

CHAPTER 4

**Scat piling: purposeful behaviour
or physical convenience ?**

ABSTRACT

Three main theories have been developed to explain the existence of local depositions of faeces or scat piling: allelomimetic behaviour, parasite avoidance and social signalling. Twelve species in the *Egernia* genus have been recorded as scat piling, but no research has previously been conducted to quantify the behaviour or to investigate its significance. *Egernia whitii* (White's skink) were captured and housed in aquaria as both singletons and in small related groups so that the position of each scat deposited over a period of several months could be recorded. Heat locations and time periods were manipulated to test several existing hypotheses. The spatial distribution of each scat was analysed using Nearest Neighbour Analysis (NNA) and Monte-Carlo simulations. Scat piling was found to be a purposeful behaviour cued by chemosensory rather than visual signals, but there was no thermoregulatory association, and burrow entrances were not the focus of the behaviour. Both individuals and groups of two, three and four related skinks were found to coordinate their behaviour by depositing their scats in a cluster in a discrete area of their permanent enclosure. In addition, field records from Wedge Island show that >10% of active *E. whitii* (diurnal skinks) were captured while refuging with sleeping *Nephrurus milii* (nocturnal geckos). Species from these two families of lizards are the only lizard taxa that are currently known to deposit their scats in piles. When these species occur in the same habitat it is possible that scat piles act as chemosensory signals or markers in interspecific identification. Refuge sharing between these two species may indicate interspecific cooperation facilitated by scat piling. Chemosensory signals derived from scats may be concentrated by deposition in one location to allow information exchange for multiple uses: between individuals, groups and species.

INTRODUCTION

General introduction

Animal scats have served humanity in the pursuit of information about the location,

food and habits of animal species for many thousands of years, but the formal consideration of scatology as a subsection of zoology has been more recent (Seton 1925). Researchers are now able to detect increasingly complex information from animal faeces. Some examples of this include home range parameters (Chame 2003), territorial warnings (Zuri *et al.* 1997), parasitic fauna (Gavin *et al.* 2005), parasite avoidance strategies (Hutchings *et al.* 2003, Apio *et al.* 2005) disease transmission between wildlife and domestic animals (Daniels *et al.* 2003), seed dispersal (Nogales *et al.* 2005), plant-animal mutualisms (Traveset & Riera 2005), food sources for small animal and bird species (Page *et al.* 1999), and the role of herbivore latrines in nutrient recycling (Feeley 2005).

Sophisticated technology can be employed to sample DNA (Reed *et al.* 1997, Smith *et al.* 2006), prey DNA (Deagle *et al.* 2005), and to monitor stress hormone levels in free-ranging animals (Bonier *et al.* 2004) in a non-invasive way, from animal scats. Similarly, historical data are collected on biology (Allmon 2004), botany (Hastorp 1999), biodiversity (Adrain & Westrop 2003), and parasites (Bouchet *et al.* 2003) during paleoecological investigations.

Apio *et al.* (2006) point out two principle aspects about the spatial **distribution** of faeces, that is, that random depositions within a home range are distinct from localised depositions. Species of ungulates (Qureshi *et al.* 2004, Apio *et al.* 2006) camelids (Portman & Myers 2004), rhinoceros (Ripley 1952, Ripley 1958), rabbits (Sneddon 1991), wolves (Sliwa 1996, Sillero-Zubiri & Macdonald 1998) primates (Irwin *et al.* 2004), lizards (Carpenter & Duvall 1995, Bull *et al.* 1999), and dasyurids (Belcher 2003, Belcher & Darrant 2004) plus otters (Rostain *et al.* 2004), badgers (Stewart *et al.* 2001, Begg *et al.* 2003), racoons (Page *et al.* 1999, Gavin *et al.* 2005) and tapirs (Quiroga-Castro & Roldán 2001) restrict their scat depositions to limited areas as part of their behavioural repertoire. The establishment of localised depositions is practised by solitary animals and pairs (Qureshi *et al.* 2004), and groups of individuals (Irwin *et al.* 2004).

Terms used and theories suggested to explain localised faecal depositions

Defaecation restricted to particular areas where excrement accumulates is described by an assortment of names. Different terms are sometimes used to describe similar

behaviour, perhaps in part to distinguish between the size of droppings or the individual strategies employed by a wide range of participants. The term dung heap is usually applied to rhinoceros (Ripley 1958), latrines and middens are often used for mammals (Sagara 1995, Irwin *et al.* 2004) spraints is used for otter droppings (Rostain *et al.* 2004), and defecatoria and scat piling are terms that have been used for lizards (Carpenter & Duvall 1995, Bull *et al.* 1999). Scat piling is a descriptive term describing the multiple depositions of faeces or scats by either individuals, or groups of individuals, at a specific site, where they accumulate to form clusters or piles.

