



Dominance and aggression in captive gidgee skinks (*Egernia stokesii*)

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Dominance is a key component of behaviour in many animal species and is central to social system dynamics, resource acquisition, individual fitness and ultimately reproductive success. We investigated dominance interactions and social behaviours in a group of captive juvenile gidgee skinks (*Egernia stokesii*). We hypothesised that a dominance hierarchy existed within the group, and that aggressive behaviours would be used to secure limited resources, especially high-value resources. We also hypothesised that body weight would be positively correlated with dominance and aggressive behaviours. We filmed the lizards at 1200 hours for six days a week over the course of eight weeks. We exposed the lizards to three different diets, which consisted of an animal-based diet (crickets), plant-based diet (plants), and a non-feeding control (no food offered). The relative value of these resources to the skinks was established through preference tests. We identified a dominance hierarchy, with dominant individuals exhibiting more aggressive behaviours than subordinates. We found that the frequency of aggressive behaviours was significantly higher in trials where high-valued resources (crickets) were at stake. Furthermore, we found a significant positive correlation between body weight and dominance, bite and chase; larger individuals were ranked higher in the social hierarchy compared to smaller individuals. Our results demonstrate the importance of morphological and behavioural traits in determining a dominance hierarchy in *E. stokesii* and how dominance can have ecological advantages.

Keywords: dominance, aggression, body weight, behaviour, interaction, lizards

INTRODUCTION

Dominance relationships define the social structure of numerous animal species (Bush et al., 2016; Chase et al., 2002; Drews, 1993). Conflicts occur when animals compete for limited resources such as food, refuges and mates, and the outcome of these conflicts can have major ecological consequences (Huyghe et al., 2005; Wong & Candolin, 2005). For example, where a clear hierarchy exists, higher-ranking individuals tend to deny subordinates access to limited resources and as a result, increase their own reproductive success (Wroblewski et al., 2009). Thus, identifying the traits associated with dominance is important to our understanding of the phenotypic evolution of animal species (Huyghe et al., 2005). For instance, a link between bite force and dominance explains the evolution of larger heads in some species of lizards (Bull & Pamula, 1996; Huyghe et al., 2005; Pratt et al., 1992).

Morphological traits such as body weight play a crucial role in dominance (Smith & Parker, 1976; Carpenter, 1995), but behavioural traits, such as aggression, can also have a major influence (Huang et al., 2011; Wilson et al., 2011). For example, aggressive individuals often out-compete less aggressive individuals for limited resources (Duckworth, 2006; Arnott & Elwood, 2009; Herrel et al.,

2009). It has been found that aggressive behaviour can correlate both positively (Payne & Swanson, 1970) and negatively (McEvoy et al., 2013) with morphological characters such as body weight. Additionally, aggressive behaviours and interactions are often most frequent when resources are of high value. For instance, wasps avoid low-value resources guarded by aggressive rivals but become more likely to challenge the rival when the value of the resource increases (Tibbetts, 2008). Therefore, resource-dependent aggression is likely to be an important mechanism underlying the evolution of social costs.

Dominance hierarchies have been identified in several lizard species (Robson & Miles, 2000; Henningsen & Irschick, 2012; Bush et al., 2016), but lizards have not been thoroughly studied in the dominance literature. The conspicuous displays of iguanids have stimulated a wealth of research that has moulded herpetology's knowledge of social and dominant behaviours in lizards (Stamps, 1977; Ord et al. 2002). By contrast, the largest and most speciose family of lizards, the Scincidae, has received far less attention. This is despite the fact both aggression (Cooper & Vitt, 1987; Torr & Shine, 1996; Jennings & Thompson, 1999; Stapley, 2006; Myers & Paulissen, 2017) and social hierarchies have been identified in various skink species (Done & Heatwole, 1977; Whittier & Martin,

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1992). For example, Myers & Paulissen (2017) found that little brown skinks (*Scincella lateralis*) aggressively interact with each other when they are in close proximity and always establish dominance relationships during paired encounters. Riley et al. (2017) found that dominant tree skinks (*Egernia striolata*) displayed invariable aggression and that dominance relationships had profound effects on an individual's behaviour and fitness. Additionally, rainbow skinks (*Carlia rostralis*) have been found to significantly increase the behaviour frequencies when paired with another skink and express dominance in a linear fashion (Whittier & Martin, 1992).

Lizards are increasingly being recognised as excellent model systems for studying questions regarding the evolution of complex sociality (Whiting & While, 2017). However, few studies have recorded fine scale information on social interactions within a group of juveniles and how this may mediate social group processes, such as the emergence of dominance hierarchies. Dominance hierarchies and territorial behaviours have been previously observed in juvenile lizards (Stamps & Tanaka, 1981; Stamps, 1983a, 1983b; Stamps & Krishnan, 1997), but this is yet to be tested in *Egernia* or other skink species.

