occur because of lack of space or suitable crevices, but may benefit individuals in some way. Two possible benefits, enhanced thermoregulation and group vigilance will be discussed in the next two chapters of this thesis.

In conclusion, these experiments suggest that ecological constraints are not the primary cause of group-living in this species. A shortage of crevices may once have forced lizards to aggregate, but they have developed not just a tolerance for conspecifics, but perhaps a tendency to actively seek them out. The finding that related juveniles are more likely to aggregate suggests delayed dispersal does occur in this species, supporting genetic data (Gardner, 1999), that groups in *E. stokesii* consist of family members and form primarily due to delayed dispersal of offspring.

Chapter 6

6 Thermal advantages to grouping behaviour.

6.1 Introduction

Thermal advantages to group-living have been reported among a wide range of taxa. Huddling in cool conditions can reduce cold stress by reducing the surface area to volume ratio, by sharing body heat and assist in the prevention of moisture loss at a time when animals are unlikely to be able to seek out additional water (White and Lasiewski, 1971).

Animals, especially ectotherms, may also be able to maintain a higher temperature if aggregated during the night when ambient temperatures drop below optimal, even during the active season. This may be particularly important to ectothermic species. Galapagos Marine Iguanas, *Amblyrhynchus cristatus*, form sleeping piles at night and experiments have revealed that the lizard closest to the centre of the pile has a higher temperature at dawn than those sleeping solitarily or on the outside of piles (Dee Boersma, 1982). Dee Boersma (1982) predicted that behavioural adaptations designed to increase body temperature at night should occur more often in herbivorous lizards, presumably because digestion of vegetable matter takes longer and is up to 60% less efficient than the digestion of protein (Iverson, 1982).

If thermal benefits are important in the formation of groups, then grouping behaviour should alter when temperature does. This hypothesis predicts that a) lizards in groups will maintain a higher temperature when ambient temperature is decreased than lizards living alone and b) the tendency of *E. stokesii* to form groups will increase at lower temperatures

6.2 *Experiment 1 –cooling of solitary and grouped lizards.*

6.2.1 Methods

Experiments were conducted in outside pens (see Chapter 2 for dimensions) over two evenings on the 8th & 9th May, 2000. Data for analysis were collected on both evenings for just over three hours (16:25-19:35). These two days had similar prevailing weather conditions (Table 6-1).

Table 6-1 Prevailing weather conditions for the two days of the experiment.
(Taken from the Bureau of Meteorology records for the Adelaide Airport weather station).

	8th May, 2000	**9th May, 2000**
Sunset	17:27 hrs	17:26 hrs
Rainfall (mm)	0	0
Minimum temperature (degrees Celsius)	6.9	8.1
Maximum temperature (degrees Celsius)	19.2	18.6

Adult lizards of a similar size (~200 grams) were selected from the captive population living in semi-natural outdoor enclosures at Flinders University. Twenty four lizards were divided into three groups of six and two groups of three. Four other lizards were kept as individuals. Groups only contained individuals that had been living together, to avoid possible antagonism.

A focal animal was randomly chosen from each size group to have its body temperature monitored. Equal numbers of females and males were used for this experiment but sex was not taken into account during the analysis. Body temperature was measured by inserting a temperature probe (Tinytag Gemini miniature temperature data logger) approximately 5 cm into the cloaca of the lizard. The logger and probe were taped to the tail of the lizard using 8cm silver duct tape. The protective casing was removed from around the logger to make it easier to affix to the lizard, and to reduce the bulk that the lizard had strapped to its tail. A small, plastic resealable bag was used to protect the loggers from moisture during the experiment. The logger recorded body temperature at 10 minute intervals.

Focal lizards and their groups were then placed into white plastic buckets with a height of 40cm and diameter of 28.5cm. The buckets were used to help keep the lizards together so that any effect of physical contact of group members on temperature could be ascertained. Ambient temperature was recorded using the same type of logger. The probe was placed in a separate bucket next to where the lizards were held. The buckets were placed in the outside pens where the lizards had been living. Ambient temperature was recorded for the duration of both trials also at ten minute intervals.

Lizards were left undisturbed for the duration of the experiment. At 20:00hrs on each night, they were weighed and measured and had the probe and logger removed. They were returned to their normal pen before 21:30hrs. Two groups of each size and two individuals had their temperature measured on each night. Different lizards were used on each night.

6.2.2 Results- experiment 1.

Data obtained from probes that became dislodged during the experiment were discarded. This left seven lizards with data for each 10 minute interval between 16:25 hrs and 19:25 hrs. Three lizards alone, and four in groups.

A Repeated Measures ANOVA with Time as the Within Subjects factor and Group Size as the Between Subjects factor was used to analyse the data. The body temperature of a lizard held alone was on average, significantly lower (by 2°C) throughout the experiment than that of an average animal in a group (RMANOVA: $F_{1,5}$=6.95, p=0.046*) (Figure 6-1).

Each time interval was then analysed separately, using an independent samples t-test. The results of examining the difference between the cloacal temperatures of lizards alone and in groups at each different temperature are shown in Table 6-2. Before sunset (17:26-17:27 hrs) there was no difference in the temperature between focal lizards from the two treatments (Table 6-2), but from 17:35 hrs onwards, lizards in groups were significantly warmer than those kept by themselves (Figure 6-1).

The body temperature of lizards by themselves reached ambient temperature at 19:15 hrs, the mean body temperature for lizards in groups remained approximately 2 degrees warmer than ambient until at least the end of the experiment (19:35 hrs) (Figure 6-1).

Figure 6-1 Temperature over time for individuals, groups of six and ambient temperature for both nights of data.

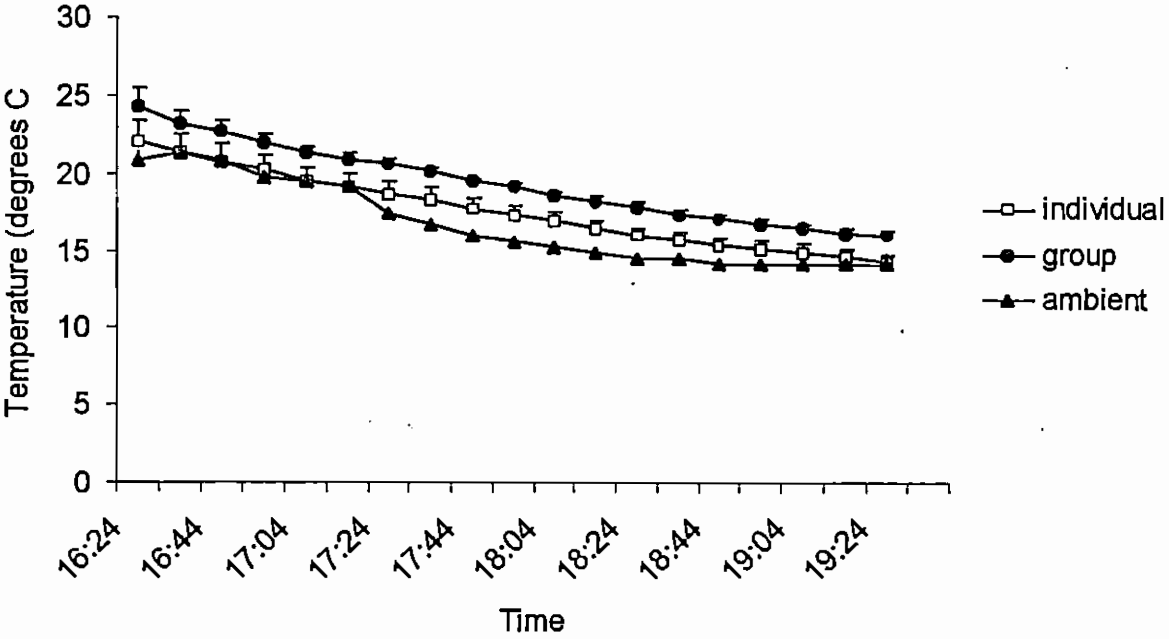


Table 6-2 Summary of independent samples t test on the differences in temperature at each time interval for between grouped and alone lizards (means are combined for both days) (* denotes significance at the 5% level).

Time	Mean for alone n = 3	Mean for group n = 4	T statistic	P value
17:05	19.50 (0.91)	21.65 (0.45)	2.32	0.068
17:15	19.13 (0.87)	21.65 (0.45)	2.34	0.067
17:25	18.67 (0.83)	20.82 (0.40)	2.56	0.051*
17:35	18.30 (0.80)	20.30 (0.30)	2.63	0.046*
17:45	17.70 (0.70)	19.75 (0.32)	2.95	0.032*
17:55	17.30 (0.64)	19.40 (0.30)	3.30	0.022*
18:05	16.90 (0.66)	18.85 (0.38)	2.75	0.04*
18:15	16.43 (0.57)	18.53 (0.40)	3.14	0.026*
18:25	15.97 (0.55)	18.15 (0.38)	3.41	0.019*
18:35	15.73 (0.43)	17.73 (0.44)	3.15	0.025*
18:45	15.37 (0.45)	17.38 (0.42)	3.25	0.023*
18:55	15.17 (0.52)	17.03 (0.44)	2.72	0.042*
19:05	14.77 (0.52)	16.75 (0.38)	3.16	0.025*
19:15	14.53 (0.43)	16.43 (0.40)	3.19	0.024*
19:25	14.30 (0.42)	16.23 (0.37)	3.46	0.018*
19:35	14.30 (0.42)	15.98 (0.32)	3.30	0.023*

6.3 *Experiment 2. Proportion of lizards in aggregations at different temperatures.*

6.3.1 Methods –Experiment 2.

During October 1999, an experiment was conducted to examine the effect of temperature on the level of aggregation in *E. stokesii*.

Twenty four lizards were selected from laboratory colonies housed in semi-natural, outdoor enclosures (see Chapter 2). The lizards were either sub-adult (18 months – 4 years) or adult. They were divided into six groups of four lizards and were placed into inside pits made of stainless steel and measuring 114cm x 81cm x 50cm each.

A plastic shelter was placed in each of the four corners of each pit and a lamp for heat was suspended over the centre of the pen. The heat lamp was switched on for 8 hrs from 9am-5pm daily during the experiment. Fluorescent room lights provided light in accordance with outside daylight hours for approximately 12 hours from 7am – 7pm. When heat lamps were on, lizards could thermoregulate to 35°C. When heat lamps were switched off, pen temperature was the same as room temperature.

The room temperature was set at 16°C, 22°C or 28°C. Overnight aggregation of the lizards was measured at these temperatures. At each temperature, lizards were left to acclimatise for two days, then their overnight position and therefore level of aggregation was recorded at 7am on the third day, before the heat lamps came on.

6.3.2 Results –Experiment 2.

Aggregation results are shown in Table 6-3. Lizards formed complete aggregations (where all the lizards in the pen were under one shelter) only at the two lower temperatures,16 & 22°C. There were 3/24 (12.5%) solitary lizards at 16°C, compared with 13/24 (54.2%) when the temperature was 28 ° C (Table 6-3).

Table 6-3 Summary of frequency of aggregation for the three experimental temperatures (numbers in brackets represent the number of lizards involved).

Temperature (°C)	Frequency of 4-lizard aggregations	Frequency of 3-lizard aggregations	Frequency of 2-lizard aggregations	Frequency of solitary lizards	Total number of lizards
16	2(8)	3(9)	2(4)	3	24
22	1(4)	2(6)	2(4)	10	24
28	0	1(3)	4(8)	13	24

The proportion of lizards in aggregations was significantly different among the three different temperatures (Figure 6-2: Table 6-4). At 16°C, 17/24 (70.8%) of lizards were found with at least two others under a shelter (aggregation of three or more individuals), while at 28 °C, only 3/24 (12.5%) lizards were found in a group of three, and none were found in a group of four (Table 6-4).

Figure 6-2 Percentage of lizards found in an aggregation (three or more lizards in the same shelter) or alone or paired at different temperatures.

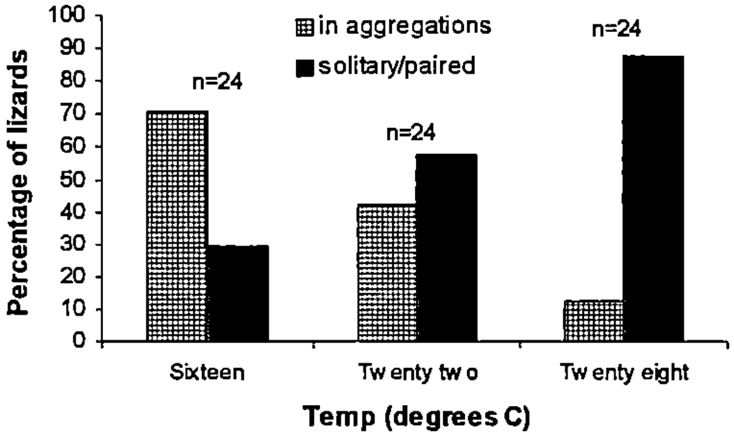


Table 6-4 Summary of Chi-square analysis on the proportion of lizards choosing to aggregate at the three different temperatures (16, 22 & 28 °C).

Comparison	**Chi-square value (df)**	**P value**
All three groups 16, 22 & 28 ° C	19.6 (2)	<0.001 *
Group 1 vs Group 3 16 vs 28 ° C	14.5 (1)	<0.001 *
Group 1 vs Group 2 16 vs 22 ° C	3.05 (1)	0.05<p<0.10
Group 3 vs Group 2 28 vs 22 ° C	5.38 (1)	0.01<p<0.025*

6.4 Discussion.

Lizard physiology is strongly influenced by body temperature (Huey and Slatkin, 1976). Aggregation may give heliothermic reptiles opportunities to thermoregulate when basking is not available, such as after sunset or on sunless days during winter.

Previous observations (Chapter 5) showed that increased aggregation may be associated with cooler temperatures. The experiments presented here provide further evidence that aggregation reduces heat loss when ambient temperature decreases (experiment 1) and that lizard aggregation increases at cooler temperatures (experiment 2).

In experiment 1, lizards in groups maintained a higher temperature for at least two hours after sunset than those alone. On average, lizards living in groups began the experiment at a higher temperature than those alone, and they maintained this higher temperature during the rest of the experiment. This suggests that cooling from optimal temperature had started before internal temperature was monitored. A further experiment, monitoring the lizards' temperature for a whole day would be useful to confirm this.

Graves and Duvall (1987), in an investigation of thermoregulation and aggregation in Prairie Rattlesnakes (*Crotalus viridis viridis),* showed that they maintained a higher temperature when aggregated during the first 14hrs after being placed in a controlled temperature environment, set at 5.5°C. However, after 20hrs, there was no significant difference in temperature between alone and grouped snakes.

In their study, Graves and Duvall (1987) found a significant interaction effect of group size and time, suggesting that snakes by themselves lost heat more rapidly than those in groups. This was not shown in this experiment on *E. stokesii*, this could be because the experiment was not conducted over a long enough period, and therefore it did not monitor the time from when both alone and grouped lizards were at optimal temperature, to when both treatments reached their lowest body temperature.

Dee Boersma (1982) suggested that aggregation should increase when food is abundant and lizards have been foraging during the day. Presumably, maintaining a higher body temperature after dark could enhance digestion, even with falling ambient temperatures. By grouping together, lizards reduce heat loss, allowing for faster metabolic rates, at least in the early part of the night.

A higher temperature and therefore higher metabolic rate, could also be a cost to a lizard, since more energy is used and thus a higher feeding rate is required (Huey and Slatkin, 1976). In herbivorous lizards, this might be outweighed by the benefits of increased digestion efficiency, which may not be as important in carnivorous/omnivorous species, since more energy per gram is obtained from animal tissue than from plant material (Pough, 1973).

In experiment 2, a greater proportion of lizards were in aggregations at 16°C, compared with the same lizards at 22°C and 28 °C, again suggesting that being aggregated may assist a lizard in reducing heat loss. Aggregation in cooler temperatures occurs in other temperature zone lizard species such as *Urosaursus ornatus.* Vitt (1974), found up to 155 individuals under the bark of a single mesquite stump. He assumed that this behaviour was due to a shortage of available overwintering sites, but this was not tested for. Calculations by White and Lasiewski (1971) suggest aggregated rattlesnakes, (*Crotalus viridis)* may be able to maintain a temperature of 9°C above the average temperature of the den site. Klauber (1937) in White and Lasiewski (1971) suggests that aggregation increases in *C. viridis* depending on the severity of winter conditions.

Although *E. stokesii* has been found in groups all year round (Duffield and Bull, 2001), experiments in this chapter suggest that group-living allows lizards to maintain a higher temperature than if they were alone which may mean lizards can avoid lethally cold temperatures, or increase their winter activity. Aggregation in winter could be more important physiologically to the lizards, than during other times of the year.

Chapter 7

7 Group predator avoidance in *Egernia stokesii*.

7.1 Introduction

Before examining possible predator detection advantages to grouping behaviour in *E. stokesii,* this chapter will review some of the more common as well as a few of the more striking and unusual behaviours exhibited by reptiles, and in particular, lizards.

7.1.1 Antipredator behaviour in reptiles

Reptiles exhibit a diverse range of antipredator defences such as camouflage, caudal autotomy and distraction. However group strategies of predator avoidance are not a commonly employed predator avoidance strategy (Greene, 1988).

Colour

Cryptic colouration and behaviour are among the most commonly employed tactics for predator avoidance in reptiles (Cooper and Greenberg, 1992).

Cryptic colouration involves the matching of the animal's body colour to a random sample of its habitat (Endler, 1978). As in other taxa, changes in phenotype often reflect changes in environment. Those animals that best match the features of the new area are not predated upon as often as those that differ from the colour of the surroundings. In a population of the lizard, *Mabuya vittata,* occuring in the Goksu Delta in southeastern Turkey, 93% of individuals are uniformly coloured in the hills and dunes, while in the agricultural areas, where grass coverage is high, 74% percent of lizards are striped. This change in colouration frequencies from one population to the next matches with changes in the surrounding environment (Van Der Winden *et al.*, 1995).

Vetter and Brodie (1977) experimentally manipulated the background colour of the cryptically coloured Flying Gecko, *Ptychozoon kuhli*, and found that it chose a brown background (the colour of its usual habitat and closest to its own body colour) significantly more often over either tan or white (brown was selected 61% of the time when tan was the alternative and 51% of the time when white was the alternative). Trials in which lizards were judged to make no choice were also fewer when brown was one of the choices. They also found that many individuals, forced to live on substrates that were different from their own skin pigment, gradually changed their colour to blend in better with the new background (Vetter and Brodie, 1977).

Green Iguanas, *Iguana iguana*, change their colour throughout their lifetime. Juveniles are bright green to blend in with the foliage, while adult colour varies with habitat (Greene *et al.*, 1978). Tail colouration varies in three species of *Eumeces* throughout the lifetime of the lizard. Juveniles have bright blue tails that distract potential predators from other vital body parts while adults have cryptically coloured tails that blend in with the environment. Differences in the cost of tail loss between juveniles and adults are thought to be responsible for this radical change in colouration (Vitt and Cooper, 1986).

Many reptiles use rock piles and tree logs for shelter and are drably coloured to match this type of environment (Gibbons, 1983). Bright colours are usually found on ventral surfaces or dewlaps (Greene, 1988). This is thought to reduce predation risk while still enabling the animal to use the coloured surfaces for intraspecific communication; the colours are exposed to the intended recipient during courtship or fighting displays (Cooper and Greenberg, 1992).

Peninsula Dragons, *Ctenophorus fionni,* exhibit sexual dimorphism, with the male having a darker coloured body and a yellow or orange chest patch covering up to 23% of their ventral surface. Although this area is not easily visible to predators, male mortality is higher in virtually all life stages in this species with life expectancy of males only 68% that of females (Johnston, 1997). Differences in colouration make males less camouflaged than females, which may increase their vulnerability to predation.

Reptiles also use colour to mimic other species, especially unpalatable or poisonous ones (Pough, 1988). Juveniles of the lizard *Pedioplanis lugubris* are coloured black and white to mimic the unpalatable and acid-spitting "oogpister" beetle that is more common and occurs sympatrically with the lizard. Juveniles also walk with a unique "arch back" that resembles the beetle's gait. Both the colouring and the unusual gait disappear a few months before the lizards reach sexual maturity (Huey and Pianka, 1977).

In regions of the world where the venomous banded coral snake occurs, up to 28% of Anilid, Boid and Colubrid snake species show permanent coral snake-like patterning, while the normally solid black *Liophis epinephalus,* when threatened, produces red pigment in bands across its body to appear like the coral snake (Pough, 1988).

Caudal autotomy

Another common antipredator behaviour employed by lizards is escape by caudal autotomy. Lizards disconnect their tail from their body when it is grabbed by a predator. The tail is sometimes enough to satisfy the predator which then does not pursue the lizard, or the tail acts as a decoy while the lizard escapes (Arnold, 1988). This behaviour is so highly developed in the tropical gecko, *Carphodactyl laevis,* that the tail "squeaks" (caused by air being drawn in and forced out during muscle contractions –(D.O'Connor - pers comm), the noise causing an additional distraction for the escaping lizard.

In staged encounters with a predator (the Spotted Night Snake, *Hypsiglena ochrorhyncha)*, tailless geckos (*Coleonyx variegatus)*, were never observed to escape predation, while 37% of those that began the trials with full tails escaped capture by detaching their tail. The predator always targeted the thickest part of the gecko, in those with tails intact. This was the base of the tail, meaning geckos had some chance of autotomising the tail and escaping. Those without tails were bitten on the body and consumed (Congdon *et al.,* 1974).

Downes (2000) also found that tailless lizards were more likely to be consumed by a predator, but only one that relies on visual stimuli for capture. Tailless lizards were not preferred prey for the Yellow-Faced Whip Snake, *Demansia psammophis,* but rather the reduction in locomotor performance of tailless lizards, and the fact that they could no longer use autotomy as an escape mechanism contributed to their being taken more often than lizards with tails intact.

Freezing

In a study by Leal and Rodriguez-Robles (1995), 13 different antipredator behaviours were displayed by *Anolis cristatellus*, an iguanid lizard from South America. These included body thrashing, head bobbing, flight and biting. However, the most common behaviour observed was immobility or "freezing". This behaviour is adopted when the lizard perceives a predator's threat. If the lizard is camouflaged, it further reduces the risk of detection. Leal and Rodriguez-Robles (1995) found freezing to be the least costly escape behaviour, (requiring minimum energy) exhibited by this species and was generally employed when the lizard was first exposed to the potential predator.

The success of this strategy probably depends on how long the lizard can maintain the fixed position and the method of prey detection used by the predator. This strategy is probably most effective against diurnal, actively foraging predators such as the snake, *Alsophis portoricensis*, the species used in predation trials on *Anolis* *cristatellus* by Leal and Rodriguez-Robles, (1995). *Alsophis portoricensis* was never observed to attack *Anolis cristatellus* when it was immobile, only striking after the lizard had moved (Leal and Rodriguez-Robles, 1995).

A more extreme version of freezing has been observed in many species of snakes, including *Farancia abacura* (Doody *et al.*, 1996). "Death-feigning" occurs when an individual discharges the contents of its cloacal cavity, then curls up and remains motionless, resisting any attempt to get it to respond to stimuli. This behaviour has been observed to last for up to one hour in *F. abacura* (Doody *et al.*, 1996). The Eastern Slender Glass lizard, *Ophisaurus longicaudus* has also been shown to exhibit behaviour resembling death-feigning, a behaviour thought to be unusual for lacertids (Smith, 1994).

Offence

Offensive behaviour is also a common and effective antipredator strategy. The use of venom by many members of the Elapid family is often not just for prey capture but also to convince potential predators to leave them alone. Venom is uncommon in lizards, restricted to only the Helodermatid Family, which comprises two species, the Gila Monster, *Heloderma suspectum*, and the Mexican Beaded Lizard, *H. horridum*, (Greene, 1988). These two lizards have the lowest maximum sprint speeds of all saurans. Envenomation may mean that rapid escape is no longer required (Beck *et al.*, 1995).

One of the most interesting examples of offensive behaviour used against predators in lizards is blood-squirting which occurs in the horned lizard, *Phrynosoma cornutum.* When threatened, and particularly when touched, this lizard squirts blood at its assailant from its orbital sinuses (Middendorf and Sherbrooke, 1992).

Distraction

Distraction of predators has been observed in many different species of reptiles, including Kukri snakes, *Oligodon cyclurus,* which evert their hemipenes when a potential predator manages to capture them. It is thought that the contrast between the white of the ventral surface and the pink of the hemipenis distracts the predator from the head of the snake long enough for it to strike at its captor (Wuster and Cox, 1992).

In an experiment to examine the antipredator advantages of the seemingly paradoxical bright blue tails of juvenile *Eumeces laticeps*, Cooper and Vitt (1991) found that lizards which had their tails experimentally blackened were never bitten on the tail, but always on the body and were always consumed. In contrast, nearly 48% of lizards with blue tails either painted or left unpainted (the natural colour of the tail in juveniles is bright blue) were bitten on the tail and their overall survivorship was higher (Cooper and Vitt, 1991).

Locomotory escape

Perhaps the most obvious antipredator behaviour for lizards or snakes is simply to run or slither away. In lizards, maximum sprint speed generally increases with increasing body size. Endurance has, not surprisingly, been related to average daily movement distance (reviewed in Garland and Losos, 1994).

