



## Behavioural phenotype modulates group size effects in a lizard

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Behaviour is a highly labile trait that can be rapidly modified to mitigate the effects of changing environmental conditions. Among the biotic and abiotic factors acting to prompt plastic responses, the social environment has been proposed as being one of the primary modulating forces on behaviour. Being part of a group has particular influence on the expression of risky behaviour in that added eyes and ears serve to decrease a group member's vulnerability to predation resulting in the mean behavioural expression of behaviours such as activity and/or exploration increasing with group size. A large body of work has documented such group size effects. However, as this process may operate at the individual level it is unclear how the social environment affects the consistent expression of personality. Thus, we examined the interactive effects of behavioural phenotype and social context on the stability of individual behaviour in the delicate skink, *Lampropholis delicata*. Lizards were exposed to a series of assays measuring activity, exploration and boldness in groups of one, two, four and eight. Repeatability was determined across group size treatments and the combined effects of social context and behavioural type on behavioural plasticity were assessed. We found that the predicted patterns of group size effects were only observed when each lizard's behavioural phenotype was considered. Inactive and shy lizards increased their behaviour with increasing group size whereas active and bold lizards exhibited the opposite pattern. Additionally, the degree to which an individual adjusted its behavioural response was contingent upon its behavioural phenotype, with slow lizards showing higher levels of responsiveness than fast lizards. Despite this plasticity, between-individual differences in the expression of activity, exploration and boldness persisted. Thus, our study provides strong evidence that the effects of an individual's personality are stronger than those of group size.

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Behaviour has long been recognized as being a highly labile trait (Briffa et al., 2013; Dingemans & Wolf, 2010; Piersma & Drent, 2003). Plasticity enables individuals to rapidly modify their behavioural responses as a means of mitigating the effects of changes in the environmental conditions they experience. Among the biotic and abiotic factors acting to prompt such plastic responses in behavioural expression, the social environment has been proposed as being one of the primary modulating forces (Jolles, Aaron Taylor, & Manica, 2016; Webster & Ward, 2011).

The influence of the social environment is particularly relevant among prey animals which are often faced with the challenge of coping with the trade-off between predation and starvation (Treisman, 1975). Resources, such as food and refuges, must regularly be acquired, thereby increasing an individual's exposure to predators. Aggregating into groups has evolved as a behavioural

mechanism that serves to mitigate the negative impacts of this conflict (Goldenberg, Borchering, & Heynen, 2014). By grouping, individuals can use social cues as a way of gaining more accurate risk-related information (Webster & Ward, 2011). Thus, vulnerability to predation is decreased as more eyes and ears increase the rate of predator detection and reduce the chance of capture through dilutionary effects (Webster & Ward, 2011).

Classical ecological models explaining the relationship between predation costs and behaviour predict that the frequency and magnitude of adjustments in behaviour of group members often scale with the size of the group (Alexander, 1974). Logically, the perception of predation risk is reduced as the size of the group increases. Individuals are thereby less constrained in how they act, resulting in higher expression of risky behaviours (i.e. being active in open habitat or resuming activity after a perceived threat). Collectively, these individual adjustments contribute to the overall plastic responses expressed by the group (Rieucau, Morand-Ferron, & Giraldeau, 2010).

In alignment with these theoretical predictions, group size effects have been widely demonstrated empirically across a range of

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species (Barbosa, 2002; Beauchamp, 1998; Blumstein, Daniel, & Evans, 2001; Elgar, 1989; Jolles et al., 2016; Morelli et al., 2019; Ward, 2012; Webster, Ward, & Hart, 2007). Among these studies, most of which have focused on mammals and birds within the context of antipredator behaviour (i.e. vigilance; Barbosa, 2002; Beauchamp, 1998; Blumstein, Evans et al., 2001; Elgar, 1989; Morelli et al., 2019), the expression of risky behaviours by the group was found to increase with the presence of more members. Time dedicated to scanning or distances at which flight was initiated were all lower among individuals in large groups. Reduction in antipredator behaviour enabled group members to then dedicate more time to other fitness-related behaviours, such as foraging. Despite such overwhelming support, however, a lack of group size effects has still been observed (Beauchamp, 2008; Blumstein, Evans et al., 2001; Cameron & du Toit, 2005; Goldenberg et al., 2014; Treves, Drescher, & Ingrisano, 2001). In these studies, relationships were either not significant or in the opposite direction predicted by vigilance models.

These previous findings of group size effects all represent shifts in the average behaviour of the group, suggesting that all group members respond to the level of per capita risk in a similar manner. However, it has recently been postulated that the impacts of group size may instead operate on the individual level where an individual's personality drives group level responses (Dumke et al., 2016; Laskowski & Bell, 2014). Personality is defined by consistent differences between individuals in the expression of behaviour across time and/or context (Stamps & Groothuis, 2010). Under this premise, each individual exhibits its own personality phenotype that falls along a behavioural axis (i.e. shy–bold or active–inactive). Indeed, it is well established that individuals often differ consistently from one another in their expression of behaviour (birds: Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; fish: Bell & Sih, 2007; amphibians: Smith & Douppnik, 2005; reptiles: Carter, Goldizen, & Heinsohn, 2012; invertebrates: Johnson & Sih, 2007; mammals: Lantová et al., 2011). Such pronounced plasticity, which is observed in the individual expression of behaviour arising from shifts in the social environment, seemingly challenges the concept of animal personality. However, the existence of personality does not necessarily imply the absence of plasticity in behaviour (Roche et al., 2016). Rather, the key feature of personality is that individuals maintain their rank order differences despite modulating their behavioural responses as a function of varying external cues, such as group size. As a result, those with fast behavioural phenotypes (i.e. high levels of activity, exploration, boldness and aggression) under one set of conditions remain fast under different conditions while those expressing slow behavioural phenotypes (i.e. low levels of behaviour) remain slow.

Whether the effects of the social environment are strong enough for interindividual repeatability to be compromised, eroding an individual's expression of personality, is still unknown (Webster & Ward, 2011). Empirical tests exploring the factors acting to either promote or inhibit the stability of personality are currently lacking (Jolles et al., 2016; Laskowski & Bell, 2014). The few studies to have considered the impact of social context on behavioural consistency (Jolles et al., 2016; Laskowski & Bell, 2014; Magnhagen & Bunnefeld, 2009; Piyapong et al., 2010; Stöwe & Kotschal, 2007; van Oers, Klunder, & Drent, 2005) have shown that individuals did in fact retain their distinctive personalities, exhibiting stable interindividual differences, despite the presence of conspecifics triggering the predicted group size effects. It was also notable that not all individuals were shown to be equally responsive to changes in the social environment. Different behavioural phenotypes were found to vary in the level and/or direction of their responses (Magnhagen & Bunnefeld, 2009; van Oers et al., 2005). For instance, boldness was assessed among perch, *Perca*

*fluviatilis*, when alone as well as when in a group (Magnhagen & Bunnefeld, 2009). Focal fish were consistent in the expression of their individual behavioural phenotypes yet still responded plastically as the social context changed. Feeding rate in an open environment increased when they shifted from being solitary to being in the presence of conspecifics. However, bold fish altered their behaviour to a lesser degree between treatments than did shy fish.