The gidgee spiny-tailed skink (*Egernia stokesii*) is a medium sized viviparous lizard endemic to Australia. They typically live in low open shrub land and inhabit the crevices of limestone rocks; the spines on their tails are adapted to prevent predators from extracting them from these shelters (Chapple, 2003). They are active predators and opportunistic omnivores, with their diet comprising of both insects and plant material (Cogger, 1996). Little is known about the natural history of *E. stokesii*, however, they exhibit a high level of social complexity (Greer, 1989; Stow et al., 2001; Duffield & Bull, 2002; Chapple, 2003). A number of 'sophisticated' social behaviours have been observed in *Egernia* spp. and other lizards, such as mate choice (Cooper & Vitt, 1993), monogamy (Bull, 2000; Gardner et al., 2002; O'Connor & Shine, 2003), mate guarding (Olsson & Shine, 1998), kin recognition (Bull et al., 2000, 2001), parental care (While et al., 2009) and aggressive territory protection (Jennings & Thompson, 1999; Chapple, 2003). Whilst the available literature highlights the social behaviours of *Egernia* spp., it is not yet known how such behaviours determine their social structure. However, the existence of stable social groups in nature provides a context in which dominance hierarchies are likely to evolve.

The foregoing illustrates the significant gaps in the understanding of *E. stokesii* social interactions and its impact on this species' ecology. Considering that *E. stokesii* are gregarious (Gardner et al., 2001) and the dearth of information that exists on their social system dynamics, we sought to investigate the possibility of a dominance hierarchy in captive, juvenile *E. stokesii* housed at ZSL London Zoo, and the social behaviours associated with dominance. We tested the hypothesis that *E. stokesii* will demonstrate some degree of dominance hierarchy and use aggressive behaviours to acquire limited food resources; and that the strength of pattern would be dependent on the value of resources over which lizards compete. In addition, we hypothesised that there would be a significant relationship between dominance and

body weight. We addressed these questions by firstly observing the interactions within the group to measure dominance, and then measuring the effect of diet, body weight and dominance on the frequency of aggressive behaviours observed. From this, we can explain what type of structure, if any, exists within the group and the outcome of interactions can allow for a hierarchy to be identified (Valderrábano-Ibarra et al., 2007).

METHODS

Ethics statement

The study design and methods were assessed and approved by the Ethics Committee at ZSL (Zoological Project Database number WAB59). They established that all experiments were non-invasive, and the welfare of the lizards was not risked or compromised. Lizards were fed using a central food presentation which is the zoo's usual feeding method, as this allows keepers to count all lizards, ensure they are all feeding and in good health. In nature *E. stokesii* are social and no lizards had previously been harmed whilst being fed in this manner. Their condition was monitored closely and aggression between individuals would have been stopped if it had escalated to levels of potential harm. For ease of identification, the lizards were marked with a small dot of non-toxic paint, which is the standard procedure at ZSL London Zoo; these markings were in place before the study and remain in use after its completion. All lizards remained in the living collection at ZSL after the end of the study.

Study animals

The study was conducted using seven juvenile gidgee spiny-tailed skinks (*Egernia stokesii*) housed in the reptile house at ZSL London Zoo, England. All lizards were captive bred and produced by the same breeding group of five unsexed animals. The lizards were unsexed and 25 (n=4), 24 (n=2) and 23 (n=1) months of age. Lizards had individual markings (a pink dot) on different areas of the body; the dorsal aspect of the back-left foot (lizard 1), back-right foot (lizard 2), pelvic area (lizard 3), front-right foot (lizard 4), front-left foot (lizard 5), back-right and front-left feet (lizard 6) or front-right and back-left feet (lizard 7), and will be referred to by their number from here on after (e.g. 'L2' is lizard 2, bearing a marking on the hind right foot). The trials were completed between the 21st of June and the 16th of August 2017.

Enclosure and husbandry

The trials were carried out in the lizard's usual enclosure, with dimensions 152 x 75 x 90 cm (length x width x height). The enclosure was made out of wood, mesh and glass, and had a substrate of 70:30 mix of Breedon amber gravel (Breedon Special Aggregates, UK) to peat free compost (Amenity and Horticulture Supplies, UK). It contained a small water dish, rocks, bark, logs and branches in order to provide crevice like shelters (Fig. 1). Lighting switched on at 07.00 h and was set on a 12 hour cycle. Their enclosure was lit using two Arcadia 100W mercury vapour lamps (Arcadia Reptile, UK) and a set of four 60 cm UVB-emitting T5 lamp (12 % UVB) (Arcadia Reptile, UK) mounted within a hydroponic lighting unit (Growth Technology, UK). This