Hypotheses on the existence of communal latrines have developed along three main themes. Leuthold (1977) attributes latrine areas to allelomimetic behaviour. This proximate explanation may arise because some observers have described the odour of faeces as triggering defaecation, often on top of the old droppings (Sneddon 1991, Apio *et al.* 2006). Parasite avoidance is another, but ultimate possible explanation, particularly for grazing herbivores which might seek to limit the gastro-intestinal contamination of their food supply by restricting their waste products to communal sites (Apio *et al.* 2006). However, the most complex and interesting explanation concerns the social function of localised defaecation sites.

In 1943 Burt defined home range as the area over which an animal normally travels, and territory as the area which is defended (*op cit.* Belcher & Darrant 2004). The social role of mammal faeces in communication is most frequently interpreted by researchers as being territorially directed (Sneddon 1991, Roper *et al.* 1993, Zuri *et al.* 1997, Belcher & Darrant 2004). However there are indications that the communal deposition of animal scats may communicate a great deal more than prior occupation or an endeavour to demarcate and maintain territorial habitat.

Carnivore species have characteristic and complex secretions which adhere to their faeces during defaecation and provide intra and interspecific information about territory, sex, reproductive state and movements (Gorman & Trowbridge 1989, *op. cit.* Chame 2003). Irwin *et al.* (2004) have suggested advertisement of sexual receptivity as one of the multiple functions for latrine behaviour in lemurs. In some species, notably lemurs and lizards, scat-piles are combined with other forms of scent-marking (Irwin *et al.* 2004, pers. obs.). Mammalian herbivores are not able to

detect the presence of parasites and must rely on cues such as faecal odour to avoid infection (Hutchings 2003). Sneddon (1991) reports different scat piling behaviour between rabbits of different age, sex and social-status classes and suggests communal sites as an efficient method of information exchange. It is possible that latrine behaviours utilise a range of strategies concurrently, including chemosensory communication, parasite avoidance and seed dispersal, and that these adaptive evolutionary strategies are supported by allelomimetic mechanisms.

Scat piling in gekkonids

Carpenter & Duvall (1995) investigated ‘fecal scent marking’ in a gecko species (*Coleonyx variegates*), and found that chemical cues are important in coordination of gecko faecal deposition patterns, and that they are likely to recognise the scent of their own faeces. In their study, scat-piles, or in their terminology ‘defecatoria’, were most likely to be established by individuals away from their diurnal refuges and, significantly, away from areas marked by conspecifics. No familiar groups were used in these experiments although anecdotal accounts of scat piling occurring when several geckos were housed together were reported.

Following in the footsteps of Carpenter and Duvall, Shah *et al.* (2006) demonstrated scat piling by pairs as well as individual thick tailed geckos (*Nephrurus milii*) but were unable to establish that older scats deposited previously cued the behaviour, or confirm that retreat sites were selected on the basis of scat presence.

Social behaviour and communication

Species using communal latrines possess well-developed chemosensory abilities (eg. Sneddon 1991), and the localised deposition of faeces is necessarily supported by high levels of social cooperation. Noë (2006) defines cooperation as ‘all interactions or series of interactions that, as a rule (or ‘on average’), result in net gain for all participants’. Social behaviour has been defined as ‘any behaviour exhibited by a group of animals that interact with each other’ (Martin & Hine 2000). Crozier (1999) defines social behaviour as ‘behaviour directed differentially at members of the same species, thus including sexual behaviour’. He further identifies a society as a group of cooperating individuals of the same species involving reciprocal communication and going beyond sexual behaviour. Communication is therefore an

important aspect of social behaviour.

Moore (1999) defines communication as ‘the transfer of information between animals using visual, audible or chemical means’. As many members of the *Egernia* genus are unique among Australian lizards in forming stable social aggregations (Greer 1989, Hutchinson 1993, Gardener *et al.* 2001, Fuller *et al.* 2005), an investigation of their scat piling behaviour (this chapter), and the role of scats in their basic communication systems, were initiated for *Egernia whitii* (next chapter)

Scat piling in the *Egernia* genus

Scat piling in some species within the *Egernia* genus has been reported anecdotally since Hickman’s observations of captive *E. whitii* in 1960. Members of the *Egernia* genus may be terrestrial, saxicolous, or semi-arboreal, and most terrestrial habitats support at least one species (Greer 1989). There are currently twelve *Egernia* species which span these varied habitats that have been described as scat piling.

Saxicolous or rock dwelling species include *E. cunninghami* (Barwick 1965), *E. hosmeri* (Stammer 1976), *E. stokesii* (Duffield & Bull 1998) and *E. kingii* (Ehmann 1992). *E. striolata* (Bustard 1970) is arboreal over much of its range, but uses fallen timber and exfoliating slabs of rock in some areas and *E. coventryi* (Douch 1994 & Clemann 1997 *op. cit.* Chapple 2003) inhabits saltmarshes.