Semi-aquatic species, such as *Sphenomorphus quoyi* escape predation by leaping into nearby slow-moving rivers or creeks to avoid capture (Done and Heatwole, 1977). Green Iguanas (*Iguana iguana*) also escape predation by diving, swimming and even remaining hidden underwater (Greene *et al.*, 1978).

Evolution of antipredator behaviour

Many species of reptile possess a repertoire of antipredator behaviours enabling them to adjust to the type of predator and the environmental conditions at the time of attack. For example, juvenile Garter Snakes, *Thamnophis radix*, use locomotory escape (crawling) until sufficient build up of lactate has occurred, when they switch to offensive displays to evade capture (Arnold and Bennett, 1984).

Locomotory escape and aggression are influenced strongly by the body temperature of the lizards (Hertz *et al.*, 1982), while the evolution of antipredator behaviour is often linked to the intensity of predation (Greene, 1988). Spiny-tailed Iguanas, *Ctenosaura hemilopha*, on Cerralvo Island where there are few predators, show a significantly reduced approach distance (a mean of 5.8m compared with 30.9m for mainland populations) and less overall wariness to the presence of a human than conspecifics on the mainland near La Paz City. This change in antipredator behaviour has occurred relatively recently because iguanas were probably introduced onto the island by man (Blazquez *et al.*, 1997). Lizards from mainland populations of *Podarcis hispanica* are smaller and significantly faster than those from the island population. Lizards on the mainland must contend with both higher predator diversity and fewer hiding opportunities (Van Damme *et al.*, 1998).

Predator avoidance in Velvet Geckos, *Oedura lesueurii,* represents another example of the evolution of antipredator behaviour, the result of changes in predation pressure. Geckos from all populations presented with the odour from Broad-headed snakes, *Hoplocephalus bungaroides,* showed several general predator avoidance tactics such as running, reversing or crawling. However, those from populations where Broad-headed snakes co-occur with the geckos exhibited significantly more crawling and adpressing behaviour, which has been associated with specifically avoiding the prey capture technique of this snake. Phylogenetic allozyme analysis suggests that this type of antipredator behaviour is ancestral, and those populations without snakes have decreased these behaviours as a result of relaxation of predation pressure (Downes, 2000).

Individuals are also able to alter their predator avoidance behaviour in order to maximise their chances of escape while minimising the costs of predation avoidance. Hallel and Bouskilla (1997) found that *Laudakia stellio brachydactyla,* a desert agamid, altered its escape behaviour in response to changes in body temperature and basking sites. Colder lizards had shorter flight distances (distance between the lizard and a refuge when basking) as did those on camouflaged perches, while animals at any temperature fled earlier when they were far from their refuges.

In birds and mammals, another commonly employed strategy to reduce the risk of predation is for individuals to group together and increase their overall vigilance to predators, without having to increase their individual investment in antipredator behaviour (the so-called "many eyes" hypothesis) (Pulliam, 1973; reviewed in Chapter 1). In fact, in many cases, individual vigilance behaviour has been shown to decrease, giving members of a group additional time and energy to engage in other activities (Lima, 1995).

7.1.2 Group vigilance

Group-living may confer thermoregulatory advantages to an organism (Chapter 6), greater reproductive success (Packer *et al.*, 1991) or increased hunting capacity (reviewed in Wilson, 2000), but if it increases the chance that an individual will be taken by a predator then it is unlikely to be a favourable evolutionary strategy – "nothing is so detrimental to an animal's fitness than being killed by a predator" (Lima and Dill, 1990). However, many studies of the effects of group-living on predator avoidance have found that it can decrease an individual's chance of being eaten, even though groups may be easier for a predator to detect than individuals (Hamilton, 1971). This "safety in numbers" effect has generally been explained by one of two hypotheses, although some argue that these need not be mutually exclusive (Bednekoff and Lima, 1998a):-

1) The "dilution effect" (Hamilton, 1971) – If a group of animals is no more conspicuous to a predator than an animal on its own then the probability that any single animal from that group will be taken is reduced because there is a high chance that another individual will be targeted (Foster and Treherne, 1981).

2) The "many eyes" hypothesis (Lima, 1995)- Group members are afforded the opportunity of reducing their individual vigilance to predators because other individuals in the group are also vigilant. Individuals are still alerted to a potential threat as quickly or more quickly than when they are alone (Pulliam, 1973).

Both hypotheses suggest that membership of a group may benefit individuals. The "many eyes hypothesis" goes further to suggest that not only are individuals less likely to be preyed upon in a group, but they may be able to reduce their vigilance to predators and devote time and energy to other important functions. Intrinsic to the "many eyes" hypothesis, is the assumption that if members of the group are alerted, either by an alarm call or signal, or by the fleeing of another group member, the whole group is alerted (collective detection) (Chapter 1). This hypothesis does not necessarily assume that individuals monitor the vigilance of the other group members, but rather that scans are random and independent between members of the same group (Bednekoff and Lima, 1998b). If this is the case, then the overall vigilance of the group will still be higher than the individual vigilance of its members.

Differentiating between the dilution effect and collective detection can be difficult since just showing that individual vigilance decreases as group size increases can be explained by either hypothesis (Roberts, 1996). Individuals in larger groups may just perceive that they are at a reduced risk, and will therefore be less vigilant (dilution effect), rather than taking any notice of the vigilance behaviour of other group members. To demonstrate the "many eyes" hypothesis, groups must show collective detection, that is, an animal should respond more quickly to a potential threat when in a group than when alone.

Vigilance behaviour can be delegated to individual members of social groups. Meerkats *(Suricata suricatta)* in the Kalahari Desert live in groups of up to 30 individuals which include dominants, breeding animals, helpers, juveniles and pups (Clutton-Brock *et al.,* 1999).While foraging, these groups appoint "raised guards" (a member of the group that watches for predators from a raised position in a tree or on a rock) for 55% of group foraging time. Similar species such as dwarf mongooses, also have members of the group that perform guard duties, but these animals are usually of a low status in the group. Meerkats share guard duty evenly among adults of the group (Clutton-Brock *et al.,* 1999).

In previous studies, guarding had been assumed to be a result of some form of altruism, either through kin selection or reciprocal altruism (Hamilton, 1978; Trivers, 1978). Clutton-Brock *et al.*, (1999) showed that individuals can benefit from guarding by being both the first alerted to danger and also by being significantly closer to safety than foraging animals. Guarding behaviour in these animals is not necessarily altruistic and has evolved because it favours the guard, not just the group. Presumably this level of sophistication in an antipredator strategy has evolved partly due to the nature of foraging in meerkats. They are not able to dig for their main prey items, fossorial invertebrates and small vertebrates, and scan for predators simultaneously (Clutton-Brock *et al.*, 1999).

Most studies of group vigilance have involved socially foraging animals. In most models explaining decreased individual scanning behaviour with increased group size, feeding and scanning behaviours were thought to be mutually exclusive (Quenette, 1990) - that is, animals were considered only to be vigilant when not feeding, and vice versa. This enables researchers to partition the time budget of the animal between vigilant and non-vigilant activities, with the presumption that there is no overlap between the two activities.

However, foraging groups present a problem. Decreased scanning could result from an increase in competition in large groups, so group members scan less and forage more (Roberts, 1996). Studying a species that does not forage socially eliminates this as a confounding factor. A species that engages in other behaviours in a group (such as basking) may simplify the interpretation of reduced vigilance in groups. *E. stokesii* does not forage socially, but it does bask with others in close proximity. Examining the vigilance behaviour of basking animals should minimise the confounding effect of increased competition.

Vigilance behaviour need not be confined to the detection of potential threats. It can also be associated with detecting conspecifics or prey (Dimond and Lazarus, 1974). In this chapter, vigilance, defined as sustained heightened awareness directed at either potential attackers or at conspecifics (the differences were not examined) was investigated.

There are two main ways in which group members alert others to potential predators. One involves the differentiation of work roles with members taking turns at guard duty. The other involves a less structured, but perhaps no less effective strategy where group members are alerted by the reaction of an individual to the approach of a predator and follow that animal to safety regardless of whether they themselves have detected the danger. When these instances have been reported in lizards, it has remained unclear whether individuals reduce their own vigilance when group members are around. The response of the entire group to one lizard's reaction may be an additional mechanism of predator detection, rather than a way to reduce their own time allocation to antipredator behaviour (Greene, 1988).

Reptiles have a lower metabolic rate than birds or mammals, they require less food, and feed less often (Bennett, 1983). Therefore opportunities for researchers to observe antipredator behaviour during foraging in reptiles are reduced. However, many lizards need to bask in an open area, exposed to sunlight, to aid thermoregulation and digestion (Heatwole and Taylor, 1987). During this time they are particularly vulnerable to predation for two reasons. Firstly they must have a large proportion of their body exposed, and therefore more at risk of predation, and secondly, they take some time to reach optimal temperature, which can limit their ability to escape from a potential threat (Hertz *et al.*, 1982; Xiang *et al.*, 1996).

During these high risk periods, lizards may need to be more vigilant to avoid predation and may benefit from basking in groups, if groups are able to detect a potential threat sooner than individuals basking alone. It may allow them to engage in other activities while basking, such as resting and social interactions.

7.1.2.1 Antipredator behaviours of individual *E. stokesii*

The most noticeable morphological antipredator trait in *E. stokesii* is its dorsal scales which are highly spinose and keeled and are used both to deter a potential predator if it is grabbed, and also to prevent its removal from rock crevices (Greer, 1989). The scales are positioned to give resistance to removal from the crevice and this is further enhanced by the animal filling its lungs and bloating out so it fills the crevice and is more difficult to remove (Barwick, 1965; pers. obs). *E. stokesii* is one of only two species in the *Egernia* genus *(E. depressa* is the other) that has lost the ability to autotomise its tail (Greer, 1989). When the lizard enters a crevice after retreating from a predator, it positions itself in such a way that the tail lies between the body of the lizard and a potential threat (pers. obs). This behaviour is common among species in the *Egernia* genus (Greer, 1989).

Similar behaviour has been observed and tested in the Cape Girdled Lizard, *Cordylus cordylus,* by Cooper *et al.*, (1999). *C. cordylus* is similar to *E. stokesii* in that it is also saxicolous and has a spiny tail that cannot be autotomised. Experiments on *C. cordylus* show a preference for deep, horizontal crevices at ground height (Cooper *et al.,* 1999). *E. stokesii* is found in both vertical and horizontal crevices throughout its southern range. Preference appears to depend on availability, but could be a response to predation pressure. Cooper *et al.*, (1999) suggest that preference for crevice orientation may depend on the predator they are escaping from. Horizontal crevices give protection from threats that are above the lizards such as raptors, while vertical crevices might be preferred where snakes are common predators. These hypotheses remain untested in *E.stokesii.*

E. stokesii is seldom seen more than a few metres from a rock crevice in the southern part of its range, (Chapter 1) and often bask in groups which will tend to flee if disturbed collectively (G. Duffield pers. comm). This aspect of their behaviour suggests a possible antipredator function of grouping.

7.2 Group predator avoidance in E. stokesii.

Three different indicators were used to investigate predator avoidance in groups of lizards housed in semi-natural outdoor pens during the 1996/97 & 1999/2000 seasons. These indicators were time out of crevice, time vigilant and how close a focal lizard allowed a potential threat to approach before fleeing.

7.2.1 Time out of crevice.

If an animal derives some security from being in a group, it might spend more time out from the relative safety of its crevice when it is in a group than when it is alone. This would benefit the individual by allowing more time for feeding, thermoregulation and social interactions. To examine this, the amount of time lizards spent emerged from a crevice when living in a group and when living alone was compared.

Shuttling behaviour, as defined by the number of times that a lizard comes out from a crevice in a set period of time might also be influenced by being alone or grouped. Heliotherms use shuttling to optimise thermoregulation (Heatwole and Taylor, 1987), but if perceived predation risk increases, lizards may alter their behaviour either shuttling less to avoid movement associated with coming out of a crevice, or if risk increases with the length of time out of the crevice, they shuttle more. Thermoregulatory shuttling may be more common in a group situation if lizards perceive that predation risk is reduced and they can respond only to their thermoregulatory requirements.

7.2.2 Time vigilant.

Secondly, if a group of lizards is as vigilant or more so to predators than a lizard by itself, then an individual lizard living in a group should be able to spend less time vigilant to predators during high risk activities such as basking. If this hypothesis is correct, individual lizards should be less vigilant when in a group than when alone.

"Vigilance" in most studies of social groups is usually assessed by the amount of scanning behaviour (mechanical action of the head) (Lima and Dill, 1990). However, physiological definitions of vigilance are not limited to scanning behaviour. Vigilance can include any kind of heightened awareness of the environment, designed to detect a stimulus (Dimond and Lazarus, 1974). Conversely, reduced vigilance could occur if one or more senses is blocked. This could occur if one or both eyes are closed.

E. stokesii does not appear to exhibit stereotyped scanning behaviour but rather reacts to a startling sound or sight by turning the head either sideways or upwards (see Chapter 3). These head movements were recorded during all trials, but a more a common and measurable indication of reduced vigilance that could be relatively easily observed and recorded was required. Eye closure during basking was examined in *E. stokesii* as a possible indicator of reduced awareness or vigilance (Kavanau, 1997).

Members of the *Egernia* genus, like scincids in general, have highly developed chemosenses. Female *E. stokesii* can differentiate between their own and other juveniles (Main and Bull, 1996; reviewed in Chapter 1), they can also differentiate between group members and non-group members, from either scats or body secretions (Bull *et al.,* 2000a; reviewed in Chapter 1) suggesting that recognition of individuals is possible just from chemical signals. A closely related species, *Egernia striolata* has been shown to differentiate between individuals based on genetic relatedness. In a study by Bull, *et al.,* (2001b) lizards directed twice the number of tongue flicks at body secretions from an unfamiliar, distantly related lizard as they did to the secretions of a closely related, but still unfamiliar lizard. Taken together, these studies suggest that members of the *Egernia* genus have a sophisticated sense of chemoreception.

Specific research on the vision and hearing of members of the *Egernia* genus could not be found. However, research on *Tiliqua rugosa,* a member of the closely related genus, *Tiliqua*, and also a large, long-lived omnivorous skink (Bull, 1994), suggests that although olfaction and hearing are the primary senses used by this lizard, the wide field of view that this lizard has is characteristic of an animal which uses sight as a means of predator detection (Kerr, 2001).

Another skink species, *Eumeces okadae* can discriminate between worker and queen ants, based on body proportions (Hasegawa and Taniguchi, 1993). The same species relies on the yellow spots of the poisonous beetle, *Dischisuss mirandus* to tell it apart from the edible species (*Harpalus sp.)*. Lizards directed significantly more tongue flicks toward the poisonous beetle when it was painted black than to the unpainted control, suggesting that it uses the yellow spots as a visual warning (Hasegawa and Taniguchi 1994). Taken together, these results suggest that although vision may not be the primary sense used by scincids, it is still important in both foraging and avoiding predators.

Reptiles have been shown to exhibit two forms of eye closure (Mathews, 1999). Synchronous eye closure (SEC), where both eyes are closed at the same time, is usually associated with a prone posture and indicates behavioural sleep (Campbell and Tofler, 1984). Asynchronous eye closure (ASEC) is where only one eye is closed at any one time (Mathews 1999).

Mathews and Amlaner (2000) investigated the relationship between ASEC and behavioural sleep in the Common Fence Lizard, *Scleroporus occidentalis.* They found that ASEC occurred significantly more during the light phase of their experiment, compared with the dark phase and ASEC was correlated with an alert body posture where the head and thorax were elevated above the terrarium floor. They also suggested that there was no increase in arousal latency during ASEC, which suggests ASEC is not equivalent to behavioural sleep, but since so far there is no reliable way of measuring EEG in reptiles, they could not rule out that it may be associated with unihemispheric sleep as it is in many species of birds and mammals (Rattenborg *et al.*, 1999).

In other experiments on eye state in *S. occidentalis* the presence of a potential predator caused a decrease in SEC and an increase in ASEC relative to when the lizards were presented with a novel moving object or with an empty cage. This suggests that ASEC may be a compromise between the physiological benefits of unihemispheric sleep and the ecological imperative of detecting predators (Mathews, 1999). An alternative hypothesis suggests that ASEC may assist in the prevention of evaporative water loss from the moist eye surface in small lizard species, while still allowing one eye open for predator detection (Kavanau, 1997).

E. stokesii exhibits both SEC and ASEC during periods of basking and while resting in crevices (see Chapter 3). Previous observations showed that tongue-flicking never occurred when the lizards' eyes were closed, suggesting that when lizards close their eyes, they are not swapping vigilance to visual stimuli with enhanced chemosensory awareness. Eye closure ceased immediately if the animal was disturbed. Sudden opening of the eyes was often accompanied by a head turn or tilt toward the source of the stimulus (Chapter 3).

In this experiment, if a lizard had one or more eyes closed, it was assumed to be less vigilant to potential threats since any visual detection of approaching predators would be reduced or eliminated. If living in a group reduces the risk of predation, and having one or more eyes closed is a sign of reduced vigilance, then lizards in a group should open their eyes less than those living alone. This may assist in reducing water loss through the eye surface (Chapter 3).

7.2.3 Threat detection.

Thirdly, if lizards basking in a group derive increased protection from predators by being alerted to a potential threat more quickly, then they should respond more rapidly to a staged approach by a potential predator when they are grouped as compared to when they are alone. For species of birds and mammals, alarm calling is the most obvious way in which group members can alert others. In lizards that do not call, individuals within a group may respond to predator avoidance behaviour by another group member, and thus benefit from group membership (Lima, 1990).

Collective detection, where all members of a group are alerted to a threat when just one of them detects it (Lima, 1995) has been extensively documented in birds and mammals (see Elgar, 1989 and Quenette, 1990 for reviews). Anecdotal evidence for it also exists for reptiles. Groups of *Iguana iguana* have been observed simultaneously fleeing from a potential threat, even if only one lizard has detected the potential predator (Greene, 1988). Mouton *et al.*, (1999) has observed the same response in the group-living Armadillo Lizard, *Cordylus cataphractus* from South Africa.

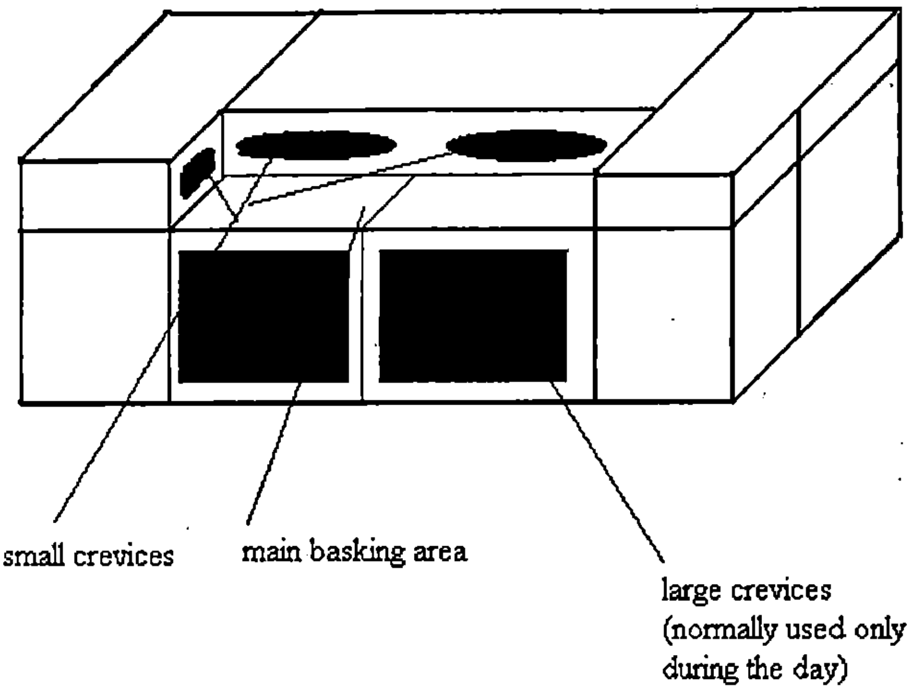
Collective detection in *E. stokesii* was investigated by determining if there was a difference in approach distance (distance between the lizard and a potential predator when the lizard chose to flee to safety) (Bulova, 1994) when a focal lizard was basking alone or in a group. If lizards were alerted to danger earlier by the presence of other group members, then the approach distance should be greater when lizards were in groups, than when they were alone.

7.3 Time out of refuge.

7.3.1 Methods for time out of refuge - 1996/97 Season

This experiment involved 35 *E. stokesii* captured from the field (see Chapter 2). They were housed in separate aquaria on a 12:12 photoperiod at 25°C over winter 1996, then placed in outside pens in early November, 1996. Pens measured 3m x 1.4m and were enclosed by chicken wire to prevent animals being taken by aerial predators. One end of each pen had a pile of seven concrete (cinder) blocks, three small (39cm x 19cm x 9cm) and four large (39cm x 19cm x 14cm). The concrete blocks were hollow, the small ones providing crevices of (4cm x 13cm) (generally preferred as overnighting refuges by the lizards) and the four large blocks provided two large crevices (8.5cm x 15cm) within the pile (Figure 7-1). There was no other shelter in the pen.

Figure 7-1 Diagram of crevice setup for antipredator experiments.



Lizards were housed either individually or in groups to determine if amount and frequency of time out of the refuge, and vigilance behaviour were influenced by group membership.

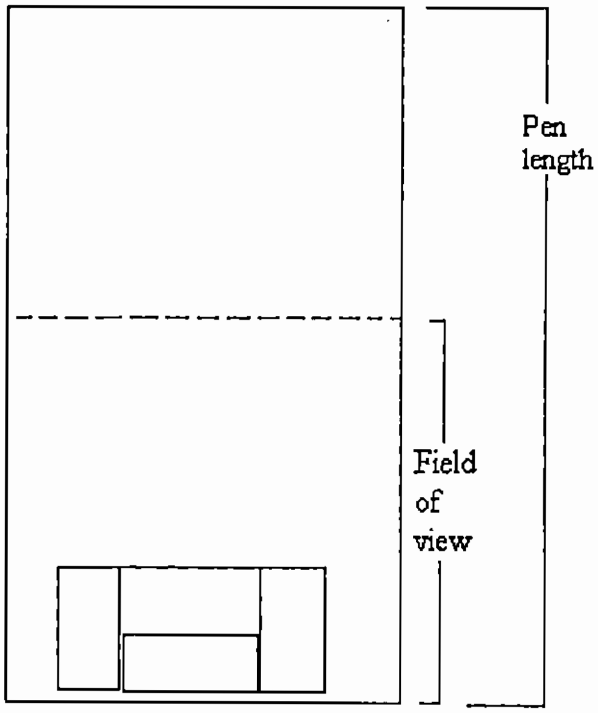
In the 1996/97 season family groups of lizards were compared to lizards living alone. Family groups of either a female and her three offspring, or groups of four juvenile siblings. Relatedness was known because all animals were from clutches born in captivity from 1995 onwards. The adult females used in the experiment had been collected from the field gravid in either 1995 or 1996 (see Chapter 2). The juveniles were aged from 7 to 18 months old. Status, defined as either adult or juvenile, was taken into account in the analysis of the data.

There were 14 pens used in this experiment, seven contained family groups of four lizards and seven pens contained individual lizards. Four of these contained one adult female and three of her offspring. They were allowed to acclimatise in their new surroundings for six weeks before filming began. Lizards were individually paint marked with non-toxic, water soluble paint to allow them to be easily recognised when in a group. They retained their paint markings for the alone trial as well, to remove any affect of paint marking on approach distance.

The treatments (either grouped or alone) were randomly allocated to each pen and each treatment was separated by 77cm high galvanised iron walls so lizards could not see others outside of their pens, even when perched on the highest basking areas (28cm high).

Egernia stokesii is sensitive to the presence of humans. Initially, attempts were made to observe the animals over a wall or from a hide. However, most animals were immediately aware of human presence and froze or scuttled into their crevice. Thus, video recording of behaviour was the preferred method of data collection. To obtain data on the activity of the lizards, a camera was placed 1.8 metres above the concrete block pile. The field of view of this camera extended to about halfway down the length of the pen (Figure 7-2).

Figure 7-2 Birds eye view of crevice set up showing field of view of the above camera.



The study involved up to four filming sessions per pen. Each session lasted three hours. From the camera above the brick pile, general activity of each lizard, time out of crevice (reported in seconds) and the number of times out of the crevice during the three hour filming session could be measured.

If a lizard disappeared from view during the filming session and was not seen again by the end of the filming session, it was assumed it had gone into the crevice at the time when it was lost from view. This may tend to underestimate time out, if the unseen lizard had spent the time in the other half of the cage. However, previous observations suggested lizards rarely stayed away from the block pile for extended periods. Also, the aim of this experiment was not to get an estimate of the absolute active time of a lizard, only to compare between grouped and alone individuals. Since this criterium was used for both treatments, the underestimate should not bias the results.

