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Impacts of caudal autotomy on personality

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Caudal autotomy, the voluntary shedding of a tail, is a last-ditch strategy used by many lizard species to escape from predators. There are several costs associated with caudal autotomy that may cause lizards to change their behaviour during tail regeneration. These behavioural changes may be dependent upon individual differences in response to autotomy (e.g. trait or state-dependent differences) and/or the degree of tail loss, as many lizards have the capacity to only partially shed their tail which probably entails fewer costs relative to complete autotomy. However, no study, to our knowledge, has considered how caudal autotomy, or the extent of autotomy, affects individual behavioural variation. Accordingly, we investigated the effects of both partial and complete tail loss on individual behavioural variation in delicate skinks, *Lampropholis delicata*. We found that lizards that experienced complete tail loss, on average, became less active and explorative and had much slower sprint speeds following autotomy. These lizards also became more predictable and consistent in their behaviour, exhibiting a notable decrease in their within-individual behavioural variance. In contrast, we did not see any significant behavioural effects in lizards that experienced partial tail loss. We also found a positive among-individual correlation between activity/exploration and neophilia, but tail loss had no effect on the structure of this syndrome. Our results suggest that complete tail loss may impose effects on traits more closely associated with locomotion and predator escape ability, while also constraining an individual's capacity for differential behavioural expression.

Animals have evolved a remarkable diversity of defensive tactics to evade or escape predators. Such strategies include increasing the use of refugia or concealed microhabitats (Michelangeli & Wong, 2014), flocking or shoaling behaviours (Carere et al., 2009), defensive weaponry (Straile & Halbich, 2000), crypsis or camouflage (Morgans & Ord, 2013) and aposematic displays (Umbers & Mappes, 2015). Yet, despite the multitude of evolved antipredator strategies, few forms of predator avoidance are as dramatic as autotomy, the ‘voluntary’ shedding of an animal's limb or appendage. This defensive tactic has independently evolved in diverse taxa (Emberts, Escalante, & Bateman, 2019), including vertebrates (e.g. amphibians and reptiles; Bateman & Fleming, 2009) and invertebrates (e.g. cephalopods, crustaceans, spiders and insects: Maginnis, 2006), but has been most widely studied in lizards where caudal (tail) autotomy occurs in 13 of the 20 known families (Bateman & Fleming, 2009). Lizards generally employ caudal autotomy as a last effort to escape the grasp of a predator, but also includes postautotomy tail thrashing which acts to distract the predator, providing valuable time for the attacked lizard to flee. Several studies have now demonstrated that the act of caudal autotomy substantially increases an individual's chances of survival from a predatory attack (Arnold, 1988; Bateman & Fleming, 2009).

While the antipredator benefits of caudal autotomy are clear, there are also costs associated with losing a tail (Maginnis, 2006). For example, caudal autotomy typically results in a loss of energy, with caudal lipid reserves being the major fat supply for many lizard species (Chapple & Swain, 2002a; Cromie & Chapple, 2013). Tail loss can also lead to decreased stride rate, endurance, jump trajectory/stability and overall locomotor performance (Chapple & Swain, 2002b; Downes & Shine, 2001; Gillis, Kuo, & Irschick, 2013; Medger, Verbrugt, & Bateman, 2008). However, tail loss does not always result in movement costs, with studies documenting that some species sprint faster after caudal autotomy (Kelehear & Webb,

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2006; Martin & Avery, 1998). Furthermore, following tail loss, lizards can no longer employ caudal autotomy as a defensive tactic until they have sufficiently regenerated their tail, thus must become more reliant on other antipredator strategies (Arnold, 1988; Bateman & Fleming, 2009). It has also been reported that tail loss can compromise immunity and lead to higher parasite infection rates (Argaez, Solano-Zavaleta, & Zúñiga-Vega, 2018). Together, loss of energy stores, compromised mobility and immunity and increased predation risk may lead lizards to change their behaviour during tail regeneration (Downes & Shine, 2001). For instance, tailless lizards may engage in more cryptic behaviour, increase refuge use and exhibit fewer risk-taking behaviours (Cooper, 2007). Alternatively, to compensate for energy loss and compromised physiology during tail regeneration, tailless lizards may spend more time active and foraging, despite the potentially greater vulnerability to predators (Cooper & Wilson, 2008).

Even before autotomy has occurred, individuals tend to vary in whole suites of traits, suggesting that they may also vary in how they respond to autotomy. Consistent individual differences in behaviour, also known as animal personality, may therefore be expected to alter the effects of autonomy on later individual behavioural expression. Animal personality is often used to describe both the phenomenon of consistent between-individual differences in average behaviour (Reale et al., 2010; Roche et al., 2016), and correlations between behaviours across time and space (i.e. behavioural syndromes; Sih, Bell, & Johnson, 2004). For example, individuals that are found to be consistently more aggressive are also commonly found to take more risks across diverse contexts (e.g. predation risk, response to novelty) relative to less aggressive individuals (i.e. this would be considered an aggressive—bold behavioural syndrome). A key characteristic of animal personalities is that they are relatively inflexible in that an individual's response to a given situation is often mediated by its fixed behavioural tendencies. However, given that physiological and morphological mechanisms often underlie behaviour and behavioural correlations (Biro & Stamps, 2008), and that physiology and morphology are often compromised following tail loss (Naya & Bodonozvic 2006), individuals experiencing autotomy may adopt behaviours on either extreme of a behavioural spectrum (e.g. either become very active or inactive), thus increasing the predictability of their behavioural expression during tail regeneration. Currently, we have a very limited understanding of how autotomy affects individual behavioural variation. One recent study found that consistently bold brown anoles, *Anolis sagrei*, compensated for being bolder by increasing their propensity for caudal autotomy (Kuo, Irschick, & Lailvaux, 2015), while another study found a similar compensatory effect in damselfly larvae, *Ischnura pumilio* (Delnat, Debecker, & Stoks, 2017).

Many studies investigating the impacts of caudal autotomy on individual performance typically only consider the effects of complete tail loss. Tail loss occurs through fracture planes within the caudal vertebrae, with lizards often shedding their tail a few vertebrae proximal to where they are grasped by an attacker (Bateman & Fleming, 2009). Thus, in many species and situations, complete tail loss seems to be relatively rare, whereas partial tail loss seems to be a more common outcome in natural populations, with lizards being able to limit the amount of tail shed during autotomy. The ability to partially shed the tail probably limits the subsequent costs of caudal autotomy and reduces the tail regeneration time. Indeed, some research suggests that weakened movement following tail loss is only significant until more than half of the tail is lost (Cooper & Smith, 2009; Lin & Ji, 2005).

In this study we investigated the effects of both partial and complete tail loss on individual behavioural variation in delicate skinks, *Lampropholis delicata*. The delicate skink is a small lizard (34–55 mm adult snout—vent length [SVL]) that is abundant throughout southeastern Australia. Our previous work has shown that both male and female delicate skinks exhibit a common behavioural syndrome between activity, exploratory behaviour and sociability whereby lizards with high activity levels tend to be more exploratory and social (i.e. spend more time with conspecifics) than lizards with low activity levels which express the opposite characteristics (i.e. low exploratory and social tendencies; Michelangeli, Wong, & Chapple, 2016; Michelangeli, Chapple, & Wong, 2016). Activity and exploration tendencies have also been found to be positively correlated within and between four geographically and phylogenetically distinct populations of the delicate skink across southeastern Australia (Michelangeli, Chapple, Goulet, Bertram, & Wong, 2019).

