

# Scat on the doorstep: Refuge choice in a group-living lizard is influenced by the presence of scat piles

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**Abstract** Group living often requires strong levels of communication between individuals. This communication is usually studied in the context of visual or auditory communication. However, chemical communication is the most widely used form of communication. We examined the role of chemical communication in mediating social decisions in a group-living lizard, *Egernia stokesii*. Specifically, we examined the extent to which scat-piling, a behaviour by which individuals deposit scat in a communal area, affected the refuge choice of individual *E. stokesii*. To achieve this, we examined individual refuge choice in response to scat piles or single scats and against two types of scat stimuli, one being their own scat and the other being scat belonging to an unrelated and unfamiliar conspecific. We show that lizards behave differently when presented with a scat pile compared with a single scat, and whether the scat stimulus was their own or sourced from an unfamiliar conspecific. When scats were in piles, individuals spent more time inspecting, more time in, and more often chose the treatment refuge as their final refuge choice, at a trial's end, when the treatment was their own scat compared with when the treatment was the refuge with the unfamiliar scat. In contrast, for individual scat treatments, individuals spent more time inspecting and more often ended up in the treatment refuge with an unfamiliar scat compared with when the treatment was their own scat. These results suggest that individuals are responding to information contained within multiple components of the scats – both their volume and their source. These results have implications for understanding how social aggregations are maintained within squamates, where sociality has evolved independently from other vertebrate lineages.

**Key words:** chemical cues, *Egernia stokesii*, reptile, scat, social signals, sociality.

## INTRODUCTION

Communication is ubiquitous throughout the animal kingdom (Frings 1962; Brennan & Zufall 2006; Houck 2009). Chemical senses are the oldest form and common to all organisms; therefore, animals are pre-adapted to detect chemical signals (Wilson 1970; Wyatt 2014). Indeed, when interacting, species employ chemical signals more than any other signal (visual or auditory; Wyatt 2003). For example, chemical communication between conspecifics facilitates honest assessment of social environments such as social status, territory and reproductive availability, and for the avoidance of aggressive encounters or facilitation of cooperative behaviour (LeMaster & Mason 2002; Wyatt 2003; Kondo *et al.* 2007; le Fras Mouton & Hayward 2007; Mason & Parker 2010; Martín & Lopez 2011; Shorey 2013).

A key advantage of chemical signals is that they remain present in an area long after an animal has

left. In contrast to glandular secretions which are often costly to produce (Buesching *et al.* 2016), chemical communication from defecation allows signalers to leave public signals at a low cost, which may reduce potentially high-cost encounters whilst still conveying information on the marker's social environment. In many taxa, faeces (scat) and urine have evolved to function secondarily as a method of chemical communication (Sprenst *et al.* 2006; Moreira *et al.* 2008; Buesching *et al.* 2016). This is well-illustrated by latrines, defined as the repeated use of a specific site for defecation or urination (Irwin *et al.* 2004). Although latrines may facilitate avoidance of parasite transmission (but see Gilbert 1997; Ezenwa 2004) and predator detection (Boonstra *et al.* 1996), chemical communication is purported to be their most common function (Irwin *et al.* 2004). For example, latrines have been shown to communicate territory boundaries and social status in badgers (*Meles meles*; Buesching *et al.* 2016; Schmid *et al.* 1993) and primates (*Lepilemur* sp. and *Haplemur griseus*; Irwin *et al.* 2004), establish communication networks between widely spaced swift foxes (*Vulpes*

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Accepted for publication December 2019.

*velox*; Darden *et al.* 2008), and assess competitive and sexual information in red-backed salamanders (*Plethodon cinereus*; Mathis 1990).