E. inornata (Hutchinson 1993), *E. kintorei* (McAlpin 2001, Pearson *et al.* 2001 *op. cit.* Chapple 2003) and *E. whitii* (Hickman 1960) were previously the only known burrowers in this group but a concurrent study has added a third species, *E. multiscutata* (S. Bellamy pers. com.). *E. slateri* and *E. rugosa* (Ehmann 1992) inhabit arid sand plains, scrub and woodland, and open dry forest and woodland respectively (Greer 1989, Cogger 2000).

A number of suggestions for the prevalence of scat piling behaviour within the *Egernia* genus have been offered in the past. Ehmann (1992) proposed that the concentration of scats in one area might serve to attract insects for consumption. Barwick (1965) suggested that scat piles might coincide with a basking site at which thermoregulation becomes adequate for defaecation, or that scat piles may mark skink territories (Barwick 1965, Swan 1990), either visually or chemically.

Despite the attention that scat piling behaviour in this genus has received in Australia, the occurrence of scat piling has not previously been quantified, and no studies have been undertaken specifically to investigate its behavioural and ecological significance. This study commenced with investigations to discover whether scat piling is quantifiable in the laboratory, whether the process is physiologically related to basking and temperature, whether scat piles designate burrow entrances, and whether cues are visual or chemosensory.

MATERIALS AND METHODS

In March 2001, 24 *E. whitii* individuals captured randomly across Wedge Island in the Spencer Gulf of South Australia (35°09'S, 136°27'E) were toe clipped for skeletochronology and retained in a laboratory colony for future communication experiments. Each skink was maintained in an individual glass tank 600mm long x 305 mm wide x 300mm deep, lined with 20-30 mm of sand. Each aquarium was provided with a 190mm x 190mm x 30mm basking paver at one end supported 30 mm above the aquarium surface by two lengths of angle plastic. The intention was to provide a safe refuge that was unlikely to collapse during excavation, for fossorial skinks. Placed at the opposite end of the tank were several rocks and a flat plastic water dish of 85mm diameter. The refuge and rocks were positioned on the tank floor before sand was introduced to prevent damage to the animals by subsidence.

In addition all tanks were covered with cardboard sheets along each side to block out the presence of neighbours, and to allow time to elapse before recognition trials began. A heat lamp warmed the basking area at 32°C for eight hours a day from 8.30am to 4.30 pm, and photoperiods were 12 hours light and 12 hours dark during each 24 hour period. Experimental areas were kept at 25°C constant temperatures. Water was available continuously and they were fed three times a week – once with crickets, once with meal worms and once with vitamised vegetables and fruit sprinkled with reptile supplement.

In December 2003, 10 skinks were captured on Wedge Island for laboratory experiments and housed in identical conditions to the 24 individuals previously captured. Four of this group were gravid females which were used in scat piling trials. As soon as the neonates arrived they were exposed to ultraviolet lights which

were coordinated to turn on and off in synchrony with the heat lamps, to aid their absorption of calcium until they reached ≥ 60 mm SVL.

During early December in 2004, 10 gravid females were captured and retained for sibling relationship observations. These skinks were housed in identical conditions to the 4 gravid females previously captured, with one exception. The internal layout of the tanks was altered post-partum. After the first birth each tank was provided with a series of quarter pavers spaced by 15-20 mm, and covered with half pavers to form three smaller refuges along the side of the tank and end wall. The water dish was placed on top of the bricks, and rocks were placed diagonally opposite under the heat lamp. This layout reflected a concern that separate refuges might be required for larger litters of new individuals in the field.

At the start of each experiment each tank and its equipment was washed thoroughly with hot soapy water and sprayed with ethanol 70% before fresh sand was laid down. All preparations were made using Microflex[®] powder-free disposable latex gloves. Tanks were not cleaned between treatments, but scats were removed between treatments. Representations of each tank, with sketches of individual rocks to mirror the precise position and layout, were printed and duplicated for scat position records. For measurement purposes the length along the left template side was designated the Y axis, and the front width was designated as the X axis.

A fresh template was used daily to graphically record the position of scats deposited in situ to the nearest mm of the midpoint, beginning with those closest to the X-Y intersection. Exact X-Y coordinates were calculated in millimetres using a ratio of 6.67:1 to fit the actual measurements of the 305 mm x 600 mm tanks. Data were transferred to a mean distance file, in which the distance between each scat was calculated and averaged for each treatment.

During the experiments scats were removed immediately after measurement at the completion of the time period, to ensure that no visual cues were present at the start of the new treatment and minimise potential allelomimetic effects. Measurements took place at the same time each day, and scats were monitored over three different time periods: 24 hour, 48 hour and 72 hour intervals, four times, two times and two times respectively for each individual over a four week time period. There were eight treatments for each individual in the singleton experiments.

After completion of the first experiment, and still using 24 individual skinks, all tanks were reversed so that the heat lamps warmed the opposite end. Scats were again measured, counted and recorded over three different time periods: 24 hour, 48 hour and 72 hour intervals, four times, two times and two times respectively for each individual over a four week time period to detect any change in deposition patterns. There were eight heat treatments for each individual in the singleton experiments.