Filming sessions began either in the morning (0930-1030) or in the afternoon (1430-1530h) and ran for three hours. Each of the 14 pens was filmed in two morning and two afternoon sessions between December 1996 and May 1997. Recording was done in rounds, so that all pens were recorded once before the next round, but within a round, pens were filmed in random order. Some filming sessions had to be repeated due to technical failure. This usually consisted if a cord came loose during the filming session or the camera stopping because of overheating. These sessions were repeated as soon after they were detected as possible, although occasionally a few of the next round of filming had occurred before the error was detected during tape playback. Each pen was randomly allocated to an order and a morning or afternoon session in each round. Not all repeats were completed by the end of the season, but all pens were filmed at least twice before May, 1997.

Above ground shade temperature was recorded at the start of each filming and was taken into account in the data analysis. Filming was performed on sunny days when forecast temperatures were between 22-34 °C. If any rain fell during the three hours that filming took place, filming was repeated at a later date.

7.3.2 Methods for emergence time in the 1990/2000 Season.

During the 1999/2000 season, the differences in behaviour between lizards in different group sizes were examined. In November 1999, lizards were selected from the captive population and placed into group sizes of 1, 2, 3 & 6. Each group size was replicated three times (total of 12 groups of animals for the experiment). Groups were made up of adults and sub adults. Adults were at least five years old, sub-adults were three or four years old. At 2-3 years of age, siblings can become aggressive towards each other (pers. obs). Therefore, for this experiment, groups of unrelated individuals were used. An effect of being in a group was expected, as previous work had shown that *E. stokesii* preferred to group and could recognise familiar group members, regardless of relatedness (Bull *et al.*, 2000a).

Each of the twelve pens was filmed once for three hours in the morning between 26th January and 13th April, 2000. The block pile was slightly modified from the 1996/97 season (Figure 7-3). Lizards tend to bask on the highest point that they can reach, so in 1999/2000 they were provided with only one high area, rather than several, meaning there was a greater chance of getting them within the field of view of the video camera, which was focussed on that one high area.

Figure 7-3 Set up for vigilance experiment in the 1999/2000 season. Only one small block was placed on top of the larger blocks for this experiment. This was done to encourage the lizards to bask in one small area where the camera was focused.

The overhead camera was set up in the same way as in the 1996/97 season. Another camera in the pen was used to assess if lizards' eyes were open or closed while basking. In some pens, the eye state could not be observed for long enough to assay the level of vigilance for any lizard in that pen. These pens had to be filmed again to obtain sufficient data on the eye state of the lizard while basking, so activity was recorded as well. The time out for each pen was averaged over the two filming sessions

7.3.2.1 Analysis.

To meet the assumption of independence of samples for statistical analysis, each pen was used as a replicate. Where pens contained groups of lizards, data were obtained for each individual, but the average for the group was used in the analysis. Where there were multiple days of filming for each pen (as occurred with all pens in the 1996/97 experiment), the mean for the pen over all the available morning sessions, and then over all the available afternoon sessions was used . The mean for each pen of the total time in seconds that lizards were fully emerged from their crevice and the mean number of times they emerged were also analysed

Where possible, groups were compared using parametric tests, either t-tests or ANOVA. A two-way ANOVA was used to compare the effect of treatment (alone or in a group) and status (adult or juvenile) on the total emergence time and number of times lizards emerged from their crevice. Where morning and afternoon samples from the same pen were analysed, Repeated Measures ANOVA with time of day as the "within subjects" factor was used.

7.4 Results – Emergence from the crevice.

7.4.1 1996/97 season.

There were 2-4 successful overhead filmings per pen when at least one lizard emerged. In 13 filmings, no lizards emerged during the three hour session. In the seven group pens, there was a total of 28 lizards divided into groups of four. One lizard (Pen N8) was not used in the analysis because it died during the experiment on 11th March, 1997 before any successful filming of emergence times for that pen. That left 27 lizards in groups.

All individual lizards (7/7) and all lizards in groups (27/27) emerged from their crevice during at least one filming session (Table 7-1). Pens were taken as independent samples in the design of this experiment. Therefore unless otherwise stated, all means reported for activity data are the means of the pens involved in that treatment. For pens with groups of lizards, this involved taking the average of all the lizards that emerged during filming for that pen. The average of multiple filmings of each lizard was also taken. Only the time out once a lizard had emerged was used in obtaining the mean time out for each lizard. Alternatively, the emergence time and number of times out could have been calculated for every lizard at every filming, which would have included times when lizards did not emerge. This analysis showed the same trends to those reported here (Lanham and Bull, in prep).

Table 7-1 Details of filming for vigilance experiment for 1996/97 experiment. "Number emerged" column indicates the number of lizards that emerged during that filming session. "No" indicates that an above video was not recording for that day. This occurred a few times in the beginning of the experiment for single lizards because it did not seem necessary to film from overhead for single lizards, until it was found that it was not always possible to see the emergence and retreat of a lizard from just the side camera (see Section 7.6.1 for explanation of side camera). Technical failure is abbreviated as "TF".

Pen	Pen id	Round	Date	Number of lizards and status	Side camera	Above camera	Number emerged	Starting time	Starting temp. (degrees C)
1	N1	1	13/12/96	1 adult	Yes	TF	N/A	10am	27
		2	30/01/97		Yes	Yes	1	3pm	30
		3	13/03/97		Yes	TF	N/A	3:25pm	28
		4	9/04/97		Yes	Yes	0	1:55pm	33
2	N2	1	17/12/96	4 juveniles	Yes	TF	N/A	2pm	26
		2	12/02/97		Yes	Yes	4	11am	21
		3	7/03/97		Yes	Yes	4	3:40pm	34
		4	26/03/97		Yes	Yes	1	nr	nr
3	N4	1	10/01/97	1 adult	Yes	Yes	1	10am	24
		2	19/02/97		Yes	Yes	1	9:25am	30
		3	6/03/97		Yes	Yes	1	10:15am	18
		4	20/03/97		Yes	Yes	0	3:40pm	27
4	N5	1	19/12/96	1a & 3 j's	Yes	Yes	1	2:50pm	28
		2	29/01/97		Yes	Yes	4	10:37am	19
		3	26/02/97		Yes	TF	N/A	3:05pm	36
		4	14/03/97		Yes	Yes	3	10:45am	19
5	N6	1	17/01/97	4 juveniles	Yes	Yes	3	3:18pm	34
		2	13/02/97		Yes	Yes	4	10:30am	23
		3	18/03/97		Yes	Yes	4	10:35am	20
		4	8/04/97		Yes	Yes	3	1:50pm	29
6	N7	1	17/01/97	1a & 3 j's	Yes	TF	N/A	10:40am	20
		2	7/03/97		Yes	Yes	3	11am	21
		3	8/04/97		Yes	Yes	3	11am	19
		4	29/04/97		Yes	Yes	3	2pm	37
		5	12/05/97	rpt due to TF	Yes	Yes	0	2:15pm	22
7	N8 juvenile died 11/03/97	1	16/01/97	1a & 3 j's	Yes	TF	N/A	2:35pm	34
		2	22/04/97	1a & 2 j's	Yes	Yes	0	10:30am	21
		3	29/04/97	1a & 2 j's	TF	Yes	3	10:30am	25
		4	13/05/97	1a & 2 j's	Yes	Yes	2	10:40am	18

Table 7.1 continued...

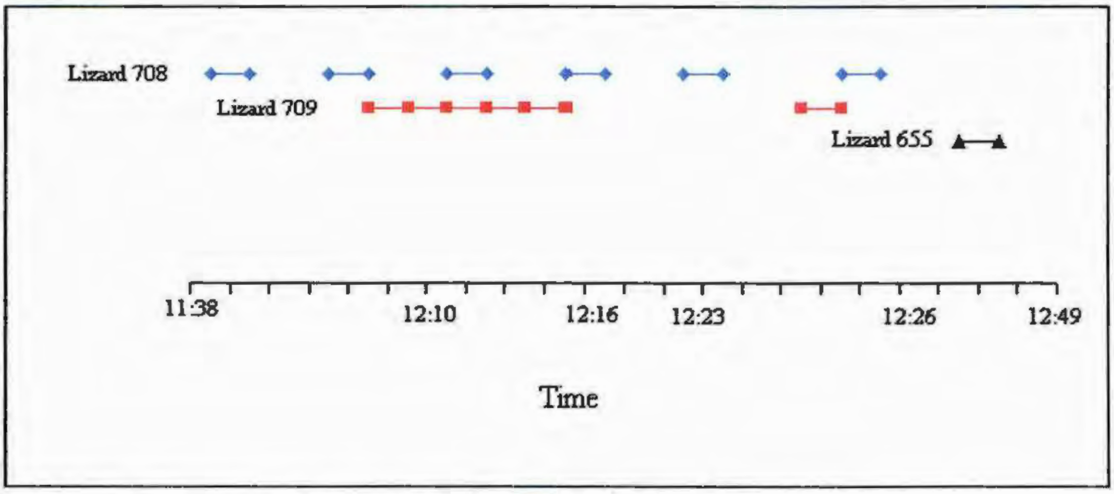
8	S1	1	13/12/96	1 juvenile	Yes	No	N/A	3pm	40
		2	24/01/97		Yes	Yes	0	10:10am	18
		3	24/02/97		Yes	Yes	1	3:30pm	27
		4	13/03/97		Yes	Yes	0	10:15am	16
9	S2	1	22/01/97	1a & 3 j's	Yes	Yes	4	9:45am	21
		2	29/01/97		Yes	TF	N/A	3pm	33
	*rpt due t	2(rept)	26/02/97		Yes	Yes	3	10:35am	19
	TF	3	10/03/97		Yes	Yes	3	3:30pm	33
		4	9/04/97		Yes	Yes	2	11:20am	24
10	S4	1	16/12/97	1 juvenile	Yes	No	N/A	10am	22
		2	12/02/97		Yes	Yes	1	3pm	29
		3	5/03/97		Yes	Yes	1	10:45am	17
		4	17/03/97		Yes	TF	N/A	10:30am	18
11	S5	1	11/12/96	1 juvenile	Yes	Yes	1	2pm	26
		2	22/01/97		Yes	Yes	0	2pm	26
		3	25/02/97		Yes	Yes	0	10am	18
		4	10/03/97		Yes	Yes	0	10:45am	17
12	S6	1	10/12/96	4 juveniles	Yes	Yes	3	11:30am	24
		2	30/01/97		Yes	Yes	4	10:40am	23
		3	3/03/97		Yes	Yes	1	3:15pm	30
		4	14/03/97		Yes	Yes	3	3:30pm	31
13	S7	1	15/01/97	1 adult	Yes	Yes	0	2:40pm	28
		2	23/01/97		Yes	Yes	0	10am	21
		3	21/02/97		Yes	Yes	1	3:15pm	40
		4	13/04/97		Yes	Yes	1	11am	30
14	S8	1	12/12/96	1 juvenile	Yes	Yes	1	1:52pm	38
		2	21/02/97		Yes	Yes	0	9am	28
		3	25/02/97		Yes	Yes	1	3pm	35
		4	11/03/97		Yes	Yes	0	3:30pm	34

7.4.2 Emergence from the crevice.

7.4.2.1 *Illustration of a typical session.*

Figure 7-4 shows the results of a typical filming session. Lines represent the time that a particular lizard spent out of its crevice. Lizard 708 emerged 6 times for a total of 23:58 mins (1438 secs). Lizard 709 emerged twice for a total of 10:47 mins (647 secs). Lizard 655 (mother) emerged once, for 6:22 mins (382 secs). Times were averaged for each pen. For this pen, the average time out per lizard was 13 mins, 42.33 secs (822 secs). The average number of times emerged per lizard was 3.0.

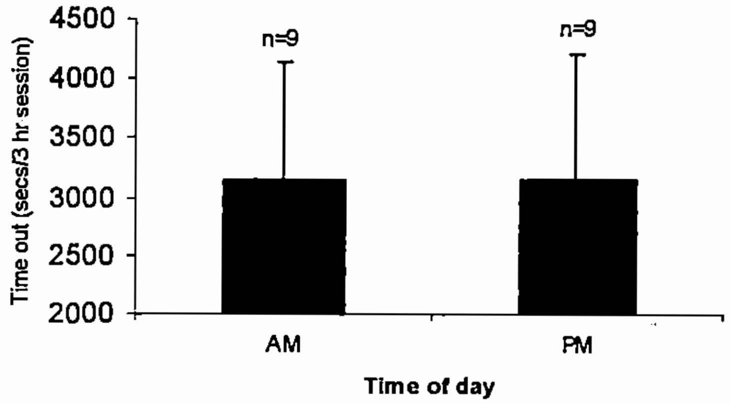
Figure 7-4 Part of a typical filming session for a group of lizards (Pen S2, 26/02/97). Only the part where lizards emerged is shown, three out of four lizards are shown, the fourth did not emerge during the filming session. The average time out per lizard was 13:42 mins (822 seconds). The average number of times emerged per lizard is 3.0.



7.4.3 Effect of time of day.

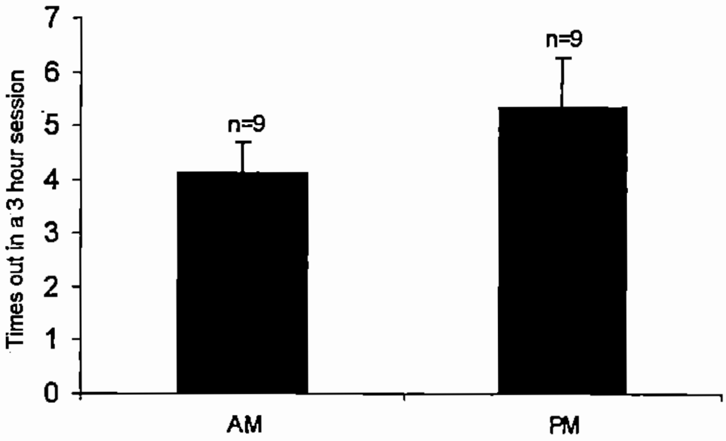
The differences in activity between morning and afternoon filming sessions were initially analysed. A subset of the activity data was analysed using Repeated Measures ANOVA with time of day (morning or afternoon) as the "Within Subjects" factor and treatment (single or grouped) as the "Between Subjects" factor. The subset included only the three single and six group pens where there were recordings for both morning and afternoon sessions. However, this sub-sample was used to give an indication of whether the lizards within each pen were behaving differently between morning and afternoon sessions. These data showed that time of day did not significantly affect the average amount of time that lizards spent out of their crevice (Figure 7-5).

Figure 7-5 Mean of total time out for repeated measures analysis of morning and afternoon filming sessions (pens as replicates) (RMANOVA: $F_{1,7}$=0.087 p=0.77) (1996/1996/97 data only).



The total number of times out for lizards within each pen was analysed in the same way. There was also no significant difference between morning and afternoon sessions for this measure of activity (Figure 7-6).

Figure 7-6 Mean number of times out per pen which contained lizards that came out during both a morning and afternoon session. (RMANOVA: $F_{1,7}$= 3.22, p = 0.12).



7.4.4 Temperature and activity

7.4.4.1 Total time out.

Temperature did not significantly affect total time out of crevice for all observations (Figure 7-7), nor number of times out during a 3 hour filming session (Figure 7-8).

Figure 7-7 Total time out of crevice for all sessions when lizards emerged versus temperature reading when filming began ($R^2 = 0.18$, $p=0.44$) (35 observations).

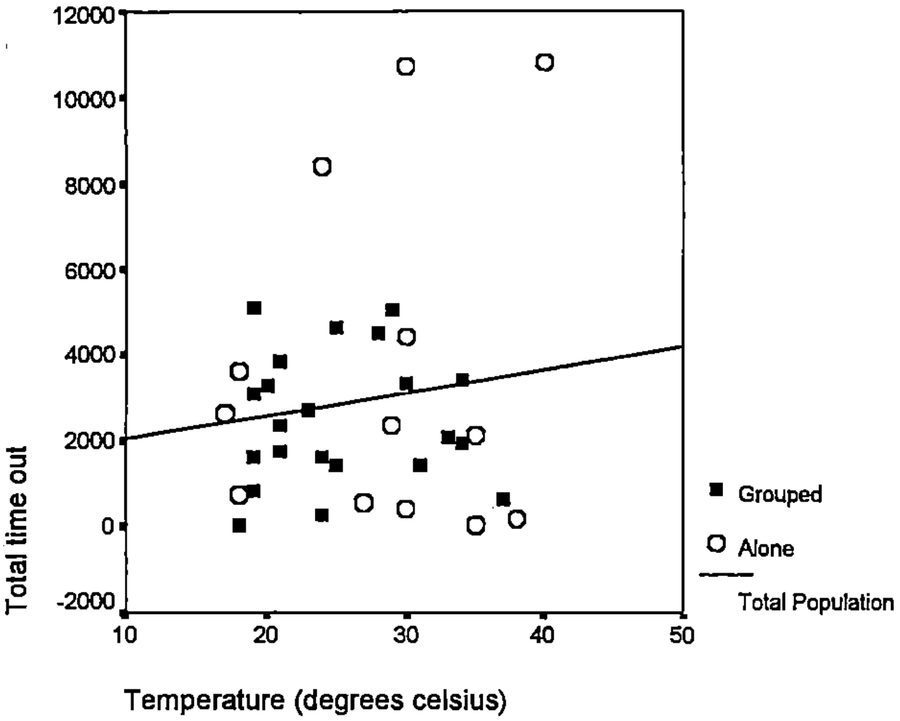
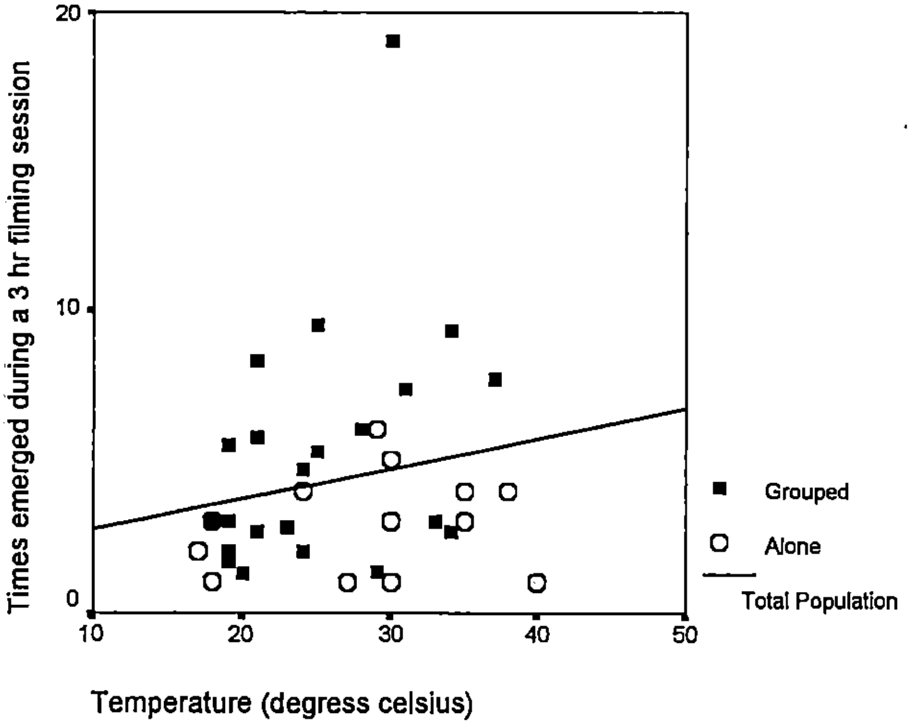


Figure 7-8 Times emerged during a filming session (Regression line is shown, $R^2=0.036$, $p=0.28$) (35 observations).



Since neither time of day nor ambient temperature affected the amount of time lizards were out of their crevice, or the number of times emerged, the data were pooled for all afternoon and morning sessions to produce an overall mean amount of time out (in seconds) and number of times out for each pen. This value was used in all subsequent analyses.

7.4.5 Treatment and status.

The effect of both the lizard status (adult or juvenile) and the treatment of the pen (alone or group) was examined using a Two-way ANOVA with status and treatment as factors and total time out and number of times out (when lizards emerged) as dependent variables. The mean of all sessions for each adult and juvenile living alone was compared to the mean for each adult living in a group (as there was only ever one adult in a group), and the mean of juveniles in a group.

Overall, adults spent more time out of their crevice than juveniles (Table 7-2: Figure 7-9). There was no significant difference between individuals or groups in time out, but there was a significant interaction between status and treatment. Being in a group affected adults and juveniles differently (Table 7-2). Juveniles spent more time out in the group treatment (mean =2291 seconds/ 3 hrs) than when alone (mean =1140 secs/3 hrs), while adults spent more time out in the alone treatment (mean = 6429 secs/3 hrs) than in a group one (mean = 2895 secs/ 3 hrs) (Figure 7-9) and section 7.4.5.2).

The mean number of times out from the crevice was not significantly different between treatments or between adults and juveniles (Table 7-2) (Figure 7-10).

Table 7-2. Summary of Two-way ANOVA on Treatment (grouped or alone) and Status (adult or juvenile) on total time out during a 3 hr filming session (in seconds) (1996/97 data only). (* denotes significance at the 5% level).

Source of variation	**Mean square**	**df**	**F statistic**	**P value**
Treatment (grouped or alone)	5.82×10^6	1	1.76	0.21
Status (adult or juvenile)	3.56×10^7	1	10.74	0.01*
Status x Treatment	2.25×10^7	1	6.80	0.02*
Error	4.64×10^7	14		

Table 7-3 Summary of Two-way ANOVA for treatment and status on number of times emerged in a 3 hr session (1996/1996/97 data only).

Source of variation	**Mean square**	**df**	**F statistic**	**P value**
Treatment (grouped or alone)	11.94	1	3.06	0.10
Status (adult or juvenile)	0.12	1	0.03	0.87
Status x Treatment	0.32	1	0.08	0.78
Error	54.70	14		

Figure 7-9 Mean total time out (seconds/ 3 hr session) for adults and juveniles alone and in groups (1996/1996/97 data only) (see Table 7-2 for analysis).

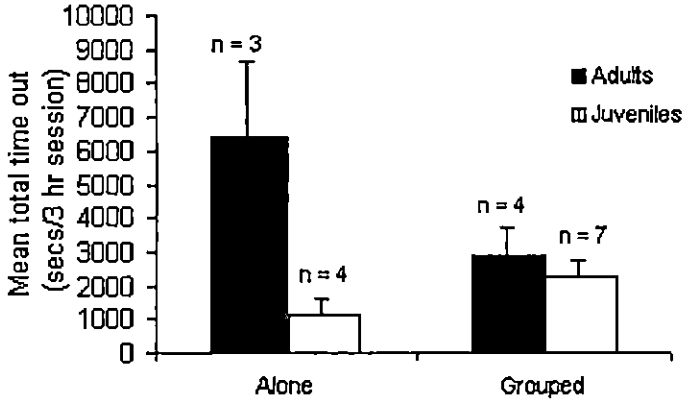
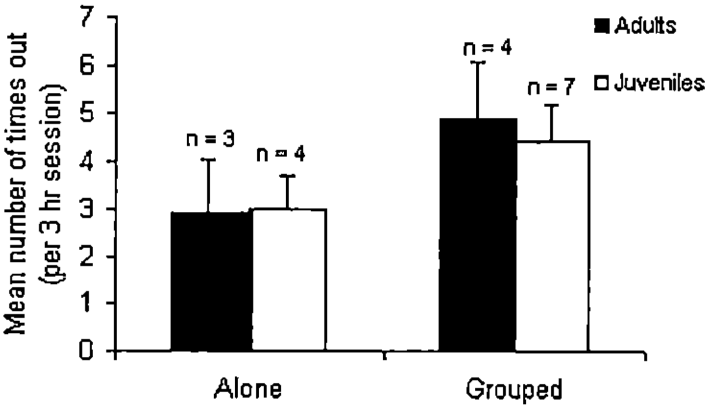


Figure 7-10 Mean number of times emerged per pen for juveniles and adults alone and in groups in a 3 hr filming session (analysis in Table 7-2) (1996/97 data only).



7.4.5.1 Juveniles

The significant interaction between treatment and status found in the Two-way ANOVA (Table 7-2), suggested that juveniles were behaving differently from adults in their response to being alone or grouped. In order to determine the relative effects of grouping on each age class, the data for juveniles by themselves (ie the 4 pens with single juveniles were compared with the 3 pens with all-juvenile groups) were analysed. Juveniles in groups spent significantly more time out per 3 hr filming session (mean=2291 secs, SE= 598 secs) than juveniles that were alone (mean=1140 secs, SE = 474 secs) (Figure 7-11).

There was no significant difference in the number of times that juveniles emerged between those living in groups and those living alone (Figure 7-12).

Figure 7-11 Mean total time out for juveniles only (1996/97 data only) (Independent samples t-test on natural log transformed data, equal variances assumed: t=2.24, p=0.052).