While the majority of evidence for latrine use has come from mammals, it has also been documented in squamate reptiles (Bull *et al.* 1999; Martín & Lopez 2011; Fenner & Bull 2011b; Ebrahimi *et al.* 2016). Individuals of some lizard species repeatedly deposit scat in the same area, resulting in the accumulation of scat material, referred to as 'scat-piling' (Chapple 2003). Several explanations for this behaviour have been proposed. The simplest explanation is that scat-piling is the outcome of convenience; that is, scat piles are produced primarily in morning basking areas where adequate temperatures induce defecation (Chapple 2003). On the other hand, scat-piling may have a functional explanation. For example, scat-piling has been shown to reduce parasite transmission under direct sunlight and desiccation (Hallas & Bull 2006) or attract prey (insects) close to a group's home range, where the lizards feed opportunistically whilst reducing rates of predation (Chapple 2003). Alternatively, scat-piling may function as a social marker, playing a crucial role in the mediation of individual and group recognition (Chapple 2003; Bellamy 2006). Indeed, previous studies have shown that lizards can distinguish between familiar and unfamiliar conspecific scat (Bull *et al.* 1999; Bull *et al.* 2000; Bellamy 2006; Moreira *et al.* 2008; Wilgers & Horne 2009). Despite this, few studies to date have focused on space use and refuge choice. Fenner *et al.* (2015) found that rather than scat-piling, *Tiliqua rugosa* (sleepy lizard) scat haphazardly within their home range. In contrast, *Tiliqua adelaidensis* (pygmy bluetongue) consistently scat in a direction aligned with the refuge of the nearest neighbour (Fenner & Bull 2011b). *Nephurus milii* (thick-tailed gecko) do create scat piles, yet Shah *et al.* (2006) found the presence of scat piles did not influence refuge choice, at least not in captive lizards. Thus, the role of scat-piling in lizard refuge choice, with consequences for spacing of individuals and groups, remains unclear.

Scat-piling has been observed in eleven species of skinks within the sub-family of Egerniinae (Chapple 2003), seven of which live in aggregations (Gardner *et al.* 2015). Skinks have well-developed vomeronasal organs (Cooper 1996), which suggest a high level of discrimination may be possible within Egerniinae. Given the potential function of scat-piling as a social signal, it is pertinent to investigate the behaviour in aggregating *Egernia* species. In this study, we explored the influence of scats on *Egernia stokesii* refuge choice. *Egernia stokesii* form stable social groups and exhibit high levels of monogamy and natal philopatry (Gardner *et al.* 2001; Gardner *et al.* 2002; Pearson *et al.* 2016). Distributed across semi-arid regions of Australia (Cogger 1983), *E. stokesii*

populations commonly occupy rocky outcrops where individuals reside in rock crevice refuges and bask on rocks outside crevice entrances. The availability of rocky crevices limits both the number of lizards and number of social groups within an outcrop (Gardner *et al.* 2007).

*Egernia stokesii* commonly produce scat piles at the entrance to, or on top of, crevices (Bull *et al.* 1999; Duffield & Bull 2002), and *E. stokesii* can identify group from non-group members based on chemical cues from scats (Bull *et al.* 2000). Here, we explored the influence of single scat and scat piles, sourced from both the focal lizard and an unfamiliar, unrelated conspecific, on *E. stokesii* refuge choice. We hypothesised that scat piles, but not single scats, would influence refuge choice. Specifically, we predicted that lizard final crevice choice and the time spent inspecting crevices would be more influenced by the presence of a scat pile than the presence of a single scat. Further, we predicted that lizards would spend more time inspecting, and choose as their final refuge choice at a trial's end, a crevice with their own scat, rather than unfamiliar scat, present.

## METHODS

### Lizard and scat source

*Egernia stokesii* (gidgee skink) were obtained from two sources. First, 14 adult lizards were sourced from the Flinders University Animal House, having been previously collected between 1993 and 1998 from various regions across South Australia (Main & Bull 1996; Arida & Bull 2008). These lizards had been housed in a seminatural but captive enclosure for up to 20 years. Second, we sourced five recently caught (January 2015) adult lizards from Witchelina Station, South Australia (31°54'S; 138°25'E). The importance of using these two sources of lizards is that they were unrelated and had never been in contact with each other. Thus, each group acted as an unfamiliar source of scat for the other, which was an important factor in experimental design, that is, when trialling captive lizards (CGS), the unfamiliar scat stimuli, were sourced from wild lizards (WGS), and vice versa.

