CSIRO PUBLISHING
www.publish.csiro.au/journals/ajz *Australian Journal of Zoology*, 2006, **54**, 271–275

Social aggregation by thick-tailed geckos (*Nephrurus milii*, Gekkonidae): does scat piling play a role?

Bansi Shah[A,B,C], *Simon Hudson*[A] *and Richard Shine*[A]

[A]School of Biological Sciences A08, University of Sydney, NSW 2006, Australia.
[B]Present address: PO Box 2189, Warwick, WA 6024, Australia.
[C]Corresponding author. Email: bansi@conservationsafaris.com

Abstract. Communal deposition of faeces into scat piles plays a role in pheromonal communication among group members in many 'social' vertebrates, including the scincid lizard *Egernia stokesii*. How general is this apparent link between scat piling and sociality? Thick-tailed geckos (*Nephrurus milii*, Gekkonidae) are large nocturnally active lizards that are widely distributed across southern Australia. They spend the daylight hours inactive inside retreat sites, typically rock crevices or burrows. Unusually among geckos, these animals often form groups of several individuals at these times. Our observations of captive *N. milii* showed that they also form discrete scat piles. However, habitat-selection experiments suggested that adding scats to a crevice did not modify the lizards' probability of using that crevice. Thus, although *Nephrurus milii* scat pile (at least in captivity), communal faeces deposits do not appear to serve a social role in this taxon.

Introduction

In many mammal species that form social groups, pheromonal cues from communally deposited faeces help to maintain group cohesion (Jarvis 1985; Sneddon 1991; Roper *et al*. 1993; Vila *et al*. 1993). Similarly, red-backed salamanders (*Plethodon cinereus*) use scats as territorial advertisements and for individual recognition (Jaeger 1981, 1986; Jaeger *et al*. 1986; Horne and Jaeger 1988). Thus, scat piling (the deposition of faeces by individuals in a specific place so that they accumulate into piles: Bull *et al*. 1999) is a phylogenetically widespread and potentially important behaviour in the context of social organisation.

Both scat piling and social groupings occur in a variety of lizard species (e.g. Bull *et al*. 2000; Chapple 2003; Fuller *et al*. 2005). Most lizards reported to scat pile belong to the Australian scincid genus *Egernia* (Bull *et al*. 1999; Chapple 2003): at least six of the 26 species of *Egernia*, including *E. stokesii* (White 1976; Swan 1990) and *E. striolata* (Bustard 1970), scat pile close to their basking sites (Greer 1989), while *Egernia hosmeri* has communal scat piles (Stammer 1976). *Egernia* species also display complex social behaviour involving stable long-term groups (Bull *et al*. 2000, 2001; Lanham and Bull 2000; Gardner *et al*. 2001; O'Connor and Shine 2002; Chapple 2003). The apparent correlation between sociality and scat piling suggests the possibility of a causal connection. In support of this inference, *E. striolata* use chemosensory cues to discriminate between their own scats and those of conspecifics (Bull *et al*. 1999).

Egernia species are not the only lizards to exhibit either (or both) scat piling or aggregative behaviour, and both of these traits probably occur more widely than is evident from published reports. For example, western banded geckos (*Coleonyx variegatus*) also scat pile (Carpenter and Duvall 1995), as do captive spiny-tailed geckos (*Diplodactylus intermedius*) and leaf-tailed geckos (*Phyllurus platurus*) (B. Shah, unpublished data). Social aggregations also are known in gekkonids (e.g. *Hoplodactylus duvauceli*: Robb 1980; *Coleonyx variegatus*: Greenberg 1943; Cooper *et al*. 1985). Notably, one gecko from southern Australia (the thick-tailed gecko, *Nephrurus milii*, Gekkonidae) forms aggregations both in the field (Kearney *et al*. 2001; Shah 2002) and under laboratory conditions (Shah *et al*. 2004). This phylogenetically independent evolution of aggregative behaviour offers an ideal opportunity to examine the consistency of the putative link between scat piling and sociality.

