

SOCIALITY IN LIZARDS: WHY DO THICK-TAILED GECKOS (*NEPHRURUS MILII*) AGGREGATE?

by

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Summary

Unusually among lizards, Australian thick-tailed geckos (*Nephrurus milii*) aggregate in their diurnal retreat-sites. They continue to do this in the laboratory, even when excess shelters are available. We manipulated cues available to captive lizards to investigate three putative advantages to aggregation: enhanced social interactions, avoidance of predators, and control over rates of heat or water flux. Trials in which we prevented physical contact with conspecifics eliminated the aggregative response, suggesting that chemical and visual cues alone do not stimulate aggregation. Adding the scent of a predatory snake did not modify the degree of aggregation, nor did changes in mean ambient temperature or humidity. However, geckos exposed to decreasing temperatures huddled more closely with each other within shelters, and huddled geckos heated and cooled more slowly than did similar-sized solitary animals. We suggest that aggregative behaviour in *Nephrurus milii* has evolved to provide facultative control over rates of thermal exchange, an advantage because *Nephrurus* are large, live in cool variable climates, and occupy retreat-sites (rock crevices with high exposure to solar radiation) that experience highly variable thermal regimes. These attributes are shared by another group of lizards, the scincid genus *Egernia*, that exhibit the most complex sociality yet described among squamate reptiles. The initial stimulus for group formation in both geckos and skinks may have been thermal control, preadapting the scincids to further elaboration of social behaviour.

Keywords: aggregation, reptile, sociality, thermoregulation.

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Introduction

To understand the evolution of sociality in vertebrates, we need detailed studies of species that represent phylogenetically independent origins and losses of this behaviour (Harvey & Pagel, 1991). However, although this topic has stimulated a massive scientific literature, research has focused disproportionately on a relatively small number of lineages (especially mammals and birds: *e.g.* Hoogland, 1983; Legge & Cockburn, 2000; East & Hofer, 2001). Many taxa within these lineages have attracted study, but most do not constitute evolutionarily independent examples of social organization. For example, parental care of offspring is widespread among endothermic vertebrates, and the ancestral mating system of modern birds may well have involved monogamous pair-bonding (Temrin & Sillen-Tullberg, 1994). If so, the number of genuinely independent evolutionary origins of sociality in endotherms may be low. To better understand the selective forces that have shaped patterns of vertebrate social organization, we need information from lineages that represent independent origins of sociality. Squamate reptiles offer a valuable opportunity in this respect. Most species of lizards and snakes appear to have relatively simple social systems, with individuals typically solitary for most of the time. However, there are anecdotal reports of aggregations in taxa from a diverse array of lineages (Greenberg, 1943; Brattstrom, 1974; Cooper *et al.*, 1985; Cooper & Gartska, 1987; Mouton *et al.*, 1999). Parental care is rare within squamate reptiles (Shine, 1988; Somma, 1990; Shine *et al.*, 1997), further simplifying potential selective forces and thus, facilitating analysis.

Detailed research on squamate sociality has focused on a single lizard lineage that displays the most complex patterns of social organization yet reported for reptiles. This lineage comprises large viviparous scincid lizards belonging to the closely-related genera *Egernia* and *Tiliqua*, both widespread in southern Australia (Cogger, 2000). This work has documented many phenomena not previously suspected to occur within reptiles, including long-term monogamy and stable social groupings of closely-related individuals (Bull, 1988; Bull *et al.*, 1998, 1999, 2000; Gardner *et al.*, 2001; Stow *et al.*, 2001; O'Connor & Shine, 2003). However, this concentration of research again raises the problem of phylogenetic independence of case-studies. Ideally, we need analyses of other reptile lineages that display independent evolutionary origins of sociality.