In a third experiment the average of all X-Y measurements for each distribution of scats was calculated, and the average distance to the nearest burrow, plus the average distance to the average of the burrow entrances was calculated from the average scat coordinate to detect any patterns.

In a fourth experiment group scat piling activity was assessed using mothers and their progeny. In February 2004 two females gave birth to one juvenile and two females gave birth to two juveniles. All juveniles survived and had reached adult size when scat piling trials began 14 months after their births. In February 2005 the second group of gravid females began to deliver young. One female gave birth to one juvenile, five females gave birth to two juveniles, and four females gave birth to three juveniles. Six newborn individuals failed to survive the neonatal period. Scats from the remaining juveniles were measured ten weeks from birth to avoid any possible effects due to very early juvenile status, such as reduced mobility.

Measurements for groups took place over a seven day period at the same time each day, using identical handling protocols. However measurements for this experiment were taken directly in the tank using plastic rulers 600mm and 305 mm respectively in length, with the resulting coordinates recorded and analysed as before.

The records of 335 captures were examined to discover the proportion of *E. whitii* found refuging with other lizard species to investigate interspecific refuge sharing between known scat piling lizards.

Nearest Neighbour Analysis

Spatial distribution (point pattern) can be categorised as dispersed, random or clustered using Nearest Neighbour Analysis (NNA) to compare the observed spacing of the scat distribution to an expected random pattern. However, assessing the deposition pattern of scats in my experimental tanks was not straightforward because

of the existence of border or edge effects. While parametric statistics (Clark & Evans 1954) can be used for assessing whether distributions of points (in this case scats) in a two-dimensional space are clustered, random or over dispersed, these do not deal with border or edge effects (Imfeld 2000). I therefore used non-parametric Monte-Carlo simulations to see if scats were clustered. For this I used the program Resampling Stats ® 4.1 (Simon 1990).

For each experimental terrarium I measured the average nearest neighbour distance, by finding the minimum distance from each scat to all other scats (giving an observed r_o value). The expected distribution of r was then calculated by randomly drawing a set of N co-ordinates (where N = the number of scats in the terrarium) from a uniform distribution of ($X = 0 - 305$) and ($Y = 0 - 600$), calculating the simulated average nearest neighbour (r_s), and then repeating this procedure 1000 times, keeping each r_s value from each iteration.

I could then determine whether the observed Average Nearest Neighbour (ANN) distance was smaller than expected by determining the proportion of the simulated distances that were equal to or smaller than the r_o . This procedure was repeated for each terrarium, since the number of scats per terrarium varied. The significance of the observed ANN (r_o) was then estimated as the proportion of simulated ANN's that were smaller than the observed value.

RESULTS

Singletons

Scat deposition in one, two and three day trials varied significantly from random distribution in all singleton replicates for both heat treatments ($N = 24$, $P = > 0.001$). Despite the removal of scats at the end of each time trial during treatments *E. whitii* continued to deposit scats in the same area, persisting even when their tanks were reversed and heat was directed from the opposite end. As there were no relationships between visual cues or heat in the deposition of scats, scat coordinates were pooled for analyses. Table 1 documents the results, indicating sex when known.

Table 1: Mean number (± 1 SE) of scats in each scat pile for singletons in scat piling experiments (N = 24). Right hand column gives the number of scat piles that were significantly clustered (Monte Carlo test for average nearest neighbour) at the $< .001$ level.

| Sex | Number of scat-piles | Mean number ± 1 SE | Range | Number of scat piles with highly significant ANN (<0.001) |
|---------------|----------------------|------------------------|------------|---|
| Male | 13 | 27.4 \pm 1.4 | 16 | 13 |
| Female | 8 | 27.1 \pm 2.0 | 20 | 8 |
| Unknown | 3 | 28.3 \pm 2.9 | 10 | 3 |
| Totals | 24 | N/A | N/A | 24 |

Groups

A total of 33 related groups of two, three and four adults or adult and juveniles formed distinct scat-piles (Table 2). Two groups, made up of two mother and daughter pairs (one juvenile daughter and one adult daughter, N = 4 individuals), did not show a significant result during testing using Monte Carlo simulations. These were the only all-female groups.