The aims of our study were to determine the effect of caudal autotomy on (1) consistent individual differences in behaviour (behavioural repeatability and variance) and (2) behavioural correlations (or behavioural syndromes). Specifically, we aimed to test a number of predictions. First, given that caudal autotomy is expected to reduce locomotor function due to morphological and physiological constraints, we hypothesized that tail loss would lead to a decrease in behaviours that are more reliant on locomotion (e.g. activity, exploration, sprinting). Moreover, we also predicted that individuals that experience tail loss would become more predictable in these behaviours, because their capacity for differential behavioural expression would also be constrained by reduced locomotor capacities. However, our third prediction was that the effect of caudal autotomy would be dependent on the degree of tail loss, whereby lizards experiencing full tail loss would exhibit the most drastic shift in personality. Finally, we also hypothesized that caudal autotomy would not greatly alter the structure of behavioural syndromes because correlated behavioural traits affected by tail loss would shift in the same direction and thus remain coupled.

METHODS

Animal Collection and Husbandry

Delicate skinks were collected from Sydney, Australia in October 2014, just after the species' breeding season. We caught lizards by hand and by mealworm fishing, as these methods do not preferentially trap individuals with particular personalities (Michelangeli, Wong et al., 2016).

We only retained adult males (SVL > 34 mm; Wilson & Swan 2013) with complete tails (tail length > SVL) for experiments. Females were not used in this study because gravidity can influence the behaviour of females and we could not guarantee that females were not gravid. Lizards were transported back to our laboratory for behavioural experiments. They were tagged with a minimally invasive unique permanent identification code using different colour combinations of Visual Implant Elastomer (Northwest Marine Technology, Anacortes, WA, U.S.A.), allowing us to track individuals throughout experiments. Focal skinks were housed in groups of up to four in plastic containers (300 × 230 mm and 370 mm high). A basking area, consisting of a heat lamp over two terracotta tiles, was provided at one end of each housing container, providing a thermal gradient within containers (22–32 °C) and allowing lizards to thermoregulate from 0800 to 1800 h. Small plastic pots were added to provide shelter. UV lighting was placed above the containers and was activated from 0800 to 1800 h. All housing containers were in a temperature-controlled room with an ambient temperature of approximately 22–23 °C and room lighting from 0700 to 2100 h daily. Skinks were fed a diet of crickets, *Acheta domesticus*, dusted in a vitamin supplement (Reptivite), three times per week, and water was available ad libitum.

Experimental Procedure

Skinks were randomly assigned to one of three treatment groups: no tail loss (i.e. control, $N = 18$), partial tail loss ($N = 19$) and complete tail loss ($N = 19$). There was no difference in the SVL between the three treatment groups (mean SVL ± SE; control: 39.5 ± 0.53 mm; partial: 39.1 ± 0.33 mm; complete: 39.3 ± 0.45 mm; ANOVA: $F_{2,\,53} = 0.153$, $P = 0.859$). Each treatment group experienced the following experimental procedure.

Stage 1: pretreatment assays

Before tail loss treatments were applied, we first tested each individual through a series of assays (outlined in detail below under *Assays*) to examine variation and correlation among four traits: activity/exploration, sociability, neophilia and sprint speed. Assays that could have the greatest influence upon behaviour were carried out last to reduce potential carryover effects (Bell, 2012). To assess behavioural repeatability, we tested individuals in each behavioural assay twice, with each retest occurring 1 week apart to examine short-term repeatability (Bell, Hankison, & Laskowski, 2009). All assays were conducted between 0900 and 1500 h within temperature-controlled rooms that matched the lizards' housing temperature (22–23 °C) and were video-recorded using Panasonic HC-V130 cameras. We thoroughly washed experimental equipment between trials with hot water and scentless dishwashing detergent to prevent scent contamination.

Stage 2: application of tail loss treatment

Once the pretreatment assays were completed, skinks in the 'partial' and 'complete' tail loss groups underwent intravertebral tail autotomy. Specifically, caudal autotomy was stimulated by pinching the tail with fine forceps (sensu Cromie & Chapple, 2012). Complete tail loss equated to the removal of a full tail, where lizards had their tails removed at approximately 10 mm posterior to the base of the tail. Partial tail loss involved skinks experiencing a break half-way along the length of the tail from the tail's base (see Appendix Fig. A1). Control lizards retained their full-length tail but experienced a similar handling procedure to control for potential behavioural changes brought about by handling stress alone (Wise & Jaeger, 1998). The skink was conscious during this procedure given that autotomy is under neurological control (Bateman & Fleming, 2009). Following tail loss, Betadine (an antiseptic) was applied to the tail stump and the lizard was returned to its housing container.

Stage 3: post-treatment assays

One week after the tail loss treatment was applied, skinks were again tested twice for each behavioural assay using the same experimental procedure outlined in Stage 1. Overall, this protocol allowed us to test for the effects of caudal autonomy on behavioural variation and behavioural correlations.

Behavioural Assays

Nondirected activity test: activity and exploratory tendencies

To measure activity and exploratory tendencies, skinks were allowed to move freely for 30 min in an opaque walled experimental arena (550 × 320 mm and 240 mm high) marked with 20 equal grid squares. Skinks were allowed to acclimate under transparent containers for 10 min prior to the trial. We counted the transitions between grid squares each skink made during the 30 min trial, with more transitions equating to a higher activity score. We have previously found that activity is strongly and positively correlated with exploratory behaviour in delicate skinks from Sydney (Goulet et al., 2018; Michelangeli, Wong et al., 2016; Michelangeli, Chapple et al., 2016; Michelangeli, Chapple et al., 2019; Michelangeli, Goulet, Kang, Wong, & Chapple, 2018; Moule, Michelangeli, Thompson, & Chapple, 2016), as well as within and between four geographically and phylogenetically distinct populations across Australia (Michelangeli, Chapple, et al., 2019). Thus, we considered the behavioural measurements taken from this assay to be an accurate proxy for testing both activity and exploratory tendencies.

Sociability test

Delicate skinks are frequently observed basking in groups of varied sizes in the wild, from small groups (ca. 2–10 individuals) to basking alone (Chapple, Simmonds, & Wong, 2011). Thus, to test the social behaviour of skinks, we conducted a dichotomous choice experiment, whereby we offered focal lizards a choice between basking with a group of conspecifics and basking alone (see detailed methods outlined in Michelangeli, Wong et al., 2016; Michelangeli, Chapple et al., 2016; Michelangeli, Smith, Wong, & Chapple, 2017; Michelangeli, Chapple, et al., 2019, see Appendix Fig. A2 for an illustration of the assay). Briefly, focal lizards were placed into a test arena that was split into three zones: a social zone, asocial zone and neutral zone. The social zone comprised a basking site that was divided in half by a clear Perspex partition that ran the length of the arena. Three stimulus lizards were placed behind the partition. The asocial zone at the opposite end of the arena was identical but contained no lizards. We recorded the amount of time lizards spent basking in the social zone over 30 min.

Response to a novel food item: neophilia

To measure an individual's willingness to forage or accept a novel food item, we allowed lizards to freely explore an opaque walled experimental arena, marked with 20 equal grid squares, that contained a novel food item (ca. 0.25 g of mashed banana inside a petri dish) placed at one end of the arena. Mashed banana has previously been used as a novel food item for skinks, and skinks have been observed to eat banana when offered it (e.g. Spiegel, Leu, Sih, Godfrey, & Bull, 2015). Furthermore, these lizards are commonly found in urban systems, and thus probably interact with, even adopt, food items that are outside their natural diet (Moule et al., 2016). Skinks were allowed to acclimate under transparent containers for 10 min prior to the trial. We recorded the time a lizard spent in the 'novel food zone' (four equal grid squares around the novel food item) as a measure of foraging neophilia.