Each lizard was identified by a unique microchip (AVID, Norco, California, USA) and isolated indoors (25°C) in separate containers (2980 × 1450 mm) for two weeks prior to experimentation. During this time, lizards were provided with a basking light and basking brick (photoperiod 0800-1700) and a refuge (see Experimental Design below). Lizards were fed weekly with vegetable mash and provided with water *ad libitum*.

### Experimental design

Experiments were conducted from March to September 2016 using three enclosures. Each enclosure consisted of a large circular galvanised open-topped pen (1 m

height  $\times$  1.5 m diameter) prepared with 20 mm depth fine-sand flooring. We created artificial crevices by placing two identical parallel pavers (300  $\times$  300 mm), propped up on one side with a wood block (70  $\times$  45 mm) to provide a gap (Appendix S1, Supporting Information). This design was previously determined as suitable crevices for *E. stokesii* (Arida & Bull 2008). Each pen contained two crevices. We fitted each pen with a GoPro Hero session™ camera (960  $\times$  540 pixels, 60 frames per second), mounted at a distance of ~860 mm above each pen, to provide footage of the entire pen during each experiment. Each experimental pen also utilised a plastic tub cover (150  $\times$  150  $\times$  100 mm) attached to string, allowing tubs to be lifted from outside the room to minimise human interference (see Appendix S2, Supporting Information, for experimental pen set-up).

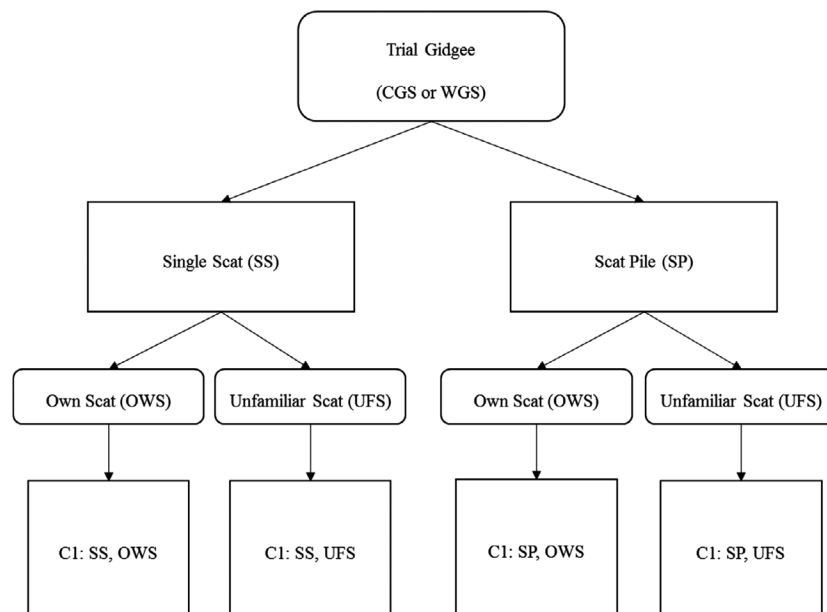
Two experiments were conducted (Fig. 1). There was a minimum of 5 days between each individual's separate trial, and we randomised the order of experimental treatment combination for each individual. First, a single scat was placed on the sand 20 mm adjacent to the entrance of one of the crevices whereas the entrance to the other crevice contained no scat and acted as a control. This design was replicated in the second experiment, except that a pile of scat was placed at the crevice entrance rather than a single scat. The crevice site that contained the scat was randomly chosen in each trial. Each experiment had two treatments, either the origin of the scat was sourced from the treatment lizard or it was sourced from an unrelated, unfamiliar lizard (from the opposite population). This resulted in four treatments overall (Fig. 1).