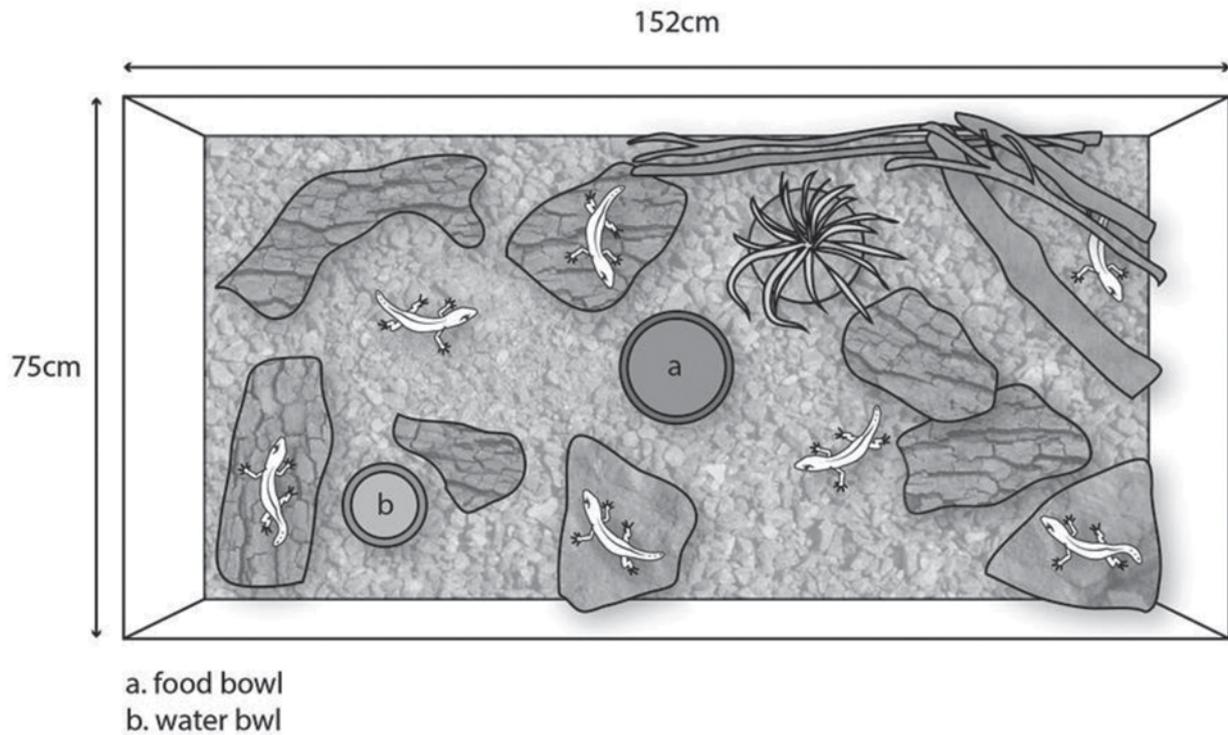


Figure 1. A diagram of the lizards’ enclosure consisting of gravel and peat free compost, rocks, bark, logs and branches. **(a)** The bowl used to present food on throughout test trials. **(b)** A small water dish available to the skinks at all times.

Table 1. An ethogram devised for the gidgee skinks (*E. stokesii*), consisting of state and event behaviours followed by their definitions.

Type	Behaviour	Definition
	Bite	Lizards grabs or attempts to grab another lizard with its jaws.
	Lunge	Rapid jumping movement by one lizard towards a conspecific
Event	Nudge	Lizard moves so that its body comes into contact with a conspecific and then pushes forward and displaces that lizard from the food bowl.
	Chase	Lizard rapidly follows another fleeing lizard.
	Flee	Lizard rapidly retreats from another chasing lizard.
State	Other	Lizard displays any other behaviour that is not listed.
	Out of sight	Lizard is not visible.

combination of lighting provided two bask zones, with UVB gradient between 0-3.3 across the entire enclosure and 1.7-3 within bask zones, and a thermal gradient of 26 °C throughout the day and 22-25 °C during the night and bask zone temperatures of 35 °C. Faeces were removed, clean water provided, and their enclosure was misted daily. The lizards were fed on Mondays, Wednesdays, Fridays and Sundays. The enclosure and set up for test trials remained the same throughout.

Food preference trials

Prior to feeding trials, a choice test was conducted to establish whether crickets or plants were considered more favourable by the lizards. Each lizard received four

trials whereby they were presented with two food bowls, one containing dead crickets (*Acheta domestica*) and the other plants. The bowl they approached first was scored as either a 1 (crickets) or 0 (plants) and then the means were calculated. We used a one-tailed one-sample sign test to test for a significant difference in food choice.

Behavioural assessment

Based on observation of the lizards, an ethogram was devised with a timeline recording sheet with state and event behaviours recorded (Table 1). Behavioural observations were based on video footage and we used focal sampling to record what each lizard was doing at each 1-minute interval and tally any event behaviours observed during each test period. As the lizards are fast moving and behaviours are instantaneous, short observation windows were used. This approach has been established for species with similar activity patterns (Januszczak et al., 2016). All observations were conducted by the same observer (HB).