Table 2: Mean number (± 1 SE) of scats in each scat pile for small groups of relatives in scat piling experiments (N = 14). Composite results giving the number of scat piles that were significantly clustered (Monte Carlo test for average nearest neighbour) are recorded in categories of significance: <0.001 , ≤ 0.005 , ≤ 0.05 , with two groups recording nil significance in the right hand column.

| Group composition (14 groups) | Mean number ± 1 SE | Range | Number of groups < 0.001 | Number of groups ≤ 0.005 | Number of groups ≤ 0.05 | Number of groups Non sig. |
|---------------------------------|------------------------|------------|----------------------------|-------------------------------|------------------------------|---------------------------|
| Adult & 1 juvenile (6 groups) | 14.8 \pm 1.2 | 9 | 3 | 1 | 1 | 1 (P = 0.13) |
| Adult & 2 juveniles (1 group) | 21.0 \pm 0.0 | 0 | | 1 | | |
| Adult & 3 juveniles (3 groups) | 39.0 \pm 2.1 | 7 | 3 | | | |
| Two related adults (2 groups) | 16.5 \pm 0.5 | 1 | 1 | | | 1 (P = 0.076) |
| Three related adults (2 groups) | 20.5 \pm 1.5 | 3 | 2 | | | |
| Totals | N/A | N/A | 9 | 2 | 1 | 2 |
| Skinks per group | N/A | N/A | 26 | 5 | 2 | 4 |

Comparison of singleton and group results

Histograms were prepared to compare the results of singleton experiments with group results. Figures 1 & 2 show tight clustering in singleton scat-piles.

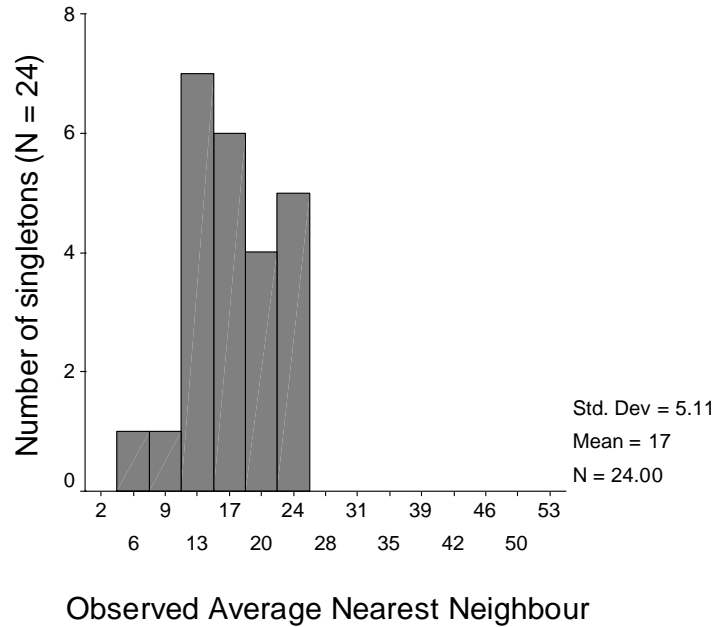


Figure 1: Observed average nearest neighbour (r_o) of individual scat piles.

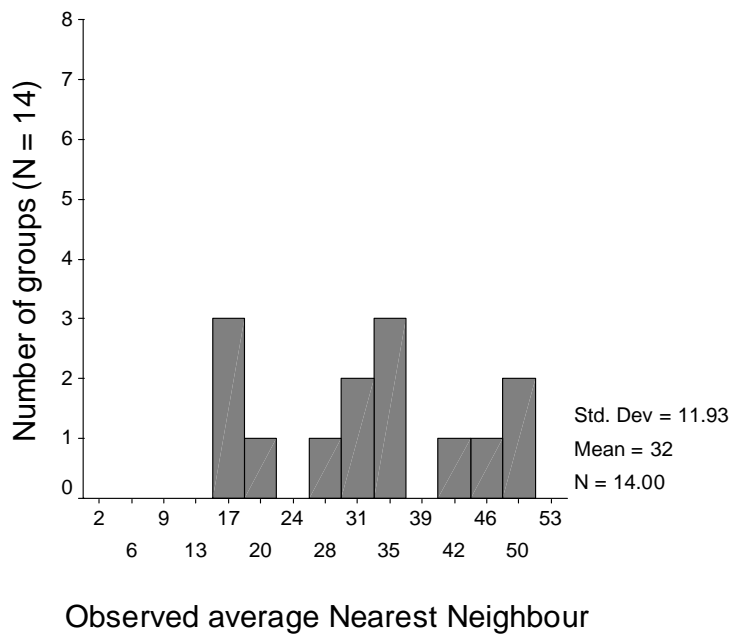


Figure 2: Observed average nearest neighbour (r_o) of group scat piles.

A One-way between-groups ANOVA was conducted to explore the relationship of scat positioning to the number of skinks scat piling, as measured by Average Nearest Neighbour (ANN) statistics. The four groups were divided according to the number of individuals in them (Group 1: singletons, Group 2: two individuals, Group 3: Three individuals and Group 4: four individuals). Robust Tests of Equality of Means were used as a measure of the homogeneity of variances (Welch 0.006 and Brown-Forsythe 0.001) which violated the Levene's test. There was a statistically significant difference of >0.001 in the mean ANN scores between groups. Figure 3 shows an error bar graph of the observed ANN against group size. Post-hoc comparisons using Turkey HSD and Bonferroni indicated that Group 2 differed significantly in ANN with both singletons and groups of three and four (Turkey HSD = >0.001 for singletons and groups of four, 0.036 for groups of three, Bonferroni = >0.001 for singletons and groups of four and 0.45).