The Australian gekkonid lizard *Nephurus milii* offers exactly this opportunity. Unlike most other gekkonids (which are found solitarily in the wild: Bustard, 1970, 1971; Cooper *et al.*, 1985), thick-tailed geckos aggregate in groups of up to 20 individuals within their diurnal retreat-sites (Kearney *et al.*, 2001; Shah, 2002). This behaviour is not a simple result of limited shelter-sites, because lizards continue to aggregate even when surplus shelters are available (Shah, 2002). Thus, we conducted laboratory experiments to explore cues that stimulate aggregation. We focused on three possible benefits: (1) social interaction; (2) predator avoidance; and (3) control over rates of thermal or hydric exchange with the environment.

Methods

Study species and housing conditions

Thick-tailed geckos (*Nephurus milii*) are large terrestrial lizards, averaging approximately 80 mm SVL as adults (Cogger, 2000). They are nocturnal and feed mainly on insects, spiders and scorpions, occasionally eating smaller lizards of other species (Cronin, 2001). Thick-tailed geckos range from the east to west coasts of southern Australia, occurring in a variety of habitats including sclerophyll forests, arid scrublands and rocky hills (Swan, 1990; Cogger, 2000). By day the geckos shelter in burrows under slabs of rocks and beneath loose bark (Swan, 1990; Johnstone & Werner, 2001). Field surveys have shown that such aggregations occur more often than expected by chance, and that groups vary widely in composition (*i.e.* most age-sex groups can be found together: Kearney *et al.*, 2001; Shah, 2002). Captive lizards aggregate even in the presence of surplus shelter-sites, indicating that these geckos actively select retreat-sites containing conspecifics (Shah, 2002).

We collected 123 animals by hand after turning rocks at Mt Korong (36°45'S, 144°17'E) in Victoria, approximately 250 km north-west of Melbourne (Australia) in July 2001. The lizards were transported to the University of Sydney where they were maintained either in pairs or as solitary individuals (depending on whether they had been captured together or not) in plastic boxes measuring 220 × 220 × 70 mm (for paired juveniles and solitary adults) or 290 × 215 × 65 mm (for paired adults). Lizards > 60 mm SVL were classed as adults, following How *et al.* (1990) and Kearney *et al.* (2001). Plastic shelters were provided within each cage; one for solitary individuals and two for paired individuals. Heating tape running beneath the back of each cage provided a thermal gradient from 20 to 29°C during daylight hours; at night the heating tape was switched off, allowing the cage to cool to room temperature (20°C). Shelter-items were provided within each cage. Crickets were provided twice-weekly as food, and water was available *ad libitum*. At the conclusion of the study (May 2002), all lizards were returned to their sites of capture and released unharmed.

Social interactions

If aggregation by thick-tailed geckos reflects benefits associated with social interactions (*e.g.* reproductive opportunities; development of dominance hierarchies), a gecko's age/sex class

should affect whether it selects or avoids conspecifics and if so, which ones. To test this hypothesis, we monitored shelter-site selection by a gecko when one of two alternative shelters contained another gecko.

Experiments were conducted between October 2001 and February 2002 in 25 plastic bins ($28 \times 36 \times 19.5$ cm for most trials; $57 \times 36 \times 19.5$ cm for predator-scent study). Experimental units contained two identical plastic trays ($13 \times 13 \times 2.2$ cm) inverted to act as shelters, each with a 4 cm wide opening to allow entry. Each unit had an opaque cover with ventilation holes to eliminate extraneous cues. Experiments were set up in the afternoon and animals were left in experimental units overnight (from 1600 to 0830 h). In the morning, we recorded the shelter under which each experimental gecko was resting. Geckos that had not selected a shelter at the time of checking ($N = 3$, from 181 trials) were excluded from the results. Lizards were given at least one night's rest between successive experiments and each gecko combination was only used once per experiment. Following each experiment, all shelters were soaked in hot soapy water for 30 minutes, then vigorously scrubbed, soaked for another 30 minutes in hot water, rinsed and air-dried.