While the studies mentioned above provide some evidence suggesting that individual behaviour expressed when alone is positively linked to their behavioural propensities when in a group, the focal animals were limited to two contexts: social and asocial. Only a single study that we are aware of has examined the stability of behavioural responses across multiple group sizes (Riceucau, Morand-Ferron, & Gialdeau, 2010). In this study, the authors assayed variation in boldness of nutmeg mannikins, *Lonchura punctulata*, across four group sizes (zero, one, three and five) and found that, despite exhibiting personality, individuals all decreased their level of vigilance with increasing group size. Given the density-dependent nature of behavioural responses, the level of influence of social processes, such as group size effects, may potentially be stronger as the number of group members increases (Webster and Ward, 2010). Thus, more research investigating how changes in the social environment affect personality across the full range of ecologically relevant group sizes is clearly needed. Equally important is determining whether the social context affects all behaviours and individual phenotypes equally. Together, such work would serve to broaden our understanding of how individual variation in behaviour is shaped by social processes under natural conditions and could also provide insight into why group size effects are not always detected.

To this end, we examined the effect of social context on the expression and stability of individual behaviour across naturally occurring group sizes using a gregarious lizard species, the delicate skink, *Lampropholis delicata*. This skink affords a unique opportunity to test for group size effects and the role that personality plays in this process as individual consistency in behavioural traits, as well as the expression of an activity–exploration syndrome, has already been well documented in this species (Michelangeli, Chapple, Goulet, Bertram, & Wong, 2019; Michelangeli, Chapple, & Wong, 2016; Michelangeli, Wong, & Chapple, 2016; Moule, Michelangeli, Thompson, & Chapple, 2016). However, individual behaviour has only been evaluated in terms of time, sex and geography, but the effects of group size have not been explored.

Specifically, we sought to determine whether (1) variation in group size affects the stability of individual expression of personality, (2) social context has differential effects across the primary behavioural axes and (3) behavioural types vary in their level of responsiveness (i.e. plasticity) to changes in group size. To answer these questions we carried out a series of behavioural assays measuring activity, exploration and boldness across groups of one, two, four and eight. Behavioural repeatability across group size treatments was determined and the combined effects of social context and behavioural type on the level of behavioural plasticity were assessed.

## METHODS

### *Study Species and Field Collection*

The delicate skink is a small (30–55 mm adult snout–vent length) heliotherm that is locally abundant and geographically widespread in eastern Australia (Chapple, Hoskin, Chapple, & Thompson, 2011). This species occurs in moist habitats, including rainforests, wet sclerophyll forests, woodlands, heaths and urban

settings (Chapple et al., 2014). Forty adult (snout–vent length > 30 mm) male lizards with complete tails were collected from the Sydney region (New South Wales, Australia: 3353'40.24'S, 15110'48.59'E) in September 2014. Each was marked with a unique visible implant elastomer (Northwest Marine Technology, Anacortes, WA, U.S.A.) colour code and transported back to the animal housing facility at Monash University (Clayton, Victoria, Australia). Lizards were housed in groups of six and maintained at 20 °C with a 14:10 h light:dark cycle (0600–2000 hours). The housing containers were lined with newspaper and external heat provided a thermal gradient of 20–35 °C. Crickets, *Acheta domesticus*, were fed three times weekly and water was provided ad libitum.

### Behavioural Experiments

Experiments were conducted from October 2014 to January 2015. All lizards were in a postabsorptive state (fasted for 48 h) during each of the trials as digestion can affect behaviour (Shine, 2003). Behaviour was evaluated in the context of activity, exploration and boldness across four group sizes (one, two, four and eight individuals) following standard methodology (Goulet et al., 2018; Michelangeli et al., 2018). Group sizes were based on natural grouping tendencies observed in this species in the wild as well as those used in a previous study on this species investigating group size effects (Downes & Hoefer, 2004; D. Littlewood, C.T. Goulet & D. G. Chapple, personal observations). Lizards were randomly assigned as either focal ( $N = 20$ ) or stimulus ( $N = 20$ ) prior to the experiments. Focal lizards were housed separately from stimulus lizards to prevent the effects of social recognition. Each group consisted of a single focal lizard and the required number of stimulus lizards. All focal lizards completed each behavioural assay four times, once for each group size, with at least 2 days between assays. To minimize the risk of carryover effects, lizards went through the behavioural assays in a fixed order, outlined below, where assays that would have the greatest impact upon behaviour were at the end of the experimental schedule. However, the order in which the focal lizards experienced each group size was randomized to control for order effects and habituation. This sequence was predetermined for each focal group and maintained throughout the study.

Assays were conducted within opaque experimental arenas (550 × 320 mm and 240 mm high) located in a temperature-controlled room (20 °C). Each trial consisted of a 10 min acclimation period where lizards were placed within a clear plastic container followed by a 30 min test period. Lizard behaviour was recorded using Panasonic HCV130 video recorders suspended above the test arena and data were analysed using Jwatcher (Blumstein 2006). All equipment used was washed with soapy water between trials to remove chemical cues.

### Activity

Activity was measured by placing lizards into a test arena marked with 20 grid squares (80 × 110 mm; Fig. A1a). The number of benign transitions ( $\geq$  half of body over grid line) between squares was recorded. The term benign transitions is used to distinguish between activity within a nonthreatening context and activity within a risky situation (see methods describing the boldness assays below).

### Exploration

An opaque Perspex partition was placed in the centre of the arena, dividing it in half (Fig. A1b). The partition was a trapezium

(flush with the base of the experimental arena, tapering to a 15 mm gap at 100 mm in height). This required the lizards to climb and squeeze into the gaps to reach the other compartment. The time it took the focal lizard to manoeuvre around the obstacle and reach the other compartment was recorded. Individuals that did not reach the goal by the end of the trial were assigned 30 min.

### Boldness

Boldness was assessed in two contexts: basking site selection and simulated predator attack. For the basking site selection assays, the arena was divided into three equal zones: open basking site, an intermediate no-preference zone and sheltered basking site (Fig. A1c). Both basking site zones included a heat lamp (40 W) suspended above a ceramic tile (100 × 100 mm) to encourage natural thermoregulatory behaviour. However, the sheltered basking site also had an opaque plastic shelter placed over the basking tile to provide a safe refuge. The intermediate zone was empty. The time spent in each zone was recorded.