Behavioural observations

On test days, the lizards were filmed for 15 minutes at 12.00 h. This time ensured that they had sufficient basking time to reach optimum temperature for activity before trials. The lizards received three types of diet; animal-based consisting of three live crickets each, plant-based consisting of 15 g of plant material (dandelions and clovers) between them, and a control where no food was offered. The goal of the control was to determine the baseline behaviour and dominance interactions of the lizards when they received no food. The purpose of the animal-based diet was to see how the lizards interact

with one another when presented with a high-energy and palatable food item. The purpose of the plant-based diet was to see if the interactions observed were similar when presented with lower-energy and less palatable food items. From a husbandry aspect, it was important for the keepers to know when and what the lizards were being fed and thus the diets could not be randomised or reversed in this case. However, we conducted 48 trials (16 of each diet) and so it is unlikely that sequencing or events on specific days had an effect. Animal-based trials were conducted on Mondays and Wednesdays and plant-based trials were conducted on Fridays and Sundays. The control trials were carried out on non-feeding days (Tuesdays and Thursdays). A camera was placed on a tripod above the lizards' enclosure, capturing as much of the enclosure as possible.

All dyadic dominance interactions were recorded using the Altmann (1974) sampling method, that is, all agonistic interactions where there was a clear winner and loser. It is important to highlight the distinction between 'aggressive' and 'dominant' animals; the former describes animals displaying a higher frequency of aggressive behaviours, while the latter describes animals that tend to win in agonistic encounters. In each encounter, all participating lizards were recorded, and we documented the initiating individual, the target, winner and loser. A loss was determined by the displacement of a lizard in control trials, and displacement of a lizard from the food bowl in animal and plant-based trials, whilst the winner did not retreat or stole the conspecific's food.

Statistical analysis

SPSS 22 was used to conduct statistical analyses, with a significance level set at $p \leq 0.05$. Due to the limited sample size we decided that non-parametric analysis was appropriate (Siegel & Castellan, 1988).

To examine the possibility of a hierarchy, dominance ranks were calculated using the Elo rating method (Albers & de Vries, 2001; Neumann et al., 2011), initially developed to rank chess players in tournaments (Elo 1961, 1978) and subsequently widely used to assess dominance within groups (Albers & de Vries, 2001). Elo ratings are based on the sequence in which dyadic dominance interactions occur, rather than the outcome of interactions alone. For instance, after each interaction, the winner gains points and the loser loses points. At the start of the Elo rating process, each lizard started with a predefined rating of 1000. The amount chosen had no impact on the difference between lizard ratings (Albers & de Vries, 2001). After each interaction, each lizard's rating was updated according to the expected outcome: the probability of that individual winning (and losing). For example, a high-rating lizard (L1) winning over a low-rating lizard (L2) would increase L1's rating by a small amount and decrease L2's rating by the same amount. If, however, L2 won the interaction, this would increase L2's rating by a larger amount and decrease L1's by the same amount, as this was an unexpected outcome. The amount of points gained and lost during an interaction (k) was set at 100 (see Appendix 1). The value of k makes little difference to results; when using three different values of k , Albers & de Vries (2001) found dominance

hierarchies to be unidirectional and significantly linear for all values of k .

Generalised estimating equations (GEE) with exchangeable working correlation structure, to account for repeated measures from the individual, and Poisson link function was used to examine the effect of diet (AB, PB, C), dominance and body weight on the frequency of aggressive behaviours. The behaviours assessed were bite, lunge, nudge, chase, flee and other. Results are presented as rate ratio (95 % confidence intervals). For significant effects detected by the GEEs, Wald chi-square post hoc tests were then conducted to compare means. Spearman's rank correlation was used to assess the relationship between dominance and body weight.

RESULTS

Food preference trials

The results from the choice tests revealed that the lizards showed a significant preference for crickets compared to plants ($Z6 = 2.65$; $p = 0.004$). In the behavioural observations, we found that the frequency of aggressive behaviours varied with diet. Aggressive behaviour frequencies differed significantly between individuals and these behaviours increased in the presence of food (crickets and plants) compared to a non-feeding control.

Behavioural observations

Overall, 183 dyadic dominance interactions were observed. Using the Elo rating method to calculate dominance ratings, we found that L1 was the most dominant individual with an Elo rating of 1200, followed by L2 (1128), L3 (1112), L6 (968), L4 (949), L5 (828) and L7 (656) (see Tables 2 and 3). As observations were conducted over a nine-week period, we were unable to quantify stability of dominance over time; a general overview is displayed in Figure 2.