To establish responses of specific sex and age groups of geckos to individuals of other age and sex groups, we restrained a gecko inside one shelter to give the experimental lizard a choice between that gecko and the second shelter containing an object the same size as the restrained gecko. To restrain a lizard within one shelter, we inserted plastic mesh to divide each shelter diagonally into two halves. Holes in the mesh divider were large enough (4×5 mm) to allow geckos to obtain scent cues via tongue-flicking the restrained conspecific. One half of the shelter was thus enclosed to restrain a lizard (bounded by two sides of the shelter and the mesh), with the other half identical except for an opening providing access into the shelter for the experimental gecko. Restrained geckos had room to move around; they settled down quickly, and attempts to escape the shelter were very rare.

Each evening, the geckos to be restrained were placed behind the divider of one shelter and a gecko-sized wooden clothes-peg was placed behind the divider of the other shelter. An experimental gecko was placed in the centre of each experimental unit, with the other gecko remaining behind its divider throughout the trial. For consistency, the two geckos in each trial had not been collected or housed together. We conducted experiments using sex/age classes of lizards (J = juvenile, AF = adult female, AM = adult male) in the following combinations (experimental *vs* restrained, sample size; see Table 1): J *vs* J ($N = 56$); J *vs* 3J ($N = 28$); J *vs* AM ($N = 20$); J *vs* AF ($N = 32$); J *vs* AF + 2J ($N = 16$); AM *vs* AF ($N = 16$); AM *vs* AM ($N = 12$); AM *vs* J ($N = 20$); AF *vs* AF ($N = 8$); AF *vs* AM ($N = 32$); AF *vs* J ($N = 16$). Sample sizes varied because of availability of lizards. In some cases we expanded sample sizes by using some lizards twice (with different combinations of individuals in the two trials) to increase statistical power. This procedure violates the assumption of statistical independence among trials. Such non-independence may affect the validity of statistical analyses if individuals show consistent tendencies either to aggregate with other lizards or to select solitary retreat sites (Leger & Didrichson, 1994). However, preliminary analyses of the data showed no significant consistency among individual lizards in this respect (contingency-table analyses, all $p > 0.05$).

Predator avoidance

If aggregation by thick-tailed geckos functions to reduce vulnerability to predation (*e.g.* by vigilance, predator-swamping or communal defence), we would expect cues associated

TABLE 1. *Results of trials testing aggregative responses by juvenile and adult thick-tailed geckos when one to three geckos were restrained*

Experimental gecko	Experimental stimulus	Attraction/Avoidance	Result	χ^2 values and significance
Juvenile	1 juvenile	None	29/53 pairs together	0.47 ^{NS}
	Adult male	None	7/20 pairs together	1.80 ^{NS}
	Adult female	Avoidance	9/32 pairs together	6.13*
	3 juveniles	None	9/26 pairs together	2.46 ^{NS}
	1 adult female and 2 juveniles	None	9/15 pairs together	0.60 ^{NS}
Adult male	Adult female	None	6/16 pairs together	0.09 ^{NS}
	Adult male	None	6/11 pairs together	1.00 ^{NS}
	Juvenile	None	8/20 pairs together	0.80 ^{NS}
Adult female	Adult female	None	3/8 pairs together	0.50 ^{NS}
	Adult male	None	20/32 pairs together	2.00 ^{NS}
	Juvenile	None	10/16 pairs together	1.0 ^{NS}

* $\chi^2_{crit}(p=0.05, df=1) = 3.841$, ** $\chi^2_{crit}(p=0.005, df=1) = 7.879$, ^{NS} = not significant. The single significant result ($p < 0.05$) obtained prior to application of the Bonferroni technique, is shown in boldface font; this result fell above $p = 0.05$ after Bonferroni correction.