Methods

Study species

Thick-tailed geckos are relatively large (adults average 80 mm snout–vent length), nocturnal, terrestrial lizards that occur across southern Australia from the east to west coasts (Cogger 2000). They occur in a variety of habitats including arid scrublands and rocky hills (Swan 1990; Cogger 2000), sheltering under slabs of rock, in burrows and beneath loose bark while inactive (Swan 1990; Johnstone and Werner 2001). In the field, aggregations within these diurnal retreat-sites may contain up to nine animals, and may include male, female and juvenile individuals (Kearney *et al*. 2001).

Laboratory studies

We collected animals from Mt Korong (36°45′S, 144°17′E) in Victoria, ~200 km north-west of Melbourne (Australia) in July 2001. The lizards were transported to the University of Sydney where they were maintained in plastic enclosures. Pairs were housed in the groupings in

 10.1071/ZO06012 0004-959X/06/040271

which they were encountered in the field, with the 10 adult pairs in larger enclosures (290 × 215 × 65 mm) than the 30 juvenile pairs and 23 solitary adults (220 × 220 × 70 mm). Plastic shelters were provided within each enclosure, one for solitary individuals and two for paired individuals. Heating tape running beneath the back of each enclosure provided a thermal gradient from 20 to 29°C during daylight hours; at night the heating tape was switched off, allowing the enclosure to cool to room temperature (20°C). Crickets were provided twice weekly as food, and water was available *ad libitum*.

Do geckos scat pile?

We cleaned the animals' 'home' enclosures (see above) and then added 2–3 cm-deep fresh washed sand to each enclosure. Following this initial clean, scats were left in the enclosures where they were deposited. All paired juvenile geckos' enclosures were checked after 2 weeks, while the enclosures containing paired adult geckos and solitary adult geckos were checked after 5 weeks, to allow enough time for scats to be deposited (adult geckos produce fewer, larger scats than do juvenile geckos). We divided each enclosure into several equal-sized quadrats, using a template made out of bamboo sticks, and then counted the number of scats per quadrat in each enclosure. Because adult pairs were housed in larger plastic enclosures than solitary adults and juvenile pairs, paired adults' enclosures were divided into 12 quadrats (72.5 × 71.5 mm each) whereas solitary adult and paired juveniles' enclosures were divided into nine quadrats (73 × 73 mm each).

All enclosures containing two geckos had two plastic half-pipe shelters (120 mm long, 50 mm diameter), whereas solitary geckos had one. Shelters in each enclosure overlapped two to four quadrats and water bowls overlapped one or two quadrats. This overlap was the same for all three groups of geckos and enclosures being compared to each other. Data on scat locations were analysed for each enclosure against a null hypothesis of equal frequencies of scat deposition in each quadrat, using a *G*-test. Because one potential explanation for non-random accumulation of scats was simply that they were deposited in shelters where animals spent most of their time, we then repeated these tests after excluding all quadrats containing shelters (i.e. comparing among quadrats used by active animals only). To compare datasets obtained for solitary adults and paired juveniles (housed in same-sized enclosures), we conducted a one-factor ANOVA incorporating spatial covariance (spatial spherical covariance structure, using SAS mixed-procedure approach).

Does the location of previous scats determine subsequent defecation location?

To test whether juvenile geckos used the presence of a scat pile containing some of their own scats as a cue to deposit more scats on the pile, we used 28 experimental units (360 × 280 × 195 mm) with a sand substrate, and natural light–dark cycles. Each unit contained two plastic shelters (130 × 130 × 22 mm). Twenty-eight juvenile geckos were chosen randomly, and a pile containing 10 scats of varying age (up to 1 month old) from each gecko's home enclosure was placed inside one of the two shelters (selected randomly) in each unit. Geckos were placed in experimental units at 1700 hours, left overnight, and removed at 0930 hours the following morning. Of the 28 geckos, 16 had deposited one or more scats. The units were divided into two and the freshly deposited scats were scored as either in the same half of the enclosure as the scat pile, or in the 'empty' half. Data collected for new scat deposition were analysed using a Pearson's Chi-square to test the null hypothesis that equal numbers of scats were deposited in the side of the cage with versus without the experimentally placed scat pile.