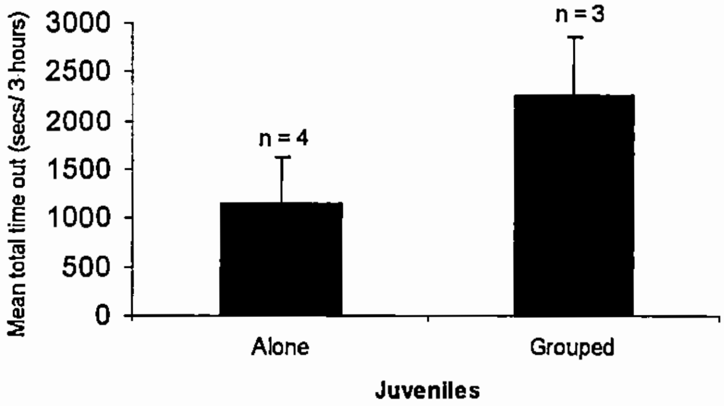
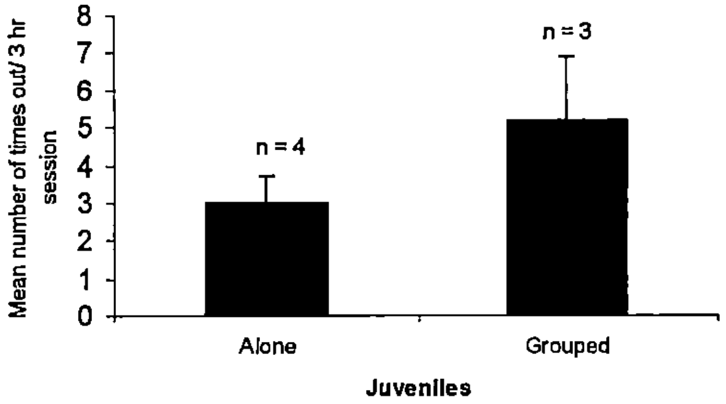


Figure 7-12 Mean number of times out in a 3 hr session for juveniles alone and in groups (Independent samples t-test, equal variances not assumed: t = 1.02, p= 0.35, df = 5) (1996/97 data only)



The data for juveniles in groups of only other juveniles were compared to those that were living in groups with an adult (their mother) present. There was no significant difference in time emerged or number of times out in this comparison (Figure 7-13: Figure 7-14).

Figure 7-13 Comparison of total time out for juveniles in groups with an adult and those in groups of juveniles only (Independent samples t-test, equal variances not assumed: t = 0.28, p = 0.79, df = 5) (1996/97 data only).

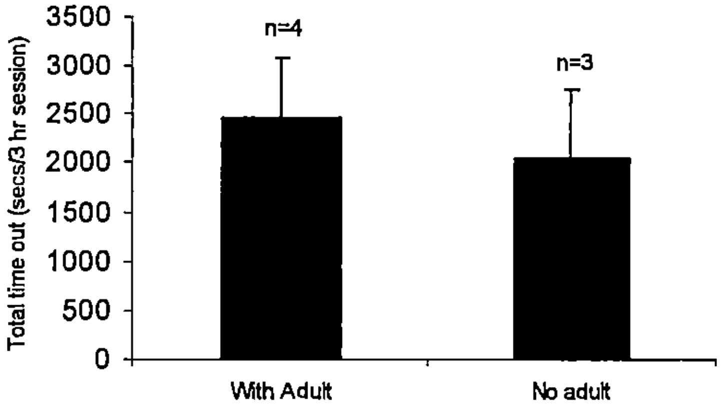
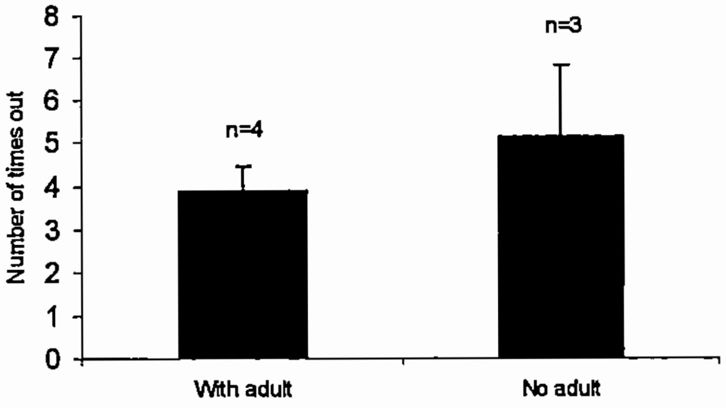


Figure 7-14 Comparison of number of times out for juveniles in groups with an adult and those in groups of juveniles only (Independent samples t test, equal variances not assumed: t = 0.65, p = 0.57, df = 5) (1996/97 data only).



7.4.5.2 Adults

Although adults showed a trend towards spending more time out when alone than in a group (Figure 7-9), this was not significant (Table 7-4). They also showed a tendency to emerge fewer times when alone, compared to adults in groups (Figure 7-10), although this also was not significant (Table 7-4).

Table 7-4 Summary of results of independent samples t-test on adult lizards in groups or alone.

Dependent variable	Treatment	Mean	Standard error	t statistic	df	P value
Total time out (secs)	Alone	6429.7	2164.9	1.53	5	0.24
	Grouped	2895.3	798.4			
Number of times out (secs)	Alone	2.9	1.2	1.18	5	0.29
	Grouped	4.9	1.2			

7.4.6 Summary and Discussion of 1996/97 emergence results.

Treatment (alone or grouped) did not significantly affect emergence time or number of times emerged. However, a significant difference in how adult and juvenile *E. stokesii* responded to being alone or grouped was found and may have influenced this result. Juveniles spent significantly more time out when they were in a group, suggesting that they may gain security from living with conspecifics.

In the field, juveniles have a higher overall mortality than adults (Duffield and Bull, 2001). Survivorship is 61% for juveniles in their first year, and only 33% at the end of their fourth year, compared with 97% for adults (reviewed in Chapter 1). Although all the factors that influence these figures have not been quantified, both kestrels (*Falco sp*) and brown snakes (*Pseudonaja textilis)* have been observed taking adult *E. stokesii*. Juveniles may be more susceptible to predation because they are more easily grasped by a predator, due to their smaller size. They may also be more naive to the dangers of predation. Since juvenile mortality is up to ten times that of adults and if predation is reduced in a group, either by enhanced vigilance to predators or by dilution, then juveniles may gain more from living in a group than adults.

Another possible explanation is that there is social transmission of information in *E. stokesii* and juveniles might be spending more time out in groups to in order to obtain foraging information. However, increased time out from shelter should increase the possibility of predation which would represent a cost to this type of information gathering. Also, if this hypothesis is correct, juveniles in groups containing an adult would be expected to come out more often, since information from adults is likely to be more valuable to their survival. There was no difference in time out between groups containing an adult and those containing only juveniles.

Table 7-5 Summary of filming for 1999/2000 experiments. * denotes a recording when lizards from the adjoining pen managed to dig into the filming pen, thus invalidating the data. ++ Tape was mislabelled and so the repeat was not performed for this individual. Abbreviations: nr= not recorded.

Pen	Pen id	Date	Number of lizards and sex	Side camera	Above camera	Number emerged	Starting time	Starting temp. (degrees C)
1	N1	15/02/00 26/03/00	3 - unknown sex	No data Yes	Yes Yes	1 1	10am 10:50am	nr 18
2	N2	24/02/00	1	Yes	Yes	1	10am	19
3	N4	5/02/00	3	* Not able to be included in analysis.				
4	N5	7/02/00	6 - 1 female 5 unknowns	Yes	Yes	3	10am	21
5	N6	26/01/00	1 female	No data+	Yes	1	10:15am	20
6	N8	13/04/00	2 - 1 female 1 unknown	Yes	Yes	2	10:10am	22
7	S1	27/01/00	3-1 female 1 male 1 unknown	Yes	Yes	2	10:50am	19
8	S2	31/01/00	6 - 1 male, 3 females, 2 unknown	Yes	Yes	5	9:40am	25
9	S4	28/02/00	2 unknown	Yes	Yes	2	10:05am	21
10	S5	8/03/00	2 -1 female, 1 unknown	Yes	Yes	2	10am	20
11	S6	3/04/00	6- 2 female, 4 unknown	Yes	Yes	5	9:55am	20
12	S8	12/02/00 2/04/00	1 female	No data Yes	Yes Yes	1 1	10:40am 10:10am	19 24

7.5.2 Effect of group size on emergence behaviour.

Single factor ANOVA showed no significant difference among groups in the mean time that lizards spent emerged (Figure 7-15). However, there was a difference among groups in the number of times emerged (Figure 7-16). Post hoc Bonferroni tests showed lizards in groups of three had significantly more emergences than those in any other group size. There was no significant difference between the other group sizes for number of times emerged (Table 7-6).

Figure 7-15 Total time out for lizards - alone (1) and in groups of two (2), three (3) and six (6) for 2000 experiments (Single factor ANOVA on natural log transformed data: $F_{3,7}$=0.64, p=0.61) (1999/2000 data only).

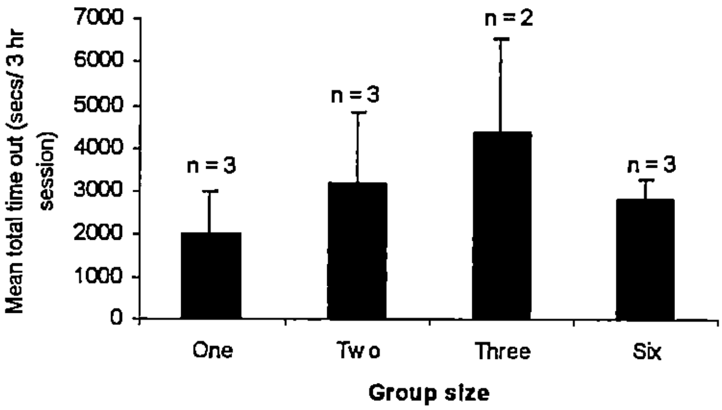


Figure 7-16 Mean number of times emerged from the crevice during a three hour filming session for group sizes of 1, 2, 3 & 6 (Single factor ANOVA: $F_{3,7}$=21.95, p=0.00*) (1999/2000 data only).

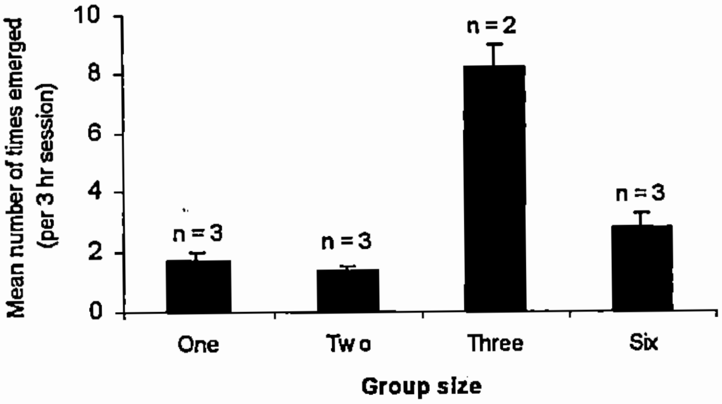


Table 7-6 Summary of Bonferroni post hoc test on ln transformed times emerged per 3 hr session (1999/2000 data only). (* denotes significance at the 0.05% level).

Group size vs	Group size	Mean difference	Standard error	P value
1	2	0.15	0.19	1.0
	3	-1.42	0.21	0.00*
	6	-0.42	0.19	0.34
2	1	-0.15	0.19	1.00
	3	-1.57	0.21	0.00*
	6	-0.57	0.19	0.11
3	1	1.42	0.21	0.00*
	2	1.57	0.21	0.00*
	6	1.0	0.21	0.01*
6	1	0.42	0.19	0.34
	2	0.57	0.19	0.11
	3	-1.00	0.21	0.01*

7.5.3 Combined activity data – For both 1996/97 &1999/2000 seasons.

Due to the differences in juvenile and adult behaviour found in the 1996/97 data (see Section 7.4.5), only adult data from that experiment were pooled with all data from the1999/2000 season. Analysis of the combined data was conducted to discover if:

a) There was an overall effect of being either alone or grouped for both seasons.
b) Small groups (1 or 2 individuals) behaved differently to larger groups (3-6 individuals)
c) Season (ie the year that the experiment was conducted) influenced the total time emerged or number of times out.

7.5.3.1 Alone or Grouped treatments

No significant difference was found for either parameter measuring emergence behaviour for lizards living alone or in groups (Figure 7-17 : Figure 7-18).

Figure 7-17 Mean amount of time emerged for lizards alone and in groups (Independent samples t-test on natural log transformed data, equal variances assumed: $t_{16} = 0.31$, p = 0.76) (1996/97 & 1999/2000 data combined).

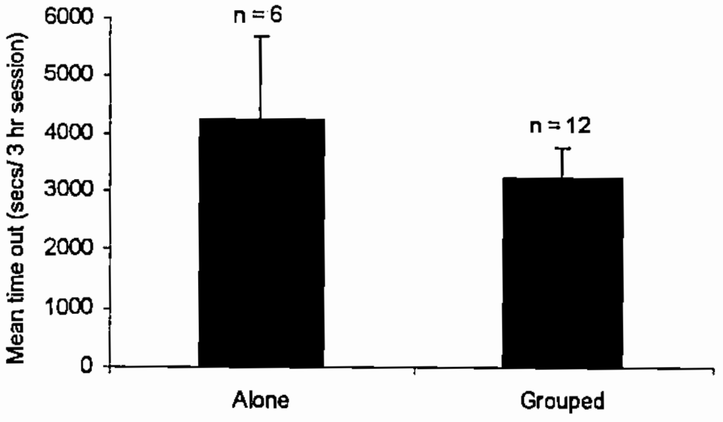
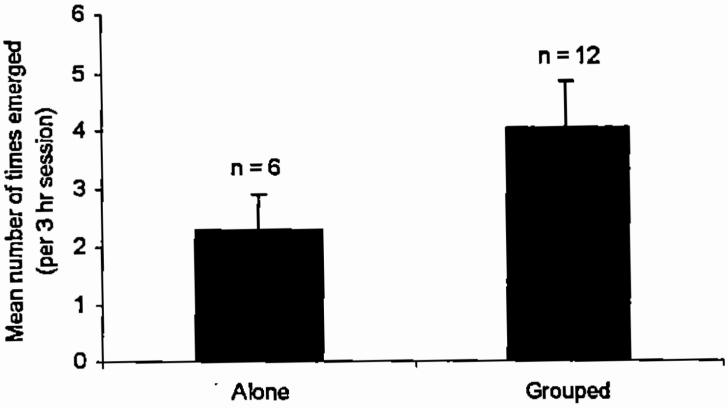


Figure 7-18 Mean number of times emerged in a three hour filming sessions for lizards alone and in groups (Independent samples t-test on ln transformed data, equal variances assumed: t_{16} = 1.49, p = 0.16) (1996/97 & 1999/2000 data combined).



7.5.3.2 Small versus large groups.

Lizards living alone or in pairs were compared with those living in groups of three or more individuals. Season did not affect either measure of emergence behaviour (Table 7-7). Total amount of time emerged was not significantly different between small and large groups (Figure 7-19). However, the number of times emerged during a three hour filming session did differ between small and large groups with lizards in large groups coming out an average of 4.93 times (SE =0.88), while those alone or in pairs only came out on average 1.96 (SE = 0.42) times per session (Figure 7-20 : Table 7-7).

Figure 7-19 Mean time emerged for lizards in small groups (1-2 lizards) compared to those in large groups (3 –6 lizards).

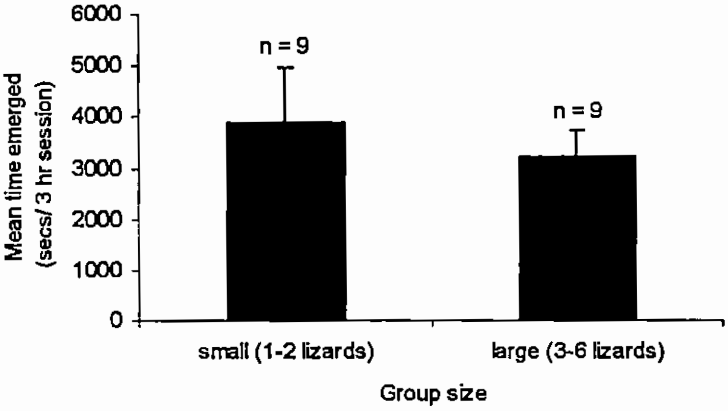


Figure 7-20 Comparison of number of times emerged for small (1-2 lizards) and large (3-6 lizards) groups (analysis in Table 7-7).

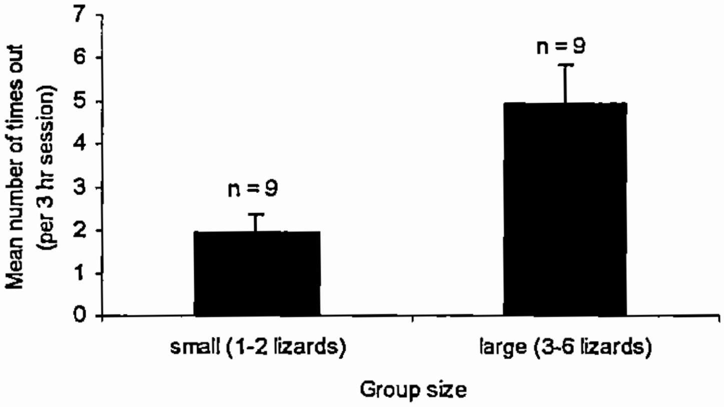


Table 7-7 Summary of results of Two way ANOVA comparing effect of season and small versus large groups (All data have been ln transformed to meet the assumptions of ANOVA).

Source of variation	Dependent variable	Mean square	df	F statistic	p value
Small vs large groups	Total time out	0.15	1	0.41	0.53
	Times out	3.11	1	10.85	0.01 *
Season	Total time out	0.78	1	2.10	0.17
	Times out	0.34	1	1.18	0.30
Season x group	Total time out	1.61	1	4.35	0.06
	Times out	0.19	1	0.68	0.42
Error	Total time out	0.37	14		
	Times out	0.29	14		

7.5.3.3 Removal of groups of three lizards from analysis.

Finally, lizards in groups of three were removed from the analysis to ensure that the results were not biased by the high values that this treatment produced. The high values for both parameters of emergence behaviour suggested that they could represent an outgroup. As with previous results, there was no difference in the mean amount of time that lizards in small (1 & 2 individuals) groups emerged compared with those in large (4 & 6 individuals) groups (Figure 7-21). Lizards in large groups still came out significantly more often than those in small groups (Figure 7-22: Table 7-8).

Figure 7-21 Total time emerged for small (1-2 lizards) and large (4 & 6 lizards) groups. (Groups of 3 lizards removed) (see Table 7-8 for analysis) (1996/97 & 1999/2000 data combined).

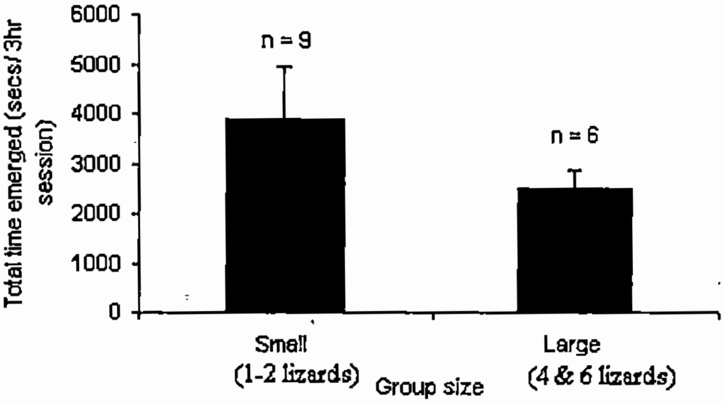


Figure 7-22 Mean number of times emerged per lizard for small and large groups, with group 3 removed.

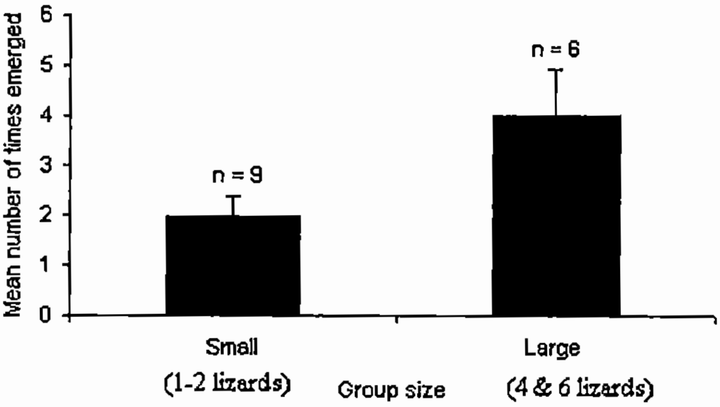


Table 7-8 Summary of analysis with groups of three lizards removed. Comparing small groups (1 & 2 lizards) with large groups (4 & 6 lizards). Analysis was on ln transformed data, using independent samples t-test (equal variances not assumed) (* denotes significance at the 5% level).

Group size	Dependent variable	Sample size	Mean	Standard error	t statistic	p value
Small (1 & 2)	Total time out	9	3892.8	1058.7	0.62	0.55
Large (4 & 6)	Total time out	6	2504.2	357.9		
Small	Times emerged	9	2.0	0.4	2.79	0.02 *
Large	Times emerged	6	4.0	0.9		

7.5.4 Summary and discussion of 1999/2000 and combined 1996/97 & 1999/2000 results

Both the 1999/2000 data and the combined data showed the same results. Lizards in different group sizes differed in the number of times they emerged during a session. Animals in smaller groups (1-2) lizards came out fewer times than those in larger groups (3-6), although, unlike the juveniles in the 1996/97 experiment, there was no difference in the total time spent out of the crevice. This suggests that lizards in small groups are coming out less often, but for longer periods of time than those in larger groups.

If shuttling behaviour (regulating an organisms temperature by moving between shade or cover and sunlight) is important to a heliotherm's ability to thermoregulate effectively (Heatwole and Taylor, 1987), then these results may indicate a reluctance by animals living alone or in small groups to fully utilise the thermal properties of the environment, perhaps due to a fear of predation. Lizards in larger groups may be able to adjust their thermoregulatory behaviour more precisely to remain at or near their optimal temperature, with less fear of predation, due to early warning from other group members, or from a lower probability of being taken when more lizards are around.

Future experiments could compare thermoregulatory precision in lizards by monitoring lizard body temperature in a group and when living solitarily. This would involve an extension of the previous chapter's experiments. Lizards would wear a thermocouple that would monitor body temperature over several days. The amount of time spent at optimal temperature during the course of one or more days could be compared among different group sizes.

Alternatively, the stimulus created by more lizards in the same sized area may mean that animals in a larger group move in and out of their refuge more often due to cues from other group members (either as a result of a perceived threat or as part of their normal activity). This could be either a benefit or cost to group-living. If lizards in a larger group are being warned of pending danger more often (even if sometimes it is only perceived danger) they may have a higher probability of escaping predation. However, if this increased "skittishness" results in higher energy expenditure, especially when food is scarce, this could represent a cost to group living, especially during drought or other periods of low resources.

There was no difference between seasons in the results obtained, but only adult data from 1996/97 were used. Juveniles were shown to respond differently (section 7.4.5.1) and so were excluded from the combined analysis.

7.6 Eyes open behaviour.

7.6.1 Methods for eyes open data for 1996/97 and 1999/2000 data.

For the experiments described in the previous section (beginning 7.3.1), a second camera was used to monitor the eye state of basking individuals. It was mounted on a tripod directly in front of the crevice pile 0.8m away from it (Figure 7-1). In both seasons, repeat filmings were made if lizards did not emerge from their crevice at any time during the 3 hr filming session, or if they did not bask in the field of view of the second camera. Repeats were made only until data were obtained for at least one session for a lizard from each pen.

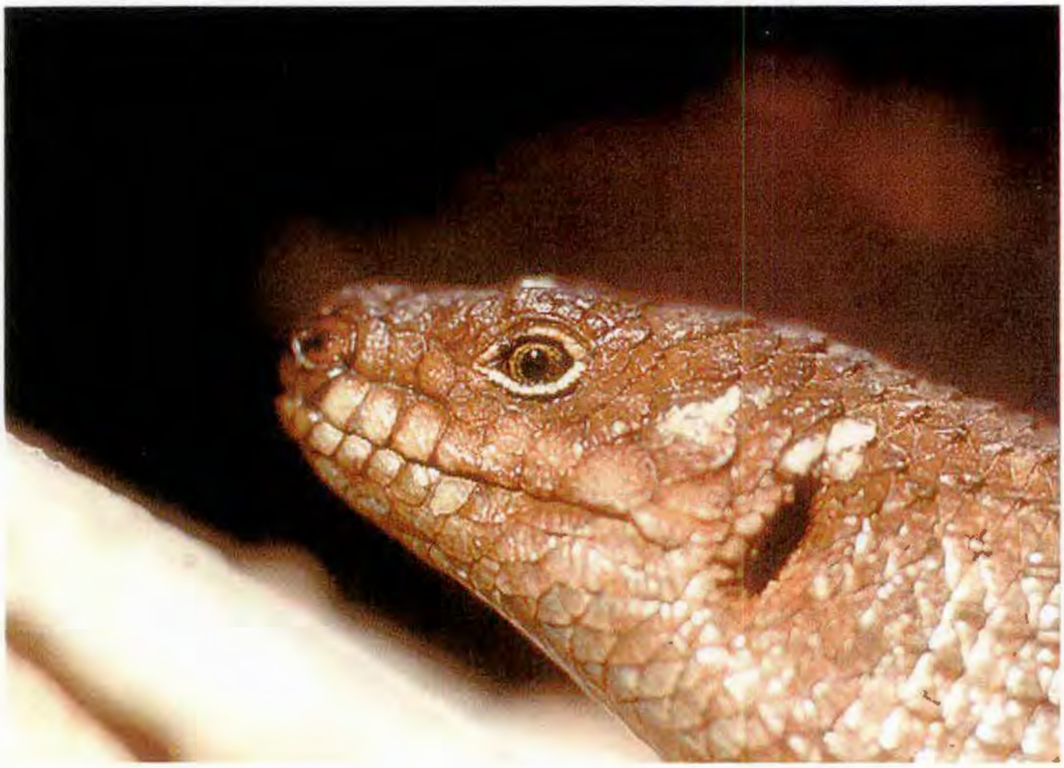
The camera was zoomed in and focused on a small area of the basking surface. When a lizard basked with its head in the camera's focal area, it was possible to ascertain when the eye facing the camera was open or closed. Recordings of the eye state of a lizard was only possible when it was positioned parallel to the camera and in the field of view– this was usually for only a short period in each filming session. Only sequences where at least 50 secs of continuous data of the eye state (either open or closed) of the eye closest to the camera were used. If the lizard moved off in that time, that sequence was discarded.