Each morning before experiments began, the experimental pens were set-up with fresh sand and clean, dry crevices. We trialled 14 captive gidgee skinks (CGS) and five wild gidgee skinks (WGS). Each lizard was tested opportunistically depending upon scat availability. Only freshly

deposited scat (maximum 24 h old) was used in single scat treatments (Bull *et al.* 1999). Scat pile treatments (five scats per lizard) were collected and stored away from UV light at 14°C in a sealed glass desiccator containing silicon crystal until five scats were collected. We chose five scats to represent a small pile in the wild (M. Gardner, pers. observ., 1998). At the beginning of each trial, lizards were introduced to their pens and left for five minutes to settle before plastic tub covers were lifted and the trial began. The trials were filmed undisturbed for seven continuous hours. For the duration of the trial, the lizards did not receive food or water and basking lights were absent so that crevice choice was not influenced by these factors. Further, Arida and Bull (2008) found lizards explored more without basking lights, behaviours suitable for this study. Following each trial, lizards were returned to their isolated pen, the sand in the experimental enclosure was removed, and the crevices were cleaned thoroughly with water to remove any remaining scents. A single observer scored each video, based on three variables incorporating behaviours previously described by (Arida & Bull 2008; Table 1).

## Statistics

We ran individual models on the three key behavioural indicators of discrimination: (i) the proportion of time spent inspecting each crevice, (ii) the proportion of time spent in each crevice and (iii) the final crevice site choice (see Table 1 for a detailed description of each of these behaviours). For these models, we ran generalised linear mixed models with either a binomial (time spent inspecting, final crevice site choice) or a negative binomial (time spent in) distribution using the *lme4* package (Bates *et al.* 2014) in R. For the two percentage time models, we



**Fig. 1.** *Egernia stokesii* crevice choice experimental design ( $n = 19$ , captive gidgee skinks (CGS), wild gidgee skinks (WGS)). Treatments were single scat (SS), scat piles (SP), own scat (OWS) and unfamiliar scat (UFS). C1 indicates crevices with scat stimuli. In each experiment, individuals were given a choice of the stimulus vs a control of no stimulus.

**Table 1.** Description of *Egernia stokesii* behaviours recorded during crevice choice experiments

Behaviour	Description
Final crevice site choice (0 or 1)	The crevice the treatment lizard is in at the end of the seven hours of filming and the lights are off, being stimuli crevice (1) or control crevice (0)
Time spent in crevice (h:mm:ss)	The proportion of time spent in the crevice (based on the time from when the animals head and forelimbs entered the crevice until the time the animals body (up to hind legs) left the crevice)
Time spent inspecting crevice (h:mm:ss)	The proportion of time the animal spent in close proximity to the crevice, including its head sitting in the crevice opening and the time spent on top of the crevice

initially included scat deposit type (single *vs.* pile), source (own *vs.* other) and crevice site (control *vs.* stimuli) as fixed factors and individual identification and population of origin as random effects. Where a significant three-way interaction was found, we then ran models for each crevice site type separately. For the final crevice site model, we did not include crevice site (control *vs.* stimuli) as a factor, because the response variable was either the control or the stimuli crevice. All models were checked for violation of assumptions. All linear models were fitted using the *car* package (Fox 2002) in R, to generate type III  $\chi^2$ -tests of fixed effects. When interactions were non-significant, results for main effects are presented from models excluding the interactions.

**RESULTS**

We found a significant three-way interaction between scat, source and crevice site for the models for both

time spent inspecting and time spent in the crevice site (Tables 2 and 3). To unpack this interaction, we re-ran each of these models for the stimuli and the control crevice separately.

For time spent inspecting the control site, we found a significant two-way interaction between scat and source (Table 2). Specifically, while individuals spent more time inspecting the control crevice site when the stimuli crevice site had both an unfamiliar scat on its own and in a pile, this effect was greatest when the stimuli crevice site had unfamiliar scat in a pile (Fig. 2). For the stimuli crevice site, individuals spent more time inspecting the crevice with a single scat when it was unfamiliar yet, for scat piles, individuals spent more time inspecting the crevice when the pile was composed of their own, rather than unfamiliar, scat (Fig. 2), but this interaction did not reach statistical significance (Table 2).

For time spent in the crevice site, we found no significant effect of scat deposit type or source on the amount of time spent in the crevice site for either the stimuli crevice or the control crevice (Table 3). Inspection of the data suggested that individuals spent more time in the stimuli crevice when their own, rather than unfamiliar, scat was in a pile with no difference between own and unfamiliar source when there was a single scat (Fig. 3). In line with these results, individuals spent more time in the control crevice when the crevice contained unfamiliar scat in a pile or when the crevice contained a single scat of their own (Fig. 3).