Do geckos select retreat sites based on scat presence?

If scat piles act as social signals to the lizards and provide information about conspecifics, geckos might either preferentially select a shelter site containing scats from their own enclosure, or avoid it. We used the same experiment as above and recorded whether the lizards selected retreat sites with or without the scat piles added experimentally.

Results

Do geckos scat pile?

Every pair of juvenile geckos showed significant scat piling after 2 weeks, against the null hypothesis of equal rates of scat deposition per quadrat ($\chi^2 > 15.51$, d.f. = 8, $P < 0.05$ in every case). Of these, more than half of the paired juveniles piled more than 80% of all scats in a single quadrat, or two adjacent quadrats. All 10 pairs of adult geckos, and 22 out of 23 solitary adult geckos, also showed significant levels of scat piling after 5 weeks ($\chi^2 > 19.68$, d.f. = 11, $P < 0.05$ in each of these cases). This result was not an artefact of lizards defecating in their diurnal retreat sites: 28 of 30 paired juveniles, 10 of 10 paired adults and 22 of 23 solitary adults showed non-random scat deposition even if analysis was restricted to quadrats that did not contain shelters (for all of these cases, $\chi^2 > 9.49$, d.f. = 4, $P < 0.05$). Because paired juvenile and solitary adults were housed in same-sized enclosures with the same number of quadrats, we could directly compare these two datasets with a one-factor spatial spherical covariance ANOVA with age class as the factor and quadrat as the repeated measure. The analysis confirmed that, in both cases, some quadrats received significantly more scats than others ($F_{8,430} = 3.85$, $P < 0.0002$) (see Fig. 1), but that adults and juveniles did not differ overall in the number of scats produced over the durations of these experiments ($F_{1,430} = 0.23$, $P = 0.63$), nor in the distribution of scats among quadrats (interaction, $F_{8,430} = 0.81$, $P = 0.59$).

Does the location of previous scats determine subsequent defecation location?

Juvenile geckos showed no significant tendency to deposit fresh scats next to or on scat piles containing their own scats (nine of 16 geckos deposited scats on or next to the scat piles; $\chi^2 = 0.25$, d.f. = 1, $P > 0.05$).

Do geckos select retreat sites based on scat presence?

Seventeen of 28 individuals selected shelters containing piles of scats. Thus, the geckos did not modify their choice of retreat sites on the basis of the presence of scats ($\chi^2 = 2.43$, d.f. = 1, $P > 0.05$).

Discussion

Both adult and juvenile thick-tailed geckos scat piled within their enclosures. Juvenile geckos scat piled when housed in pairs; adult geckos scat piled both when housed individually and when housed in pairs. This pattern was not due to defecation within retreat sites, because scat piling was also non-random within quadrats that did not contain shelters. Over half of juvenile pairs concentrated their scats in two or fewer quadrats.

Amongst geckos, only the western banded gecko (*Coleonyx variegatus*) and Texas banded geckos (*Coleonyx brevis*) have been reported to scat pile in the field (Carpenter and Duvall 1995). Western banded geckos formed scat piles when housed individually, and also in an arena that had been previously marked via scat piling by a member of the opposite sex (Carpenter and Duvall 1995). Carpenter and Duvall (1995) also observed communal defecation when several geckos were housed together in a common terrarium. The lizards in that study scat piled in shelters in 61% of trials, usually in shelters that were not used as diurnal retreat sites (Carpenter and Duvall 1995). Similarly, we observed that thick-tailed geckos that scat piled in shelters tended to do so in only one of the two available shelters, mostly the one not used as a diurnal retreat site. This behaviour may reduce disease transmission, or scent cues that might otherwise attract predators (Ford and Burghardt 1993; Carpenter and Duvall 1995). Scat deposition outside the shelters was highly non-random also, suggesting that scat piling was not simply an artefact of restricted movements by the geckos.