with predator presence to elicit a higher degree of aggregation (Wilson, 1975; Hoogland, 1983; Pitcher & Parrish, 1993). Thick-tailed geckos recognise and avoid scent cues from the sympatric lizard-eating snake *Pseudechis porphyriacus* when selecting shelter-sites (Shah, 2002). In the present trials, we tested whether the presence of predator scent modified the degree to which a juvenile gecko aggregated with a group of three other (restrained) juvenile geckos. Cotton rope was placed inside the cage of a captive snake (*P. porphyriacus*) for several weeks to pick up its scent. Each experimental unit contained a 15 cm long piece of rope between the two shelters and two 10 cm long pieces perpendicular to the central one. To allow sufficient space for distribution of these scent stimuli, these trials were conducted in enclosures twice the size of those used for the other trials reported in this paper. Three juvenile geckos were restrained behind the divider of one shelter while the other shelter contained a peg. Fourteen such groups were tested, plus 28 control groups (*i.e.* identical except for predator scent). An experimental lizard was placed in each unit and allowed to roam freely overnight. In the morning, we scored its retreat-site selection.

Humidity

If the main function of aggregation in thick-tailed geckos is to reduce water loss, then we expect that high humidity should reduce or eliminate the grouping response (Tanaka, 2000). To test this prediction, we compared aggregation by juvenile geckos in enclosures with dry sand ($N = 28$) to enclosures with wet sand ($N = 29$). For the latter treatment we added

two litres of water to the sand substrate. Two alternate plastic shelters ($13 \times 13 \times 2.2$ cm) were available to the two experimental geckos, both of which were free to move around the experimental unit (*i.e.* neither was restrained). Opaque covers were placed on all experimental units. Data-loggers (Hobo RH, Onset Computer Corporation) were placed inside shelters in extra units (*i.e.* not containing lizards) to measure humidity under both treatment conditions.

Temperature

If geckos aggregate to influence rates of heating or cooling, the ambient thermal environment during trials may influence the degree of aggregation (Boersma, 1982). We manipulated two aspects of the thermal environment in this respect:

(1) *Mean air temperature.* The room was set to 28, 20 or 16°C during trials, mimicking the range of conditions that these lizards are likely to experience in natural habitats at different times of the year (Kearney, 2002). We used 27 different pairs of juvenile geckos at each temperature, with both animals able to move freely around the arena and select their retreat-sites.

(2) *Heating and cooling.* If huddling with another gecko increases thermal inertia and thus, retards rates of heating and cooling, we might expect that aggregation responses would depend not on absolute temperature (as manipulated in the above trials) but on rates of change in ambient temperature. This hypothesis identifies the actual physical contact between lizards as the important variable, not simply whether the lizard selects a retreat-site containing another lizard. Thus, we need to measure physical contact within retreat-sites rather than common use of shelters.

To test this hypothesis, we exposed lizards to changing temperatures. Ambient temperature in the room was 18°C. Plastic cages ($22 \times 22 \times 7$ cm), each containing one plastic shelter ($13 \times 13 \times 2.2$ cm) and a pair of juvenile geckos, were left to equilibrate to room temperature and then placed on substrates at 10, 18 or 29°C. After one hour, we scored whether or not geckos were in physical contact with each other within the shelter. We tested eight pairs of lizards at each temperature.

Consequences of aggregation for rates of thermal exchange

Because the changing-temperature experiment revealed a significant effect on huddling (see below), we explored the idea that a gecko in physical contact with a conspecific would heat and/or cool more slowly than when solitary. To test this, we measured body temperatures of juvenile geckos both when alone and when huddled with an adult conspecific. Fifteen replicates were tested for each experimental group and for each of the experiments below. To measure heating rates, we set three incubators to 10°C. Ten cages ($22 \times 13 \times 7$ cm) were placed in each. Within each cage, a juvenile gecko was placed (either alone or with an adult conspecific) in a plastic half-pipe shelter (5 cm diameter, 12 cm long), resting on the transparent base of the experimental container. After two hours (sufficient for body temperatures to equilibrate in pilot studies), we checked whether or not the paired geckos were in contact by looking through the clear bottom of the experimental container. We then turned each incubator up to 28°C. At the end of an hour, we again checked whether or not the geckos were in contact and then took core body temperatures of all juvenile geckos with a thermocouple wire inserted 7 mm into the cloaca.