Sprinting performance

Sprint speed is often used as an index for the individual's optimal performance capacity and is a key trait that allows lizards to escape predators (Brodie & Russell, 1999; Husak, 2006). While sprint speed is not typically considered a behavioural trait per se, we used it here as a proxy for the many behavioural traits, particularly those related to antipredator strategies, that are likely to underlie sprinting speed and other similar metrics of performance (Brodie & Russell, 1999). To test a lizard's sprint speed, we first warmed lizards to 30 °C (the optimal temperature for maximal sprint speeds; Cromie & Chapple, 2012; Goulet, Thompson, Michelangeli, Wong, & Chapple, 2017) in temperature-controlled chambers for 30 min. After this warming period, lizards were then encouraged to sprint (by lightly tapping the tail/tail stump with a paintbrush) down a 1 m racetrack (10 cm width: Goulet et al., 2017) that was set at our desired test temperature (i.e. 30 °C). The sprinting performance of lizards was determined by photodiode sensors positioned at 25 cm intervals along the racetrack. A velocity measurement was recorded for each of the segments between the four sensors. Following their first run, lizards were returned to the thermal chamber and allowed to rest for 30 min before being run down the racetrack again. In total, we recorded eight sprint speed measurements for each lizard, with the fastest 25 cm interval speed designated an individual's maximal sprint speed.

Ethical Note

Research was conducted in accordance with appropriate collection and research permits (SL101038, SL101202, SL101203) and was approved by the Monash University Animal Welfare Committee (BSCI/2014/11). Visible Implant Elastomer (VIE) is a commonly used tagging method in small animals. It has been successfully used in delicate skinks with no negative effects (Goulet et al., 2017; Michelangeli, Wong et al., 2016; Michelangeli, Chapple et al., 2016; Michelangeli et al., 2017; Michelangeli, Chapple et al., 2019; Michelangeli, Goulet et al., 2018). Tagging with VIE involves injecting one to four limbs of a lizard with a biologically inert material. The handling time during VIE is less than 2 min for trained personnel and very fine 28-gauge needles were used to reduce pain. On completion of this study, lizards were maintained in our housing facility and were then used in future ethically approved research projects.

Statistical Analysis

Data were analysed using *R* version 3.3.2 (R Core Development Team, 2016). We used the Bayesian package MCMCglmm (Hadfield et al., 2010) for mixed modelling. To model the response to novelty (i.e. neophilia) data, we used a Poisson error distribution, but for all other data, we used a Gaussian error distribution. Models were checked for adequate mixing, autocorrelation and convergence. We also compared models with different priors to ensure that results were not heavily influenced by our choice of prior (they did not; results not shown). In our results we report posterior modes for all estimated parameters (fixed and random) and the associated 95% credible intervals (CIs).

Effect of caudal autotomy on mean behaviour

To examine how caudal autotomy influenced mean behaviour, we performed Bayesian univariate mixed models. Models contained treatment, stage (pre- and post-treatment), treatment $*$ stage interaction and SVL as fixed factors and individual ID as a random factor to take the repeated measures design into account. Given that our hypothesis was that tail loss would influence behaviour after autotomy, we were testing for a significant treatment $*$ stage interaction. Each behavioural variable (number of grid transitions, time spent basking with conspecifics, time spent near novel food item and maximal sprint speed) was modelled separately.

Effect of caudal autotomy on behavioural variances

Repeatability represents the proportion of variation attributed to between-individual differences in a trait and is calculated using the formula: among-individual variance (V_A)/total phenotypic variance (within-individual variance (V_W) + V_A). Thus, a repeatability higher than 0.5 would suggest that most of the observed trait variation is due to differences between individuals (Nakagawa & Schielzeth, 2010). Across studies of multiple taxa, the average repeatability of behavioural traits is around 0.37 (Bell et al., 2009). To estimate and compare repeatability and the associated variance components (i.e. V_A and V_W) of traits before and after caudal autotomy, we used separate Bayesian bivariate mixed models for each treatment and behaviour. Specifically, for each treatment and trait, models contained both the pre- and post-treatment behavioural scores as response variables and SVL and trial number as fixed factors. Individual ID was included as the random effect and the bivariate model allowed us to estimate the individual behavioural variance components separately for pre- and post-treatment measurements. We report the repeatability, V_A and V_W, as well as the differences in the variance components between pre- and post-treatment scores (ΔV_A and ΔV_W). The bivariate model also allowed us to estimate the among-individual covariance between pre- and post-treatment behaviours (e.g. to test whether the most active individuals pretreatment were also the most active post-treatment). The covariance estimates were standardized to correlations and inference was based on overlap of the 95% CIs with zero.

Effect of caudal autotomy on behavioural correlations

To examine whether caudal autotomy affected correlations between behavioural traits at the among-individual level, we performed multiresponse Bayesian mixed models. All four behavioural traits (number of grid transitions, time spent basking with conspecifics, time spent near novel food item and maximal sprint speed) were included as multivariate response variables and we included trial and SVL as fixed predictors. We estimated the among-individual behavioural covariances pre- and post-treatment in each treatment separately. To provide an indicator of the magnitude of difference in correlation between pre- and post-treatment behaviours, we also report the average difference in their pairwise correlations (Δr_A). Statistical inference for these differences was based on the following scale: $0 < \Delta r_A < 0.3$, no to low effect; $0.3 < \Delta r_A < 0.6$, medium effect; $r_A > 0.6$. strong effect (sensu Royauté, Buddle, & Vincent, 2015; Nakagawa & Cuthill, 2007).

RESULTS

Effect of Caudal Autotomy on Mean Behaviour

We found evidence of a treatment $*$ stage interaction in the models associated with activity and maximal sprint speeds (Appendix Table A1), suggesting that tail loss treatment, on average, had an effect on these behaviours. To further disentangle these interactions, we explored each treatment group separately. Complete tail loss lizards made significantly fewer grid transitions (i.e. activity; estimates [95% CIs]: -15.03 [-25.93, -4.96]; Fig. 1a) and were significantly slower sprinters (-14.90 [-25.51, -4.40]; Fig. 1d) after than before autotomy. In contrast, control lizards and lizards that only experienced partial tail loss exhibited no difference in activity (control: -1.50 [-11.42, 8.79]; partial: -6.79 [-15.70, 2.39]) or maximal sprint speed (control: 1.33 [-6.101, 9.27]; partial: 4.71 [-1.77, 10.83]; Fig. 1) between pre- and post-treatment. Notably, lizards experiencing partial tail loss increased sprint speed after autotomy, although the magnitude of this increase was nonsignificant (i.e. CIs overlap zero). We found no indication that the average neophilia and social behaviour of lizards were influenced by caudal autotomy (Table A1, Fig. 1).