Both skinks (Bull *et al*. 1999) and geckos (Carpenter and Duvall 1995) can differentiate between their own scats and those of conspecifics, as well as from control substances. Western banded geckos deposited more scats in the end of the arena containing an extract of their own faecal scent (Carpenter and Duvall 1995). Thick-tailed geckos in our

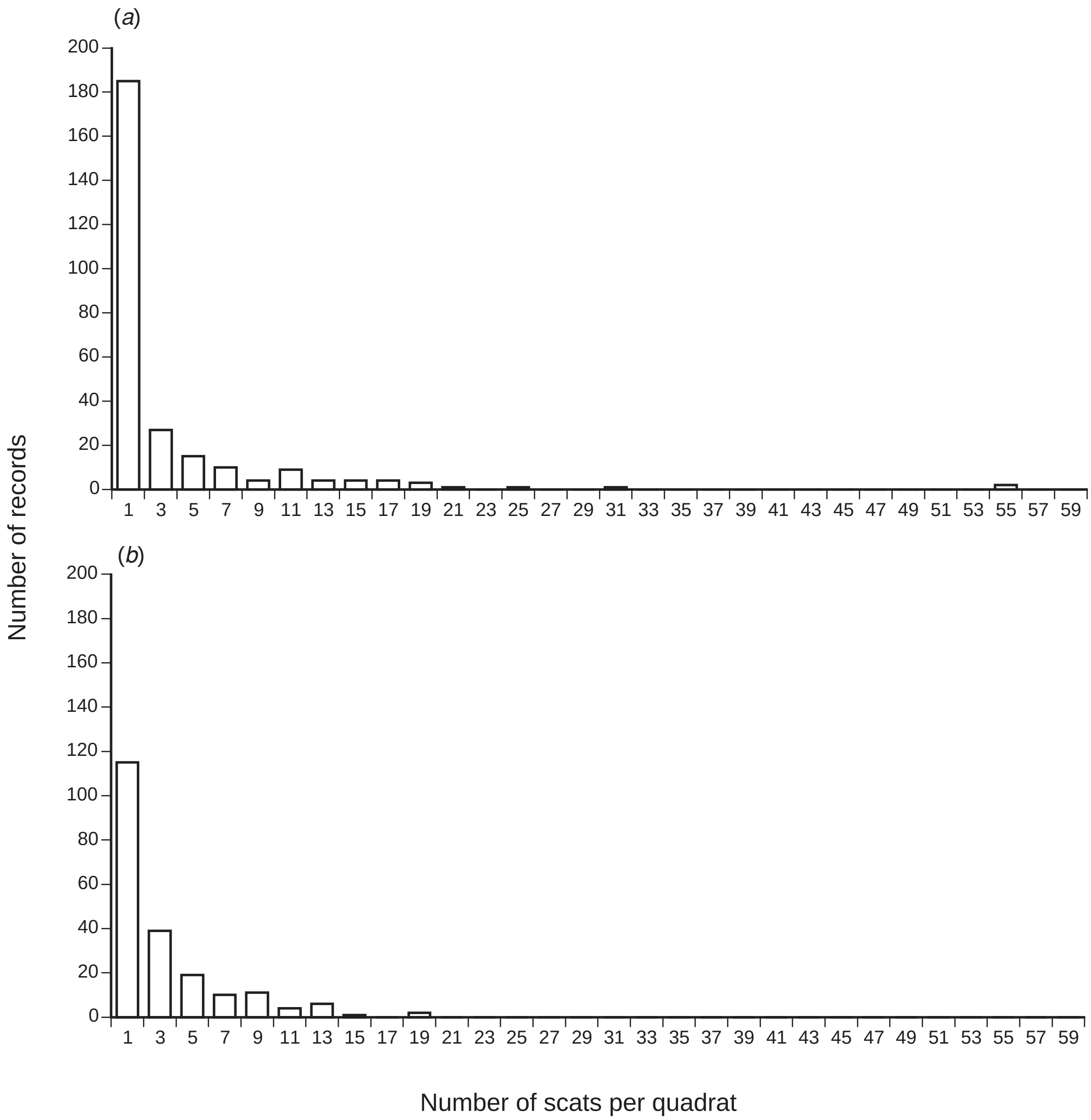

Fig. 1. Number of scats deposited per quadrat by captive thick-tailed geckos. Data are for (*a*) juveniles and (*b*) adults. Scat piling by both age groups resulted in most quadrats receiving no scats but a few quadrats receiving many scats.

study, however, did not preferentially defecate on piles containing their own scats. Some of the scats we used in these trials were relatively old, and thus may have provided few chemical cues (Carpenter and Duvall 1995; Bull *et al*. 1999). However, non-social explanations for scat piling are plausible also. For example, some species of nocturnal lizards may defecate in diurnal shelters because they attain optimal body temperatures for digestion only during the day (Carpenter and Duvall 1995).