Usually only one eye of any lizard was visible at any one time. It was always the eye furthest from the crevice that could be viewed from the camera. *E. stokesii* exhibits asynchronous eye closure (see Chapter3 and section 7.1.2) , meaning they can close one eye while the other remains open. This behaviour has frequently been observed in both captive and field populations. By recording the eye state of the eye furthest from the crevice probably underestimated the period that the lizard had one or both eyes closed. If an animal was relying on sighting a potential threat, and it wanted to close one eye, it would be expected to close the eye closest to the crevice more often, while keeping the eye furthest from the crevice open. In this experiment, the assumption was made that if the eye closest to the camera was closed, then the animal had reduced its vigilance compared to when it was open. This was likely to be a conservative estimate of the eye closure of the lizard.

Lizards have not been observed tongue flicking during asynchronous eye closure (ASEC) (pers obs) and they were not observed tongue flicking when their eye closest to the camera was closed, suggesting they do not compensate for partial loss of sight by increasing their chemosensory sampling of the environment.

E. stokesii has small eyes (6mm x 3mm) and they are normally dark brown, the surrounding area is only slightly lighter than the iris (Figure 7-23). To assist with the detection of eye state in the video recording, the lower eyelid of the lizards were painted with a light shade (white or pale pink) of a non-toxic, water-soluble paint immediately before filming commenced. The bottom eyelid covers most of the eye and is the lid that is moveable, and therefore able to be closed in *E. stokesii* (Greer, 1989).

Figure 7-23 Close up of the eye of *E.stokesii*. Note little difference in eye colour to surrounding skin colour. Painting of the lower lid (this covers most of the eye when the lizard shuts it) with non-toxic, water-soluble paint was used to enhance visibility on the video.



7.6.1.1 Comparison of eye closure for lizards living alone and in groups

The amount of time (secs) when each lizard had the eye closest to the camera closed was recorded and an average for the pen was computed for the filming session. This was then converted to secs/min so comparisons could be made between grouped and alone lizards.

7.6.1.2 Comparison of eye closure for lizards basking alone and in groups

Some of the data collected for the previous section were taken from lizards that were basking alone, although they were living in a group. If there was an antipredator advantage to group-living, then lizards basking in a group should also show a reduction in eyes open behaviour compared to those basking alone (though not necessarily living alone), since this is when they would stand to gain most from group membership. Data for lizards basking alone and in groups for both seasons were combined.

For every focal animal that eye state during basking had been recorded for also had the number of lizards basking with it recorded. The average number of lizards that each focal animal basked with was used to determine which category the lizard was placed in. If the average was zero as it was for all the alone lizards and for one group in 1996/97 and two in 1999/2000, then those lizards were considered to be basking alone, while if the value was greater than 0.5, as it was for the other groups, then the lizards were considered to have been basking in a group.

For the 1996/97 season, estimates of the time that at least one member of the group had its eye(s) open could be made for six out of the seven pens. An individual may get an advantage from closing its eyes more when in a group, but if the group significantly reduces its overall vigilance to predators, it may be more susceptible to predation than a lizard basking alone that keeps its eyes open all the time.

7.6.1.3 Head turns

As well as recording eye state as a measure of vigilance, the number of head turns or tilts (see Chapter 3 for a description) was also recorded. These have been associated with vigilance or scanning behaviour in many species of birds and mammals (see Elgar, 1989 for a review). Many studies have shown a decrease in this behaviour, and implied a reduction in vigilance with increased group size (Lima, 1995). Any sideways or upward movement of the head of the lizard was recorded for a basking session that met the criteria for the collection of data for eyes open/eyes closed.

7.6.1.4 Analysis of vigilance data

Where possible, parametric methods of comparing means between samples (both independent samples and paired t-tests) were used to compare means. Where applicable, data were appropriately transformed to meet the assumptions of normality and homoscedasticity. There were two instances when this was not possible: when there was no variation in one of the groups (1999/2000 eyes open data for lizards living alone) a Mann-Whitney U non-parametric alternative to the independent samples t-test to test between alone and grouped lizards (all group sizes combined) was used and a Kruskal-Wallis nonparametric alternative to a one-way ANOVA when each group size was analysed separately. When comparing basking groups, data could not be transformed to fit the assumption of normality for a t-test, so a non-parametric alternative to the independent samples t-test was used (Mann-Whitney U test).

Each season was examined separately, then data were combined from both years, first testing if there was any significant difference between seasons. Pen N8 in the 1996/97 season, contained only three lizards, since one died just before the start of filming. This pen was analysed as part of the group data when 1996/97 was analysed on its own (all other groups contained four individuals), but it was analysed as a group of three instead of four when the combined data were analysed.

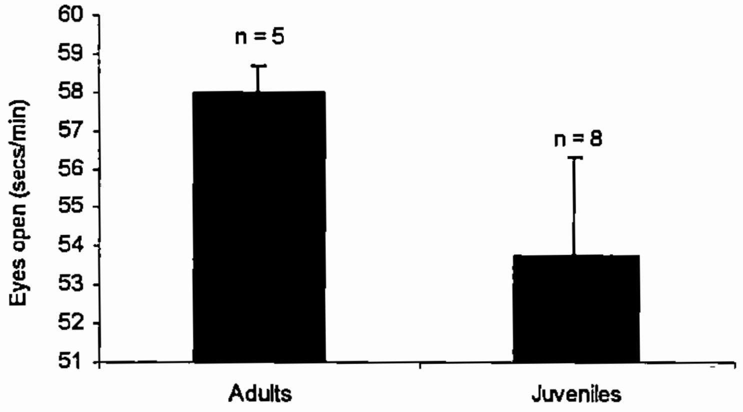
7.6.2 Results

Some pens had lizards that never basked in front of the camera, and so therefore no data could be collected for those pens. Most groups had only one or two sessions containing video footage from the side camera that was suitable for analysis. Data for the solitary treatment were even harder to get, with most lizards alone only basking within sight of the camera once out of the four filming sessions. Some pens had to have additional repeats to obtain any data on solitary lizards. Even with this increased effort, only five out of the seven individuals had sufficient data recorded for them to be used in the analysis.

7.6.2.1 Eyes open per minute for adults and juveniles.

Adult and juvenile *E. stokesii* were compared for the amount of time they spent with their eyes open while basking. There was no significant difference between them (Figure 7-24). For further analysis, adult and juvenile data were combined to obtain an overall average for each pen.

Figure 7-24 Eyes open (secs/min) while basking for adult and juvenile lizards (independent samples t-test, equal variances not assumed: $t_8 = 1.58$, $p = 0.15$) (1996/97 data only).



7.6.2.2 1996/97 data - Individual versus group for eyes open

Means of eyes open per minute for lizards living in a group were then compared to those for lizards living alone. A limited number of videos also recorded eye state of several members of the group and thus an estimate of total group vigilance for six out of the seven groups was made. This then made up three groups of data, an estimate of eyes open (secs/min) for lizards living alone, an estimate for individual lizards in a group and an estimate of the amount of time that at least one lizard in the group that was basking had its eyes open.

Individual lizards living alone spent nearly all their recorded basking time with their eyes open (mean = 59.5 secs/min, SE = 0.5). Lizards living in a group spent significantly less time with their eyes open (mean eyes open = 52.7, SE =2.5) (Figure 7-25 : Table 7-9). Mean eyes open (secs/min) for whole groups was significantly higher than individual vigilance in groups, (mean eyes open = 58.9 secs/minute, SE = 1.1), but not significantly different from animals living alone (Table 7-9). Data could not be analysed using just one test for all three groups as data for the group as a whole was an aggregate of the data for individuals in a group and was therefore related. A series of t-tests were used for this analysis (Table 7-9).

Figure 7-25 Pen means for eyes open per min for lizards living alone, lizards living in a group, and total eyes open for the group as a whole. (1996/97 data only).

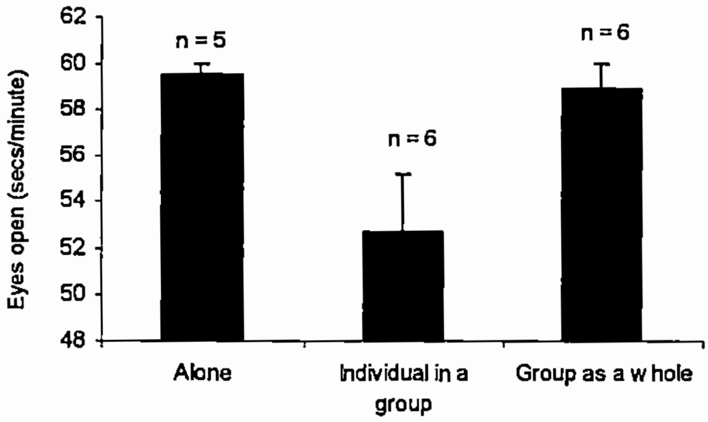


Table 7-9 Summary of analysis of eyes open (secs/min) for the following groups: 1 = lizards living alone, 2 = individuals in a group, 3 = eyes open for the whole group.

Comparison of groups	Test	t statistic	df	p value
1 vs 2	independent samples t test (equality of variances not assumed)	2.65	9	0.042
2 vs 3	paired samples t test	2.80	5	0.038
1 vs 3	independent samples t test (equality of variances not assumed)	0.49	9	0.64

7.6.2.3 Eye state of two lizards basking (1996/97 season)

Analysis on eyes open per minute for groups as a whole were based on a small number of replicates because it was rare to have two lizards with their eyes in view of the side camera simultaneously. Data from four out of the five groups consisted of one or both lizards remaining vigilant throughout the session or each lizard took a short turn of closing its eyes. However, one sequence filmed on 10/12/96 of a group of four lizards (pen s6: Table 7-1) did show two lizards opening and closing their eyes during the same period.

The overlap lasted for 4:01 minutes from 12:11:08-12:15:09. During this period, lizard 44 closed its eyes for 77 secs, while lizard 40 had its eyes closed for 48 secs. The total time during this period when both lizards had their eye(s) closed was only 26 secs (Table 7-10).

Figure 7-26 Graph of alternating eye closure for two lizards filmed simultaneously. The lines show when the lizard had its eye(s) open. The blanks in the lines represent periods when each lizard had its eyes closed. Summaries for each lizard are shown in Table 7-10.

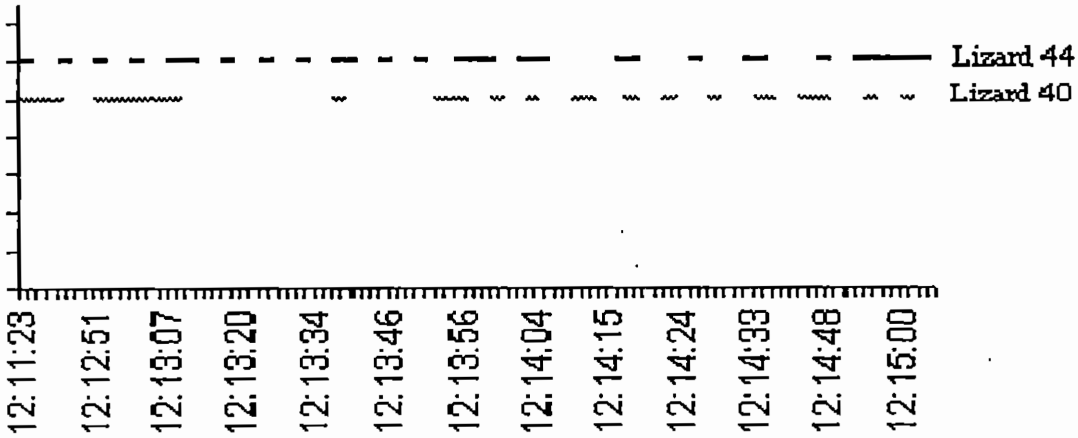


Table 7-10 Summary of data from two lizards (#40 and #44) basking together, exhibiting alternating eye closure

	Lizard 40	**Lizard 44**	**Total for the period**
Total number of seconds with eyes closed	48	74	26
Eyes open/minute (secs)	41.58	48.05	53.33
Eyes closed /minute (secs)	18.42	11.95	6.67

The maximum time when both lizards had their eyes closed was 5 secs at any one time, with most bouts of synchronous eye closure lasting only 2-3 secs (Figure 7-26). While it is difficult to determine if the amount of mutual eye closure exhibited by these two lizards was less than would be expected by chance, especially as there was only one recorded instance of this type of behaviour, there are two things worthy of comment.

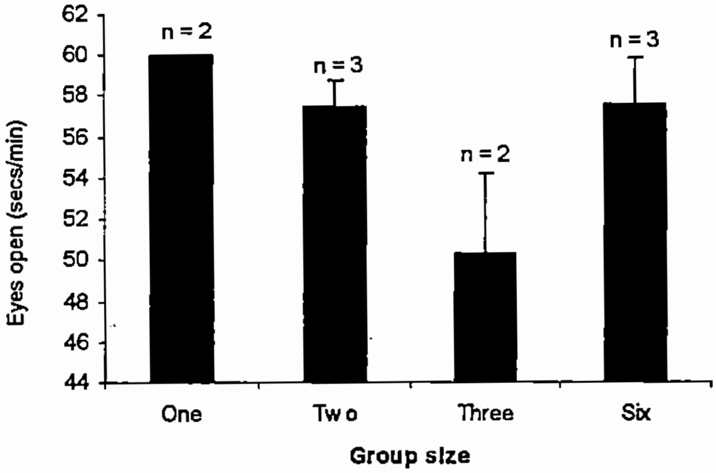
Firstly, these two lizards exhibited one of the highest amounts of eye closure per minute (12.0 and 18.4 secs/min respectively) recorded in the experiment. Secondly, casual observation of groups in outside pens have revealed similar behaviour, where lizards alternate their eye closure with another. It may be that the limited field of view of the camera prevented more data collection of lizards in close proximity to each other and that these groups may have exhibited lower eyes open/min than the data obtained for the rest of the experiment. There were several instances when lizards spent long periods of time basking in close proximity (as determined by the overhead camera), but due to the small field of view of the side camera, usually only one lizard's eye state for the required amount of time could be determined

7.6.3 1999/2000 Vigilance data.

More group sizes were added to the experimental design in the 1999/2000 season. This increase in the number of group sizes observed was to determine if the reduction in individual time spent with eyes open in a group, applied to groups larger than four, and also to see if there was a gradual decline in this behaviour in groups of two or three individuals.

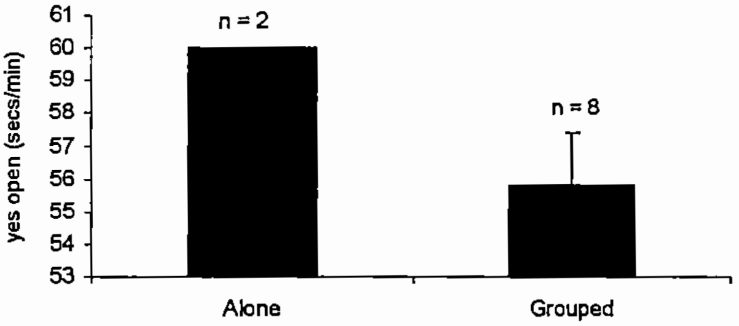
As in 1996/97, lizards living alone were highly vigilant (mean eyes open for individuals was 60 secs/minute), while groups of 2 & 3 were the least vigilant (mean eyes open = 57.4 and 50.3 respectively). Data were analysed using a Kruskal-Wallis non-parametric alternative to a One way ANOVA due to the lack of variability in the alone treatment. The trend in the 1999/2000 data was similar to the 1996/97 results, although there was no statistically significant difference among groups in eyes open when basking (Kruskal-Wallis nonparametric test: $X^2_3 = 3.33$, p=0.34) (Figure 7-27).

Figure 7-27 Eyes open per individual per pen (secs/min) for lizards living alone and in groups of 2, 3, and 6 (Kruskal-Wallis nonparametric test: $X^2_3 = 3.33$, p=0.34) (1999/2000 data only).



Group data were then combined and alone and grouped treatments were compared (all group sizes were combined into one category). No significant difference was found between alone and grouped treatments (Mann Whitney U: U= 2.0, p=0.18) (Figure 7-28).

Figure 7-28 Eyes open per minute for alone and grouped (all group sizes combined) (Mann Whitney U: U= 2.0, p=0.18) (1999/2000 data only)



7.6.3.1 1996/97 and 1999/2000 Vigilance data combined.

There was no significant difference between the two different seasons (1996/97 and 1999/2000) in the amount of time lizards spent basking with their eyes open.

When analysed together, the two data sets showed there was a significant difference between the amount of eyes open/min for lizards in the five different group sizes (Figure 7-29 : Table 7-11), and when lizards living alone were compared with grouped lizards (all group sizes combined) (Figure 7-30). There was a gradual decrease in eyes open per minute from the highest value of 59.6 secs/min for lizards living alone down to a mean of 51.8 secs/min for lizards in groups of four. However, it then increased to the second highest value in the analysis of 57.9 secs/min for lizards in groups of six (Figure 7-29). The average time spent with eyes open for grouped lizards was 54.4 secs/min, significantly lower than 59.6 secs/min for lizards living alone (Figure 7-30). The differences discovered in the analysis came primarily from a significant difference between alone lizards and those in groups of four (Table 7-11).

Figure 7-29 Eyes open (secs/minute) for different group sizes (1-6 animals) (1996/97 & 1999/2000 data combined)

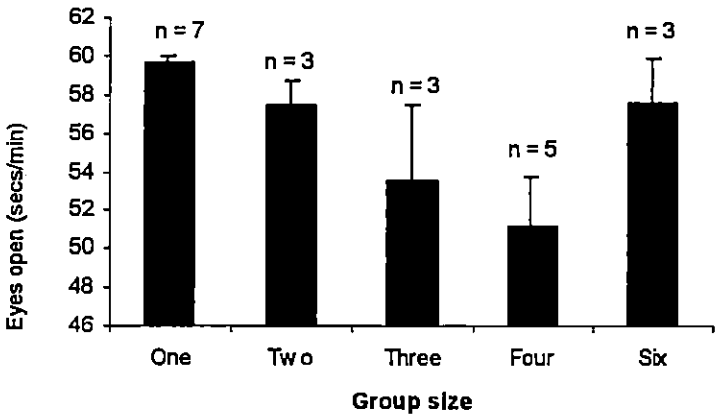


Figure 7-30 Vigilance behaviour (eyes open per minute) for alone and grouped (all group sizes combined) (Independent samples t-test, equal variances not assumed: t = 3.70, p = 0.00*) (1996/97 & 2000 data combined)

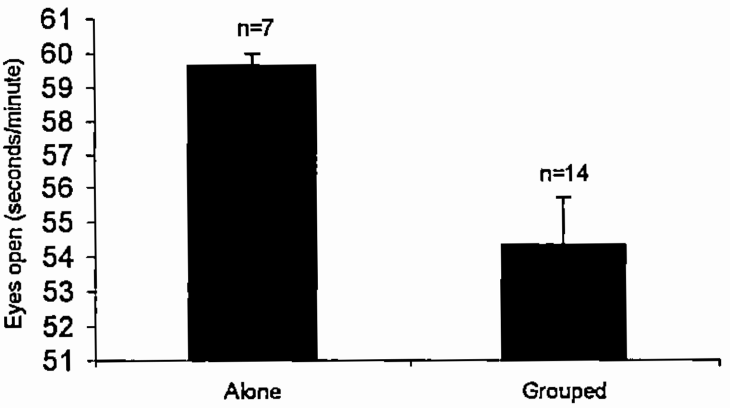


Table 7-11 Summary of results of Two way Anova on year and group size (1996/97 & 1999/2000 data combined)

Dependent Variable: eyes op/min

Source	Type III Sum of Squares	df	Mean Square	F statistic	p value
Corrected Model	300.25	6	50.04	3.45	.03
Intercept	53784.30	1	53784.30	3707.45	.00
Groupsize	294.30	4	73.57	5.07	.01
YEAR	38.35	1	38.35	2.64	.13
Groupsize x year	47.15	1	47.15	3.25	.09
Error	203.10	14	14.51		
Total	66704.76	21			
Corrected Total	503.35	20			

Table 7-12 Summary of results of Bonferroni post hoc tests on eyes open for each group size for both seasons combined (1996/97 & 1999/2000 data combined) (note that group sizes of one and four are significantly different).

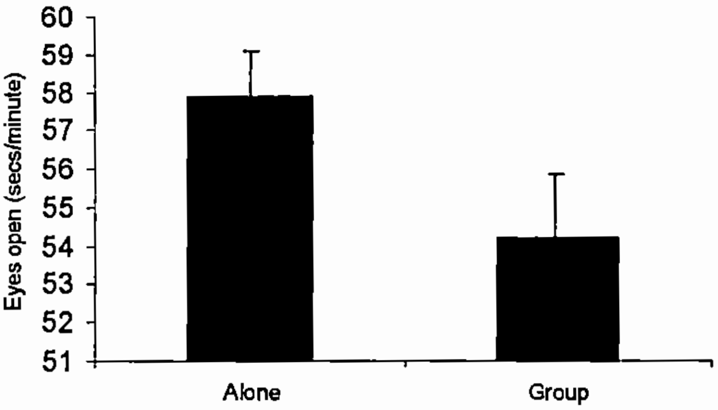
Dependent Variable: eyes op/min
Bonferroni

Groupsize vs	Groupsize	Mean difference between values	Standard error	p value
1	2	2.23	2.63	1.00
	3	6.10	2.63	.36
	4	8.41	2.23	.02
	6	2.12	2.63	1.00
2	1	-2.23	2.63	1.00
	3	3.87	3.11	1.00
	4	6.18	2.78	.43
	6	-.12	3.11	1.00
3	1	-6.10	2.63	.36
	2	-3.87	3.11	1.00
	4	2.32	2.78	1.00
	6	-3.98	3.11	1.00
4	1	-8.41	2.23	.02
	2	-6.18	2.78	.43
	3	-2.32	2.78	1.00
	6	-6.30	2.78	.40
6	1	-2.12	2.63	1.00
	2	.12	3.11	1.00
	3	3.98	3.11	1.00
	4	6.30	2.78	.40

7.6.3.2 *Groups of basking lizards.*

Lizards that lived in groups sometimes still basked alone. The previous sections included data in the grouped treatment from lizards that were basking alone, although they were living in a group. This section compares lizards that were basking alone to those basking in groups, regardless of if they were in an alone or group treatment. Lizards basking in groups spent significantly less time per minute with their eyes open than those basking alone Figure 7-31). This represents the same trend as the group living data reported in the previous section (eg Figure 7-30).

Figure 7-31 Mean of eyes open per minute for lizards basking alone and in groups (Mann-Whitney U non-parametric test: U=25.00, p= 0.04*) (1996/97 & 2000 data combined)



7.6.4 Head turns

The mean number of head turns per minute of basking time did not vary between alone and grouped lizards during the 1996/97 experiment (Figure 7-32). There was also no significant difference among groups in the mean number of head turns per minute for the 1999/2000 experiment (Figure 7-33).

When data for both seasons were combined, there was also no difference in the mean number of head turns per minute for any group size (Figure 7-34).

Figure 7-32 Mean number of head turns or tilts per min for lizards alone and in groups (independent samples t-test, equal variances assumed: t=0.941, df = 8, p=0.38) (1996/97 data only).

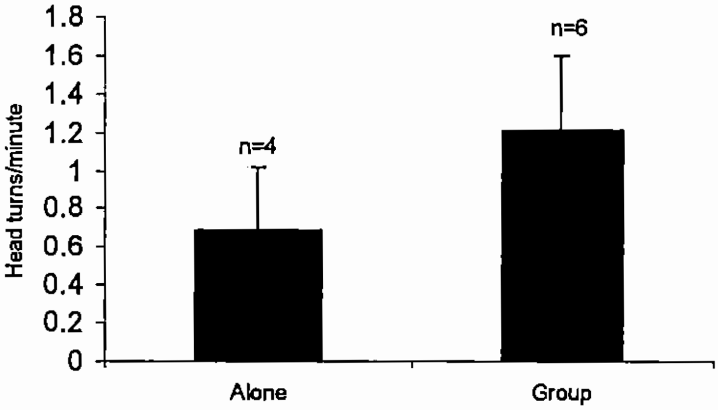


Figure 7-33 Mean number of head turns/minute for group sizes of 1, 2, 3 & 6. (Single factor ANOVA: $F_{3,6}$=1.62, p=0.28) (1999/2000 data only).