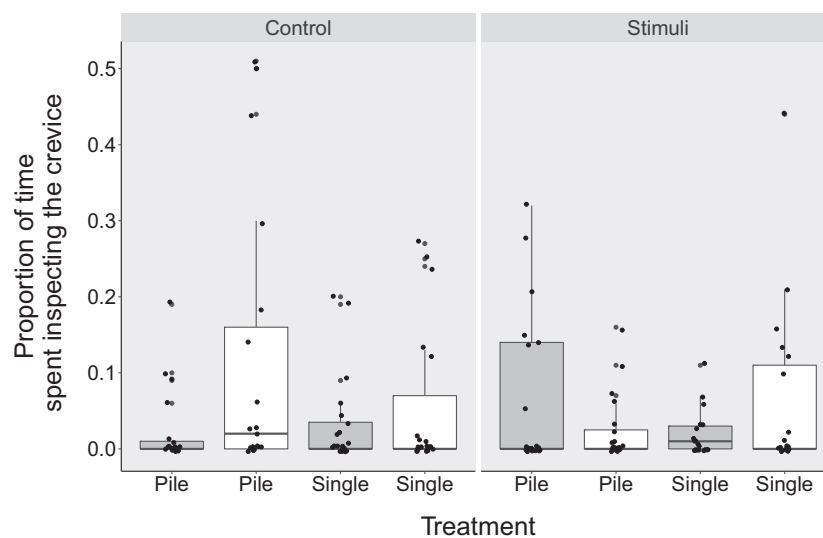
There was a strong two-way interaction between scat deposit type and source in mediating final crevice site choice (Scat deposit type  $\times$  Source:  $\chi^2 = 7.04$ ,  $P = 0.008$ ; Scat deposit type:  $\chi^2 = 0.01$ ,  $P = 0.99$ , Source:  $\chi^2 = 0.13$ ,  $P = 0.71$ ). Specifically, even though an equal number of lizards settled in control *vs.* the stimulus crevice overall (38 out of 76), there was a difference in the frequency of settlement that was dependent on both the scat deposit

**Table 2.** Outputs of a generalised linear mixed model examining the time *E. stokesii* spent inspecting each crevice site. Fixed factors included whether the crevice site was the control *vs.* the stimuli crevice (the one with the scat outside), the scats were in a pile or single, and the source of the scats that is whether they were the lizards own scat (OWS) or a scat from an unfamiliar individual (UFS). We include outputs from the full model and the reduced model, run on the stimuli and control crevice separately. Significant effects are in bold

Factors	Full model		Stimuli crevice		Control crevice	
	$\chi^2$	$P$	$\chi^2$	$P$	$\chi^2$	$P$
Single scat or scat pile	0.97	0.325	1.68	0.19	1.39	0.24
OWS or UFS	<b>11.02</b>	<b>0.001</b>	1.82	0.18	<b>14.43</b>	<b>&lt;0.001</b>
Single scat or scat pile * OWS or UFS	3.77	0.052	2.60	0.11	<b>5.44</b>	<b>0.02</b>
Control or stimuli	<b>7.66</b>	<b>0.006</b>	–	–	–	–
Control or stimuli * OWS or UFS	<b>4.93</b>	<b>0.026</b>	–	–	–	–
Single scat or scat pile* control or stimuli	<b>12.90</b>	<b>&lt;0.001</b>	–	–	–	–
Single scat or scat pile* OWS or UFS * control or stimuli	<b>8.98</b>	<b>0.003</b>	–	–	–	–

**Table 3.** Outputs of a generalised linear mixed model examining the time *E. stokesii* spent in each crevice site. Fixed factors included whether the crevice site was the control *vs.* the stimuli crevice (the one with the scat outside), the scats were in a pile or single, and the source of the scats that is whether they were the lizards own scat (OWS) or a scat from an unfamiliar individual (UFS). We include outputs from the full model and the reduced model, run on the stimuli and control crevice separately. Significant effects are in bold