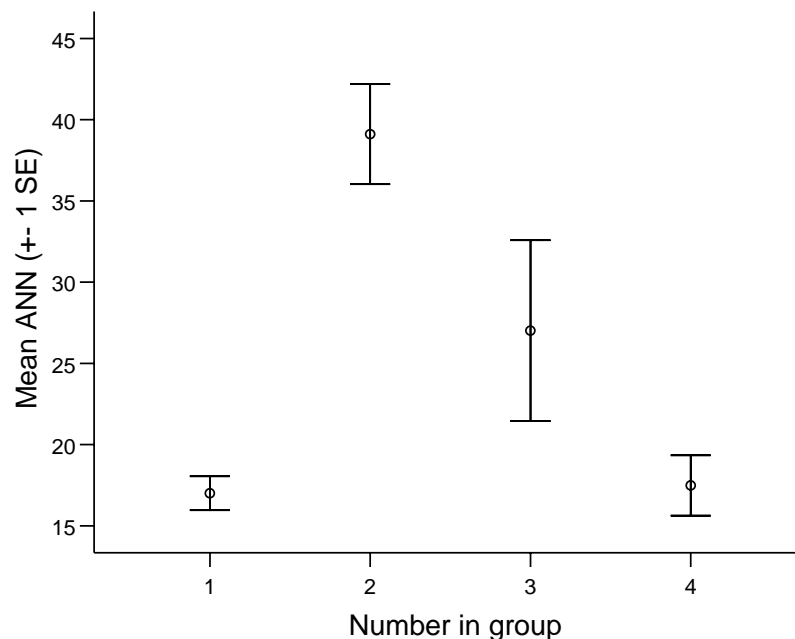


Figure 3: Mean Average Nearest Neighbour as a function of group number.

Average burrow entrance coordinates and average scat coordinates

Figure 4 shows the average scat coordinates for each of 24 skinks over a four week period, and Figure 5 shows the average burrow entrance coordinates.

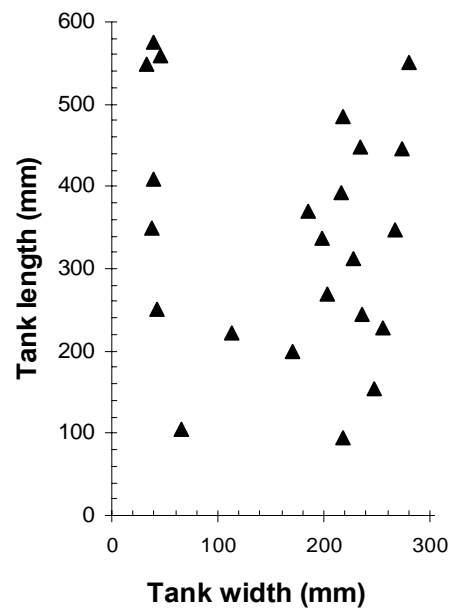


Figure 4: Mean X-Y coordinates (centroids) for scat piles for singleton lizards. Note the wide variation in the mean values.

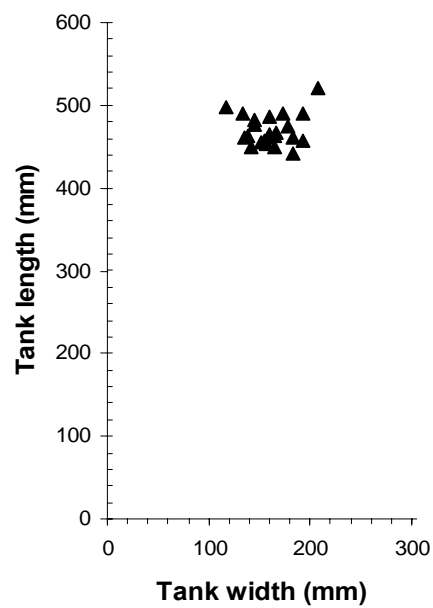


Figure 5: Individual burrow entrances for each of the singleton experiments, averaged and combined, for comparison with scat-pile averages.

These were calculated to investigate the proximate factor that scat pile placements might be uniformly close to burrow entrances to signal the immediate presence of the occupant, or uniformly distant from burrow entrances to dissociate their chemosensory signal from the territory holder.

Within the confines of the tank dimensions, there was no relationship between the refuge or burrow entrance and the position of the scat pile. Scats were found deposited in clusters in discrete positions, individually selected without regard to distance from refuge entrance.