For the simulated predatory attack assays, a test arena marked with 20 grid squares (80 × 110 mm) was divided into three zones: basking zone, an intermediate neutral zone and shelter zone (Fig. A1d). The basking and intermediate zones were set up as previously described while the shelter zone consisted of a plastic refuge. Unlike the previous assays, the lizards were given 10 min to freely acclimate within the arena. After the acclimation period a plastic bird model (700 mm wing span; 50 mm beak to tail length) was flown low over the test arena three times at a predetermined pace (Michelangeli, Chapple, & Wong, 2016; Michelangeli, Wong, & Chapple, 2016). The time spent basking in each zone and the number of risky transitions after the simulated predator attack were recorded.

### Ethical Note

All animal care and experimental procedures were approved by the Monash University Animal Ethics Committee (BSCI/2014/13). Lizards were collected by hand to minimize by-catch under scientific collection permits (New South Wales: SL101425, Victoria: 1007284). Only adult males were collected and used in the study to ensure removing animals from the wild would not impact population viability. Lizards were housed in temperature-controlled animal housing facility at Monash University, Melbourne, Australia. The captive environment was designed to promote natural behaviours in terms of circadian cycle (14:10 h light:dark cycle), social structure and thermoregulation. Specifically, as a gregarious species, individuals were housed in groups of six within plastic containers (300 × 230 mm and 370 mm high) to allow for natural social interactions to occur. Refuges and basking sites provided a thermal gradient of 20–35 °C which enabled all lizards equal opportunity to behaviourally thermoregulate within their preferred temperature range (20–25 °C). Lizards were monitored daily to assess body condition and fed a vitamin-enriched diet (crickets sprinkled with vitamin supplement) three times weekly. Standard experimental procedures were employed that have been found not to cause any long-term negative effects (Goulet et al., 2018; Michelangeli et al., 2018). State legislation prevented the release of captive animals; thus, lizards were kept in captivity once the study was complete and reused for additional research projects and education purposes to maximize the amount of data collected from them.

### Statistical Analyses

All statistical analysis was conducted using R version 3.3.2 (R Development Core Team 2016). Data were checked for normality (Shapiro–Wilk test) and homogeneity of variance (Fligner–Killeen test) where appropriate. Boldness metrics were found to be correlated; thus, a single measure between pairs of correlated metrics considered to be most representative of an individual's level of boldness (i.e. time in basking zone following simulated predator attack versus time in refuge) was used in the analyses. We therefore included time spent in the basking zone under benign conditions (before simulated predator attack), time spent basking under risky conditions (after predator attack) and the number of risky transitions.

Each lizard's behavioural phenotype was assigned as being either active or inactive, exploratory or nonexploratory and bold or shy according to whether they scored above or below the median score for each behaviour when tested alone. Median scores were calculated separately for each trial number block (four trials per block for each behaviour) to account for order effects as a function of group size. A generalized linear mixed-effect model (GLMM) with a Poisson distribution was then used to investigate the influence of group size on activity and to test whether individuals differing in behavioural phenotype were affected similarly by social context. The number of benign transitions was the response factor while group size, behavioural type and their interaction as well as trial number were included as fixed factors. Individual identity (ID) and group size were assigned as random factors. By including both ID and group size as random effects, individual intercepts estimated personality while plasticity estimates were represented by the slope of the interaction between ID and group size (Betini & Norris, 2012). Post hoc analyses (package: 'lsmeans') were performed to identify which paired comparisons were significant.

Markov chain Monte Carlo linear mixed-effects models (MCMCglmm R package: Hadfield, 2010) were used to evaluate the influence of group size on exploratory and boldness behaviour. Time to cross the barrier was modelled with a log-normal distribution, times spent basking under benign and risky conditions were modelled with a Gaussian distribution and the number of risky transitions was modelled using a Poisson distribution. Group size, behavioural type and their interaction as well as trial number were included as fixed factors and ID and group size as random factors. Prior to running the models, variation in Markov chain lengths, prior specification, thinning intervals and burn-in lengths were explored to obtain models that had adequate sampling of the posterior distribution and showed limited autocorrelation among samples. For the final models, default diffuse uniform priors were used for fixed effects and a random effect variance–covariance matrix prior specification  $V = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$  and  $\nu = 0.002$  for random effects (Hadfield, 2010). Models were run for 10 million iterations with the first 200 000 discarded (burn-in) that were sampled every 5000 iterations (thinning interval), which resulted in an effective sample size of <1000. Trace plots were visually inspected to ensure chains had good mixing. Autocorrelation among samples was assessed to ensure levels were low (lag < 0.1) using the autocorr function in the R package coda (Plummer, Best, Cowles, & Vines, 2010). Parameter estimates were considered significant when the credible intervals did not include zero (Hadfield, 2010).

Adjusted repeatability of behaviour across group sizes was then calculated using the variance components from the GLMMs described above (ratio of among-individual variation to total

phenotypic variation) implemented using the 'rptR' package. Parametric bootstrapping provided 95% confidence intervals (CIs) and statistical significance was evaluated with likelihood ratio tests. Adjusted repeatability was also performed for each behavioural phenotype separately. Nonoverlapping CIs indicated that repeatabilities varied between behavioural phenotypes.

Finally, best linear unbiased predictors (BLUPS) of the random effects were extracted from each of the GLMM models to test for correlation between personality and plasticity (within-individual variation) as a way of assessing the level of responsiveness among behavioural phenotypes. Negative correlations would be indicative of a high level of plasticity for individuals expressing a low behavioural phenotype (i.e. inactive, nonexploratory or shy) while a positive relationship would indicate that high behavioural phenotypes were more responsive to changes in group size. ANOVAs were then used to evaluate the difference in levels of plastic responses between behaviours. Where significant differences were identified, post hoc analyses (package: 'lsmeans') were performed to identify which paired comparisons were significant.

## RESULTS

### Repeatability

Overall, all behaviours were repeatable across group sizes except for the boldness measure of time spent basking under benign conditions ( $R = 0.003$ , 95% CIs = 0.00–0.49). Lizards exhibited the highest level of consistency in their expression of activity ( $R = 0.49$ , 95% CIs = 0.25–0.70). Repeatability in exploratory behaviour (time taken to cross the barrier) was moderate ( $R = 0.26$ , 95% CIs = 0.07–0.52) while two measures of bold behaviour, the time spent basking and the number of transitions under risky conditions, were low ( $R = 0.09$ , 95% CIs = 0.001–0.42;  $R = 0.15$ , 95% CIs = 0.02–0.41, respectively). When considering repeatability among behavioural types, inactive and active lizards had similar levels of repeatability in the number of benign transitions across group sizes ( $R = 0.54$ , 95% CIs = 0.21–0.79;  $R = 0.51$ , 95% CIs = 0.12–0.78, respectively). By contrast, exploratory and bold phenotypes differed in their levels of consistency. Non-exploratory lizards exhibited moderate repeatability in the time to cross the barrier ( $R = 0.28$ , 95% CIs = 0.08–0.53) while exploratory individuals were not consistent in their latencies to cross the barrier across group size treatments ( $R = 0.34$ , 95% CIs = 0.00–0.93). Bold lizards were consistent in the time they spent basking under risky conditions ( $R = 0.19$ , 95% CIs = 0.01–0.63) as well as in the number of risky transitions they made ( $R = 0.36$ , 95% CIs = 0.11–0.69); however, these individuals were not consistent in the amount of time spent basking under benign conditions ( $R = 0.003$ , 95% CIs = 0.00–0.49). By contrast, shy lizards exhibited the opposite pattern where the time spent basking under benign conditions was repeatable ( $R = 0.00$ , 95% CIs = 0.00–0.41;  $R = 0.00$ , 95% CIs = 0.00–0.42, respectively), yet they were not consistent in either the number of risky transitions or the time spent basking after the simulated predator attack ( $R = 0.26$ , 95% CIs = 0.01–0.61).