Factors	Full model		Stimuli crevice		Control crevice	
	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
Single scat or scat pile	1.05	0.31	0.42	0.52	1.04	0.31
OWS or UFS	2.71	0.10	2.67	0.10	2.67	0.10
Single scat or scat pile * OWS or UFS	2.72	0.10	2.00	0.16	2.68	0.10
Control or stimuli	2.71	0.10	–	–	–	–
Control or stimuli * OWS or UFS	1.43	0.23	–	–	–	–
Single scat or scat pile* control or stimuli	<b>5.41</b>	<b>0.02</b>	–	–	–	–
Single scat or scat pile* OWS or UFS * control or stimuli	<b>4.72</b>	<b>0.03</b>	–	–	–	–



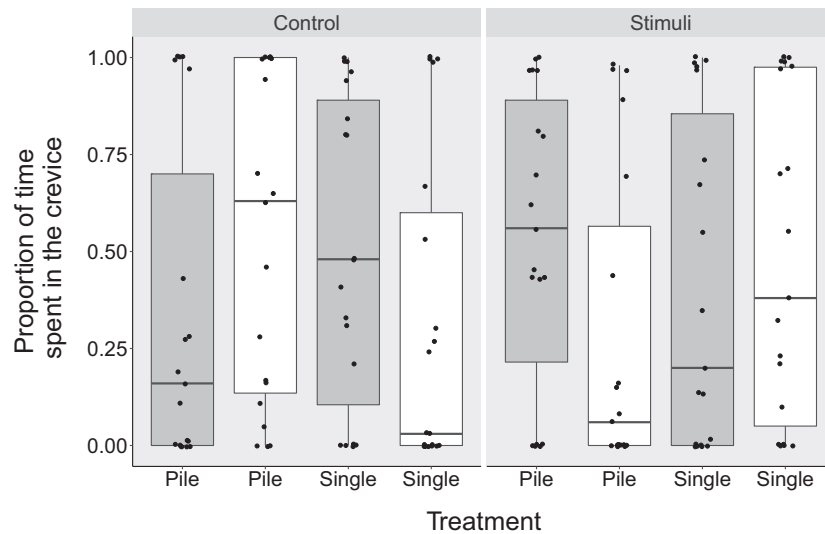
**Fig. 2.** Time *Egermia stokesii* spent inspecting control and stimuli crevice sites. Showing differences in response to the treatment of the stimuli crevice: the type of scat presented (pile *vs.* single) and the source of the scat (own (grey bars) *vs.* unfamiliar (white bars)).

type and the source. More lizards settled in the stimulus crevice when there was a pile of their own scats compared with a pile of unfamiliar scats and when there was a single unfamiliar scat compared with a single familiar scat (Table 4). The amount of time spent in a crevice site during the trial was a strong predictor of whether that lizard was in that crevice site at the end of the trial (e.g. final crevice site choice;  $\chi^2 = 8.08$ ,  $P = 0.004$ ).

## DISCUSSION

We investigated whether refuge choice in a group-living lizard was influenced by source of scat (unfamiliar and unrelated) compared with their own scat, as well as the size of the stimulus – pile or single scat.

Our study has several important findings. First, lizards appeared to behave differently when presented with a scat pile compared with a single scat and that this was influenced by whether the scat pile stimulus was their own or sourced from an unfamiliar conspecific. Specifically, for scat piles, when presented with the control or treatment scat, individuals tended to choose the crevice site with their own scat compared with when they had the choice between the control and the crevice site with the unfamiliar scat. In contrast, for single scats, individuals tended to choose the crevice site with an unfamiliar scat. Behavioural data supported, to some degree, these results. Specifically, individuals spent more time inspecting and more time in the crevice site that contained their own scat when it was in a pile, and more time inspecting and more time in the control crevice when



**Fig. 3.** Proportion of time *Egernia stokesii* spent in control and stimuli crevice sites. Showing differences in response to the treatment of the stimuli crevice: the type of scat presented (pile vs. single) and the source of the scat (own (grey bars) vs. unfamiliar (white bars)).