Effects of caudal autotomy on repeatability and behavioural variance

Repeatability of behavioural traits ranged between <0.01 (i.e. no evidence of repeatability) and 0.92 (very high repeatability; Appendix Table A2, Fig. 2). However, owing to the relatively low sample sizes within treatment groups for partitioning variances, there is high uncertainty (i.e. wide CIs) around our repeatability and variance estimates, and thus these estimates should be interpreted

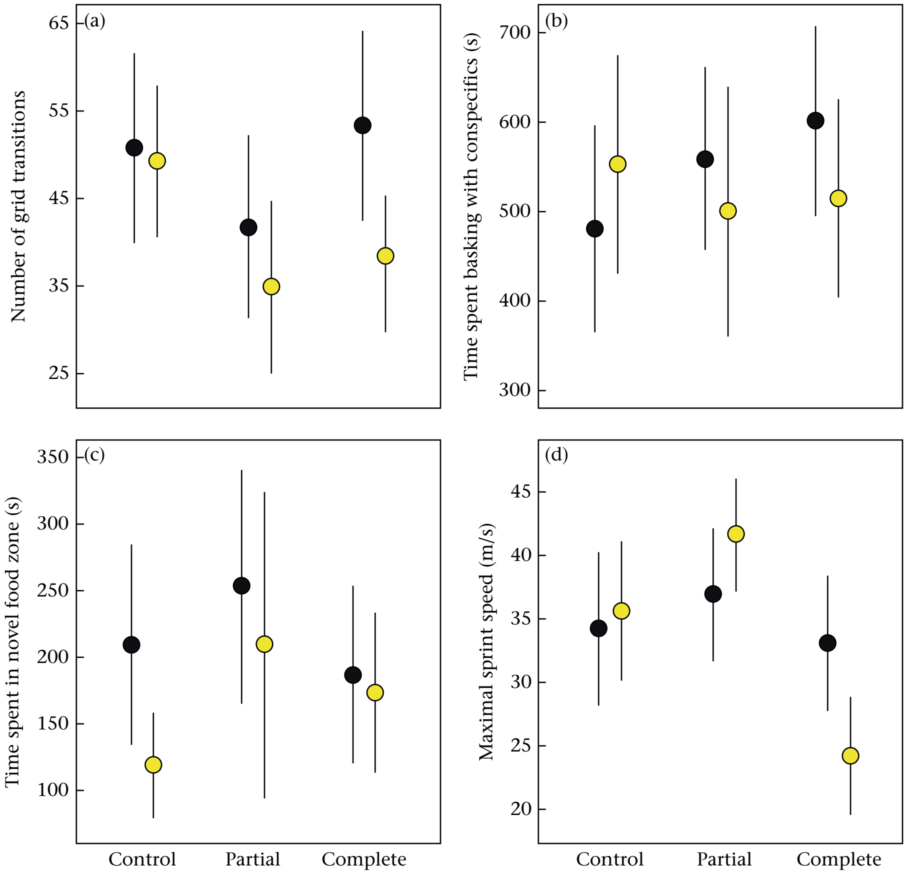

Figure 1. Average behavioural differences between tail loss treatment groups pre- (black circles) and post-treatment (yellow circles) in (a) number of grid transitions, (b) time spent basking with conspecifics, (c) time spent in the novel food zone and (d) maximal sprint speed. Values represent posterior means ± 95% credible intervals.

carefully. Nevertheless, despite low power to detect differences in variances, we still found that caudal autotomy had an effect on repeatability and behavioural variance (Appendix Tables A3, A4). Specifically, lizards that experienced complete tail loss expressed significantly higher repeatability in their activity and neophilia after autotomy (Table A2, Fig. 2). It appears that this increase in behavioural repeatability in lizards that experienced complete caudal autotomy was a result of a very apparent decrease in their within-individual variation in these behaviours after autotomy (Table A3, Fig. 3). The magnitude of this decrease in within-individual variation was significant for activity, but not for both response to a novel food item and maximal sprint speed; Table A3). These results suggest that lizards that experienced complete caudal autotomy became more predictable in their behaviour after tail loss.

In contrast, control and partial tail loss lizards expressed little difference in repeatability between pre- and post-treatment for most behaviours (Table A2, Fig. 2). However, unexpectedly, both treatment groups exhibited a noticeable decrease in repeatability for maximal sprint speeds post-treatment (Table A2, Fig. 2). This decrease in repeatability was due to an evident decrease in between-individual variation (i.e. individuals had more similar sprinting speeds after autotomy), potentially arising from a habituation effect to the test conditions (Table A3, Fig. 3). Finally, we only detected significant among-individual covariance in activity between pre- and post-treatment for control and partial tail loss lizards; that is, lizards that were more active pretreatment were also more active post-treatment (Table A3). We did not find support for among-individual covariance in the other behaviours between pre- and post-treatment.

Effect of Caudal Autotomy on Behavioural Correlations

We found limited evidence of behavioural syndromes (Appendix Table A4). When considering all lizards, we found some support for a significant positive among-individual correlation between activity (i.e. number of grid transitions) and neophilia (i.e. time spent near a novel food item; Table A4). This suggests that lizards that were more active were also more likely to spend time near a novel food item. However, the strength of this correlation declined post-treatment (Table A4). This decline does not appear to be driven by caudal autotomy, but instead, seems to be a result of a drop in the among-individual covariance between activity and response to novelty within the control group post-treatment (Table A4). Overall, it appears that for some behavioural combinations, the among-individual covariance between these behaviours decreased post-treatment, but that this decrease was not driven by any particular treatment group, suggesting that caudal autotomy had no influence on among-individual behavioural correlations (Table A4).

DISCUSSION

We found that caudal autotomy impacted delicate skink personality, but that these impacts depended on the extent of tail loss. Specifically, lizards that experienced complete tail loss were overall less active and explorative and became slower sprinters after caudal autotomy. Interestingly, these lizards also became behaviourally more predictable after autotomy, exhibiting an apparent decrease in within-individual variation in all behaviours, except sociability. In contrast, lizards that experienced partial tail loss

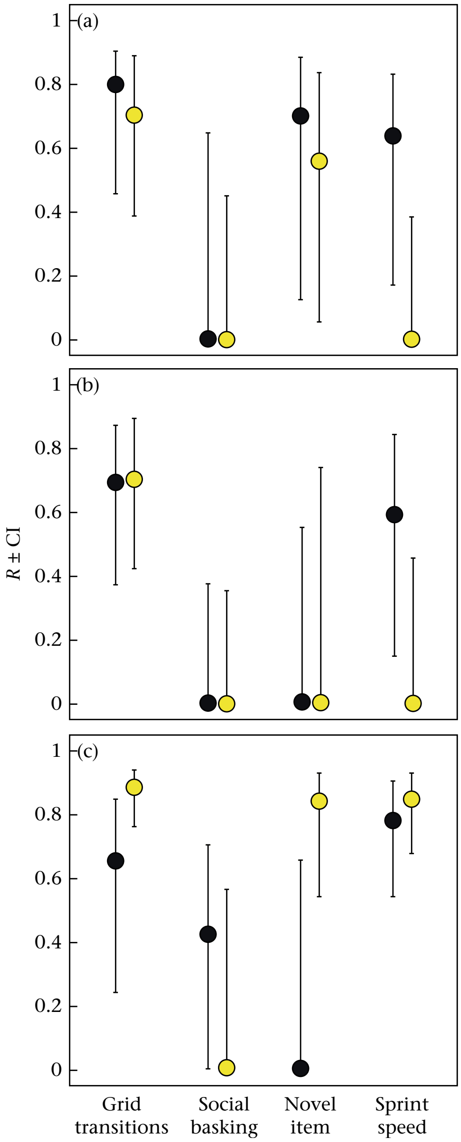

Figure 2. Repeatability estimates (R) for each trait in the tail loss treatment groups pretreatment (black circles) and post-treatment (yellow circles): (a) control, (b) partial tail loss and (c) complete tail loss. Values represent posterior modes ± 95% credible intervals (CI).

exhibited very little difference in their behaviour. In fact, on average, partial tail loss lizards increased their maximal sprint speeds after losing part of their tails. Furthermore, while we did find a positive among-individual correlation between activity/exploration and response to novelty, tail loss had no apparent influence on the structure of this behavioural syndrome. Overall, our study is one of the first to document any effects of autotomy on animal personality. It seems that complete caudal autotomy may impose greater effects on behavioural traits closely linked to locomotion and predator escape abilities. Importantly, our results also suggest that the capacity to partially shed a tail in lizards can reduce, even potentially ameliorate, the behavioural costs that are often associated with losing an entire tail.