### Group Size Effects on Behaviour

Models testing the effect of only group size without the influence of personality indicated that the expression of behaviour did not vary between group sizes (activity:  $F_3 = 0.94$ ,  $P = 0.43$ ; exploration:  $F_3 = 1.75$ ,  $P = 0.16$ ; benign basking time:  $F_3 = 1.80$ ,

$P = 0.16$ ; risky basking time:  $F_3 = 0.07$ ,  $P = 0.97$ ; number of risky transitions:  $F_3 = 1.73$ ,  $P = 0.17$ ). The expected progressive increase in the expression of activity, exploratory and boldness behaviours predicted by previous theoretical models was generally not observed (Table A1, Fig. A2a–e). The expression of each behaviour, instead, followed no apparent trend upwards or downwards except for one boldness measure, the number of risky transitions (Fig. A2e), where lizards made the fewest movements under risky conditions ( $\mu = 9 \pm 1.84$  transitions) at the smallest group size and the most ( $\mu = 17 \pm 3.25$  transitions) at the largest. However, the number of risky transitions decreased from groups of two to four ( $\mu = 14 \pm 0.99$  transitions and  $12 \pm 1.96$  transitions; respectively). A somewhat similar pattern was demonstrated in the expression of exploratory behaviour where lizards took the least amount of time to cross the barrier (high exploratory behaviour) when alone ( $\mu = 1683 \pm 68.36$  s) and the most time in a group of eight ( $\mu = 1284 \pm 149.77$  s; Fig. A2b). Like the number of risky transitions, however, the opposite trend was exhibited at intermediate group sizes. By contrast, activity and time spent basking under benign and risky conditions were highest in groups of two ( $\mu = 63 \pm 9.47$  transitions) and four ( $\mu = 692 \pm 116.60$  s). Lizards made the most benign transitions in a group of two ( $\mu = 63 \pm 9.47$  transitions; Fig. A2a) and spent the most time basking in a group of four (benign basking time:  $\mu = 679 \pm 122.79$  s; risky basking time:  $\mu = 692 \pm 116.60$  s; Fig. A2c,d), although activity, benign basking time and risky basking time were at their lowest in groups of one, two and eight, respectively.

#### Behavioural Phenotype as a Modulator of Group Size Effects

When considering behavioural type within the context of group size effects, different patterns emerge. The results of the GLMMs showed that, for activity, the number of transitions varied between groups of one and four as well as between behavioural types (Tables 1 and A1, Fig. 1a), with inactive lizards making significantly fewer benign transitions than active ones. The interaction between behavioural phenotype and group size also influenced the expression of activity (Table 1), with inactive lizards making more transitions as the number of group members increased from two to four and to eight. Furthermore, post hoc analyses revealed that mean activity level differed between inactive lizards when alone and active lizards in groups of two ( $z = -3.28$ ,  $P = 0.02$ ) and eight ( $z = -3.55$ ,  $P = 0.01$ ) as well as between inactive lizards in a group of four and active lizards in a group of eight ( $z = -4.08$ ,  $P = 0.001$ ). Trial number also influenced the number of benign transitions made (Table 1) suggesting that habituation may have played a role in an individual lizard's movement frequency.

Results of MCMC GLMMs indicated that exploration was not influenced by any of the factors (Table 2, Fig. 1b). Among boldness

behaviours, however, behavioural type influenced the amount of time a lizard spent basking under both benign (Fig. 1c) and risky conditions (Fig. 1d). Shy lizards basked less relative to bold lizards in both contexts. The interaction between behavioural type and group size affected boldness in terms of time spent basking prior to a simulated predator attack, with shy lizards basking more as group size increased while bold lizards exhibited the opposite pattern (Table 2). By contrast, the number of risky transitions was not affected by behavioural phenotype, group size or their interaction (Fig. 1e).

#### Effect of Behavioural Phenotype on Plasticity

The level of plasticity varied between behaviours ( $F_4 = 30.41$ ,  $P < 0.001$ ). Changes in social context elicited a higher level of responsiveness in the time spent basking under risky conditions relative to activity ( $t_{95} = 66.09$ ,  $P < 0.001$ ), exploration ( $t_{95} = 66.44$ ,  $P < 0.001$ ), the time spent basking under benign conditions ( $t_{95} = 66.57$ ,  $P < 0.001$ ) and the number of risky transitions ( $t_{95} = 65.71$ ,  $P < 0.001$ ). Negative correlations between individual variation in behaviour and plasticity were found for all behaviours (activity:  $R = -0.49$ ,  $P = 0.03$ ; exploration:  $R = -1.00$ ,  $P < 0.001$ ; benign basking time:  $R = -1.00$ ,  $P < 0.001$ ; risky basking time:  $R = -1.00$ ,  $P < 0.001$ ; number of risky transitions:  $R = -0.76$ ,  $P < 0.001$ ) indicating that behavioural phenotypes differed in their levels of plasticity. Slow behavioural phenotypes were more responsive than those with a fast behavioural profile.

## DISCUSSION

Classical models have long invoked an individual's perceived risk of predation as the primary driver of group size effects on behaviour, predicting that increases in the number of group members would result in higher mean expression of activity, exploration and boldness. These predictions have also been well supported empirically (activity: Awan & Geoffrey Smith, 2007; Blumstein, Daniel, & McLean, 2001; Downes & Hoefler, 2004; Webster et al., 2007; exploration: Ward, 2012; boldness: Awan & Geoffrey R. Smith, 2007a, 2007b; Downes & Hoefler, 2004; Goldenberg et al., 2014; Piyapong et al., 2010).