We found a significant overall effect of diet on the frequency of bite ($X^2 = 8.111$; $p = 0.004$) lunge ($X^2 = 23.704$; $p < 0.001$), nudge ($X^2 = 25.225$; $p < 0.001$), chase ($X^2 = 8.782$; $p = 0.012$) and flee ($X^2 = 62.316$; $p < 0.001$). Animal and plant-based diets increased the frequency of aggressive behaviours compared to the non-feeding control (Figure 3). Open-mouth threats, push downs and tail-wagging were never observed throughout the trials. Using post hoc pairwise comparisons, it was revealed that the animal-based diet caused a significant increase in lunge ($p < 0.001$), nudge ($p < 0.001$), chase ($p = 0.010$) and flee ($p < 0.001$) compared to the control, and caused a significant increase in bite ($p = 0.004$), lunge ($p < 0.001$), nudge ($p < 0.001$) and flee ($p < 0.001$) compared to plant-based. The plant-based diet caused a significant increase in lunge ($p = 0.008$) and nudge ($p = 0.004$) compared to the control. We found no significant increase in behaviour frequencies in the control compared to animal and plant-based diets (see Table 4 for summary of the GEE results).

There was a significant effect of dominance on the frequency of lunge ($X^2 = 8.111$; $p = 0.004$), nudge ($X^2 = 34.630$; $p < 0.001$) and chase ($X^2 = 21.870$; $p < 0.001$), but not for bite ($X^2 = 21.852$; $p = 0.174$) and flee ($X^2 = 2.026$; $p = 0.155$). There was a significant effect of body weight on the frequency of bite ($X^2 = 23.745$; $p = 0.053$) and flee

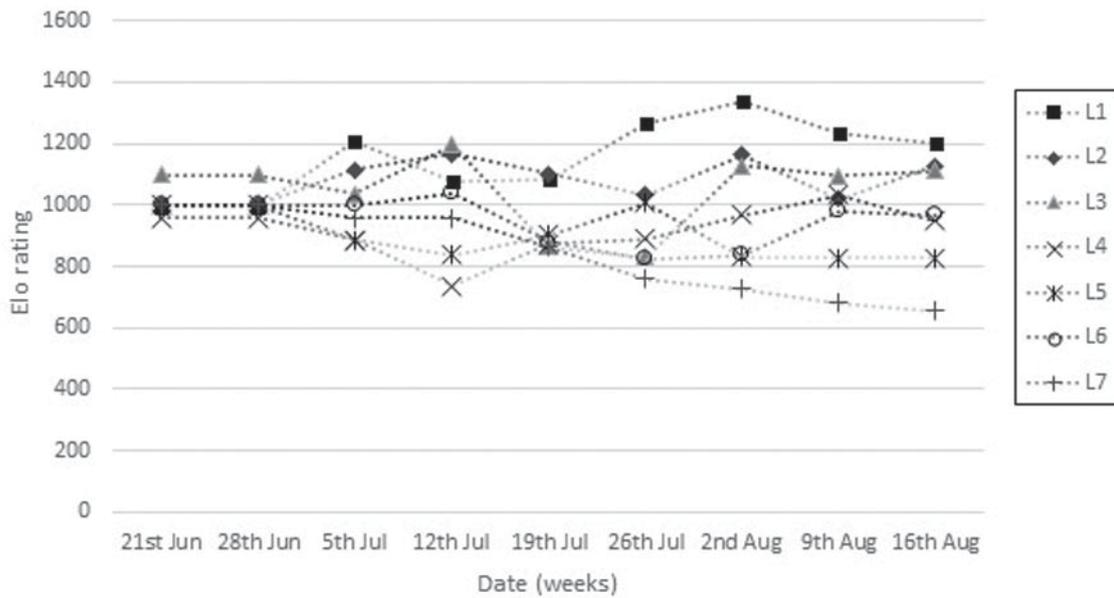


Figure 2. A general overview of dominance stability over time. Individuals are displayed on the right hand-side legend, with L1 being lizard one.