In summary, our data show that thick-tailed geckos form scat piles under laboratory conditions. However, the social significance (if any) of this behaviour remains unclear, and our data suggest that field aggregations are unlikely to reflect responses to communal scat piles. Thus, alternative explanations for the cues eliciting aggregation are required, perhaps involving thermal ecology (Shah *et al*. 2003). It seems likely that both scat piling and aggregative behaviour are widespread in lizards, and have evolved many times in separate lineages. These scats offer a rich source of pheromonal information, and hence may later be co-opted by natural selection to act as social signals (Bull *et al*. 1999). Under this scenario, we expect that future studies will show that scat piling and sociality are linked functionally in some lizard taxa but not in others. *N. milii* appears to fall into the latter group, but we caution that future studies are needed to determine whether or not scat piling by this species occurs in the field as well as in captivity.

Acknowledgments

We thank D. Brown, S. Comber, M. Kearney, N. Kearney and P. Shah for assistance with collecting geckos in the field, and M. Kearney for extensive advice and comments. This work was carried out in accordance with the University of Sydney Animal Ethics Committee and under a scientific licence from the New South Wales National Parks and Wildlife Service. Financial support was provided by the Australian Research Council (to R. Shine).

References

Bull, C. M., Griffin, C. L., and Johnston, G. R. (1999). Olfactory discrimination in scat piling lizards. *Behavioral Ecology* **10**, 136–140. doi:10.1093/beheco/10.2.136

Bull, C. M., Griffin, C. L., Lanham, E. J., and Johnston, G. R. (2000). Recognition of pheromones from group members in a gregarious lizard, *Egernia stokesii. Journal of Herpetology* **34**, 92–99. doi:10.2307/1565244

Bull, C. M., Griffin, C. L., Bonnett, M., Gardner, M. G., and Cooper, S. J. B. (2001). Discrimination between related and unrelated individuals in the Australian lizard *Egernia striolata. Behavioral Ecology and Sociobiology* **50**, 173–179. doi:10.1007/s002650100348

Bustard, H. R. (1970). A population study of the scincid lizard *Egernia striolata* in northern New South Wales. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series C* **73**, 186–213.

Carpenter, G. C., and Duvall, D. (1995). Fecal scent marking in the western banded gecko (*Coleonyx variegatus*). *Herpetologica* **51**, 33–38.

Chapple, D. (2003). Ecology, life-history, and behaviour in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs* **17**, 145–180.

Cogger, H. G. (2000). 'Reptiles and Amphibians of Australia.' 6th edn. (Reed New Holland: Sydney.)

Cooper, W. E., Jr, Caffrey, C., and Vitt, L. J. (1985). Aggregation in the banded gecko *Coleonyx variegatus. Herpetologica* **41**, 342–350.

Ford, N., and Burghardt, G. (1993). Perceptual mechanisms and the behavioural ecology of snakes. In 'Snakes. Ecology and Behaviour'. (Eds R. Seigel and J. Collins.) pp. 117–164. (McGraw-Hill: New York.)

Fuller, S. J., Bull, C. M., Murray, K., and Spencer, R. J. (2005). Clustering of related individuals in a population of the Australian lizard, *Egernia frerei. Molecular Ecology* **14**, 1207–1213. doi:10.1111/j.1365-294X.2005.02478.x

Gardner, M. G., Bull, C. M., Cooper, S. J. B., and Duffield, G. A. (2001). Genetic evidence for a family structure in stable social aggregations of the Australian lizard *Egernia stokesii. Molecular Ecology* **10**, 175–183. doi:10.1046/j.1365-294X.2001.01171.x

Greenberg, B. (1943). Social behaviour of the western banded gecko, *Coleonyx variegatus* Baird. *Physiological Zoology* **16**, 110–122.