We observed a reduction in activity levels and maximal sprint speeds in lizards that experienced complete tail loss, but not in lizards that only experienced partial tail loss. Differences in maximal sprint speeds could be a consequence of changes to weight, balance and friction as a result of caudal autotomy. A number of species have been demonstrated to reduce endurance, speed and stamina following autotomy of an appendage (e.g. spiders: Gerald, Thompson, Levine, & Wrinn, 2017; crabs: Gerald & Thiesen, 2014; lizards: Lin & Ji, 2005; Martin & Avery, 1998). As a base for muscle attachment, a lizard tail functions as a counterbalance to limit sideways movement during sprinting (Bateman & Fleming, 2009; Cooper & Smith 2009). Thus, when tails are completely lost, lizards spend more energy at every step correcting for the disequilibrium caused by no longer having a counterbalance mechanism, resulting in reductions to stride length, stability and momentum (Chapple & Swain, 2002b; Martin & Avery, 1998). On the other hand, previous research has also shown that the ability of the tail to act as a counterweight is not lost until more than two-thirds of the tail is shed (Cooper & Smith 2009). This probably explains why partial tail loss skinks in our study were even able to increase their maximal sprint speeds after caudal autotomy. Given that lizard sprint speed is often strongly correlated with predator escape ability (Husak, 2006), this would suggest that the antipredator costs of complete tail loss are far greater than those of partial tail loss. Indeed, partial autotomy of limbs has been suggested to have evolved in several taxa to mitigate the costs of autotomy (Emberts et al., 2019).

Our results also suggest that lizards that experienced tail loss converged towards a personality that was less active and explorative. Indeed, many species, including the delicate skink, have been shown to reduce activity when they undergo autotomy (Cromie & Chapple, 2012; Downes & Shine, 2001; Fromanowicz et al., 1990; Martin & Avery, 1998; Martin & Salvador, 1993). Limiting activity is thought to be a strategy to compensate for energy loss during tail or limb regeneration (Chapple & Swain, 2002b; Naya, Veloso, Munoz, & Bozinovic, 2007). Loss of appendages is often associated with increases in metabolic rate due to the physiological demands associated with tissue repair (Naya & Bodonozvic, 2006). This creates an interesting trade-off whereby individuals with autotomized limbs need to compensate for increased energy expenditure by either increasing activities related to energy acquisition (i.e. high food intake rates) and/or by diverting energy away from other energy-consuming functions such as reproduction and growth (Naya & Bodonozvic, 2006). Our results lend support for this latter trade-off because decreased overall activity is counterproductive to increased energy acquisition. Lizards in our study may have also reduced activity after tail loss as a response to minimize exposure to potential predators due to increased vulnerability as a consequence of losing an effective defensive strategy (Bateman & Fleming, 2009; Downes & Shine, 2001). Most studies have shown that individuals with autotomized appendages will modify their antipredator behaviour to compensate for weakened movement and to avoid increased predation risk (see references within Bateman & Fleming, 2009). For instance, tailless lizards have been observed to increase their flight initiation distances when approached by a simulated threat (Capizzi, Luiselli, & Vignoli, 2007; Cooper, 2007; Downes & Shine, 2001), take longer to re-emerge from a refuge after a predatory attack (Cooper & Wilson, 2010) and respond faster to the scent of a predator (Downes & Shine, 2011). Yet, there is also research suggesting that not all species modify antipredator behaviour following autotomy (e.g. frog-eyed geckos, *Teratoscincus scincus*; Lu, Ding, Ding, & Ji, 2010). For example, damselfly larvae compensate for higher risk taking by initiating caudal autotomy faster and more frequently than low risk-taking larvae (Delnat et al., 2017). This coupling of risk taking and the propensity for autotomy is suggested to increase survival of individuals that more regularly encounter predators (Carter et al., 2010; Delnat et al., 2017; Kuo et al., 2015).

Interestingly, after complete caudal autotomy, lizard behaviour generally became more predictable. Thus, it appears that autotomy