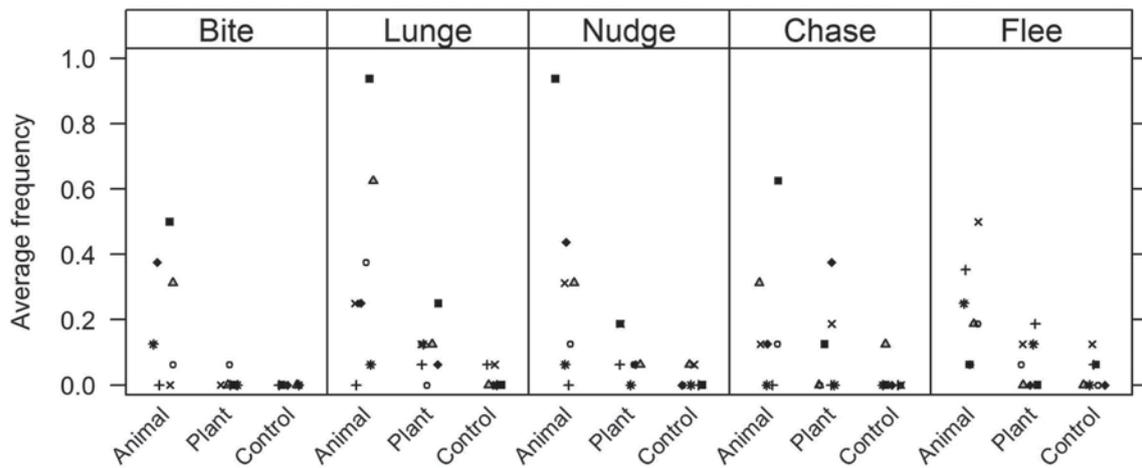


Figure 3. Shows the average frequency of behaviours for each individual in the animal-based, plant-based and control trials.

Table 2. The total frequency of interactions, wins and losses, and dominance rating for each lizard, with the most dominant individual ranked as 1 and the least dominant as 7.

ID	Weight (g)	Total Interactions	Total wins	Total Losses	Elo rating	Dominance
L1	91	92	55	37	1200	1
L2	85	73	50	23	1128	2
L3	86	62	35	27	1112	3
L6	72	38	11	27	968	4
L4	61	58	18	40	949	5
L5	58	39	12	27	828	6
L7	52	22	2	20	656	7

Table 3. The number of wins and losses between lizards in dyadic dominance interactions.

ID	L1	L2	L3	L6	L4	L5	L7
L1	-	8	13	5	17	4	4
L2	10	-	8	10	10	9	7
L3	7	2	-	8	9	5	4
L6	1	2	3	-	2	1	2
L4	2	4	1	4	-	6	1
L5	2	4	2	0	2	-	2
L7	0	0	0	0	0	2	-

Table 4. The number of wins and losses between lizards in dyadic dominance interactions.

Behaviour	Overall effect	Treatment			Dominance		Body weight	
		AB v C	PB v C	AB v PB	p-value	Rate ratio	p-value	Rate ratio
Bite	=0.004	-	-	21.8(2.6,18.3)	=0.174	1.9(0.9,1.5)	=0.053	1.2(0.9,1.5)
Lunge	<0.001	19.9(4.1,96.8)	6.0(1.6,22.6)	3.3(2.0,5.4)	=0.004	1.3(1.1,1.7)	=0.712	1.0(1.0,1.0)
Nudge	<0.001	17.5(4.5,68.2)	5.0(1.7,15.2)	3.5(2.1,5.8)	<0.001	1.7(1.4,2.0)	=0.266	1.0(0.9,1.0)
Chase	=0.012	10.9(1.7,62.8)	5.5(0.5,56.1)	1.9(0.6,6.4)	<0.001	1.5(1.2,1.7)	=0.445	1.0(1.0,1.1)
Flee	<0.001	6.4(3.1,13.1)	2.0(0.8,5.0)	3.2(2.0,5.0)	=0.155	1.2(0.9,1.5)	<0.001	0.9(0.9,1.0)

($X^2 = 14.843$; $p < 0.001$), but not for lunge ($X^2 = 0.136$; $p = 0.712$), nudge ($X^2 = 1.235$; $p = 0.266$) and chase ($X^2 = 0.583$; $p = 0.445$; Table 4). A Spearman's rank correlation found a positive correlation between bodyweight and dominance ($r_s = 0.788$; $p < 0.001$), such that heavier skinks tended to be more dominant. We found a significant positive correlation between body weight and bite ($r_s = 0.800$; $p < 0.031$) and chase ($r_s = 0.847$; $p < 0.016$), but not for lunge ($r_s = 0.571$; $p < 0.180$) or nudge ($r_s = 0.595$; $p < 0.159$). A significant negative correlation was found between bodyweight and flee ($r_s = 0.857$; $p < 0.014$).

DISCUSSION

The purpose of this study was to investigate the possibility of a dominance hierarchy in a group of captive juvenile *E. stokesii*. We hypothesised that *E. stokesii* would display a dominance hierarchy and use aggression behaviours to obtain limited resources, and that the frequency of these behaviours will be highest when competing for high value resources (crickets) compared to lower value resources (plants). The existence of dominance hierarchies was suspected in this species due to their group-living biology (Chapple, 2003) and the existence of complex social dynamics on congeners (see above). Our analyses provide three main results. First, we identified a dominance hierarchy, with dominant individuals (i.e. those that won the most confrontations) tending to exhibit more aggressive behaviours than subordinates.

This is interesting as it indicates that fighting aggressively is necessary to establish dominance; in some other taxa, the most dominant individuals engage in very few fights as other individuals don't even attempt to challenge them. Second, we found that the frequency of aggressive behaviours was highest in diets with high-valued resources (crickets). Finally, we found a significant positive correlation between body weight and dominance, bite and chase, and a significant negative correlation between body weight and flee.