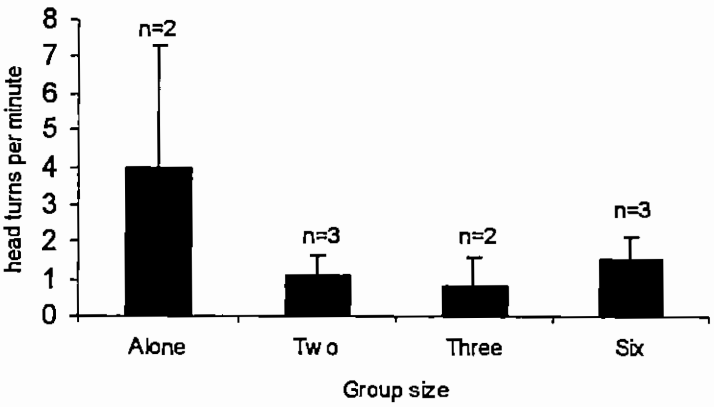
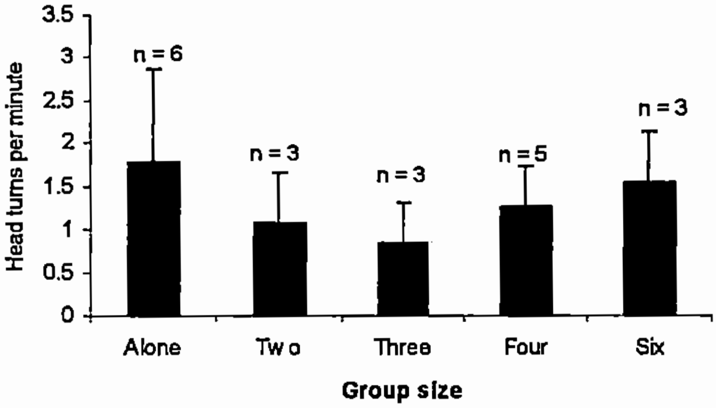


Figure 7-34 Mean number of head turns per minute for all group sizes (One way ANOVA: $F_{4,15}$= 0.18, p=0.95 (1996/97 and 1999/2000 data combined).



7.6.5 Summary and discussion of vigilance behaviour.

Vigilance behaviour in lizards may be more difficult to quantify than in some other species, but closing one or both eyes represents a reduction in input from an important source (visual system), consistent with a reduction in vigilance to a potential threat (section 7.2.2).

It is likely that in 1996/97 there were enough data to compare individuals living alone, individuals in a group and the group as a whole. The mean eyes open/min for lizards living alone was not significantly different to the mean for groups as a whole. Individuals living in a group of four lizards spent significantly less time with their eyes open than either the group as a whole or lizards living alone. This suggests that lizards are able to reduce the time with their eyes open, and therefore fully vigilant, for more time with they eyes closed when they are in a group, while the group still maintains the equivalent amount of eyes open of a single lizard.

Neither the season the experiment was conducted in (1996/97 or1999/2000) nor status (juvenile or adult) affected eyes open behaviour, so all data from both seasons were combined. Lizards living alone spent significantly more time with their eyes open than those lizards living in groups of two or more. The combined data showed a difference in the amount of time lizards in different group sizes spent with their eyes open. However, vigilance behaviour did not decline linearly with an increase in group size. Such a decline has been predicted from the "group size effect", as noted in mammals and birds (Lima, 1995).

Eyes open per minute was lowest in groups of four and then groups of three, while groups of six had the second highest value behind lizards living alone. This higher value could result from the six lizards in a pen of size 3m x 1.4m being crowded, and therefore more alert to the activity of other group members. There may be some competition for limited basking areas and lizards increased their vigilance to conspecifics, rather than to predation. Distinguishing between the two types of vigilance can be difficult, even in taxa where the effect of group size on vigilance behaviour has been well-studied (Janson, 1998).

The amount of eyes open/min was also lower in lizards basking in a group compared with lizards basking alone. This confirms the results obtained comparing lizards living alone or in a group. It also provides some evidence that lizards may close their eye(s) more often if a lizard has other conspecifics nearby to look out for potential threats, and that this effect may increase with the number of group members. The example given of two lizards basking together (section 7.6.2.3) shows two of the lowest values for eyes open per minute. The only time other time that values lower than 40 seconds/min have been observed is when a lizard has only half of its body out of the crevice. In this position, lizards close their eye(s) for up to 30 secs/minute. This was observed in two filmings and in casual sightings, but was not analysed, because there were insufficient recordings of this behaviour. However, it does suggest that perceived security (having most of the body inside a crevice) allows a lizard to close its eyes more, suggesting that the reduced rate of eyes open/minute in groups of lizards is indicative of a perception of increased security within a group and also that closing one or both eyes is a desirable behaviour for a lizard.

Head turns, which may represent scanning behaviour or a reaction to a noise or movement, were not significantly different between lizards living alone or those in groups. If head turns/tilts are similar to scanning behaviour in birds and mammals, then lizards might be expected to reduce them when in a group. In fact, grouped lizards had a slightly higher mean number of head turns /minute (although it was not statistically different from those lizards living alone).

This suggests that head turn behaviour is not the same as scanning in birds and mammals, and may actually be a response to a stimulus either seen or heard, rather than being used to detect a threat. This has also been found to be the case in other closely related scincid species. *Lampropholis guichenoti* (Torr and Shine, 1994) and *Egernia saxatilis* (D. O'Connor, pers comm).

Lizards in groups which close their eyes more, may head turn more as a result of being startled from their less vigilant state. Eyes open before and after head turning was not specifically investigated.

7.7 Collective detection.

7.7.1 Methods

This experiment was designed to test if lizards respond differently to a potential threat when they were in a group compared to when they were alone. Unrelated lizards aged 2-4 years (juveniles and sub adults) were housed outside in groups of three individuals for at least two weeks before the experiment began. To try to account for variation between lizards, trials were run on one focal lizard per group. Focal animals were selected randomly, (numbers picked from a hat) and were each filmed twice, once when alone and once when living in a group (Random blocks design, Zar, 1996). The order of these two treatments was randomised within groups to avoid any effect of habituation. Six individuals were filmed in six different groups. No animal was used in more than one group, even those that were not focal animals. Lizards were individually paint-marked with a water-soluble, non-toxic commercial model paint for easy identification (see Chapter 2).

Lizards were transferred from the main holding enclosures either alone or with their group, to a pen with galvanised steel sides (1.75m x 1.78m x 0.5m) (Figure 7-35) in a separate enclosure to the main lizard holding pens. This was more than 100 metres from any other lizards to prevent those not involved in the current trial being exposed to the stimulus. Within this pen, rocks were arranged in a pile, approximating a natural habitat for the lizards (approximate dimensions 0.95m x 0.70m x 0.40m).

Figure 7-35 Overhead view of the pen where the collective detection experiment was conducted. One rock pile in the middle was used to simulate natural scree habitat. Lizards basked on the flattest rocks on the top of the pile.

Chicken wire was placed over the top of the pen in the period between trials to prevent predation or harassment from birds. Lizards were left for 7-10 days to acclimatise to the new pen. Trials were commenced between 1000-1100hrs on sunny days when the expected maximum temperature was betweeen 22 -34°C between 19th February, 1999 – 23rd April 1999 and then again from 11th November, 1999 – 19th April, 2000.

An overhead camera was mounted on a stand 2.3m above the middle of the rock pile (Figure 7-36). The camera was connected to a TV monitor which was 7 m from the pen, in a covered area (a hide). This monitor was used to view the lizards without disturbing them. A trial was started when the focal lizard (and the rest of the group in the case of the group treatment) had emerged and been still for at least one minute.

A tape measure was laid out in a straight line from the pen, with a marker at 5 m from the pen, before the lizards emerged for their morning basking session. The observer (myself) walked from the 5 m mark toward the pen, in a straight line along the tape measure. Walking speed was kept constant, approximately 1m/sec. As soon as the lizard responded to my approach by moving, the approach distance was recorded (distance between observer and the lizard when the lizard chose to flee) (Bulova, 1994). The flight distance (distance between the lizard and a crevice was not measured) but was negligible, as all trials were conducted when the lizard was basking on the rock pile, usually only centimetres from an appropriate refuge.

“Out” of the crevice, was defined as when the lizard was fully emerged from the crevice (hind legs were visible and exposed) and therefore potentially vulnerable to predation. The lizards in the trials always basked on the rock outcrop, and usually on one of the higher rocks. Variability due to different visibilities from different sides of the rock pile was reduced by only conducting the trial when the focal lizard was basking on the side of the rock closest to the side that the approach would be made from (this was the northern side which received the sun first, so was usually the side the lizards basked on anyway).

Figure 7-36 Side view of collective detection pen set up, showing frame where video camera was attached to give an overhead view of the pen.

Once all the equipment had been set up, the lizards were left for 15-30 mins to allow them to resume basking (or begin, if they had not yet emerged for the day). The hide was approached from the opposite direction to where the lizard pen was, so that the lizards were not disturbed.

After each successful trial, the lizards were removed from the pen and the rocks were washed with water to remove any chemical traces from scats or secretions for the next trial. Lizards had been kept in the group used in the trial for at least 4 weeks before commencement of the experiment. They were allowed 10-21 days between treatments to become used to either being alone after having lived in a group, or returning to the group after solitary filming. Times between filming varied, due to the recording of other experiments and the unpredictability of the weather.

Body temperature has been implicated in the response of lizards to a potential predator (Hertz *et al.*, 1982: Hallel and Boskilla, 1997) and so body temperature of the focal lizard was measured by inserting a thermocouple into the lizard's cloaca, immediately after the conclusion of a successful trial

An additional measure to minimise extraneous variation was to keep the observer the same (myself), during all trials and ensure that the shirt the observer wore was also always the same (kept specifically for the purpose). This procedure followed similar precautions as those taken by Burger and Gochfeld, (1993) to reduce extraneous variation in approach distance.

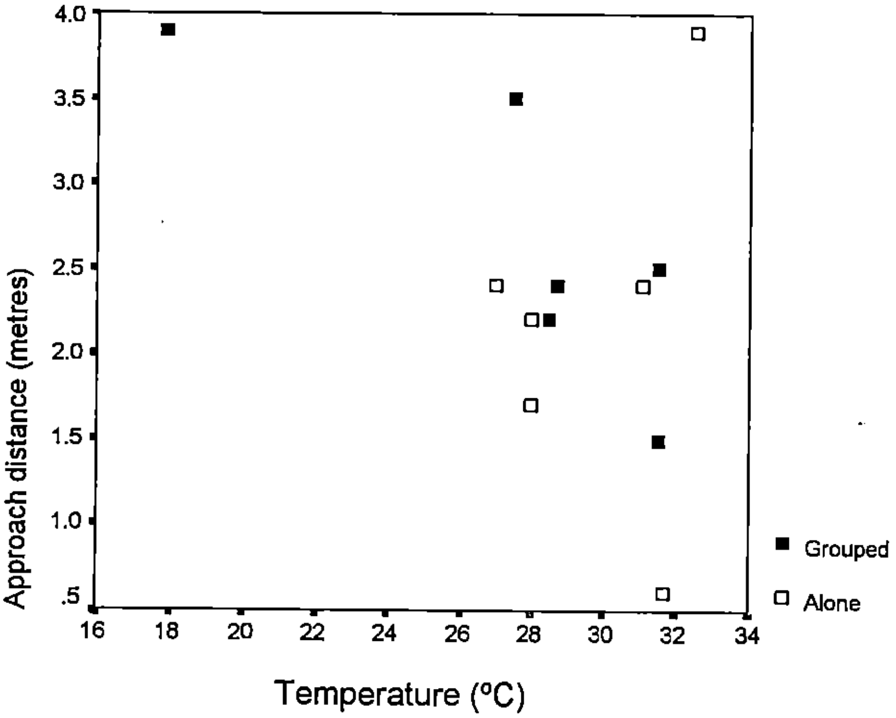
7.7.2 Results – collective detection.

7.7.2.1 Body temperature and approach distance.

Body temperature of the focal lizards did not vary significantly between treatments (Related samples t-test, t = 0.47, p = 0.66) (Figure 7-37). Approach distance was not correlated with lizard body temperature

(Pearsons correlation coefficient = -0.423, p = 0.17) (Figure 7-37).

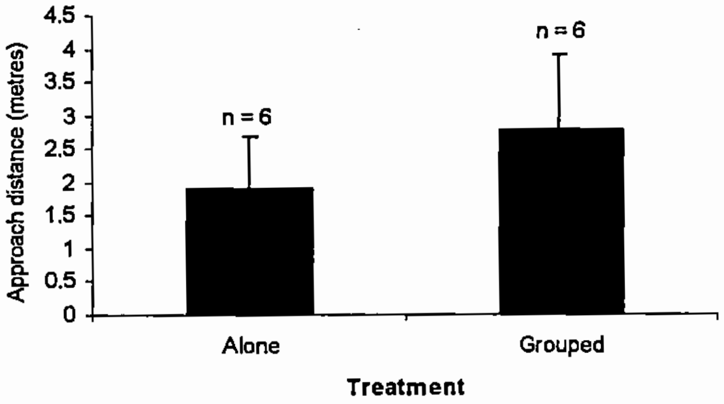
Figure 7-37 Relationship between approach distance and temperature for collective detection experiment (Pearsons correlation coefficient= -0.423, p= 0.17)



7.7.2.2 Effect of grouping on approach distance

The approach distance for focal animals living alone was significantly shorter than when those same animals were in a group (Figure 7-38).

Figure 7-38 Mean approach distance for focal lizards when they were alone and in a group (paired samples t-test: t = 2.71, p= 0.04*)



7.7.3 Summary and discussion of collective detection experiment.

Approach distance was significantly greater when a focal animal was in a group, compared to when it was alone.

This suggests that when lizards are in a group, they react earlier to a potential threat, presumably because they are alerted sooner, possibly by the response of others in the group. This kind of group response has been reported in other species of lizards such as the Armadillo Lizard, (*Cordylus cataphractus*), groups of which have been seen retreating in unison at the first sign of danger. Even when groups are separated by some distance, all lizards respond instantaneously (Mouton *et al.,* 1999). These observations suggest some form of collective detection in this species also.

The result of this experiment supports anecdotal evidence that *E. stokesii* does benefit from collective detection when basking in a group. Field observations of lizards quickly retreating as soon as one individual does (Duffield, pers. comm), suggests similar behaviour occurs as that reported by Mouton *et al.*, (1999) for *C. cataphractus*. *E. stokesiis*' closest relative, *Egernia cunninghami* also retreats when lizards that are basking around it do (D. O'Connor pers comm), but *Egernia saxatilis* which is found in many of the same areas as *E. cunninghami* does not. Individuals whose basking companion flees appears to become more alert by raising it head (still suggesting collective detection), but they do not generally flee to a refuge immediately, in the same way that *E. stokesii and E. cunninghami* do (D. O'Connor pers comm).

Several authors (eg Burger and Gochfeld, 1993; Hallel and Boskilla 1997) have identified other factors that may affect approach distance in lizards. These include flight distance, habituation and ambient temperature. In this experiment, attempts were made to control for flight distance by using one centrally located rock pile that served as shelter and as a basking surface. Lizards were never more than a few centimetres away from a suitable crevice when basking on this pile. This meant flight distance was negligible in all trials. This reduced or negated this as a possible factor in the analysis.

Habituation from the stimulus could also affect results so the order of the filming was randomised so some lizards were filmed alone first, then in a group and others were filmed the other way around. This should reduce the chance that variability between the treatments is only a result of a lizard becoming less sensitive to the stimulus. Each focal lizard was only exposed to the stimulus twice, once for each treatment, while lizards used in the group treatments were exposed only once.

Temperature is always a significant factor in any behavioural experiment, especially with ectothermic animals. Blamires (1998) found a positive relationship between ambient temperature and approach distance in *Lophognathus temporalis*. Rand (1964) found the same trend among populations of *Anolis lineatopus*. However when body temperature and approach distance were measured by Martin and Lopez (1995a) in *Psammodromus algirus*, they found no correlation between the two variables. Whitaker *et al.*, (2000) also found that defensive behaviour was not correlated with body temperature in brown snakes (*Pseudonaja textilis*), when tested at similar temperatures to those used in this experiment.

The apparent discrepancy in the results reported in these papers could occur because ambient temperature is not always correlated with body temperature in reptiles or that the response to ambient temperature varies between species. The correlation between ambient temperature and body temperature could change, depending on the time of day that it is measured. If the reptile has been out basking for a significant amount of time, then body temperature is likely to approach or exceed ambient. If the animal has only just emerged from its refuge. The fact that ambient temperature is not always a good indicator of body temperature in reptiles was why body temperature of each focal lizard was measured immediately after a successful trial.

In this experiment, variability due to temperature was reduced in two ways. Firstly, only sunny days where the expected maximum temperature was 22-34°C were used in the analysis and then body temperature was recorded from the focal animal after each successful trial. This experiment showed that body temperature did not influence approach distance , but this does not suggest this is necessarily the case when all possible environmental temperatures are assayed, since this experiment was conducted on days deliberately selected so that body temperature, and therefore activity (Hertz *et al.*, 1982) were likely to be close to optimal.

Habitat structure has also been shown to influence the escape responses of lizards (Martin and Lopez, 1995a). To account for this, the rock pile was built in such a way that there was only a few flat rocks at the top that served as good basking sites, so the field of view for any lizard out basking was very similar, thus reducing possible error caused by differences in ability to see the threat over physical obstacles..

Perception of threats may not always be detected by the visual system of a lizard, especially in skinks that have highly developed chemosenses (Schwenk, 1995). However, in these trials, a lizard was never observed tongue flicking immediately before an approach by the observer. Chemoreception may be important to *E. stokesii* in detecting more cryptic predators such as brown snakes, *Pseudonaja textilis*, but would be of little use in detecting aerial predators. Sight and sound probably alerted them to the approach but this assumption was not specifically tested.

This experiment was designed to differentiate between the two hypotheses about why animals reduce their vigilance in a group. The dilution effect predicts that animals will reduce their vigilance not because they perceive that other group members are looking out for them, but only because the probability of being eaten is reduced in a group. The "many eyes hypothesis" is dependent on collective detection (Lima, 1995) and predicts that the reduced vigilance of individuals in a group occurs because animals can utilise other group members vigilance. When one animal detects danger, other group members' respond. Showing that a lizard in a group responds sooner to a threat suggests that *E. stokesii* is forming groups to increase the likelihood of predator detection, not just as a way of reducing the chance of predation.

7.8 General discussion

Enhanced vigilance to predators has been shown to be a significant factor in the formation of groups in mammals, birds and fish (Krebs and Davies, 1993). However, the level of sociality required for animals to exhibit group vigilance has not been shown in any lizard species to date, although several species show year round group fidelity which may in have an antipredator function (eg. *Cordylus cataphractus*, Mouton *et al.*, 1999; *Sceloporus mucronatus mucronatus*, Lemos-Espinal *et al.*, 1997).

Previous observations of collective fleeing of all the members of a group at the response of just one lizard had suggested that *E. stokesii* may use grouping as an antipredator strategy. This chapter describes three different techniques that were designed to experimentally examine the effect of grouping behaviour on one aspect of predator avoidance, vigilance behaviour, comparing the behaviour of lizards living solitarily to those in groups of different sizes.

In all three experiments, differences in behaviour between lizards living alone and grouped were found. In 1996/97, when differences between age classes were tested, there was also a difference in vigilance behaviour between adults and juveniles, particularly in the way they responded to being alone or in a group.

Differences between adults and juveniles in antipredator (Greene, 1988) and thermoregulatory behaviour (Diaz, 1994) as well as phenotypic characteristics (Schmidt, 1997) have been documented in other lizard species. Juveniles of the lizard *Psammodromus algirus* appeared to be less wary and allowed closer approach before fleeing than adults (Martin and Lopez, 1995b). Stamps (1983b) found that juvenile *Anolis aeneus* actively avoided shady areas, which they then prefer as adults. This behaviour is thought to represent a predator avoidance strategy since adult *Anolis richardi* prey upon juvenile *A. aeneus*, but do not generally take adults. *A. richardi* lives mostly in shaded areas surrounding clearings.

Van Damme *et al.*, (1995) found that although juvenile *Lacerta vivipara* exhibited the same stereotyped behaviour to chemical cues from predatory snakes as adults, they basked at least 12 times less in areas with the chemical cues than in control areas, whereas adults showed no difference in the amount of time spent basking between treatments. This suggests that juvenile *L. vivipara* may be more wary than adults.

These studies not only show that ontogenetic shifts in behaviour occur in a diverse range of lizard species, they also illustrate the influence that predation pressure can have on the activity and behaviour of juvenile lizards. Reduced activity in juvenile *E. stokesii* living alone could limit foraging and thermoregulatory opportunities which may result in slower growth and therefore a longer time to first reproduction.

Adult emergence behaviour was more thoroughly investigated when the adult data from the 1996/97 season was combined with all the data from 1999/2000. No significant differences in total time out were found in these data. However, adults and sub adults from both years emerged more times during a session when in a group than when alone, although total time out was not significantly different. Lizards in group sizes of three and four came out the most number of times in a three hr filming. One possible explanation for this difference is that lizards are reacting to cues from other group members. This social transmission of information could warn group members of possible threats or may be a way of securing group coherence, especially in densely populated areas where other group members are likely to be encountered. *E. stokesii* have distinct home ranges, but are not often overtly aggressive or territorial (Chapter 1 and Chapter 3). They may rely on frequent social interactions to recognise and maintain group structure.

Huey and Slatkin (1976) suggested that predation may affect thermoregulatory behaviour. They argue that shuttling behaviour may reduce risk in a high risk predation area. If living in a group reduces predation risk, then solitary lizards should shuttle more often than those in a group. In this experiment, the opposite result was found. Predator avoidance strategies are often species specific and could depend on the tactics of the main predators of the species in question. For instance, frequent movement (associated with shuttling) might draw attention to a lizard from an aerial predator (such as those in the *Falco* genus that have been observed taking adult *E. stokesii)* and make it more prone to predation than if it remained in the one spot for longer periods.

Social interactions may stimulate lizards to move around more which may include movement in and out of the crevice. Amount of time moving or distance moved was not tested during this experiment. However, increased shuttling between open areas and crevices may represent a response by group members to perceived predators. If a solitary lizard responds to a perceived predator once or twice during a basking session by retreating to its crevice, a lizard in a group may respond the same number of times plus it may also respond to separate events initiated by other members of the group, meaning its retreats will double or triple. This would only be true if *E. stokesii* exhibited collective detection, which was the subject of the third experiment in this chapter.

Increased probability of avoiding predation is only one possible benefit of group living. Individuals in a group may be able to trade vigilance behaviour with other activities if other animals can watch out for them (Pulliam, 1973). Both adult and juvenile *E. stokesii* spent significantly more time with their eye(s) closed than lizards living by themselves, but the collective eyes open per minute did not differ to the average for lizards living alone.

So, why would a lizard want to close its eye(s) while basking anyway? In experiments on Gulls, Ball *et al.*, (1996) found that they chose to close the eye facing into the sun more often than the other eye when engaging in asynchronous eye closure but there was no difference in which eye (the left or right) the gulls closed. There was also no effect of wind on which eye was closed, suggesting that there may be a benefit in limiting direct sunlight exposure to the eye (Ball *et al.*, 1996). Further work on the physiological reasons for eye closure in lizards would be valuable.

Previous work on small heliothermic reptiles has found that they close their eyes only briefly during basking sessions. Kavanau (1997) suggests that these short bouts of eye closure during basking are used to inhibit water loss. However, in the same article he maintains that eye closure is associated with sleep in most vertebrates and that primitive sleep has been observed in many species of lizards in captivity. *E. stokesii* is found in arid to semi-arid environments where they rarely drink from pools of water, getting their moisture from their food and from infrequent rain showers, where they lick the water from the substrate (pers. obs). Moisture loss may be a problem in such an environment. Basking in direct sunlight, where humidity is low and evapotranspiration is high, moisture loss from the eyes could be a significant cost of heliothermic thermoregulation (Heatwole and Taylor, 1987). Asynchronous eye closure represents a compromise between deriving some benefits from sleep or water loss prevention and remaining aware of possible threats.

The 1999/2000 experiment was designed to investigate further if individuals in groups of different sizes are less vigilant than lizards living alone. Lizards in groups of six had their eyes open more than those in other group sizes, but not as much as those living alone. This trend was evident in the emergence data as well, with mean values for the group of six more closely resembling values for lizards living alone in both number of times emerged and emergence time.

This suggests an advantage for small groups that is lost with further increases in group size. There may be an optimal group size, perhaps the pen size, or the resources (suitable basking sites etc) may have been limiting. In order to function effectively, larger groups may need more basking sites and crevices. Although group sizes of up to 17 have been recorded in the field, only a proportion of the whole group basks at any one time (G. Duffield pers. comm). It may be that a large group is a distraction to basking lizards, causing them to remain more vigilant than they might be in a smaller group.