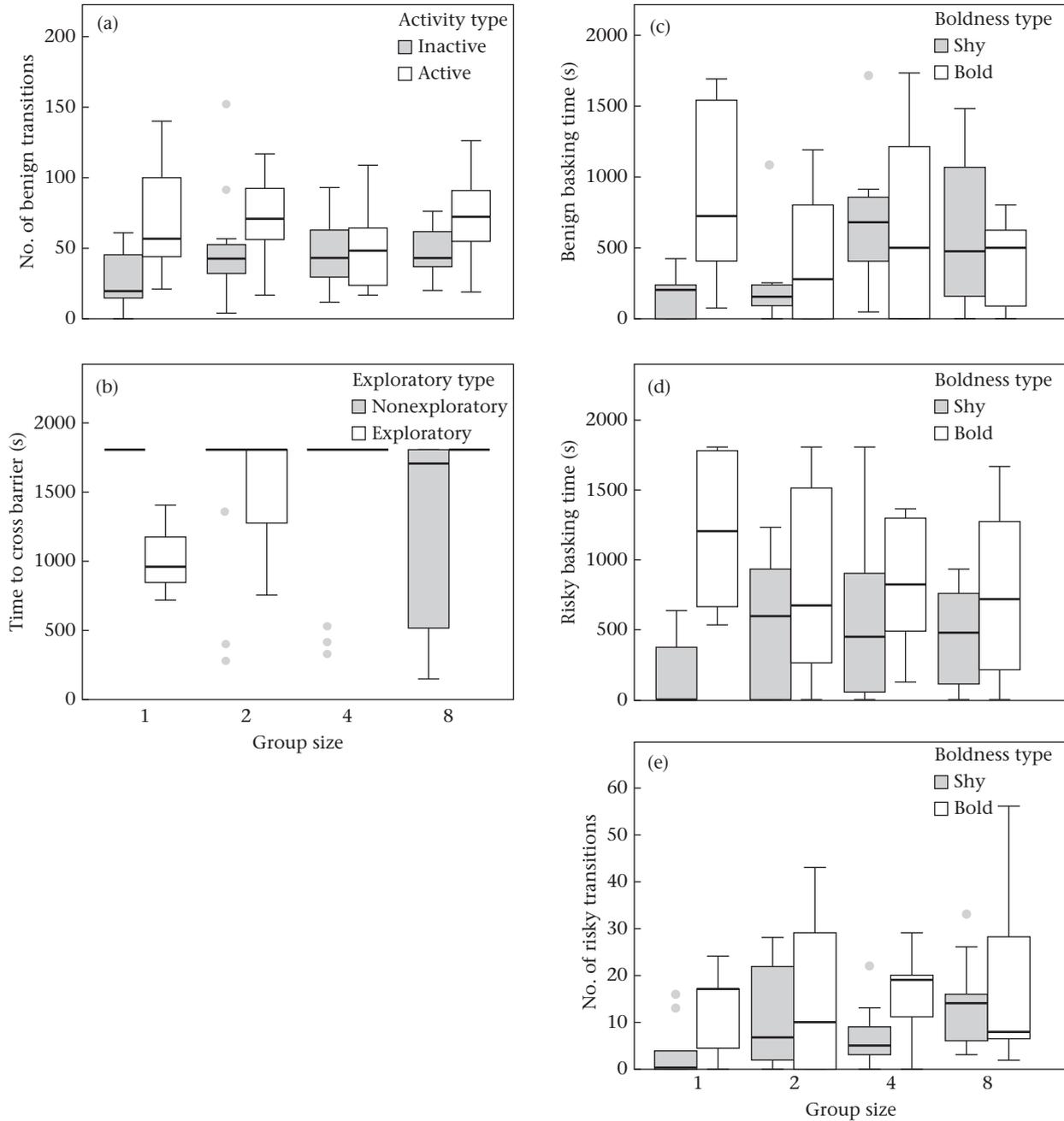
However, our study revealed complex effects of social context on the expression of individual behaviour among delicate skinks that countered many of the traditional predictions of a positive relationship between individual behaviour and social context. Instead, we found that lizards made nonlinear adjustments in their level of activity, exploration and bold behaviour which remained relatively consistent across group sizes. Differences in behavioural responses as a function of group size were only observed for activity, with lizards increasing the number of transitions they made when the number of group members increased from one to four under benign conditions. By contrast, social context had no influence on either exploratory or bold behaviour. It was expected that, as the number of group members increased, the time it took for lizards to cross the barrier would decrease, while the time spent openly basking or being active under threatening conditions would increase. Yet, this was not the case.

The apparent lack of group size effects in the expression of bold behaviour is particularly noteworthy, as these findings are in stark contrast to an earlier study on this species (Downes & Hoefler, 2004). In looking at the influence group size had on antipredator behaviour, Downes and Hoefler (2004) found that lizards spent less time inactive and immobile in the presence of a predator cue as group size increased. It makes sense that the effect of group size would be especially influential on the expression of bold behaviour in this species because, as a small heliotherm, delicate skinks are

**Table 1**  
Results of the generalized linear mixed models used to evaluate the effects of group size and individual behavioural type on activity (no. of transitions between zones) in *L. delicata*

Parameter	Estimate $\pm$ SE	$z$	$P$
Intercept	3.98 $\pm$ 0.26	15.33	< 0.001
Trial no.	-0.07 $\pm$ 0.03	2.22	0.03
Activity type: Inactive	-1.15 $\pm$ 0.34	-3.35	< 0.001
Group size 2	-0.04 $\pm$ 0.27	-0.16	0.88
Group size 4	-0.41 $\pm$ 0.20	2.02	0.04
Group size 8	-0.04 $\pm$ 0.22	-0.16	0.84
Activity type*Group size 2	0.78 $\pm$ 0.37	2.13	0.03
Activity type*Group size 4	1.12 $\pm$ 0.28	4.02	< 0.001
Activity type*Group size 8	0.71 $\pm$ 0.30	2.35	0.02

Significant values are in bold.



**Figure 1.** Behavioural responses across group sizes for each phenotype of *L. delicata*. (a) Number of benign transitions, (b) time to cross the barrier, (c) benign basking time, (d) risky basking time and (e) number of risky transitions. High values for number of benign transitions, benign basking time, risky basking time and number of risky transitions reflect high expression of activity and boldness, respectively; high values of time to cross the barrier reflect low expression of exploratory and bold behaviour. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

**Table 2**

Parameter estimates from Bayesian Markov chain Monte Carlo mixed-effect models evaluating the effect of group size, behavioural type and their interaction on exploratory and boldness behaviour

Parameter	Statistic	Exploration	Boldness		
		Time to cross	Benign basking	Risky basking	No. of risky transitions
Intercept	Posterior mean	<b>6.99</b>	<b>899.81</b>	<b>1105.79</b>	<b>1.98</b>
	Lower CrI	6.36	566.22	760.51	0.97
	Upper CrI	7.58	1232.46	1472.85	3.01
Trial no.	Posterior mean	0.001	-75.53	<b>-27.6</b>	-0.03
	Lower CrI	-0.11	-172.34	125.74	-0.30
	Upper CrI	0.11	14.50	67.89	0.22
Behavioural type	Posterior mean	0.46	<b>-550.60</b>	<b>-703.50</b>	-1.02
	Lower CrI	-0.11	-877.80	-1110.49	-2.35
	Upper CrI	1.12	-177.27	-306.19	0.27
Group size	Posterior mean	0.08	-34.12	-39.45	0.08
	Lower CrI	-0.09	-85.71	-106.65	-0.06
	Upper CrI	0.22	28.00	13.36	0.24
Behavioural type*Group size	Posterior mean	-0.16	<b>107.79</b>	65.47	0.10
	Lower CrI	-0.32	26.50	-23.52	-0.14
	Upper CrI	0.02	182.19	147.43	0.34