Cooling rates were quantified in a similar fashion (*i.e.* comparing juvenile geckos when alone *versus* when huddled with another gecko). The incubators (see above) were set to 28°C at the beginning of the trial and turned down to 10°C after two hours' equilibration. An hour later, core body temperature readings were taken for all juvenile geckos, as described above.

Results

Social interactions

The high levels of aggregation evident in the field (64% of lizards were found in aggregations: Shah, 2002) and in laboratory trials when both geckos were free to move (typically >70%: see Shah, 2002 and below) disappeared when one of the animals was restrained behind plastic mesh (Table 1). The only statistically significant deviation from the null hypothesis (expected 50 : 50 ratio) involved the avoidance of adult females by juveniles (Table 1). However, this result was no longer significant after Bonferroni correction for multiple testing (Hochberg, 1988). The proportions of aggregative responses were similar between juvenile–juvenile, adult male–male and adult female–female pairs ($\chi^2 = 0.84$, 2 df, $p = 0.66$).

Predator avoidance

Predator scent did not affect the proportion of juvenile thick-tailed geckos that aggregated in our laboratory trials (9 of 26 *vs* 5 of 14: $\chi^2 = 0.0$, 1 df, $p > 0.99$).

Humidity

The proportion of geckos aggregating was similar at high humidity (99.5% RH inside the shelter, 21 of 29 pairs together) and low humidity (77.0% RH, 20 of 28 pairs together; $\chi^2 = 0.00$, 1 df, $p > 0.99$).

Temperature

(1) *Mean air temperature.* The proportions of juvenile geckos aggregating did not differ significantly among the three thermal treatments (17 of 27 at 16°C, 20 of 27 at 20°C, 15 of 27 at 28°C; $\chi^2 = 1.27$, 1 df, $p = 0.53$).

(2) *Heating and cooling.* Significantly more geckos in the 10°C treatment (6 of 7 pairs) were in contact with each other after one hour than were geckos in either the 18°C (2 of 7) or 29°C (2 of 7) treatments ($\chi^2 = 6.11$, 2 df, $p < 0.05$). One cage in each treatment had a gecko outside the shelter, and was therefore excluded.

Consequences of aggregation for rates of thermal exchange

After one hour's heating from 10°C the core body temperatures of juvenile geckos that were in contact with adult geckos (mean \pm SE = 23.6 \pm 0.61°C, $N = 29$) were lower than those of juvenile geckos not in contact with adult geckos (25.2 \pm 0.27°C; $F_{1,28} = 7.43$, $p < 0.01$). Similarly, when cooled from 28°C towards 10°C, juvenile geckos huddled with adult geckos had higher core temperatures (mean \pm SE = 16.44 \pm 0.14°C, $N = 8$) than did juveniles not in contact with adults (15.37 \pm 0.21°C; $F_{1,7} = 19.30$, $p < 0.0001$).

Discussion

In combination with previous work in the field and laboratory (Kearney *et al.*, 2001; Shah, 2002), our data clarify potential benefits and proximate mechanisms involved in aggregation by thick-tailed geckos. We began by identifying three potential benefits to aggregation, based on previous discussions of shelter-site selection in ectotherms (Huey *et al.*, 1989; Downes & Shine, 1998; Elfström & Zucker, 1999; Lanham, 2001). We hypothesised that aggregation may benefit geckos in terms of their social interactions, predator avoidance, or rates of heat or water flux. Below, we consider each of these hypotheses in turn:

Social interactions

In many 'social' animals, it is clear that groupings reflect complex behavioural interactions among conspecifics. For example, animals within groups may thereby increase their opportunities for mating, enhance their foraging effectiveness, or benefit from group defence against conspecifics (Vine, 1971; Wilson, 1975; Lanham, 2001). If this was the case for *Nephruvus*, we would expect to see a highly non-random composition of groups in the wild.