In order to be able to reduce their individual vigilance in a group situation without compromising their safety, lizards must be able to detect and respond to the flight response of another group member. This was tested in the third experiment on collective detection in *E. stokesii*. Approach distance was significantly longer when a lizard was in a group as opposed to when it was alone, suggesting that when in a group, a lizard is alerted and responds sooner to a potential threat than when alone.

This experiment was designed to differentiate between two hypotheses about why animals reduce their vigilance in a group. The dilution effect predicts that animals will reduce their vigilance not because they perceive that other group members are looking out for them, but only because the probability of being eaten is reduced in a group. The collective detection hypothesis predicts that the reduced vigilance of individuals is because they are taking advantage of other group members' vigilance.

The previous experiment showed that lizards in groups close their eyes more, suggesting reduced vigilance. It also hinted that lizards may be able to monitor the vigilance of group members since total group vigilance did not decline, but this was not directly tested and could have occurred by chance. The third experiment tested this directly. If dilution was the primary reason for reduced vigilance then approach distance should not have been increased in a group. In fact, it would be expected to decrease, since if animals perceived that their risk of being eaten was reduced in a group, then they would be expected to allow a potential threat to get closer.

This was not the case in *E. stokesii*. Lizards in a group took flight earlier than when alone, suggesting that they gain predator detection advantages from the other lizards, and thus providing evidence for collective detection as the reason for their reduced vigilance in a group.

Future experiments could examine eye closure in a larger group in the field, where predation is possible. Animals in these experiments had no real predators, although they still appeared to respond to perceived threats in a similar way to animals in the field. *E. stokesii* becomes tame in aquariums and inside enclosures where they are fed and have their cages cleaned out regularly. However, once put in outside pens, with more lizards and where feeding occurs irregularly (see Chapter 2), animals reverted quickly to being shy and easily startled. This change in behaviour may be explained by the tendency in other lizard species to alter their antipredator behaviour based on the perception of the intensity of predation pressure (eg Blazquez *et al.*, 1997).

The results of these three experiments suggest an antipredator advantage in group-living for *E. stokesii*, especially juveniles which have higher mortality (Duffield and Bull, 2001) and thus more incentive to reduce their likelihood of predation. The fact that lizards respond to the presence of conspecifics by altering both their activity and antipredator behaviour shows a level of sociality that has, to my knowledge, not been observed in any other species of reptile. This series of experiments provide strong evidence that grouping behaviour in *E. stokesii* increases the probability of predator avoidance and reduces the need for individual vigilance. This chapter and the previous one suggest that there are at least two benefits of group-living in this species, increased thermoregulation and improved predator detection.

Chapter 8

8 Group behaviour and dominance.

8.1 Introduction

Group formation confers antipredator (Chapter 7) and thermal (Chapter 6) advantages, but it may impact on the behaviour of individuals, especially if grouping causes the formation of a hierarchical social structure, where dominant individuals place limits on the behaviour of subordinates. Subordinate individuals can have limited access to food, shelter or mating opportunities. For instance, subordinates within a population of Willow Tits (*Parus montanus*) are relegated to exposed areas of habitat, where they must spend more time vigilant to predators than their more dominant conspecifics (Ekman, 1987).

Subordinate females in many primate social groups have a lower reproductive rate than more dominant females within the group (reviewed in Chalmers, 1979). Subordinates among flocks of the Coal Tit (*Parus ater*) suffer interference competition from dominants (Barbosa *et al.*, 2000). To compensate for this, small subordinates engage in more hanging behaviour when conspecifics are around, compared to when they forage solitarily. Heavier subordinates that rarely use hanging behaviour to forage, appear to be at a disadvantage when dominant birds are around (Barbosa *et al.*, 2000).

Hierarchical social systems form in territorial species when density increases, either in captivity or as a result of limited dispersal in the field (Brattstrom, 1974). Many skink species occur in high densities, making them candidates for the formation of hierarchies (Torr and Shine, 1996).

In previous studies of such systems in lizards, hierarchies have been related to size (and therefore, potentially, age), and can be established and maintained with aggressive displays or subtle behaviours such as order of entry into a nocturnal retreat (Brattstrom, 1974). Other measures of subordination could include reduced access to favourable basking sites and difficulty establishing a territory. Subordinate juvenile *Anolis aneus* overcome this problem by acquiring territory when they refuse to leave despite repeated attacks from dominant individuals (Stamps and Krishnan, 1995). Subordinates acquired more territory if the dominant animal in the area reduced the number of times it chased off the subordinate (Stamps and Krishnan, 1995).

Traditionally, staged encounters involving two individuals have been used to assess dominance in lizards, especially iguanid and agamid species (eg Johnston, 1997). The outcome of these fights have often been correlated with size. For example, Zucker and Murray, (1996) could predict the result of 80% of these encounters in the tree lizard, *Urosaurus ornatus* based on body mass. These trials have also been used to predict mating success in polygynous systems (eg Olsson, 1994b).

In this study, one on one trials to determine dominant-subordinate relationships were not conducted, but rather dominance was deduced from behavioural interactions in groups that had been established for some time. This is more difficult to determine, but may represent a more realistic picture of the relationships among all members of the group.

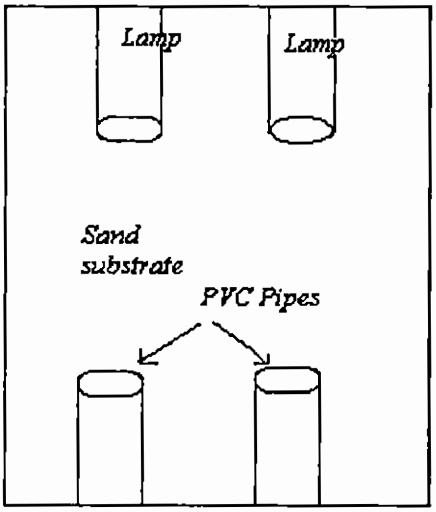
The aim of this investigation was to determine the effect of grouping on individual behaviour and to determine if there were any patterns of dominance within groups.

8.2 Methods

Six groups each of three unrelated juveniles (approximately 18 months old) were housed in 72cm x 69cm x 42cm indoor pits. Pit temperature was maintained at 18-20 °C. Windows above the pits allowed external light, providing a natural light/dark pattern. Two 40 watt globes were placed overhead in each pit. The temperature under each lamp ranged from 28-32°C. The lamps were on an automatic timer that came on for 8 hours, between 8am & 4pm each day (after natural sunrise, and before natural sunset at the time of the experiment).

There were four shelters in each pit, two under the lamps and two directly opposite the lamps (Figure 8-1). These shelters were made from 15cm long white cylindrical PVC pipe with a diameter of 5cm, smoothed at each end to prevent lizards hurting themselves on any sharp edges left over from cutting the pipe.

Figure 8-1 Diagram of pit setup.



Six groups of 18 sub adult lizards of both sexes were allowed two weeks to become familiar with each other in other similar holding pits away from the experimental area. For observations each lizard was moved to the experimental pit, either alone or with its group members, and its activity was recorded by video tape filming. Each lizard was then moved into one of the experimental pits and was filmed twice, once in its group and once alone. Thus there were 24 filming sessions, four sessions for each of the six groups. The order of filming was randomised. Lizards were allowed ten days to become familiar with either being alone or with their group in the experimental pit before filming commenced. Lizards were replaced with their group in the holding pens in between filming sessions. Experiments were conducted from 9th July, 1999 – 29th October, 1999.

Initially, filming began between 12-1230hrs and continued for 24 hours in four pilot studies. In the first few filmings, lizards seldom moved from their overnight refuge from 6pm until 8am the next morning, when the lamps came back on. Filming was then cut back to 6 hours for the twenty four experimental sessions, between 12pm–6pm. Detailed behavioural data were taken from the first three hours of filming from 12pm – 3pm. Activity at this time was unlikely to be influenced by changes in day length over the course of the study. Lizards were initially disturbed to set up the camera and to place feed bowls in their pits. Data recording commenced approximately 5 minutes after filming began. Lizards quickly resumed normal patterns of behaviour only minutes after being left undisturbed. They were left alone until after each filming was completed.

Filming of pits occurred three times per week, on Monday, Wednesday and Friday with two cameras filming at the same time, so that all six pits could be filmed in one week. Filming took place over four weeks, with time in between each filming week for lizards to adjust to the new condition. Each pit received a feed bowl containing their normal feed mixture (see Chapter 2) and then, within two minutes, filming commenced. Lizards received seven grams of food each for both treatments. This was about half as much food as they would normally receive, although they are normally only fed twice a week. This feeding regime was designed to provide a slightly limited food supply and therefore added motivation for lizards to be among the first to feed, but not so that lizards would be starved. All lizards were weighed before the experiment commenced, and again after each treatment.

8.2.1 Dominance

Lizards were all the same age, although they varied considerably in size and body mass (Table 8-1). Ranking was determined using a scoring system based on several behaviours that may represent dominance (detailed in the results section). *E. stokesii* are not particularly aggressive (Chapter 1 and Chapter 3), so more subtle behaviours such as feeding order and amount of time spent basking on top of another lizard were used to assess rank within the group. The amount of time spent for each behaviour by each lizard was recorded and then analysed using statistical comparisons of the time spent in each behaviour when the lizard was alone, compared to when it was in a group.

Statistical analysis was performed on all data using parametric methods if possible, but non parametric methods were employed in many cases because independence of replicates could not be assumed when the data came from lizards in the same group.

Table 8-1 Snout vent length and mass for all lizards used in the experiment (measurements taken just before group treatment).

Lizard no.	Group no.	SVL (mm)	Mass (grams)
114	1	160	141.3
147	1	150	101.1
274	1	165	153.6
708	2	170	179
6	2	170	164.2
14	2	165	181.3
712	3	165	168.2
41	3	130	86.6
703	3	170	182.7
477	4	135	70.2
1004	4	145	101.9
427	4	120	51
17	5	155	137.1
47	5	140	132.2
76	5	155	121.6
560	6	140	88.1
63	6	145	116.3
74	6	130	58.4

8.3 Results

8.3.1 Comparison of behaviour when grouped and alone.

Each lizard had the following behaviours recorded for it from the video playback:-

Basking – lying still under the lamp(s). This was different to the "still" record, as they had to be under a lamp to be considered basking.
Moving – lizards moved at three distinct speeds: a slow, exploring gait, often associated with tongue-flicking, a medium gait, and a fast gait, often associated with escape behaviour such as climbing the walls or while being chased by another lizard.
Still – lying motionless, but not under a lamp or in the food bowl
Eating – lizard was inside the food bowl, eating the food provided
In food bowl – lizard just lying in the food bowl, without eating. This may have been of interest to the lizards because it was a novel object, or perhaps due to the smell of food, may have had an attractive odour to the lizards.
In refuge – lizard was lying still inside one of the cylindrical PVC pipes.
Other - this included all other behaviours not listed, and usually made up less than 1 % of the time. Some of the other behaviours included digging, scatting, chasing, pushing and lunging, tail lashing and waggling and body waggling – see Chapter 3 for a full description of these behaviours.

Each lizard had all behaviours in a three hr period recorded for it when it was alone, and then for another three hrs in a group (or vice versa, if the order was reversed). Analysis was done using paired Wilcoxon signed rank tests, with data from alone and each lizard in a group as the paired factor.

Data were used for individual lizards, means were not taken for lizards in a group, although it could be argued that lizards in the same pit for the group treatment are not necessarily independent subjects, and perhaps the mean values should be used in the analysis.

There were several reasons why this was not done. Firstly, the usual argument for taking the mean of a group such as this in the field or in outside semi-natural pens, is because the weather or some other environmental factor could have affected those three lizards in the group differently to other groups and so might bias the results. (This type of analysis was done for some previous experiments). This experiment was conducted inside, with maximum light, under the same temperature conditions and all pits had the same physical environment. This reduced or eliminated variability in conditions for each trial.

Secondly, the statistical power of a paired design is in taking into account individual variation in lizard behaviour. By taking the mean of the group, this power is reduced. Non parametric methods were used, since there is no assumption of independence inherent in their application.

Finally, one of the objectives of this analysis was to look at differences among lizards within groups to see if there was any kind of hierarchical structure, and if there was, if subordinate lizards behaved differently. By taking the mean of the group as a whole, these differences would effectively be diluted.

Table 8-2 summarises the mean values for each behaviour of the percent time taken in each lizard when it was alone and when in a group. All lizards, regardless of if they were alone or grouped spent the majority of their time basking. When lizards were by themselves, they spent significantly more time basking than when in a group. When lizards were in groups they spent more time in a refuge than when they were alone. There were no other differences in the percentage of time lizards were engaged in any of the other behaviours observed.

Table 8-2 Summary of mean percentage of time for all observed behaviours comparing lizards when they were alone and when in a group (Analysed using Wilcoxon Signed Ranks test for related samples) (*denotes significance at the 5% level) (S.E.M denotes Standard Error or the Mean).

Behaviour	Mean for alone	S.E.M	Mean for when in a group	S.E.M	Z statistic	P value
Basking	62.7	3.1	44.7	5.7	2.85	0.00*
In refuge	5.1	1.9	23.4	6.4	2.39	0.02*
Moving	7.7	0.9	8.0	1.5	0.20	0.85
In food bowl	6.0	1.1	5.4	1.8	0.85	0.40
Still	12.4	1.5	11.9	2.0	0.20	0.85
Eating	1.1	0.3	0.9	0.2	0.62	0.54
Wall climbing	4.9	1.1	4.8	1.6	0.81	0.42
Other	0.2	0.04	0.2	0.1	0.25	0.81

8.3.1.1 Active and passive behaviours.

The eight behaviours observed in the previous section were grouped according to whether they were considered "active" or "passive" behaviours. Active behaviours were considered to be: wall climbing, moving, eating and other. Basking, still, time in food bowl and time in refuge were considered to be passive. No differences were found between percentage of time in either active or passive behaviours when lizards were alone or grouped (Table 8-2).

Table 8-3 Summary of statistics for percentage of time lizards spent engaged in either active and passive behaviours alone and when in a group.

	Mean for alone	S.E.M	Mean for in a group	S.E.M	Z statistic	P value
Active behaviours	13.84	1.39	13.87	2.28	0.02	0.98
Passive behaviours	86.21	1.39	85.44	2.19	0.37	0.71

8.3.2 Effect of dominance

The following behaviours and attributes were used to assess dominance among groups of *E. stokesii* in this experiment:

The proportion of group basking time that lizard spent basking on top. For each lizard, the proportion of "piggyback basking" (see Chapter 3), time when the lizard was under another and the time it was on top was determined. This behaviour is commonly seen both in field and captive populations. It was assumed that there is an advantage to the lizard on top of the pile, since it is generally this lizard that initiates the behaviour and stands to gain by getting closer to the heat source as well as deriving warmth from the lizard underneath (see Chapter 3).

The second determinant of rank was the difference in the proportion of total time in the alone and group treatment when the lizard was feeding. Any change in the time feeding in the group may result from some status related behaviours of the group. A lizard that spent more time feeding when alone was assumed to have curtailed its feeding behaviour in the group treatment. Since feeding occurred on the same day of the week every week, and the lizards were given the same amount of food per lizard every time, the assumption that their feeding requirements and therefore time spent feeding should be the same for both treatments was made. If a lizard spent less time feeding when in a group, it was assumed it was reducing this behaviour as a result of interactions with one or other of the other lizards. For example, one lizard may spend less time feeding if another has monopolised the food and prevented that lizard from feeding.

The feeding order of the group during filming was also incorporated into the analysis of dominance and in the case when one lizard chased another, the chaser and lizard being chased was used as a measure of dominance as well.

From the above behavioural observations, a ranking was assigned to each lizard in each of the six groups, by means of assigning a score to each behaviour, in the following way.

Percentage of time on top of another lizard:-

0-30%	0 points
31-60%	½ point
61-100%	1 point

Change in percentage of feeding time from alone to grouped treatment

Feeding time increased in a group	1 point
Feeding time remained the same	½ point
Feeding time decreased	0 points

Feeding order:

Fed first	1 point
Fed second	½ point
Fed third	0 points

If chasing occurred:

Chaser	1 point
Not involved	½ point
Chased	0 points

Table 8-4 shows the values observed for each lizard of these behaviours for each of the lizards in the experiment. It also shows the ranking of each lizard within a group, as determined by the scoring system above. Those lizards ranked as "3" generally fed last, spent more time underneath another lizards and spent less time feeding when they were in a group compared to when they were alone.

Table 8-4 Summary of data collected for ascertaining the rank of an individual within a group (only one group displayed any overt aggressive behaviour. The lizard marked with an * was chased several times during the analysis period by the one marked with a +)

Lizard	Group	SVL (mm)	Mass (gms)	Time in secs (out of 3 hrs) lizards involved in group basking	Percent of group basking time on top of another lizard	Time (secs) feeding when alone	Time (secs) feeding when in a group	Percent change in feeding time between alone and group treatment	Feeding order in the group	Score	Rank
114	1	160	141.3	300	54.7	184	0	-100	3.00	0.5	3
147	1	150	101.1	301	62.1	140	97	-44.33	1.00	2.5	1
274	1	165	153.6	254	65.0	108	86	-25.58	2.00	2	2
708	2	170	179	299	0	86	184	53.26	1.00	3	2+
6	2	170	164.2	30	0	65	0	-100	3.00	0	3 *
14	2	165	181.3	349	91.4	0	54	100	2.00	3.5	1
712	3	165	168.2	565	0	22	162	86.42	2.00	2.5	2
41	3	130	86.6	154	73.4	119	76	-56.58	3.00	1	3
703	3	170	182.7	548	71.9	65	86	24.42	1.00	2.5	1
477	4	135	70.2	1807	0	130	194	32.99	1.00	3	1
1004	4	145	101.9	-	-	130	324	59.88	3.00	2	3
427	4	120	51	1807	100	173	119	-45.38	2.00	2	2

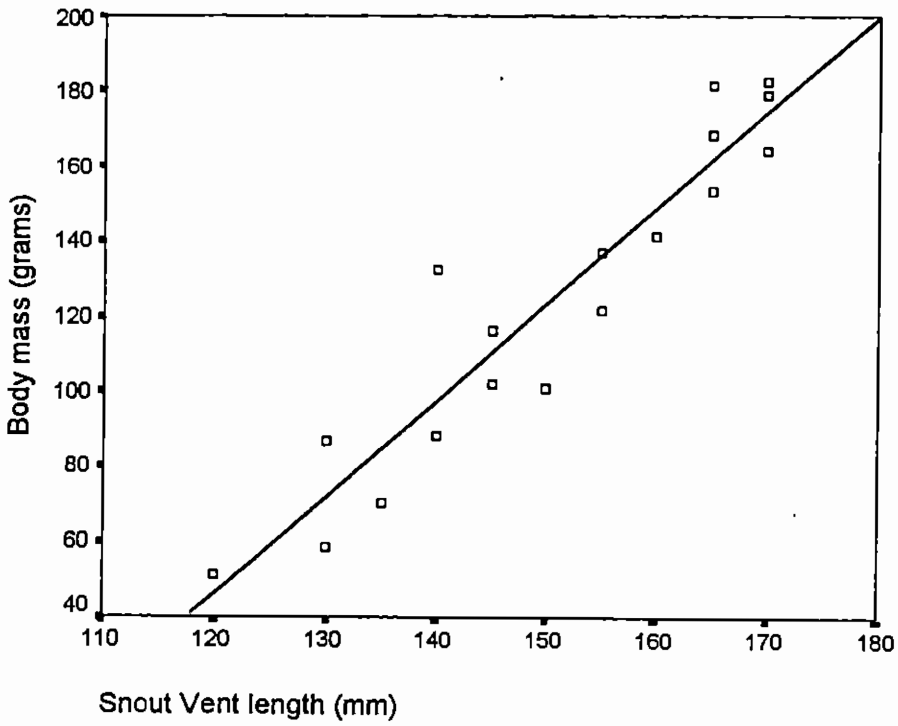
Table 8.4 continued....

Lizard	Group	SVL (mm)	Mass (gms)	Time in secs (out of 3 hrs) lizards involved in group basking	Percent of group basking time on top of another lizard	Time (secs) feeding when alone	Time (secs) feeding when in a group	Percent change in feeding time between alone and group treatment	Feeding order in the group	Score	Rank
17	5	155	137.1	55	0	11	11	0	2.00	1.5	3
47	5	140	132.2	140	0	54	54	0	3.00	2	2
76	5	155	121.6	195	100	22	43	48.84	1.00	4	1
560	6	140	88.1	344	31.7	248	22	-1027.27	3.00	0.5	3
63	6	145	116.3	343	58.6	486	86	-465.12	2.00	1	2
74	6	130	58.4	242	31.7	173	54	-220.37	1.00	1.5	1

8.3.2.1 Index of body condition

As well as comparing the SVL and mass of lizards with different rankings, an index of body condition, termed a condition index (CI), was estimated using a similar method as that used in Chapter 4. This time, however, the mass and SVL were linearly related to each other without the need to transform to meet the assumptions of regression.

Figure 8-2 Body mass versus snout vent length for determining Condition Index. Measurements are those taken just before the group treatment ($F_{1,16}$=127.25, p=0.00, R^2=0.89)



The CI did not vary among rankings ($F_{2,15}$=1.64, p = 0.23) and there were no differences among rankings in either SVL ($F_{2,15}$=0.16, p =0.86) or Body Mass ($F_{2,15}$=0.24, p =0.79).

Determining the most dominant and second most dominant lizards in four out of the six groups was difficult, sometimes two lizards had very similar values for all criteria, sometimes only separated by half a point in the scoring system. However, in three out of the six cases (Table 8-4), there was a definite “subordinate”, one that had the lowest values for all variables, ie one that fed last, spent little group time basking on top and reduced its feeding when in a group. In the case where there was a tie between two lizards with the lowest score, the subordinate was determined to be the one that fed last.

The following analyses compare only these subordinates to both the other lizards, not differentiating between ranks "1" and "2".

8.3.3 Dominance and behaviour.

8.3.3.1 Refuging behaviour.

A Repeated Measures Analysis of Variance (RMANOVA) was performed for each behavioural parameter, with treatment (alone or group) as the Within Subjects Factor and rank (subordinate versus dominant) as the Between Subjects Factor.

There was a significant effect of rank – subordinates spent 30% more time in a refuge than dominants did. There was also a significant effect of treatment –lizards in groups spent more time in refuges (as reported earlier). There was also a significant interaction effect showing increased use of refuges by subordinates in groups, while dominants showed little change between alone and group treatments(Table 8-5 : Figure 8-3).

When the data for subordinate lizards were removed from the previous analysis of time spent in refuge for lizards when they were alone and in a group (section 8.3.1), there was no difference in the proportion of time lizards spent in a refuge when they were alone and in a group (Table 8-5). This suggests that it is this difference in behaviour of the subordinates when alone and in a group that is the main cause of the difference between the alone and grouped treatments when all the lizards were analysed together.

Figure 8-3 Proportion of time spent in a refuge for "subordinate" lizards, compared to "dominant" lizards (see text for definitions).

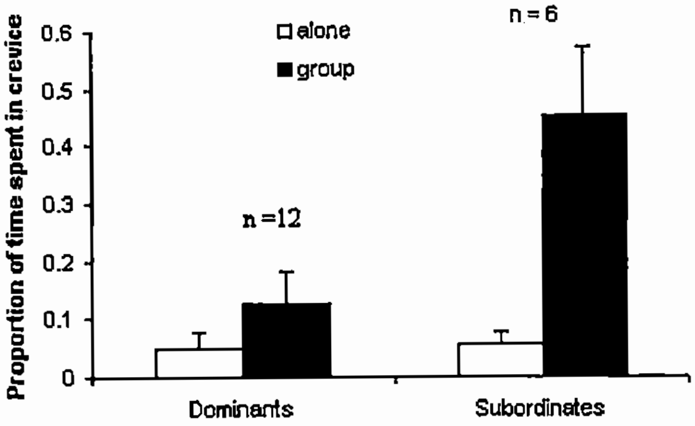


Table 8-5 Summary of results of proportion of time in refuge for subordinates and dominants in groups (*denotes significance at the 5% level).

Factors	Analysis	Statistic	df	P value
Rank (low rank vs others)	RMANOVA	7.58	1	0.01*
Treatment	RMANOVA	14.48	1	0.00*
Rank x Treatmt (alone/group)	RMANOVA	6.57	1	0.02*
Alone and Group treatments, excluding subordinates	Wilcoxon test for related samples	1.07	12	0.29

8.3.3.2 Basking behaviour.

If refuging behaviour differs between dominant and subordinate lizards, then basking behaviour may also differ. A Repeated Measures Analysis of Variance was also performed on the amount of time basking, with treatment (alone or group) as the Within Subjects Factor and rank (subordinate versus dominant) as the Between Subjects Factor.

There was a significant effect of rank. Subordinate lizards spent less time basking than dominants. There was also a significant effect of treatment. Lizards in groups spent less time basking (as reported earlier).A significant interaction effect was detected, showing less time spent basking by subordinates in groups, while dominants showed less change between alone and group treatments (Table 8-6: Figure 8-4).