Nonexploratory and shy behavioural types are included within the intercepts. Bold estimates are significant (95% credible intervals (CrI) not including 0).

often faced with the conflicting demands of thermoregulation and predator avoidance. Grouping in larger numbers could, therefore, serve as an effective antipredator strategy that mitigates the risks associated with basking in sites having higher thermal quality (i.e. open sites). Habituation could explain the absence of group size effects on risky behaviours (i.e. openly basking and being active after a simulated predatory attack) in our study. Perhaps lizards had become familiar with their test environment and/or experienced sensory fatigue. This seems unlikely, however, despite such confounding effects being observed in other studies (Goldenberg et al., 2014; Ward, 2012), as trial number had a minimal effect in all behaviours except activity and risky basking.

One explanation as to why our findings do not align with previous work may be that our assessment of behaviour relied upon a single metric, at least for activity and exploration, rather than employing a multivariate approach. Recently, White, Pascall, and Wilson (2020) criticized univariate data collection and analyses of personality traits, suggesting that a single assay was ineffective in measuring the desired behavioural phenomenon. They collected multiple metrics from an assay commonly used to assess boldness, the open field test, across seven species of poeciliid fish. They found that when a single metric was considered it corresponded to the shy–bold axis for only three species, while the behaviour measured in the other four species instead corresponded to stress response behaviour. This issue was eliminated when a multivariate approach encompassing the full suite of metrics was employed. Whether our univariate approach contributed to our inability to detect group size effects is not entirely clear. However, given that we were not making interspecific comparisons, as was the case in White et al.'s (2020) study, and we employed standard assays that have been shown to effectively define and quantify each of the behavioural axes in question of a study species, we feel that the single metrics we utilized for exploration and activity were indeed robust and did not play a role in our findings.

An alternative and highly plausible explanation is that an individual's behavioural phenotype, rather than the absolute number of group members per se, may instead be the more important factor dictating behavioural responses to changing social conditions. Indeed, the effect of group size was only observed when it was evaluated in combination with behavioural phenotype; however,

these effects were limited to only two of the five metrics that were assessed, activity behaviour and one measure of boldness. Behavioural phenotypes were found to vary in the direction of responsiveness to changes in the social environment. For example, inactive lizards followed the trend of increasing activity with increases in group size. Higher expression of activity was especially prevalent when group size shifted from one lizard to the two largest group sizes (four and eight). Likewise, not only was the time spent basking in the open prior to a simulated predator attack greatest in larger groups, but behavioural adjustments also resulted in shy lizards becoming bolder than lizards with bold behavioural profiles. The expected group size effects may not have occurred between singletons and dyads due to the density dependency of behaviour. Differential responses in behavioural expression may be elicited only when the social context changes beyond the point where the security benefits of being in a group are realized. Thus, it may be that the addition of a single lizard may afford little in terms of reduced risk if individuals perceive the same level of risk when alone as when in a group of two.

In contrast to slow phenotypes (i.e. low-level activity and boldness), fast lizards generally exhibited an average decline in behaviour. Active individuals made fewer movements when group size increased, particularly when it increased from four to eight lizards. Similarly, the time that bold lizards spent openly basking under benign conditions was highest when alone but nearly reached its lowest level in a group of eight. Furthermore, fast phenotypes also varied in how much they modified their behaviour. The negative correlations between plasticity and personality suggested that fast individuals were less responsive than slow phenotypes in that their behavioural adjustments were smaller. Other studies have had similar results (Betini & Norris, 2012; Magnhagen & Bunnefeld, 2009; Stöwe & Kotschal, 2007). For instance, among shoaling perch, it was found that social context influenced the expression of bold behaviour, but bolder individuals responded less than shy fish (Magnhagen & Bunnefeld, 2009).

Yet, despite this mounting evidence, it is still not clear why variation in the degree of plasticity among behavioural types even exists. It has been suggested that low stress responsiveness or differential acquisition rates of public information could affect the sensitivity to external cues related to risk among phenotypes

(Cornwell, McCarthy, Snyder, & Biro, 2019). Perhaps, then, fast lizards were less able to assess the variation in per capita risk across group sizes. Alternatively, this result may be explained by the compensatory hypothesis which suggests that individuals expressing lower levels of a behaviour may need to modify their behaviour to a greater degree when responding to changes in environmental conditions, such as social context, as a means of compensating for the reduction in resource acquisition from lower expressions of activity, exploration and boldness (Betini & Norris, 2012), whereas those that already express high levels of behaviour need only to adjust their behaviour slightly, if at all, to achieve high fitness (Betini & Norris, 2012). Another scenario may be the process of conformity: behavioural responses among individuals are impacted by the personality of other group members such that the behaviour of the group is pushed towards that of the least or most responsive individuals (Webster & Ward, 2011). Indeed, we did observe a convergence in behavioural expression among behavioural phenotypes towards a common response level. Slow lizards exhibited elevations in behaviour while fast lizards simultaneously showed reductions, with the magnitude of change being greater among slow phenotypes. Without having tested the behaviour of all group members, however, it is unclear whether conformity was influencing the behaviour of focal lizards. Empirical support is beginning to emerge that suggests that the composition of the group can greatly impact the behaviour of its members through social processes such as conformity or facilitation (Magnhagen & Bunnefeld, 2009; Stöwe & Kotschal, 2007; van Oers et al., 2005). Thus, this would be a promising area of future research.

Importantly, despite the plastic responses to changes in the social environment exhibited by lizards in our study, we found that the diversity of individual behaviour was not restricted by social context. Instead, between-individual differences in the expression of activity, exploration and boldness persisted. The behavioural phenotype expressed when an individual lizard was alone was found to reflect its behaviour when in a group. However, the level of consistency did vary among behaviours where those behaviours expressed under more benign conditions showed higher levels of repeatability than those expressed under riskier conditions. Additionally, slow phenotypes were more consistent when the threat of predation was lowest whereas fast phenotypes exhibited greater consistency at higher threat levels. This suggests that slow phenotypes adopted a more risk-prone behavioural strategy when the perception of risk was elevated. Similar findings have been demonstrated among ravens, *Corvus corax* (Stöwe & Kotschal, 2007). Here, slow birds reduced their latencies in approaching a novel object when in groups of siblings versus being alone while fast birds increased their levels of neophobia. As a result, slow individuals took less time to inspect the novel object when in the presence of siblings than fast individuals. Furthermore, these observed effects of social context on behaviour were not dependent upon the behavioural phenotype of the group members as the same responses were observed when focal birds were grouped with both slow and fast phenotypes.