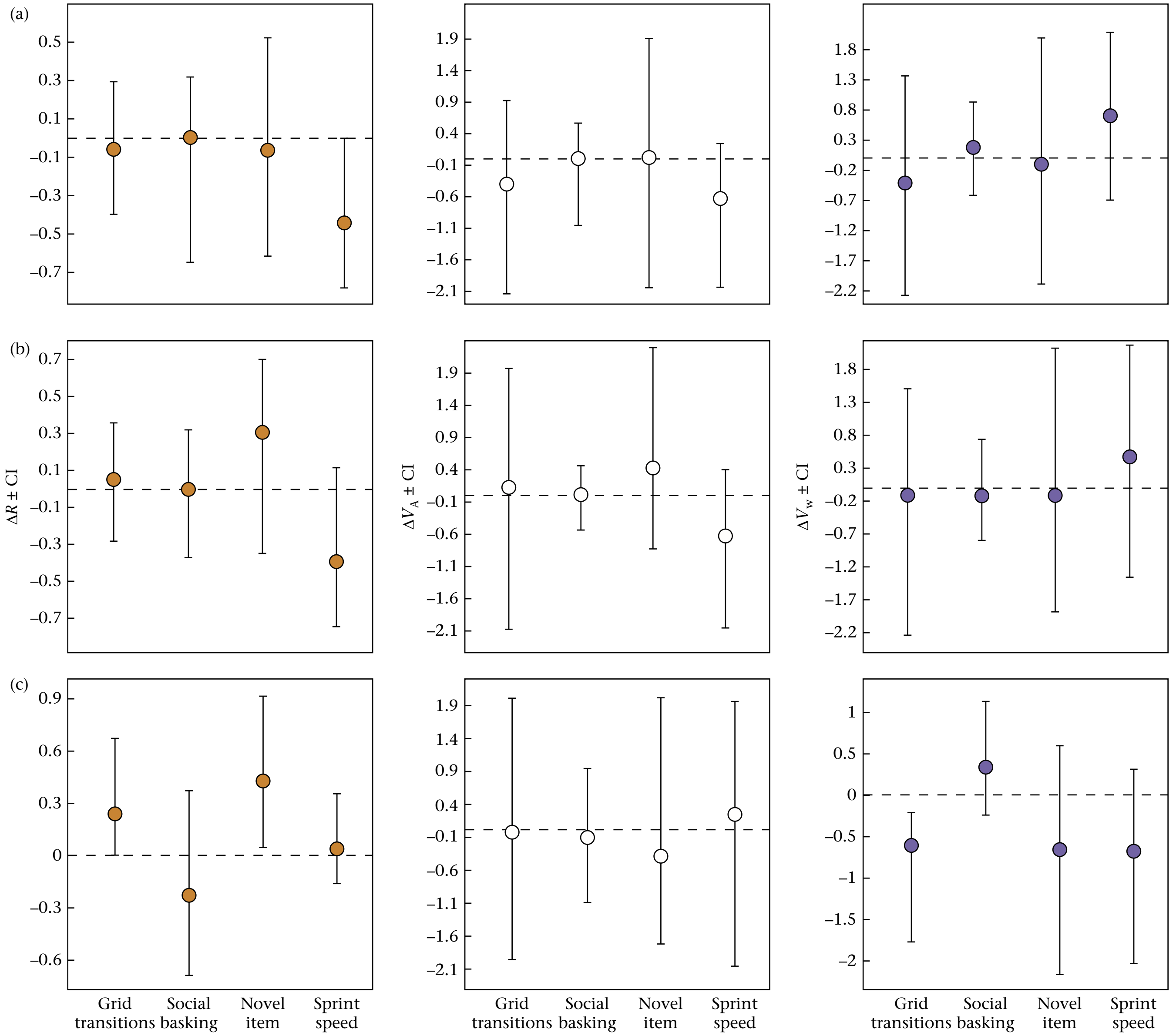

Figure 3. Differences in repeatability (ΔR; orange circles), between-individual (ΔV_A; white circles) and within-individual (ΔV_W; purple circles) variances in the tail loss treatment groups between pretreatment and post-treatment. (a) Control, (b) partial tail loss and (c) complete tail loss. Values represent posterior modes ± 95% credible intervals (CI). Positive values indicate an increase in variance after autotomy.

can generate stronger, less flexible, personality. This increase in behavioural predictability is probably a result of compromised locomotion and physiology (i.e. proximate systems that often underlie multiple behaviours; Biro & Stamps, 2008; Careau, Thomas, Humphries, & Réale, 2008), which then limits an individual's capacity for differential behavioural expression. However, this behavioural predictability is likely to be state dependent (i.e. arises when an individual has autotomized a limb); thus, a future interesting research question would be to test whether individuals become less predictable after regenerating their tails.

Tailless skinks were just as likely to bask with conspecifics and spend time near a novel food item as control skinks. It is perhaps surprising that caudal autotomy did not affect an individual's likelihood of spending time near a novel food item, given that these skinks were captured in urban environments and probably encounter novel resources regularly (Lowry et al., 2012), and that tail loss, through the need to acquire more energy for regeneration, may promote the adoption of novel food sources. One might also predict that tailless lizards would become more social following caudal autotomy because engaging in group behaviour can limit an individual's likelihood of being attacked by a predator and thus the subsequent costs of autotomy (Downes et al., 2004). On the other hand, male delicate skinks, unlike females, have been shown to be largely asocial (Michelangeli, Chapple et al., 2016), probably because most males try to avoid aggressive interactions with other males (Michelangeli et al., 2017). Thus, caudal autotomy could also negatively influence an individual's decision to bask with a group of conspecifics, particularly as tailless male lizards may be more likely to lose agonistic interactions (Fox, Heger, & Delay, 1990; Maginnis, 2006).

We found a positive correlation between activity/exploration and neophilia, and that tail loss appeared to have no effect on this correlation. We hypothesized that the influence of caudal autotomy on behavioural correlations will largely depend on whether the behavioural traits share proximal associations (e.g. genes or physiological mechanisms) that limit independence between behaviours and thus their adaptive potential (Dochtermann & Dingemanse, 2013). Under this scenario, if caudal autotomy affects one trait within the behavioural syndrome, then we should expect to see a corresponding shift in the other proximally linked behavioural trait, thus keeping these behaviours coupled. In our study we found that tail loss had no influence on syndrome structure which aligns mostly with this constraint hypothesis. However, our statistical power to detect an effect was low and the correlations we detected were relatively weak; thus, future studies are needed to more robustly test the effects of autotomy on behavioural syndromes.

Overall, our results suggest that caudal autotomy can impact personality, and we suggest that these impacts probably arise from compromised locomotion and physiology during tail loss. Lizards that experienced complete tail loss became consistently less active and explorative. In some circumstances, it appears that the amount of tail shed also matters, particularly in terms of predator escape ability, as lizards that only partially lost their tail increased their sprinting performance (albeit not significantly), whereas lizards that experienced complete tail loss significantly reduced their maximal sprint speeds. Importantly, we also found evidence to suggest that lizards become behaviourally more predictable following complete caudal autotomy. This is the first study to document any impacts of autotomy on animal personality, but further studies are needed to test the generality of our results across other taxonomic groups that have the capacity to autotomize appendages.

Author Contributions

M.M. carried out fieldwork, conducted data analysis and contributed to the drafting of the manuscript and design of experiments. B.M.W. carried out fieldwork and conducted lab experiments. K.L. conducted data analysis and contributed to the drafting of the manuscript. B.B.M.W. and D.G.C. contributed to the design of the study and drafting of the manuscript. All authors gave final approval for publication.

Data Availability

Data have been made available on Dryad Digital Repository by Michelangeli, Melki-Wegner, Laskowski, Wong, & Chapple (2020).

Declaration of Interest

We have no competing interests.

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Appendix

Table A1
Effect of tail loss treatment, stage (pre- and post-treatment) and SVL (snout–vent length) on average behaviour

Trait	Fixed effect	Estimate [95% CI]	*P*
Number of grid transitions	Intercept	43.72 [-109.12, 185.22]	0.554
	Treatment (partial)	-8.91 [-27.92, 8.36]	0.338
Random effects:	Treatment (complete)	2.71 [-15.01, 21.45]	0.760
V_A = 524.68 [317.84, 831.90]	Stage (post-treatment)	-1.62 [-11.68, 8.30]	0.750
V_W = 435.30 [365.39, 565.29]	SVL	0.18 [-3.43, 3.98]	0.937
	Treatment (partial)*Stage (post)	-5.29 [-19.07, 8.78]	0.464
	Treatment (complete)*Stage (post)	-13.43 [-27.34, 0.19]	**0.061**
Basking with conspecifics	Intercept	1.84 [-1.33, 4.83]	0.241
	Treatment (partial)	0.19 [-0.28, 0.67]	0.437
Random effects:	Treatment (complete)	0.32 [-0.15, 0.79]	0.191
V_A <0.01 [0, 0.18]	Stage (post-treatment)	0.20 [-0.26, 0.64]	0.386
V_W = 0.94 [0.76, 1.16]	SVL	-0.05 [-0.13, 0.03]	0.209
	Treatment (partial)*Stage (post)	-0.35 [-0.97, 0.28]	0.274
	Treatment (complete)*Stage (post)	-0.44 [-1.03, 0.23]	0.181
Time near novel food item	Intercept	6.08 [-3.93, 16.43]	0.243
	Treatment (partial)	0.52 [-1.01, 1.95]	0.498
Random effects:	Treatment (complete)	-0.10 [-1.57, 1.38]	0.895
V_A = 1.03 [0, 2.62]	Stage (post-treatment)	-0.71 [-2.05, 0.59]	0.277
V_W = 7.41 [5.69, 9.84]	SVL	-0.05 [-0.32, 0.19]	0.657
	Treatment (partial)*Stage (post)	-0.30 [-2.17, 1.55]	0.744
	Treatment (complete)*Stage (post)	0.19 [-1.59, 2.03]	0.841
Maximal sprint speed	Intercept	63.62 [-2.63, 124.19]	0.050
	Treatment (partial)	2.40 [-5.85, 11.00]	0.581
Random effects:	Treatment (complete)	-1.30 [-9.64, 7.38]	0.766
V_A = 60.10 [31.29, 133.43]	Stage (post-treatment)	1.31 [-4.95, 7.99]	0.697
V_W = 186.82 [151.91, 236.04]	SVL	-0.74 [-2.27, 0.92]	0.350
	Treatment (partial)*Stage (post)	3.42 [-5.57, 12.41]	0.452
	Treatment (complete)*Stage (post)	-10.22 [-19.18, -1.36]	**0.026**

Values represent posterior means with 95% credible intervals [CI]. Significance of fixed effects was based on the overlap of 95% CIs with zero. V_A and V_W indicate the variance for the among-individual and within-individual components of the phenotypic variance estimated through the random effect of individual ID. Important fixed effects are in bold.