This situation occurs in *Egernia*, where groupings are highly structured (typically consisting of adult pairs plus their offspring: Gardner *et al.*, 2001; Stow *et al.*, 2001; O'Connor & Shine, 2003). Instead, aggregations of *Nephruroides* comprise an almost-random assortment of individuals within the local population (Kearney *et al.*, 2001; Shah, 2002). Similarly, our study provided no evidence that particular sex/age groups avoided or were attracted to each other. Indeed, a physical barrier (although providing visual and chemosensory cues to another lizard's proximity) nonetheless eliminated the aggregation response observed when both lizards were free to move and therefore could be in physical contact with each other within a retreat-site.

Predator avoidance

Aggregation with conspecifics might reduce vulnerability to predation via several pathways, including increased vigilance, predator confusion, predator swamping, and communal defence (Wilson, 1975; Burger & Gochfeld, 1992; Hass & Valenzuela, in press). However, we saw no facultative increase in the degree of aggregation in the presence of a predatory snake's scent.

Humidity and temperature

We conducted two sets of trials manipulating these physical conditions. In the first, we maintained different but constant levels of either temperature or humidity, and saw no significant shift in the degree of aggregation as a result. Even though thick-tailed geckos continued to aggregate when at high humidity (99.5%), it would be interesting to measure rates of evaporative water loss of aggregated and non-aggregated lizards under high and low humidity.

In our second set of trials, we examined effects of changing temperatures on the degree of physical contact between geckos within a single shelter-site. Geckos that were exposed to decreasing temperatures huddled together more closely than did geckos that were heated or maintained in a stable thermal regime. Thus, huddling appears to be initiated by a change in temperature rather than a constant high or low temperature. Thick-tailed geckos encounter temperatures well below 10°C regularly in the wild (Shah, 2002), so our experiment used a biologically realistic range of thermal regimes. Nonetheless, temperatures under natural rocks may rarely fall as rapidly as was the case in this laboratory trial.

Not only did the rate of temperature change influence huddling in our lizards, but the reverse was also true. That is, aggregation affected (as well

as being affected by) the rate of change in temperature. Contact with another gecko reduced the rate at which the lizards heated and cooled. Similarly, grouped gidgee skinks (*Egernia stokesii*) cooled more slowly than did solitary animals (Lanham, 2001). Marine iguanas (*Amblyrhynchus cristatus*) form 'sleeping piles' overnight, where aggregated iguanas cool more slowly than solitary ones, and those at the centre of piles cool more slowly than those on the outside (Boersma, 1982). Physiological processes and locomotor performance of ectotherms often vary with temperature, and a difference of even 1 or 2°C may have a significant impact on organismal performance (Huey, 1982; Autumn *et al.*, 1999; Lanham, 2001). A modest reduction in cooling rate may therefore influence the geckos' ability to forage in the evening, or to evade predators.

Why do thick-tailed geckos aggregate?

In combination, our results suggest that grouping behaviour (sharing shelter-sites) allows the geckos to press closely against other individuals, thus increasing effective total mass, decreasing the surface area to volume ratio, and hence reducing rates of heating and cooling. The animals thus obtain significant behavioural control over rates of heat exchange, simply by minor postural adjustments that influence degree of contact with conspecifics. The major lines of evidence in support of this hypothesis are as follows:

- (i) Lizards aggregated only when they were able to have physical contact with each other. When this opportunity was eliminated, they no longer grouped.
- (ii) In the field during winter, the geckos used rocks that were more thermally stable (higher daily minima and lower daily maxima) than were nearby rocks (Shah, 2002).
- (iii) These lizards are unusual in their cold-climate distribution, large body size and use of thermally variable rocks. All of their congeners occur in warmer climates, while sympatric geckos (*Christinus marmoratus*, *Diplodactylus vittatus*, *D. intermedius* and *Heteronotia binoei*) are much smaller (Cogger, 2000). Thus, they are the only large Australian geckos occurring in such cold climates and sheltering in rock crevices (which show strong diel fluctuations in temperature), rather than soil burrows (which are thermally more stable; Williams *et al.*, 1999). Thus, thick-tailed geckos occur in situations where control over rates of heating and cooling may enhance fitness,

and are also large-bodied enough for aggregation to affect rates of heat exchange.