Greer, A. E. (1989). 'The Biology and Evolution of Australian Lizards.' (Surrey Beatty: Sydney.)

Horne, E. A., and Jaeger, R. G. (1988). Territorial pheromones of female red-backed salamanders. *Ethology* **78**, 143–152.

Jaeger, R. G. (1981). Dear enemy recognition and the costs of aggression between salamanders. *American Naturalist* **117**, 962–974. doi:10.1086/283780

Jaeger, R. G. (1986). Pheromonal markers as territorial advertisement by terrestrial salamanders. In 'Chemical Signals in Vertebrates'. (Eds D. Duvall, D. Muller-Schwarze and R. M. Silverstein.) pp. 191–203. (Plenum: New York.)

Jaeger, R. G., Goy, J. M., Tarver, M., and Marquez, C. E. (1986). Salamander territoriality: pheromonal markers as advertisement by males. *Animal Behaviour* **34**, 860–864. doi:10.1016/S0003-3472(86)80071-9

Jarvis, J. U. M. (1985). Ecological studies on *Heterocephalus glaber*, the naked mole-rat in Kenya. *National Geographical Society Research Reports* **20**, 429–437.

Johnstone, B. M., and Werner, Y. L. (2001). Hearing in some Australian geckos (Reptilia: Sauria: Gekkonomorpha) as tested electrophysiologically. *Herpetological Natural History* **8**, 49–56.

Kearney, M., Shine, R., Comber, S., and Pearson, D. (2001). Why do geckos group? An analysis of "social" aggregations in two species of Australian lizards. *Herpetologica* **57**, 411–422.

Lanham, E. J., and Bull, C. M. (2000). Maternal care and infanticide in the Australian skink *Egernia stokesii. Herpetological Review* **31**, 151–152.

O'Connor, D., and Shine, R. (2002). Lizards in 'nuclear families': a novel reptilian social system in *Egernia saxatilis. Molecular Ecology* **12**, 743–752. doi:10.1046/j.1365-294X.2003.01777.x

Robb, J. (1980). Three new species of gekkonid lizards, genera *Hoplodactylus* and *Heteropholis*, from New Zealand. *National Museum of New Zealand Records* **1**, 305–310.

Roper, T. J., Conradt, L., Butler, J., Christian, S. E., Ostler, J., and Schmid, T. K. (1993). Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. *Behaviour* **127**, 289–307.

Shah, B. (2002). Why do thick-tailed geckos (*Underwoodisaurus milii*) aggregate? B.Sc.(Honours) Thesis, University of Sydney.

Shah, B., Shine, R., Hudson, S., and Kearney, M. (2003). Sociality in lizards: why do thick-tailed geckos (*Nephrurus milii*) aggregate? *Behaviour* **140**, 1039–1052. doi:10.1163/156853903322589632

Shah, B., Shine, R., Hudson, S., and Kearney, M. (2004). An experimental study of retreat-site selection by thick-tailed geckos, *Nephrurus milii. Austral Ecology* **29**, 547–552. doi:10.1111/j.1442-9993.2004.01388.x

Sneddon, I. A. (1991). Latrine use by the European rabbit (*Oryctolagus cuniculus*). *Journal of Mammology* **72**, 769–775.

Stammer, D. (1976). Reptiles. In 'Around Mt Isa. A Guide to the Flora and Fauna'. (Ed. H. Horton.) pp. 131–159. (University of Queensland Press: Brisbane.)

Swan, G. (1990). 'A Field Guide to the Snakes and Lizards of New South Wales.' (Three Sisters Productions: Sydney.)

Vila, C., Urios, V., and Castroviejo, J. (1993). Use of faeces for scent marking in Iberian wolves (*Canis lupus*). *Canadian Journal of Zoology* **72**, 374–377.

White, J. (1976). Reptiles of the Corunna Hills. *Herpetofauna* **8**, 21–23.

Manuscript received 18 January 2006, accepted 2 June 2006