When the data for subordinate lizards were removed from the previous analysis of time in refuge in section 8.3.1, there was no difference in the proportion of time lizards spent basking when they were alone and in a group (Table 8-6), suggesting that it is the difference in behaviour of the subordinates that created the difference between the alone and grouped treatments when all the lizards were analysed together.

Figure 8-4 Proportion of time spent basking for dominant and subordinate lizards alone and in groups.

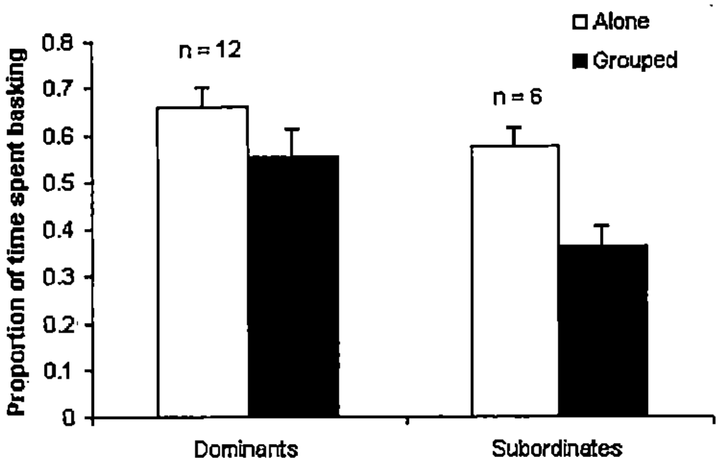


Table 8-6 Summary of results of proportion of time basking for subordinates in groups (*denotes significance at the 5% level).

Factors	Analysis	Statistic	df	P value
Rank	RMANOVA	10.03	1	0.01*
Treatment	RMANOVA	19.97	1	0.00*
Rank x Treatment (alone/group)	RMANOVA	5.67	1	0.03*
Alone and Group treatments, excluding subordinates	Wilcoxon test for related samples	1.65	12	0.10

8.3.3.3 Other behaviours

No other differences in behaviour were detected between subordinate and other lizards (Table 8-7).

Table 8-7 Summary of Repeated Measures ANOVA on other behaviours and rank.

Behaviour	Effect of Rank		Effect of Treatment		Rank x Treatment	
	F statistic	P value	F statistic	P value	F statistic	P value
Wall Climbing	1.87	0.19	0.20	0.66	2.79	0.11
Eating	0.00	0.99	0.98	0.34	0.26	0.62
Other	0.14	0.71	0.77	0.39	0.08	0.39
In food bowl	0.01	0.92	0.14	0.71	0.14	0.72
Still	0.00	0.97	0.27	0.61	1.14	0.30
Moving	0.03	0.88	0.06	0.80	2.71	0.12

8.4 Discussion

8.4.1 Behaviour when alone compared to when in a group.

Grouping altered both the amount of refuging and basking time of individuals, relative to how much time individuals spent involved in these behaviours when alone. Lizards in groups spent more time refuging than when they were alone. This was an unexpected result, since similar groups of sub adult lizards in semi-natural outdoor enclosures were found to spend more time out of their crevice than those that were in pens by themselves (Chapter 7).

There are several possible explanations for this result and the discrepancy between it and the experiment in Chapter 7. It could be that lizards are able to respond to variation in perceived predation levels. Although predators were not able to get into the outdoor enclosures used in the vigilance experiments in Chapter 7, the lizards would have been aware of birds such as Kookaburras (*Dacelo novaeguineae*) and Magpies (*Gymnorhina tibiticen*) flying overhead. Both brown and black snakes (*Pseudonaja textilis* and *Pseudechis porphyriacus*) have been found near these outdoor enclosures, and their smell might be perceptible to the lizards.

In this inside experiment, they could have perceived that predation risk was low and so social factors may have become more important. Also, basking opportunities were more limited in the inside pits because there were only two lamps to bask under on one side of the enclosure. In the outside pens, sunlight provided ample basking opportunities on any substrate in the pen. Subordinate lizards might have been denied access to the basking area in the inside pits by more dominant group members.

The design of the two experiments was different. This experiment was run as a paired design, with the same lizard used in both alone and group treatments. This was done to reduce the effect of individual variation (Zar, 1996). Also, the experiment was designed to test for differences in behaviour that might reflect dominance, most easily recognised by submissive behaviour towards a dominant lizard (Brattstrom, 1974). The difference in refuging behaviour between alone and group treatment disappeared when subordinate lizards were removed from the analysis, suggesting that most lizards in the group did not alter their behaviour, but only the lowest ranked group members spent more time in the crevice when they were in a group.

8.4.2 Dominants versus subordinates

These subordinates may be avoiding contact with other members of the group, or demonstrating their submission by remaining inactive in a refuge. Other species of lizard show subordination by a modified head bob (Stamps and Krishnan, 1994). *E. stokesii* shows little, if any stereotyped display behaviour, but may avoid contact with other group members to demonstrate submission or avoid conflict. In the one group where aggression was observed, the lizard being chased often fled to a refuge after being chased, and remained there for several minutes. The aggressor did not attempt to extract the lizard from the refuge, or to follow it in there. However, these chases were also associated with body waggling by the chaser, and could have represented attempts at courtship, rather than aggression (see Chapter 3).

E. stokesii have distinct home ranges, but are not territorial. The home ranges of group members overlap by an average of 45% in the Hawker population (Duffield and Bull, 2001). Lizards spend much of their time in contact or within close proximity of other group members. This may, at least temporarily, increase competition for food and prime sheltering and basking sites.

A hierarchical social system is likely to evolve under these conditions (Stamps, 1983; Torr and Shine, 1996). A primary objective of this chapter was to determine if hierarchies form among groups of juveniles and to establish the differences between dominant and subordinate behaviour.

Dominance relationships have been ascertained by researchers in a variety of ways. Many use the frequency and severity of aggressive acts to other group members as the main determinant of dominance (eg Chase, 1985). Others have used contests between pairs of animals and applied the outcome of those contests to the group as a whole (eg Iguchi, 1996).

In species that show low rates of aggression, such as *E. stokesii* (Chapter 3), these type of contests may not produce a clear winner and loser. Whittier and Martin (1992) in a study on the Australian skink, *Carlia rostralis* showed that this lizard responds poorly to one on one contests, with 60% having no outcome. Another confounding factor in these trials is that aggression is often mistaken for dominance, but it is not the same thing. In many species, the most aggressive group members may not have priority over limited resources, which is the ultimate benefit of establishing dominance (Francis, 1988). For example, dominants may exert authority by display or recognition by subordinates, and may not have to use aggression. Subordinates may attempt to improve their rank by aggressive behaviour, whereas dominant lizards have already proven their abilities, and do not need to be aggressive.

However, the use of other methods of establishing difference between dominants and subordinates within a group are more arbitrary, can be transitory and often do not show a linear relationship within a group (Bernstein and Gordon, 1980), (eg of a linear relationship, if A dominates B and B dominates C then A should dominate C, this is not the case in many group-living animals).

Juveniles and sub adults are generally not the most dominant animals in any group. However, they may need to dominate each other in order to gain food and access to other resources especially when those resources are limited. If adults obtain resources first, because of their size, then it may be particularly important for juveniles and sub adults to establish a hierarchy amongst themselves in order to receive access to remaining resources.

Reduced basking and activity time may represent a cost of group-living to subordinate lizards, but unequal distribution of costs within groups have been reported in other species. Dominant members of Vervet Monkey (*Cercopithecus aethiops*) troops, spend more time vigilant than subordinates and subordinate females spend more time moving than dominant females (Isbell and Young, 1993). Subordinate Pumpkinseed Sunfish (*Lepomis gibbosus*) show reduced growth rates, even whey they eat the same amount of food consumed as dominants (Blanckenhorn, 1992).

In this experiment, dominance was not correlated with body size (either mass, SVL or condition). This is unusual (Brattstrom, 1974) but may be related to the fact that lizards were all from the same cohort, with less than two months difference in age. Other studies have shown a relationship between either SVL (Whittier and Martin, 1992) or mass (Zucker and Murray, 1996), and dominance, which they have often correlated with age (Torr and Shine, 1996), since lizards have indeterminate growth.

In this experiment, lizards were, within a few months, the same age, so dominance may be established by other means. This may be why it was sometimes difficult to determine the first two ranks for each group. An interesting possibility that would require further testing, is that because subordinate lizards spend less time active and basking, they may grow at a slower rate and this might be why subordinates are smaller by the time they reach adulthood. Most previous studies of dominance in lizards has concentrated on established groups of lizards of various ages (eg Torr and Shine, 1996) and have assumed that larger body size is a causative agent of dominance, it could be that limited access to resources has meant a slower growth rate and thus a small size in subordinates.

In territorial species, fights are most likely to arise between unfamiliar lizards of the same size (Stamps and Krishnan, 1994). *E. stokesii* rarely show overt aggression to the introduction of an unfamiliar animal into a group. However, resident lizards engage in a lot of tongue-flicking under the eyes, around the mouth and towards the vent of the new lizard (pers. obs). Chemical signals may provide adequate information about the status of the new lizard, and fights may not be necessary to ascertain dominance.

This experiment provides evidence that individuals behave differently when they are alone and when are they are in a group. They also behave differently depending on the rank they occupy within the group. Subordinates modify their basking and refuging behaviour when in a group. This suggests that a hierarchy does form within groups of juveniles, which could affect their long term access to resources; especially since they may remain in the same group for up to five years (Duffield and Bull, 2001).

Chapter 9

Overview

The aim of this thesis was to expand the knowledge about the unusual grouping behaviour of *E. stokesii*. The benefits of this behaviour were the primary focus of this study, since grouping behaviour carries with it inherent costs (Alexander, 1974), so establishing the benefits to individuals is an important first step in understanding the evolution of group-living within a species. Understanding the benefits to *E. stokesii* in forming groups is particularly interesting, since until recently, lizards have not shown the sort of stable, long-term group fidelity that this species shows (Duffield and Bull, 2001).

Long-term studies of the group fidelity of this species have concentrated on one population in the Flinders Ranges of South Australia. This population occupies a small, isolated rocky outcrop containing approximately 100 lizards (Duffield and Bull, 2001). This thesis sort to establish if this behaviour extended beyond just this population. After examining the behavioural repertoire of *E. stokesii*, other populations of *E. stokesii* were surveyed and Chapter 4 of this thesis showed that although group size varies among regions, grouping behaviour still persists throughout much of the South Australian range of this lizard.

The simplest hypothesis to explain the evolution of group-living is that there is a shortage of resources or that animals are attracted to the same area, independent of the presence of conspecifics. This hypothesis was tested using both unrelated and related juveniles in pens with an excess of suitable refuge sites. Related animals were more likely to remain aggregated, although the distribution of most groups was more aggregated than would be expected by chance (Chapter 5). Grouping appears not just as a response to environmental constraints. Individuals appear to derive benefits from forming groups. An excellent extension to this experiment would be the experimental removal of groups within known populations in the field, and monitoring of surrounding groups to see if there is dispersal into the newly vacant home sites. This type of experiment would thoroughly test the "habitat saturation hypothesis" for the evolution of sociality.

Two possible benefits of grouping behaviour to individuals were then experimentally tested (Chapter 6 and 7). Both thermal and antipredator benefits were observed during the course of this study. Firstly, thermal benefits for an individual were implied by the increased tendency to form groups in cooler temperatures and by the maintenance of a higher temperature when grouped (Chapter 6). A question arising from these findings is why a lizard would want to maintain a higher overnight temperature.

Dee Boersma (1982) found that Marine Iguanas *(Amblyrhynchus cristatus)*, which, like *E. stokesii* are large, primarily herbivorous lizards, maintained a higher temperature when aggregated in overnight sleeping piles than when alone. An increased temperature would increase the metabolic rate of the lizard. This may facilitate increased digestion (Dee Boersma, 1982), which could be especially important for herbivorous lizards (Pough, 1973).

However, an increased metabolic rate means an increased rate of energy use, which would require more food. This could be why *E. stokesii* is more active during winter than closely related species such as *Tiliqua rugosa* (pers.obs: Firth and Belan, 1998). It could be beneficial to *E. stokesii* to be able to be active during winter when most of the rainfall occurs, and new growth of vegetation occurs. Overnighting in groups may facilitate increased activity on sunny days in winter, meaning lizards could take advantage of vegetation growth during this time. Further experiments would be required to test this hypothesis.

Secondly, grouping behaviour provided individual lizards with predator avoidance benefits. Juvenile lizards in groups came out more, both adults and juveniles reduced their vigilance in a group without compromising the vigilance of the group and lizards in groups reacted to a potential threat sooner than lizards by themselves (Chapter 7).

There is an obvious benefit in detecting a potential threat sooner, as shown in the collective detection component of the experiments on the antipredator advantages of grouping behaviour, but it is less clear why lizards in groups spent more time with their eyes closed. Eye closure could represent a sleeping state (Campbell and Tobler, 1984), in which case lizards basking in groups may be able to lower their energy output, or it could also reduce water loss, which might be important for a lizard living in an arid or semi-arid environment (Kavanau, 1997).

The final data chapter of this thesis (Chapter 8), showed that the benefits of grouping behaviour may not be equally shared among members of a group. Dominant lizards spent about the same amount of time engaged in refuging and basking behaviours when they were in a group as they did when they were alone. However, more subordinate lizards spent significantly less time basking when in a group than when they were housed by themselves, and they spent more time in a refuge when they were in a group, compared to when they were alone. This showed that the low level of intragroup aggression shown by *E. stokesii* may be maintained by a hierarchical social structure, which also means that costs and benefits are not shared equally among group members.

Subordination in groups of juveniles may extend to differential dispersal such as that shown in subordinate juvenile birds (eg Ellsworth and Belthoff, 1999) which may reduce the lifetime reproductive output of subordinate lizards. If such a hierarchy exists among adults in groups, *E. stokesii* may also show the sort of reproductive skew that has been used to predict the reproductive output of individuals within social groups of many birds, mammals and insects (eg Nonacs, 2000).

Since so many species within the *Egernia* genus show at least anecdotal evidence of social aggregation (Chapter 1), it may be that an ancestor of the *E. stokesii* evolved grouping behaviour when population density increased in an environment with a patchy distribution of suitable habitat. Alternatively, sociality may have been an extension of monogamy in a similar manner to the way in which cooperative breeding has been hypothesed to have evolved from the pair bond in some bird species. Long-term monogamy occurs in at least one species of a closely related family, *Tiliqua rugosa*.

The benefits of grouping behaviour that have been documented here may be the result of phylogenetic conservatism, rather than being unique to this species. Further work on both the social systems of closely related lizards, and a better understanding of the evolutionary relationships among the genus *Egernia* will help to clarify this. However, even among the *Egernia* species that have been studied so far, *E. stokesii* shows a low level of aggression and a large group size and unusual group fidelity (Duffield and Bull, 2001). Grouping behaviour may have evolved in an earlier *Egernia* species, but it has been retained and possibly increased in *Egernia stokesii*.

Territoriality is the most common spatial organisation in the lizard species studied to date. This type of social organisation is most appropriate in areas that are relatively homogenous for resources, including females. In areas where *E. stokesii* is found, both refuge and food resources are patchily distributed. Suitable rocky outcrops and vegetation occur sporadically throughout the southern distribution of this species, meaning that individuals are potentially attracted to the same areas, in the same way that sociality has been thought to evolve in arid-zone mammal species such as the Naked Mole-rat (Jarvis *et al.*, 1994).

As with most lizards (Shine, 1988), there has been evidence of only very limited, temporary parental care in this species (Lanham and Bull, 2000). Groups of lizards are unlikely to display helping behaviour, therefore philopatry of young is probably a result of a limit in suitable dispersal sites. However, groups of *E. stokesii* are not just composed of related individuals, unrelated animals group also. Group-living reptiles represent a unique system for understanding social behaviour, since there is little or no direct care of the young, so inclusive benefits for non dispersing offspring are likely to be negligible. This gives sociobiologists a chance to test alternative hypotheses for sociality, other than the inclusive fitness benefits of foregoing reproduction to help raise siblings.

Although this thesis has shown that grouping behaviour occurs throughout the rock-dwelling populations of South Australian *E. stokesii*, there is only anecdotal evidence that it occurs in the tree-dwelling populations of northern Australia. A comparative study of the group size and social organisation of these two populations would be an excellent way of examining the evolution of sociality within this species.

Many species within the *Egernia* genus show at least anecdotal evidence of sociality. Additional behavioural studies on these, as well as an overall analysis of the phylogenetic origins of social behaviour within this genus offers fertile ground for a greater understanding of the evolution of sociality in all taxa.

In conclusion, this study demonstrates that grouping in this species represents true sociality. *E. stokesii* groups even when opportunities to disperse are available and it appears to cooperate in such a group, by reducing individual vigilance in a group and by detecting a potential threat sooner. It also derives thermoregulatory advantages from the formation of social groups. Such a level of sociality has so far not been shown in any other lizard species.

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Appendix 1.

Appendix for Chapter 5.

Script file for running aggregation model. This is an example for Pen S6. 4 lizards. 1996 (Data shown in Figure 5.5, Chapter 5). This script contains the program information for S+ to run a simulation to estimate the probability of each of 12 crevices being used by an individual lizard.

```
"crevice"<-
function(x, n, esingle, etwina, etrip, etwinb, equad, etriptwin, equin)
{
    single <- 0
    twina <- 0
    trip <- 0
    twinb <- 0
    quad <- 0
    triptwin <- 0
    quin <- 0
    coincide <- 0
    expt <- c(esingle, etwina, etrip, etwinb, equad, etriptwin, equin)
    if(x == 3) {
        results <- matrix(0, nrow = 100, ncol = 3)
        summary <- vector("numeric", 3)
        explt <- vector("numeric", 3)
    }
    else if(x == 4) {
        results <- matrix(0, nrow = 100, ncol = 5)
        summary <- vector("numeric", 5)
        explt <- vector("numeric", 5)
    }
    else if(x == 5) {
        results <- matrix(0, nrow = 100, ncol = 7)
        summary <- vector("numeric", 7)
```

```
    explt <- vector("numeric", 7)
}
holes <- c(1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12)
for(i in 1:100) {
    for(j in 1:n) {
        enter <- sample(holes, x, replace = T, prob=c(0.052, 0.095, 0.043, 0.009,
0.121, 0.017, 0, 0.103, 0, 0.086, 0.36, 0.112)) ***NB: prob=c(0.052,..) is
removed for the random model which assumes equal probability of a lizard going
into any of the twelve crevices.
    #   print(enter)
        occupy <- hist(enter, breaks = c(1:12), plot = F)
        occupy <- occupy$counts[occupy$counts > 0]
        occupy <- sort(occupy)
    #   print(occupy)
        if(length(occupy) == 5) {
            single <- single + 1
        }
        else if(length(occupy) == 4) {
            if(occupy[4] == 2) {
             twina <- twina + 1
            }
            else single <- single + 1
        }
        else if(length(occupy) == 3) {
            if(occupy[3] == 3) {
             trip <- trip + 1
            }
            else if(occupy[2] == 2) {
             twinb <- twinb + 1
            }
            else if(occupy[3] == 2) {
             twina <- twina + 1
            }
            else single <- single + 1
        }
```

```
    else if(length(occupy) == 2) {
        if(occupy[2] == 4) {
          quad <- quad + 1
        }
        else if(occupy[2] == 3 && x == 5) {
          triptwin <- triptwin + 1
        }
        else if(occupy[2] == 3 && x == 4) {
          trip <- trip + 1
        }
        else if(occupy[1] == 2) {
          twinb <- twinb + 1
        }
        else twina <- twina + 1
    }
    else if(length(occupy) == 1) {
        if(occupy[1] == 3) {
          trip <- trip + 1
        }
        else if(occupy[1] == 4) {
          quad <- quad + 1
        }
        else if(occupy[1] == 5) {
          quin <- quin + 1
        }
    }
}
if(x == 3) {
    results[i, 1] <- single
    results[i, 2] <- twina
    results[i, 3] <- trip
    y <- 3
    if (single<=esingle && trip>=etrip) {
        coincide <- coincide + 1
    }
```

```
        }
        else if(x == 4) {
            results[i, 1] <- single
            results[i, 2] <- twina
            results[i, 3] <- twinb
            results[i, 4] <- trip
            results[i, 5] <- quad
            y <- 5
            if (single<=esingle && quad>=equad) {
                coincide <- coincide + 1
            }
        }
        else if(x == 5) {
            results[i, 1] <- single
            results[i, 2] <- twina
            results[i, 3] <- twinb
            results[i, 4] <- trip
            results[i, 5] <- quad
            results[i, 6] <- triptwin
            results[i, 7] <- quin
            y <- 7
            if (single<=esingle && quin>=equin) {
                coincide <- coincide + 1
            }
        }
        single <- 0
        twina <- 0
        trip <- 0
        twinb <- 0
        triptwin <- 0
        quad <- 0
        quin <- 0
    }
    print(results)
    print(coincide)
```

```
    for (m in 1:y) {
        summary[m] <- (sum(results[1:100,m])/100)
        explt[m] <- expt[m]
    }
    print(summary)
    par(mfrow = c(1,2))
    barplot(summary, ylim =c(0,20))
    barplot(explt, ylim= c(0,20))
}
```

Modifications were made to include six lizards for three pens in Experiment 1.

```
"crevice"<-
function(x, n, esingle, etwina, etrip, etwinb, equad, etriptwin, equin)
{
        single <- 0
        twina <- 0
        trip <- 0
        twinb <- 0
        quad <- 0
        triptwin <- 0
        quin <- 0
        coincide <- 0
        expt <- c(esingle, etwina, etrip, etwinb, equad, etriptwin, equin)
        if(x == 3) {
                results <- matrix(0, nrow = 100, ncol = 3)
                summary <- vector("numeric", 3)
                explt <- vector("numeric", 3)
        }
        else if(x == 4) {
                results <- matrix(0, nrow = 100, ncol = 5)
                summary <- vector("numeric", 5)
                explt <- vector("numeric", 5)
        }
        else if(x == 5) {
                results <- matrix(0, nrow = 100, ncol = 7)
                summary <- vector("numeric", 7)
                explt <- vector("numeric", 7)
        }
        holes <- c(1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12)
        for(i in 1:100) {
                for(j in 1:n) {
                        enter <- sample(holes, x, replace = T, prob=c(0, 0.208, 0.031,
0.038, 0.469, 0.038, 0, 0.177, 0, 0, 0.038, 0))
                #       print(enter)
                        occupy <- hist(enter, breaks = c(1:12), plot = F)
                        occupy <- occupy$counts[occupy$counts > 0]
                        occupy <- sort(occupy)
```

```
#       print(occupy)
        if(length(occupy) == 5) {
                single <- single + 1
        }
        else if(length(occupy) == 4) {
                if(occupy[4] == 2) {
                 twina <- twina + 1
                }
                else single <- single + 1
        }
        else if(length(occupy) == 3) {
                if(occupy[3] == 3) {
                 trip <- trip + 1
                }
                else if(occupy[2] == 2) {
                 twinb <- twinb + 1
                }
                else if(occupy[3] == 2) {
                 twina <- twina + 1
                }
                else single <- single + 1
        }
        else if(length(occupy) == 2) {
                if(occupy[2] == 4) {
                 quad <- quad + 1
                }
                else if(occupy[2] == 3 && x == 5) {
                 triptwin <- triptwin + 1
                }
                else if(occupy[2] == 3 && x == 4) {
                 trip <- trip + 1
                }
                else if(occupy[1] == 2) {
                 twinb <- twinb + 1
                }
                else twina <- twina + 1
        }
        else if(length(occupy) == 1) {
                if(occupy[1] == 3) {
                 trip <- trip + 1
                }
                else if(occupy[1] == 4) {
                 quad <- quad + 1
                }
                else if(occupy[1] == 5) {
                 quin <- quin + 1
                }
        }
}
if(x == 3) {
        results[i, 1] <- single
        results[i, 2] <- twina
```

```
            results[i, 3] <- trip
            y <- 3
            if (single==esingle && twina==etwina) {
                coincide <- coincide + 1
            }
        }
        else if(x == 4) {
            results[i, 1] <- single
            results[i, 2] <- twina
            results[i, 3] <- twinb
            results[i, 4] <- trip
            results[i, 5] <- quad
            y <- 5
            if (single==esingle && twina==etwina) {
                coincide <- coincide + 1
            }
        }
        else if(x == 5) {
            results[i, 1] <- single
            results[i, 2] <- twina
            results[i, 3] <- twinb
            results[i, 4] <- trip
            results[i, 5] <- quad
            results[i, 6] <- triptwin
            results[i, 7] <- quin
            y <- 7
            if (single<=esingle && quin>=equin) {
                coincide <- coincide + 1
            }
        }
        single <- 0
        twina <- 0
        trip <- 0
        twinb <- 0
        triptwin <- 0
        quad <- 0
        quin <- 0
    }
    print(results)
    print(coincide)
    for (m in 1:y) {
        summary[m] <- (sum(results[1:100,m])/100)
        explt[m] <- expt[m]
    }
    print(summary)
    par(mfrow = c(1,2))
    barplot(summary, ylim =c(0,20))
    barplot(explt, ylim= c(0,20))
}
```