Table A2
Repeatability (*R*) of behavioural traits with associated credible intervals [95% CIs] pre- and post-treatment for the three tail loss treatment groups

Trait	Control	Partial tail loss	Complete tail loss	All lizards
Pretreatment				
Number of grid transitions	**0.80 [0.46, 0.91]**	**0.68 [0.37, 0.86]**	**0.67 [0.25, 0.88]**	**0.60 [0.37, 0.74]**
Time basking with conspecifics	<0.01 [<0.01, 0.64]	<0.01 [<0.01, 0.37]	0.44 [<0.01, 0.73]	<0.01 [<0.01, 0.39]
Time spent near novel food item	**0.70 [0.12, 0.88]**	<0.01 [<0.01, 0.54]	<0.01 [<0.01, 0.68]	**0.37 [0.05, 0.59]**
Maximal sprint speed	**0.64 [0.17, 0.83]**	**0.58 [0.14, 0.83]**	**0.81 [0.56, 0.94]**	**0.58 [0.36, 0.73]**
Post-treatment				
Number of grid transitions	**0.70 [0.39, 0.89]**	**0.70 [0.42, 0.88]**	**0.92 [0.79, 0.97]**	**0.74 [0.59, 0.84]**
Time basking with conspecifics	<0.01 [<0.01, 0.46]	<0.01 [<0.01, 0.35]	<0.01 [<0.01, 0.58]	<0.01 [<0.01, 0.11]
Time spent near novel food item	**0.55 [0.06, 0.87]**	<0.01 [<0.01, 0.73]	**0.87 [0.56, 0.96]**	<0.01 [<0.01, 0.24]
Maximal sprint speed	<0.01 [<0.01, 0.38]	<0.01 [<0.01, 0.45]	**0.88 [0.70, 0.96]**	<0.01 [<0.01, 0.51]
Δ $R_{\mathrm{Post-Pre}}$				
Number of grid transitions	-0.06 [-0.40, 0.29]	0.24 [-0.28, 0.36]	**0.24 [<0.01, 0.67]**	
Time basking with conspecifics	<0.01 [-0.65, 0.31]	<0.01 [-0.37, 0.32]	-0.22 [-0.68, 0.37]	
Time spent near novel food item	-0.06 [-0.61, 0.52]	0.31 [-0.35, 0.70]	**0.43 [0.05, 0.91]**	
Maximal sprint speed	-0.44 [-0.78, <0.01]	-0.40 [-0.75, 0.11]	0.04 [-0.16, 0.35]	

Repeatability is calculated as the ratio of among-individual variation (V_A) to total phenotypic variation [V_A + within-individual variation (V_W)]. Difference between pre- and post-treatment repeatability (Δ $R_{\mathrm{Post-Pre}}$) was calculated such that positive values indicate an increase in repeatability post-treatment. Information on variance components can be found in Table A3. Bold scores indicate significant repeatability estimates and repeatability differences based on the overlap of CIs with zero.

Table A3
Among- (V_A) and within-individual (V_W) variances pre- and post-treatment for the three tail loss treatment groups

Trait	Among-individual variance (V_A)			Within-individual variance (V_W)			V_A Cov
	Pre	Post	ΔV_A	Pre	Post	ΔV_W	*r*
Control							
Number of grid transitions	762.96 [261.6, 1664.1]	417.22 [124.5, 1088.3]	-205.25 [-1118.1, 485.4]	262.25 [142.3, 572.8]	226.03 [119.5, 441.4]	-72.90 [-387.0, 230.8]	***0.73 [0.25 − 0.97]***
Basking with conspecifics	<0.01 [<0.01, 1.02]	<0.01 [<0.01, 0.61]	<0.01 [-1.05, 0.57]	0.66 [0.35, 1.34]	0.83 [0.49, 1.48]	0.17 [-0.62, 0.93]	-0.24 [-0.99, 0.81]
Time spent near novel food item	4.56 [<0.01, 15.25]	4.12 [<0.01, 13.25]	0.21 [-12.6, 11.7]	3.21 [1.44, 9.28]	3.29 [1.64, 9.30]	-0.37 [-6.79, 6.45]	-0.41 [-0.87, 0.36]
Maximal sprint speed	168.11 [<0.01, 440.8]	0.47 [<0.01, 141.5]	-140.06 [-446.7, 54.63]	127.32 [73.2, 297.3]	259.0 [150.0, 410.5]	97.44 [-94.4, 283.9]	0.68 [-0.56, 0.99]
Partial tail loss							
Number of grid transitions	479.02 [176.7, 1275.3]	484.49 [191.6, 1284.4]	39.69 [-697.6, 657.8]	304.4 [167.7, 594.0]	249.9 [142.7, 501.9]	-19.74 [-377.7, 254.9]	***0.90 [0.53, 0.99]***
Basking with conspecifics	<0.01 [<0.01, 0.50]	<0.01 [<0.01, 0.44]	<0.01 [-0.54, 0.46]	0.93 [0.55, 1.54]	0.82 [0.52, 1.49]	-0.11 [-0.79, 0.74]	0.98 [-0.82, 0.99]
Time spent near novel food item	0.03 [<0.01, 5.06]	0.04 [<0.01, 11.62]	2.20 [-4.3, 11.87]	4.60 [2.44, 9.36]	4.47 [2.19, 10.88]	-0.38 [-6.03, 6.81]	-0.14 [-0.86, 0.78]
Maximal sprint speed	128.50 [<0.01, 330.1]	0.39 [<0.01, 121.2]	-99.48 [-322.4, 62.30]	116.18 [58.25, 243.1]	161.40 [99.70, 293.35]	41.18 [-118.6, 189.3]	0.64 [-0.51, 0.98]
Complete tail loss							
Number of grid transitions	561.11 [27.7, 1706.2]	639.34 [341.1, 1708.4]	85.48 [-1058.7, 1292.0]	392.26 [220.4, 904.8]	70.76 [47.6, 171.9]	**-279.24 [-815.7, -96.7]**	0.38 [-0.09, 0.84]
Basking with conspecifics	0.27 [<0.01, 1.05]	<0.01 [<0.01, 1.06]	-0.11 [-1.10, 0.94]	0.45 [0.24, 0.90]	0.92 [0.48, 1.55]	0.45 [-0.24, 1.13]	0.69 [-0.51, 0.99]
Time spent near novel food item	0.02 [<0.01, 9.23]	10.68 [2.78, 30.33]	7.55 [-4.09, 28.48]	4.94 [2.30, 10.49]	2.64 [1.00, 6.01]	-2.61 [-8.62, 2.37]	0.33 [-0.44, 0.91]
Maximal sprint speed	206.67 [85.81, 590.0]	181.24 [85.55, 471.9]	-9.58 [-429.2, 302.9]	61.98 [35.64, 133.76]	29.35 [17.88, 66.95]	-34.53 [-103.4, 16.03]	0.29 [-0.21, 0.68]

Variances were calculated from bivariate mixed models and represent posterior modes and 95% credible intervals [CI]. The difference between pre- and post-treatment variances (ΔV_A, V_W) was calculated such that negative values indicate a decrease in variation post-treatment. Among-individual covariance (V_A Cov) between pre- and post-treatment behavioural scores has been standardized to a correlation coefficient (*r*) with 95% CIs. Bold values indicate significantly different variances between pre- and post-treatment assays, based on overlap of CIs with zero. Bold italicized scores indicate significant covariance.