**Table 4.** *Egernia stokesii* final stimuli crevice site choice according to the type (pile vs. single) and source (own vs. unfamiliar) of the scat

	Stimuli	
	Own	Unfamiliar
Pile	13	6
Single	7	12

the stimuli crevice contained an unfamiliar scat. Conversely, we found the opposite patterns with regards to scat source when scats were on their own. Although these results need to be treated with caution, as some failed to reach statistical significance, combined they provide some support for a role of scats, via chemical cues, in influencing lizard refuge choice. We discuss our results in the context of a number of potential scat-piling functions.

For many animals, defecation sites may have a primary function in social communication (Irwin *et al.* 2004; Apio *et al.* 2006). Social communication, via chemical cues from scats, is widespread among animal groups including amphibians (frog; Lee & Waldman 2002; Waldman & Bishop 2004), mammals (ungulates; Apio *et al.* 2006; primates; Irwin *et al.* 2004; otters; Oldham & Black 2009), monotremes (echidna; Sprent *et al.* 2006) and lizards (Wilgers & Horne 2009). However, despite the widespread use of scat-based chemical communication, the specific function of the information transmitted can differ. One potential function of scats is to indicate presence or occupancy.

The communication of presence via defecation sites has been proposed for mammals (Irwin *et al.* 2004; Kilshaw *et al.* 2009) and lizards (Labra *et al.* 2002; Fenner & Bull 2011b). Indeed, *Egernia* scat-piling may function as an indicator of residency (Bull *et al.* 1999; Bull *et al.* 2000; Chapple 2003; Fenner & Bull 2011a; Ebrahimi *et al.* 2016). This may be particularly important in saturated or patchy environments, such as that in which *E. stokesii* live, where the number of crevices within a rocky outcrop limit the number of individuals and social groups.

Further to signalling presence, chemical cues in scats may also convey more subtle information related to inter-group communication. As social interactions have fitness consequences (Silk 2007), many animals have evolved the ability to assess social familiarity. For example, latrines may communicate female and/or male presence to neighbouring groups in lemurs (*Hapalemur meridionalis*); information that may contribute to mate guarding, maintaining home ranges and reducing rates of inter-group agonism (Eppley *et al.* 2016). Investigation, rather than over-marking, of scats suggests defecation sites function in social recognition. For example, obtaining social information rather than territoriality may better explain group-living otters' (*Lontra canadensis*) strong investigative behaviours in response to foreign scat (Oldham & Black 2009). Similarly, some lizards appear to use chemical cues from scats to differentiate familiar and unfamiliar individuals (Bull *et al.* 2000; Moreira *et al.* 2008; Wilgers & Horne 2009). For example, like *E. stokesii*, *E. striolata* form aggregations, create scat piles and can discriminate between their own scats and that of conspecifics (Bull

*et al.* 1999). In contrast, although *Liopholis inornata* form scat piles, individuals do not form aggregations and cannot discriminate between their own scats and that of conspecifics (Bull *et al.* 1999). Further, Bull *et al.* (1999) report differences in the distribution of scat piles of the two species: *L. inornata* do not deposit scats in one location whereas *E. striolata* deposit their scats around a preferred basking site. The non-random placement of scat piles may provide a stronger signal for group and non-group members alike. Thus, similar to studies of other animal groups, our findings suggest that lizard scat-piling may play a role in inter-group communication with consequences for individual and group spacing.