## Conclusion

In summary, we found a pronounced level of phenotypic plasticity among delicate skinks as a function of social context. The predicted patterns of group size effects were only observed, however, when each lizard's behavioural type was considered.

Furthermore, the degree and direction in which an individual adjusted its behavioural response were contingent upon its behavioural phenotype with slow lizards being more responsive than fast lizards. Yet even though lizards behaved plastically to changes in the social environment, our results provide strong evidence that the effects of an individual's personality were stronger than that of group size. Our study emphasizes the important role personality plays in social behaviour. Thus, it is vital to evaluate context dependency of behaviour to gain greater insight into how individual variation in behaviour is shaped by social processes under natural conditions.

## Author Contributions

D.L. performed the fieldwork and laboratory experiments. C.T.G. performed the data analysis and wrote the paper. D.G.C. developed the study design and assisted with writing the paper. All authors give final approval for this publication.

## Data Availability

Data are available at Dryad at <https://doi.org/10.5061/dryad.ns1rn8prt>.

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## Appendix

**Table A1**  
Summary statistics of behaviours by group size and behavioural type of *L. delicata*

Behaviour	Group size	Behavioural type	N	Mean	SE	Minimum	Maximum
No. of transitions	1	Active	9	73	12.96	21	140
		Inactive	11	27	6.05	0	48
		Total	20	47	8.37	0	140
	2	Active	9	75	14.90	17	158
		Inactive	11	52	11.86	4	152
		Total	20	63	9.47	4	158
	4	Active	9	50	9.78	17	109
		Inactive	11	47	7.16	12	93
		Total	20	49	5.75	12	109
	8	Active	9	73	10.96	19	126
		Inactive	11	47	5.49	20	76
		Total	20	59	6.36	19	126
Time to cross (s)	1	Exploratory	3	1021	194.43	719	1384
		Nonexploratory	17	1800	0.00	1800	1800
		Total	20	1683	68.36	719	1800
	2	Exploratory	3	1453	347.00	759	1800
		Nonexploratory	17	1509	141.71	255	1800
		Total	20	1501	127.66	255	1800
	4	Exploratory	3	1800	0.00	1800	1800
		Nonexploratory	17	1459	153.89	267	1800
		Total	20	1510	133.15	267	1800
	8	Exploratory	3	1800	0.00	1800	1800
		Nonexploratory	17	1192	166.96	147	1800
		Total	20	1284	149.77	147	1800
Benign basking (s)	1	Bold	10	841	187.90	70	1687
		Shy	10	174	45.60	0	426
		Total	20	508	121.25	0	1687
	2	Bold	10	414	149.68	0	1189
		Shy	10	229	98.48	0	1078
		Total	20	322	99.74	0	1189
	4	Bold	10	649	209.75	0	1723
		Shy	10	708	139.53	50	1710
		Total	20	679	122.79	0	1723
	8	Bold	10	418	89.65	0	799
		Shy	10	627	174.66	0	1479
		Total	20	523	98.53	0	1479
Risky basking (s)	1	Bold	10	1167	161.53	531	1800
		Shy	10	187	80.44	0	636
		Total	20	677	142.64	0	1800
	2	Bold	10	803	214.64	0	1800
		Shy	10	525	162.04	0	1232
		Total	20	664	134.71	0	1800
	4	Bold	10	831	142.74	126	1361
		Shy	10	554	180.97	0	1800
		Total	20	692	116.60	0	1800
	8	Bold	10	763	174.97	0	1656
		Shy	10	464	106.87	0	929
		Total	20	613	105.47	0	1656
No. of risky transitions	1	Bold	11	12	2.46	0	24
		Shy	9	4	2.06	0	16
		Total	20	9	1.84	0	24
	2	Bold	11	16	5.13	0	43
		Shy	9	12	3.88	0	28
		Total	20	14	0.99	0	43
	4	Bold	11	16	2.54	0	29
		Shy	9	7	2.27	0	22
		Total	20	12	1.96	0	29
	8	Bold	11	19	5.27	2	56
		Shy	9	14	3.37	3	33
		Total	20	17	3.25	2	56

Activity was assessed in terms of the number of transitions made. Exploration was assessed in terms of the time to cross a barrier with lower values indicating higher expression of exploratory behaviour. The time spent basking under benign and risky conditions and the number of transitions made after a simulated predator attack were used as measures of boldness.