Agonistic encounters among conspecifics can be energetically expensive (Neat et al., 1998) and, in some cases, extremely dangerous (Clutton-Brock et al., 1979). The potential cost of engaging in an agonistic encounter must therefore be weighed against the potential pay-off of winning, which will include access to scarce resources. During a choice test, we found that *E. stokesii* showed a significant preference for crickets over plants as a food source. One explanation for this preference is that crickets have a higher energy content compared to the plant species used in our study. For example, per 100 g, adult

house crickets (*Acheta domesticus*), the taxon used in this study, have a mean energy (ME) of 120 kcal (Clayton, 2014; Nowak et al., 2016) compared to dandelions (*Taraxacum*) ME = 45 kcal (Tan et al., 2017) and clovers (*Trifolium*) ME = 12 kcal (Johansen et al., 2017), which comprised the plant-based diet. Additionally, we found that the frequency of lunge, nudge, chase and flee was significantly higher in animal-based trials (crickets) compared to control (no food offered), the frequency of bite, lunge, nudge and flee was significantly higher in animal-based compared to plant-based, and lunge and nudge was significantly higher in plant-based compared to control. This is supported by previous studies which revealed that the frequency of aggressive behaviours in juvenile lizards increases in the presence of limited, high-value resources (Stamps, 1978).

Dominance scores using the Elo rating method revealed a hierarchy in the lizards, with more dominant animals winning more agonistic encounters. However, as observations were conducted over a nine-week period, we were unable to statistically test for stability of dominance over time (see Figure 2 for general overview). Our results revealed that the frequency of lunge, nudge and chase was significantly higher in dominant lizards compared to subordinates. In support of these findings, Myers & Paulissen (2017) found that, when observing little brown skinks (*Scincella lateralis*), aggressive behaviours such as 'chasing' were only ever exhibited by dominant lizards and these individuals also displayed 'lunging' significantly more times than subordinates. In some cases, aggression has been found to override body size; Schult-Hostedde & Millar (2002) found that smaller aggressive individuals were more dominant over larger, but less aggressive, individuals. In our study, winners gained primary access to food whilst losers were often submissive and consequently displaced from the food bowl. Thus, dominance interactions leading to disparate access to resources between individuals may have evolutionary implications for skinks, as well as ecological implications for the individuals involved (Greer, 1989; Langkilde et al., 2005).

In addition to aggression, other social behaviours can be used to determine resource distribution within species, without the need for aggressive interactions. For example, *E. stokesii* display 'open-mouth threats', 'push downs' and 'tail-wagging' as a way of emphasising their size, strength or quality to warn others and compete for dominance over their opponents (Chapple, 2003). However, these display behaviours were never observed in the trials. This may be because all the animals were of relatively similar size and age, and therefore may

not have been able to use posturing before engaging in aggression. Posturing can be important for showing off size as a proxy for likelihood of winning, so lizards may not bother with this if they perceive that their opponent is so similar that they will have to resort to aggression. Displacement behaviour can also show competitive ability without aggression. When investigating competition in two closely related skinks (*Niveoscincus greeni* and *N. microlepidotus*) that have overlapping geographical distributions and similar habitat preferences, Melville (2002) found that they use displacement to access limited basking sites. Similarly, Dame & Petren (2006) found that house geckos have been displacing indo-pacific geckos on a global scale because of habitat competition. While theoretically, it should be possible for familiar animals to outcompete one another without fighting, our sample predominantly used aggressive behaviours to determine and maintain social dominance and it is for this reason we measured aggression only.

Body weight is a key determinant of dominance in various lizard species and skinks are no exception. It has been found that body weight is significantly correlated with dominance in various skinks, with larger individuals dominating smaller lizards (Whittier & Martin 1992; Torr & Shine 1996; Melville, 2002). Similarly, we identified a significant positive correlation between body weight and dominance, bite and chase, with heavier individuals being ranked higher in the social hierarchy. It is possible that *E. stokesii* assess some correlate of body width or muscle size to parse dominance relationships. In some instances, when *E. stokesii* bite and lock jaws, they fight by rolling around on the ground (Chris Michaels, pers. Obs). Therefore, it is likely that the lizard which is physically stronger wins the fight and subsequently emerges as the dominant individual. However, there will be circularity in the development of increased body weight and access to more resources to increase body weight; without data concerning body weight at hatching and subsequent development of dominance hierarchies, it is impossible to say which determines which in this case.

Social dominance, as measured herein, may also correlate with other variables. For example, testosterone levels linked to sex, which have been found to influence the rate of aggression during the formation of social hierarchies in lizard species (Greenberg et al., 1984). In our experiment, the sex of the lizards was unknown as juvenile *E. stokesii* show no sexual dimorphism and thus sexing the lizards before our experiment was not possible. Moore (1987) and Moore & Marler (1987) demonstrated that testosterone influences aggressive behaviours and that castration dramatically reduced, yet did not eliminate, territorial behaviour in free-living *Sceloporus*. The fact that no individuals reached sexual maturity in this case, means the effects of testosterone levels linked to sex are less likely to have had an impact.