There are several alternative functional explanations for *E. stokesii* scat-piling behaviour. Scat piles may function to reduce parasite transmission, deter predators or attract prey. Parasite avoidance via defecation sites is proposed for reindeer (*Rangifer tarandus platyrhynchus*; Van der Wal *et al.* 2000), red howler monkeys (*Alouatta seniculus*; Gilbert 1997) and three species of ungulates (*Madoqua kirikii*, *Gazella granti* and *Aepyceros melampus*; Ezenwa 2004). However, because lizards use tongue-flicks to explore chemical cues in scats (Bull *et al.* 2000), scat-piling may enhance parasite transmission (Hallas *et al.* 2005); therefore, the parasite avoidance function is unlikely. The use of defecation sites may help to mitigate predation risk (Boonstra *et al.* 1996). For example, lemming (*Dicrostonyx groenlandicus*) latrines are located underground during summer, when predation risk is high (Boonstra *et al.* 1996). In contrast, *Egernia* lizard scat piles are located in open areas close to refuge sites rather than concealed under rocks or within crevices (Chapple 2003). Scat-piling as a means of avoiding predators is therefore unlikely. Further, because *Egernia stokesii* is primarily herbivorous or omnivorous, rather than insectivorous (Chapple 2003), it appears scat-piling to attract insect prey is also unlikely. Thus, although we did not test these alternative functions, we suggest they play no role, or only a minor role, in *E. stokesii* scat-piling behaviour.

Our results should be interpreted within the context of a number of caveats. First, our experimental design only allowed us to compare an individual's responses to its own scat compared with an unfamiliar conspecific. Whether these results would hold if we had used scats from a related individual, or entire family group, is unknown. Second, because we did not know the relatedness of individuals within each of the two source populations, we restricted our source of unfamiliar scats to individuals of the other population. Depending on the level of divergence between source populations, this may represent a level of unfamiliarity that is not biologically realistic in the context of the communication of social information at a local scale. Third, we cannot separate the

roles of familiarity and relatedness using this design, as focal animals are both related and familiar to their own scents and unfamiliar and unrelated to the scents of the unfamiliar individuals. Combined, these caveats suggest that inferences about the extent to which scat piles may function in the social organisation of this species should be treated with caution.

Although our findings present novel insights into the use of chemical cues in *E. stokesii* refuge choice, further research is warranted to better understand the extent to which chemical communication may mediate social organisation more broadly in group-living lizards. Outstanding questions include the following: (i) 'is there is a threshold to the number of scats in a pile that elicits a response?'; (ii) 'do scat piles communicate refuge availability and suitability?'; (iii) 'do scat piles mediate mate and group choice decisions?'; (iv) 'does reproductive season or sex (of the defacator) modify the influence of scat piles on refuge choice?'; and (v) 'what molecules in scat facilitate discrimination?'

Evidence shows that lizards are able to distinguish and identify individuals from scats, presumably based on chemical signals. Yet, little is known about signal sources. Chemosignal sources include genes of the major histocompatibility complex (Beauchamp *et al.* 1985) and major urinary proteins, a class of proteins that bind and release volatile pheromones (Hurst *et al.* 2001). How these, and/or other sources, contribute to chemical signals used in lizard social communication is yet to be understood.

In conclusion, we demonstrate that the scat-piling behaviour observed in *E. stokesii* influences refuge choice, but that this is potentially dependent on the information contained within the scats. Refuge choice has implications for individual and group spacing, and thus inter-individual and inter-group communication. Our findings are therefore a step towards understanding the role of chemical communication in lizard social organisation. Whether, and how, scat piles mediate social organisation in this and other aggregating lizard species is yet to be explored. Greater insight into potential links between scat-piling and aggregating behaviours in lizards will facilitate comparison of group-living dynamics across a broader range of taxa than currently possible.

## ACKNOWLEDGEMENTS

We thank Leslie Morrison and the staff at the Flinders University Animal House for their assistance with the captive lizards, and Scarlett Graf for assistance with recently caught lizards. We also thank Michael Schwarz and Pawel Skuza for statistical assistance. This project was supported by a grant from the Australian Research Council (DP150102900) to MGG, DGC and GMW.

## CONFLICT OF INTEREST

We report no conflict of interest.

## ETHICS APPROVAL

All animals were handled following SOP-BIOL-3-06/2015-Lizard. Ethics approval for this project was granted by the Flinders University Animal Welfare Committee (project number E442/15). Captive and wild lizards were managed in compliance with the standards and procedures in the Australian Code of Practice for the use of animals for scientific purposes. Funding from Australian Research Council grant DP150102900.

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## SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

**Appendix S1.** Artificial crevice design.

**Appendix S2.** Experimental pen set up.