(iv) In an environment where mean daily minimum temperatures average 3.5°C during winter, with extremes sometimes below 0°C (Anonymous, 1993), it may be important for the geckos to retard cooling rates in the evening to facilitate locomotion, maintain physiological processes or simply to survive.

(v) During summer, temperatures under rocks frequently exceed 40°C (Kearney, 2002), high enough to kill thick-tailed geckos (Licht *et al.*, 1966). While there is a seasonal shift in rock-use from thin rocks in winter to large boulders and deep crevices in summer (Kearney, 2002), geckos may nonetheless experience occasional days with excessively high temperatures at any time throughout the year. Even small differences may be important in such cases.

(vi) Thick-tailed geckos that are aggregated can modify their rate of heat exchange by huddling with other geckos. We used just two geckos to determine whether heating and cooling rates were affected by the presence of a conspecific, but larger aggregations often occur in the field (up to 20 animals: Kearney *et al.*, 2001; Shah, 2002). Geckos may benefit not only from sheltering with a conspecific, but even more by sheltering with several conspecifics.

How can we test this hypothesis? The observation that aggregation affects (and is affected by) rates of heat exchange, does not necessarily mean that this is a major reason for the geckos to aggregate under field conditions. Further studies are required on thick-tailed gecko aggregations in the field; we predict that aggregations will be less common in *Nephrurus* populations that use logs rather than rocks as shelter-sites, and in areas and times of year when ambient temperatures are more stable. Additional experiments and mathematical modelling are needed to examine the thermal advantages of aggregation, as well as their effect on various physiological processes, activity times, and ability to evade predators.

Another clear prediction from our hypothesis is that other reptile species that share the same characteristics (large-bodied, living in rock crevices in the same climatic region) should share the same benefits from aggregation and hence, might be expected to live in groups. This should be true even for diurnally-active species, because the same advantages would apply. The reptile lineage that most closely fulfils these conditions is the scincid genus *Egernia*, often sympatric with *Nephrurus* across rocky habitats in southern Australia (Greer, 1989; Cogger, 2000). Studies on one of these species

(*E. stokesii*) have confirmed that animals form aggregations in cooler conditions, and that grouped animals cool more slowly than do solitary individuals (Lanham, 2001). Importantly, a high proportion of all *Egernia* species (especially but not exclusively the saxicolous taxa) are among the most 'social' of all lizards. Although their sociality is more complex than that of *Nephruros*, we suggest that the initial stimulus for aggregation may have been the same — control over rates of thermal exchange — in both taxa. The scincids have subsequently evolved more elaborate social systems, but the thermal benefits to aggregation may have been an important preadaptation in this respect. Aggregation may have forced individuals to interact with one another due to their close proximity, providing an opportunity for the subsequent evolution of complex sociality in the *Egernia* lineage.

More generally, research on non-traditional 'model' organisms such as lizards may provide a valuable perspective to elucidate the generality of conclusions from studies on aggregation in more 'popular' organisms such as endotherms. Aggregative behaviour in endotherms may have a primarily social function (Wilson, 1975), but our study suggests that other factors may be important in other lineages. Notably, thermoregulatory and hydric benefits may stimulate aggregation in many ectotherms, providing a platform for the subsequent evolution of more complex sociality. The evolutionary roots of complex social organisation in endothermic vertebrates may thus lie in much simpler systems in which aggregation provided passive control over rates of physical transfer between organisms and the surrounding environment.

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