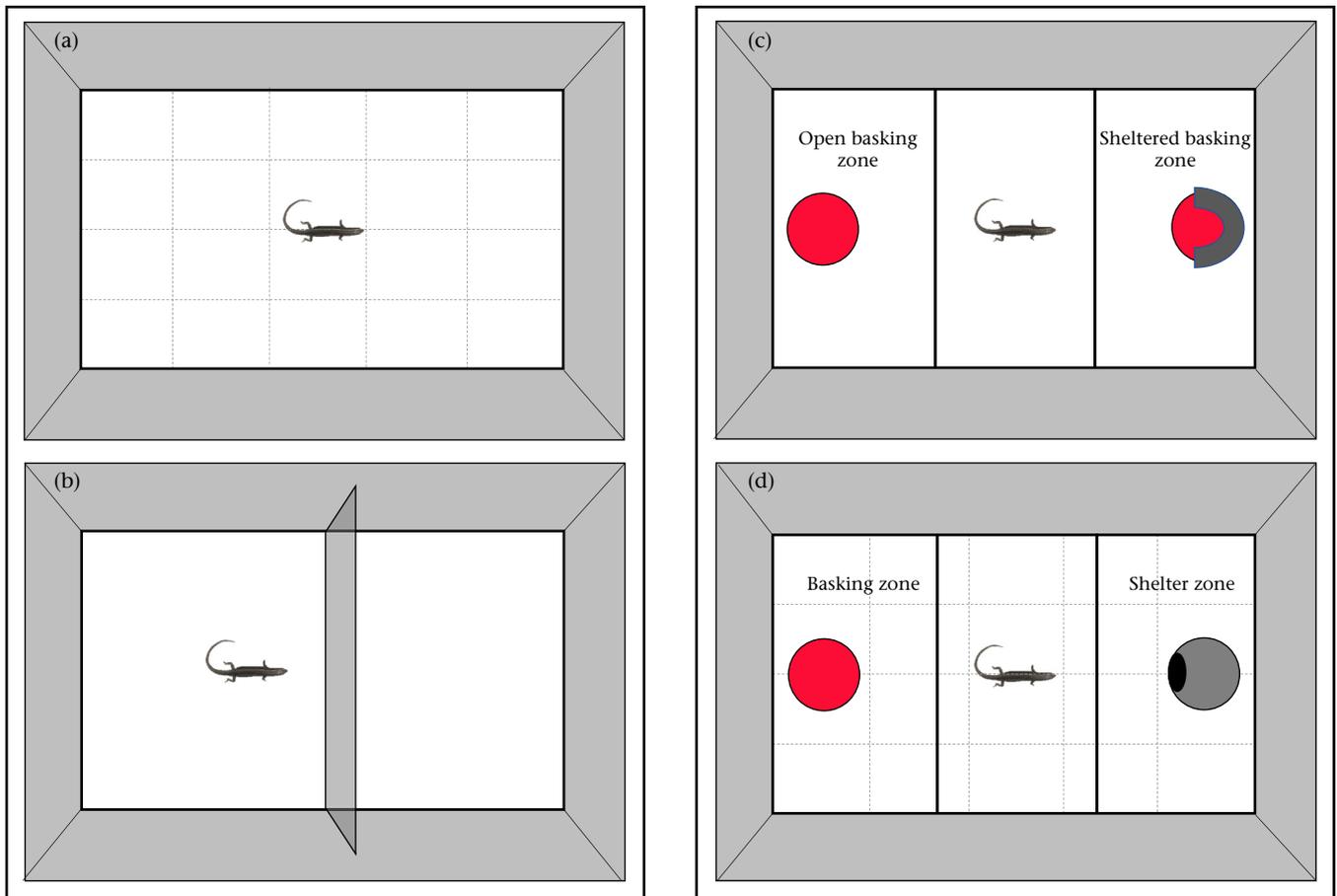
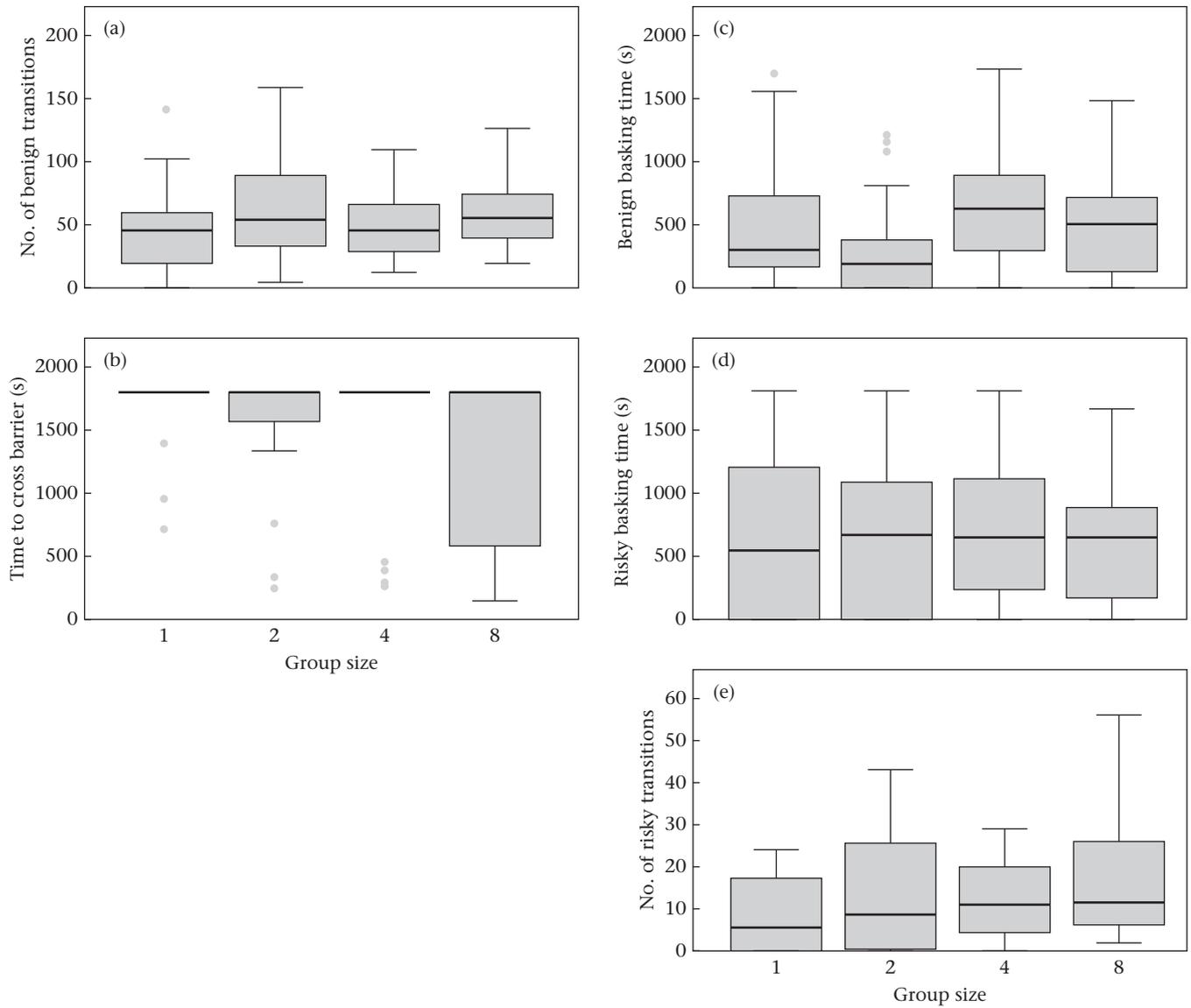


Figure A1. Schematics of experimental arenas (550 × 320 mm and 240 mm high) used in testing behavioural responses to changing social environments. (a) For testing activity, the arena was divided into 20 equally sized grid squares. The number of transitions between grid squares was used as a measure of activity. (b) For testing exploration, the arena was divided in half by a trapezium-shaped partition which was flush with the base of the arena and tapered allowing space for lizards to squeeze between either gap to reach the other compartment. Exploration was measured as the time to manoeuvre around the partition. Boldness was assessed in two contexts: (c) basking site selection and (d) simulated predator attack. For the basking site selection assay, the arena was divided into open and sheltered basking sites (left and right zones, respectively) and a no-preference zone. Time spent in either basking zone was used to quantify boldness. For the simulated predator attack, the arena marked with 20 grid squares was divided into a basking zone (left), a neutral zone (middle) and a shelter zone (right). The times spent in the zones and the number of transitions after a simulated predator attack were used to assess boldness. See Methods for further details.



**Figure A2.** Behavioural responses across group sizes of *L. delicata*. (a) Number of transitions, (b) time to cross the barrier, (c) benign basking time, (d) risky basking time and (e) number of risky transitions. High values for number of benign transitions, benign basking time, risky basking time and number of risky transitions reflect high expression of activity and boldness, respectively; high values of time to cross the barrier reflect low expression of exploratory and bold behaviour. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.