Shared refuges

In 355 recorded captures *E. whitii* were discovered refuging with other species on 34 occasions. Individuals, pairs and groups of three *E. whitii* were found in refuges with individuals or groups of up to six geckos on 29 of these occasions. However they were found only six times with either *Hemiergis peronii* or *Lerista dorsalis* (geckos also present two of these times), twice with *Ctenophorus fionni* (geckos also present one of these times), and twice with a centipede (geckos present both times). Table 3 shows the percentage of individual *E. whitii* found with each of the different species.

Table 3: The percentage of total (N = 335) *E. whitii* captures captured in refuges with other species.

| Refuge Species | % of recorded <i>E. whitii</i> population | Total number of <i>E. whitii</i> individuals |
|--|---|--|
| Gecko (<i>Nephrurus miltii</i>) | 10.7 | 36 |
| Four-toed earless skink (<i>Hemiergis peronii</i>) & Southern four-toed slider (<i>Lerista dorsalis</i>) | 1.8 | 6 |
| Peninsula dragon (<i>Ctenophorus fionni</i>) | 0.9 | 3 |
| Centipede | 0.6 | 2 |

DISCUSSION

General considerations

Both proximate and ultimate factors are likely to be involved in scat piling and it is

possible that allelomimetic behaviour may support parasite avoidance, or social or territorial signalling, or any combination of these elements. A comprehensive explanation for scat piling behaviour can not be established without investigating the use the animals themselves make of chemosensory signals in scats.

Divergent descriptions of scat piles across taxa from individual investigators may reflect subtle differences in species' behaviour, or size and landscape variation. Alternatively, and in particular within the lizard community, there maybe different levels of tolerance for conspecifics, or different levels of chemosensory receptivity. Latrine behaviour which serves different functions may also affect cooperative endeavours within participating groups. Regardless of these factors, the common outcome of latrine use for all taxa does appear to be the conferral of mutual advantages to the participants.

During scat piling trials each scat and its remnants were removed from the resident's aquarium on a daily basis. However the sandy substrate was not changed during the trial period. These measures were taken to ensure that visual cues were absent for the majority of the trial period, while at the same time allowing chemosensory cues to be available to the resident skink. Nonetheless, resident skinks continued to actively form their scat piles in the same locations, persisting even when the aquariums were turned around so that the heat source came from the opposite direction. Not surprisingly, in view of the important role chemosensory development plays in scincid lizards, visual cues were discovered to be non-essential in the process of scat piling for both singletons and groups.

Natural *E. whitii* habitat includes open woodland, scrub, grasslands, herbaceous vegetation, clearings, excavated soil, and loose rocky outcrops (Chapter 2). As one of the smaller *Egernia* species, *E. whitii* tend to produce smaller scats and consume a greater proportion by volume of invertebrates to vegetation (Hickman 1960, Duffield & Bull 1998, Chapter 2). In more open habitat lightweight deposits can dry quickly in the sun and blow away. For these reasons *E. whitii* depositions are difficult to observe under field conditions. A visual cue for deposition under these circumstances could be problematic.

During trials *E. whitii* scat piles were demonstrated to occur in a variety of heat zones within the confines of the enclosure, and the compact formation of the scat

piles made it necessary for the resident skink to travel to the same site one or more times a day to add to the pile. It is unlikely under these circumstances that the formation of scat-piles is coincidental with thermoregulation and basking in this species. Chapple (2003) proposes that the active formation of scat piles might serve some purpose in the social function of those species that exhibit complex sociality. It is possible that scat piling is a sign of social complexity. Research directed towards cryptic and hitherto overlooked species may yet be a rich source of discovery.

E. whitii did not necessarily avoid their individual or communal scat piles in the laboratory nor did they frequent them (pers. obs.). There is no evidence favouring the hypothesis that scat piles might act to attract insects for opportunistic consumption (Chapple 2003).

Anecdotal observations record that scat piles are generally located near the entrance to a permanent home site (Chapple 2003), and it has been suggested that in a rare or secretive species such as *E. rugosa*, scat piles indicate their presence in an area (Wilson & Knowles 1988 *op. cit.* Chapple 2003). There was no uniform relationship between burrow entrances and scat piles in *E. whitii* although several individuals deposited their scats directly overhead on the top surface of the refuge, and one individual formed a scat pile inside the refuge. It is likely that *E. whitii* scat piles recorded during trials remain within an unknown minimum distance from their burrows for territorial signalling. The tank sizes were much smaller than home territories on Wedge Island (unpublished data) and further testing would be required to establish the exact parameters of territorial marking.

One of the major benefits of dispersal is thought to be the avoidance of parasites found at a high density where relatives are genetically similar (Boulinier *et al.* 2001). The avoidance of parasites is an advantage that depends on minimising contact with groups of relatives to some extent to obtain fitness advantages. If contact with relatives is to be avoided, it is necessary to be able to recognise and respond appropriately to them.