Another explanation could be the slight difference in age between the lizards may have influenced social behaviours within the group. For example, Baird et al. (1996) discovered age-related differences in social behaviours in free-living collared lizards (*Crotaphytus collaris*), and Bajer et al. (2015) found that risk-taking and explorative behaviours were dependent on age in a group

of European green lizards (*Lacerta viridis*). However, the oldest and youngest only varied in age by two months (23 versus 25 months). Our experiment lasted 56 days and the rank order of the individuals tested was consistent across the whole study period. This suggests that the slight difference in age was not important in determining social status and aggression in the lizards.

The competitive behaviours observed in the lizards follow the typical pattern for skinks in both captive (Torr & Shine, 1996; Langkilde et al., 2003) and free-living populations (Carpenter & Ferguson, 1977). However, our sample was limited to seven full and half sibling lizards, which was the only sample available at the time. Small sample size is a frequent limiting factor when studying non-model organisms, especially in a zoo, but by doing so we were able to investigate social behaviours in juvenile *E. stokesii*. It may be hard to extrapolate these particular results to all *E. stokesii*. Indeed, free-living populations are faced with different biological factors (e.g. family size, breeding pairs, number of offspring) and environmental stressors (e.g. predators, abnormal weather patterns, habitat destruction) which are likely to have an impact on the social behaviours of juvenile *E. stokesii*, however this is yet to be assessed.

Nevertheless, the underlying principle that juvenile *E. stokesii* are capable of forming a dominance hierarchy is a significant finding, which is supported by previous studies addressing dominance hierarchies in juvenile lizards. For example, it was found that juvenile *Anolis aeneus* are able to form a dominance hierarchy, (Stamps, 1984). High social status has also been found to be linked to ecological advantages. When investigating growth costs of territorial overlap in juvenile *A. aeneus*, Stamps (1984) found that higher status lizards had significantly less overlap in territories than lower status lizards. This demonstrates that one of the benefits of high social status is access to high-valued resources, in this case, a more exclusive territory.

Our results demonstrate that groups of social lizards can develop a dominance hierarchy, and that dominant individuals within this hierarchy had a larger body size. It is therefore possible that dominant individuals were more likely to gain access to food resources. Moreover, the level of aggression maintaining the hierarchy is correlated with the value of the resources over which lizards are competing. Social dominance and aggressive behaviour therefore likely have fitness consequences for lizards within a hierarchy. Our results add to the small but growing field of reptile sociality and, although they are limited to a captive population, suggest that there is much behavioural and social complexity to explore in this group of animals.

Conflicts of interest

None.

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Appendix 1. Table taken from Albers & Vries (2001) to calculate the difference in Elo ratings and expected outcomes. After each interaction, this table was used to give each rating difference between the two individuals and the corresponding expected chance of winning for the individual with the highest score.

Rating difference	Expected chance of winning	Difference	Chance	Difference	Chance
0>=dif<=3	0.50	122>=dif<=129	0.67	279>=dif<=290	0.84
4>=dif<=10	0.51	130>=dif<=137	0.68	291>=dif<=302	0.85
11>=dif<=17	0.52	138>=dif<=145	0.69	303>=dif<=315	0.86
18>=dif<=25	0.53	146>=dif<=153	0.70	316>=dif<=328	0.87
26>=dif<=32	0.54	154>=dif<=162	0.71	329>=dif<=344	0.88
23>=dif<=39	0.55	163>=dif<=170	0.72	345>=dif<=357	0.89
40>=dif<=46	0.56	171>=dif<=179	0.73	358>=dif<=374	0.90
47>=dif<=53	0.57	180>=dif<=188	0.74	375>=dif<=391	0.91
54>=dif<=61	0.58	189>=dif<=197	0.75	392>=dif<=411	0.92
62>=dif<=68	0.59	198>=dif<=206	0.76	412>=dif<=432	0.93
69>=dif<=76	0.60	207>=dif<=215	0.77	433>=dif<=456	0.94
77>=dif<=83	0.61	216>=dif<=225	0.78	457>=dif<=484	0.95
84>=dif<=91	0.62	226>=dif<=235	0.79	485>=dif<=517	0.96
92>=dif<=98	0.63	236>=dif<=245	0.80	518>=dif<=559	0.97
99>=dif<=106	0.64	246>=dif<=256	0.81	560>=dif<=619	0.98
107>=dif<=113	0.65	257>=dif<=267	0.82	620>=dif<=735	0.99
114>=dif<=121	0.66	268>=dif<=278	0.83	dif<=736	1.00

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