Communication mechanisms facilitate interaction and cohesion between preferred group members, but they may also be used in avoidance and competitive strategies. Investigations of *E. striolata* scats have provided evidence that some *Egernia* scats contain a complex combination of chemical cues which may serve as signals (Bull *et*

al. 1999). Research has also established that these scat signals deteriorate over time (Bull *et al.* 1999), and in the small scincid lizard *Lamprohopolis guichenoti*, signals can no longer be used in discrimination tests effectively after 7 days (unpublished data). In a review of the ecology, life-history and behaviour of the *Egernia* genus, Chapple (2003) came to the conclusion that scat piling may be necessary to renew the signal so that it could retain its (unknown) social function.

Social signalling

In the early 1960's there was some initial recognition that secretive or cryptic lizards relied more on scent and sound than visual stimuli for sexual or species discrimination (Glinski & Krekorian 1985). However it is only more recently that research has focussed on discovering the implications of that understanding.

Scats have been used in bioassays in several contexts. The Australian lizard *E. striolata* discriminates between its own scats and those of unfamiliar conspecifics (Bull *et al.* 1998), male Iberian rock lizards discriminate between familiar and unfamiliar conspecifics through faecal pellet odours (Aragón *et al.* 2000), and the Chilean lizard, *Liolaemus tenuis*, is able to recognise its own odour from scats (Labra *et al.* 2002). These findings suggest that lizard scats might be used to produce individual signals.

Small groups of relatives and individual *E. whitii* scat pile. In their laboratory tests Carpenter & Duvall (1995) demonstrated that western banded geckos (*C. variegatus*) deposited their scats in piles when kept alone in captivity, and that unfamiliar individuals introduced after the resident had been evacuated avoided the same area when depositing their scat piles. However they did not attempt to demonstrate scat piling as a group activity in individuals held captive together, even though this behaviour had been anecdotally reported previously.

Similarly, thick-tailed geckos (*N. milii*) have also been shown to scat pile in the laboratory as individuals and also as pairs (Shah *et al.* 2006). However these investigations were concerned with crevice use rather than the discovery of a range of chemosensory signals amongst group members, and further discoveries might yet be forthcoming.

Experimental trials showed tighter clustering of scat-piles for singleton and groups of

four than groups of two or three. There were only two single sex groups and they were composed of mother and daughter combinations. These were the only two groups which failed to show a significant clustering when tested using Monte Carlo simulations. However the numbers are too limited to accept without further research.

All other groups were composed of mixed sexes. There were no all-male groups for comparison as each group comprised an adult female and her progeny. *E. whitii* males and females respond in different ways to scats used as scent cues (Chapter 5). It is plausible that because they respond differently to scent cues that they also deposit signals differently.

Furthermore, if lizard scats are used to produce individual signals, it might be expedient for females to advertise in a way that separates them or distinguishes them as individuals. Individual signals deposited separately by females could aid in offspring strategies that avoid kin competition by cooperation within the family group, but attract suitably genetically divergent mates to avoid inbreeding depression. It is possible that social signals are a major aspect of scat piling behaviour for *E. whitii*.

Members of the *Egernia* genus are not alone amongst lizards in establishing scat-piles. Individual western banded geckos (*Coleonyx variegatus*) also establish preferred defaecation sites (Carpenter & Duvall 1995), and pairs and individual thick-tailed geckos (*Nephrurus milii*) scat pile (Shah *et al.* 2006). The use of latrine areas or scat piling is clearly not restricted to diurnal or nocturnal habits.

Reports of scat piling in species of the *Egernia* genus and in geckos are intriguing from an ecological perspective. It is an activity that requires social coordination, and its existence is linked to social benefits. The social benefits arising from signalling could confer both cooperative and competitive benefits.

Permanent territorial markers would benefit conspecifics, congeners and other species, as the signal provides a means of avoiding potentially damaging agonistic interactions. The high incidence of *E. whitii* refuging with *N. milii* on Wedge Island provides an indicator of interspecific cooperation. The low incidence of retreat sharing with other skinks and centipedes points to the avoidance of other species apart from the exceptional circumstance of fleeing from human predators. However

there appears to be some plasticity when it comes to geckos. One advantage of the scat piling habit of *N. milii* might be mutual recognition between a diurnal species and nocturnal species. Theoretically, if no threat is perceived by either species concerning the other, greater access to refuges can be attained by both.

Cooperation in group scat piling, allows individual members of the group to leave chemical cues in scats which potentially indicate relatedness, or social and sexual status within the group. By the cooperative practice of scat piling these individuals validate their group membership while simultaneously providing individual scent cues and ensuring their own safety within the group.

Information concerning the social environment that is readily available to dispersing transient and potential immigrant conspecifics, or even intruders and competitors, before encountering the inhabitants would allow advantageous settlement choices to be made. In terms of population dynamics it may be adaptive for the recruitment of one or the other sex, or in contrast the niche may be fully occupied. Obtaining information concerning the sex and number of group members would allow the potential newcomer to avoid agonistic encounters.

Some or all of these benefits are possible when the multiple uses of chemosensory communication are taken into consideration in Chapter 5.

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