Table A4
Among-individual correlations (r_A) of behavioural traits between pre- and post-treatment for the three tail loss treatment groups

Trait 1	Trait 2	Pretreatment r_A [95% CI]	Post-treatment r_A [95% CI]	$\Delta r_{A\text{ Post-Pre}}$
Control				
Number of grid transitions	Basking with conspecifics	0.57 [-0.76 – 0.89]	0.16 [-0.80, 0.85]	-0.03
Number of grid transitions	Time spent near novel food item	0.51 [-0.13 – 0.90]	-0.01 [-0.61, 0.66]	**-0.39**
Number of grid transitions	Maximal sprint speed	0.04 [-0.64, 0.59]	-0.12 [-0.80, 0.77]	0.01
Basking with conspecifics	Time spent near novel food item	-0.11 [-0.75, 0.91]	0.05 [-0.75, 0.88]	0.01
Basking with conspecifics	Maximal sprint speed	-0.51 [-0.94, 0.66]	-0.09 [-0.86, 0.84]	0.14
Maximal sprint speed	Time spent near novel food item	-0.13 [-0.69, 0.63]	-0.12 [-0.85, 0.70]	0.03
Partial tail loss				
Number of grid transitions	Basking with conspecifics	0.09 [-0.79, 0.87]	0.45 [-0.63, 0.99]	**0.23**
Number of grid transitions	Time spent near novel food item	0.44 [-0.53, 0.91]	0.32 [-0.40, 0.91]	0.05
Number of grid transitions	Maximal sprint speed	-0.25 [-0.72, 0.52]	0.24 [-0.70, 0.87]	0.19
Basking with conspecifics	Time spent near novel food item	0.38 [-0.77, 0.90]	0.36 [-0.72, 0.96]	0.02
Basking with conspecifics	Maximal sprint speed	-0.34 [-0.90, 0.72]	0.45 [-0.80, 0.94]	0.13
Maximal sprint speed	Time spent near novel food item	0.06 [-0.78, 0.75]	0.39 [-0.62, 0.93]	0.09
Complete tail loss				
Number of grid transitions	Basking with conspecifics	0.60 [-0.70, 0.97]	-0.47 [-0.89, 0.70]	-0.18
Number of grid transitions	Time spent near novel food item	0.73 [-0.08, 0.97]	0.44 [-0.02, 0.79]	-0.08
Number of grid transitions	Maximal sprint speed	0.17 [-0.48, 0.62]	0.22 [-0.34, 0.59]	0.01
Basking with conspecifics	Time spent near novel food item	0.63 [-0.65, 0.99]	-0.41 [-0.86, 0.71]	**-0.36**
Basking with conspecifics	Maximal sprint speed	0.38 [-0.63, 0.85]	0.16 [-0.69, 0.82]	0.13
Maximal sprint speed	Time spent near novel food item	0.07 [-0.64, 0.59]	-0.12 [-0.58, 0.42]	0.09
All lizards				
Number of grid transitions	Basking with conspecifics	0.47 [-0.35, 0.96]	0.55 [-0.57, 0.91]	**-0.60**
Number of grid transitions	Time spent near novel food item	**0.64 [0.26, 0.92]**	**0.29 [-0.01, 0.66]**	**-0.29**
Number of grid transitions	Maximal sprint speed	-0.16 [-0.45, 0.26]	0.12 [-0.41, 0.50]	0.13
Basking with conspecifics	Time spent near novel food item	0.68 [-0.28, 0.98]	0.01 [-0.63, 0.85]	**-0.36**
Basking with conspecifics	Maximal sprint speed	-0.24 [-0.83, 0.37]	0.01 [-0.54, 0.64]	**0.23**
Maximal sprint speed	Time spent near novel food item	-0.06 [-0.54, 0.32]	-0.02 [-0.47, 0.53]	0.11

These values represent posterior modes and 95% credible intervals (CI). Bold indicates significant correlation based on nonoverlap of CIs with zero. Δr_A indicates the average effect size of the difference in among-individual correlation coefficients between pre- and post-treatment behavioural scores. Positive values represent an increase in the magnitude of the correlation post-treatment.

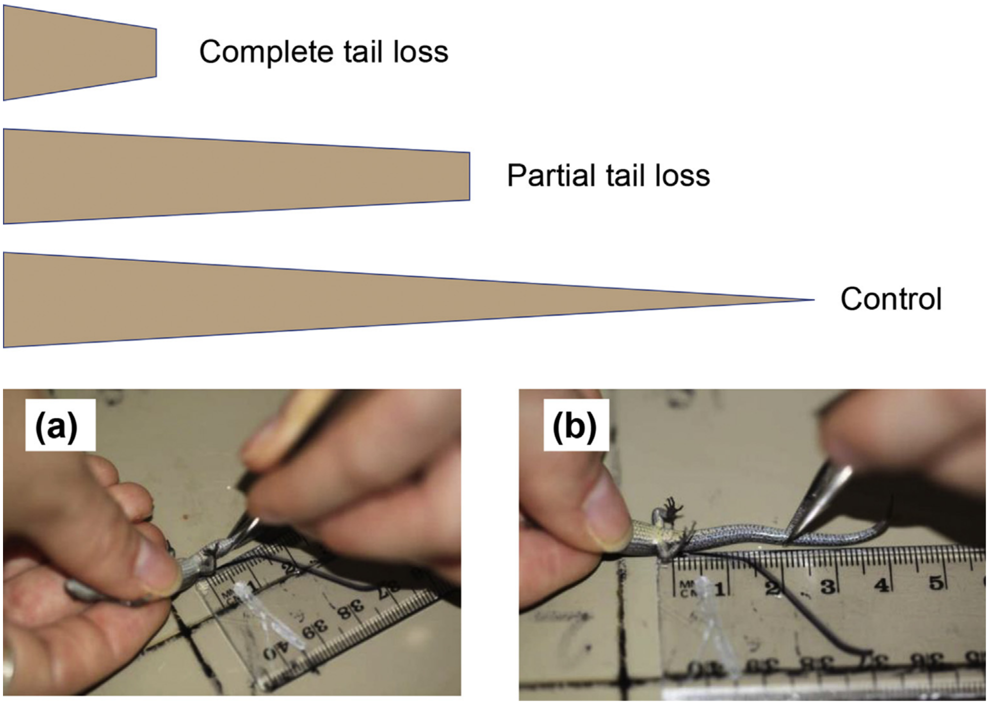

Figure A1. Tail loss treatment application. Complete tail loss: break located approximately 10 mm posterior to the tail base; partial tail loss: break positioned half-way along the length of the tail from the base; control: lizards retained their complete tail length. Tail loss was simulated by pinching the tail with fine forceps. (a) Complete tail removal; (b) partial tail removal.

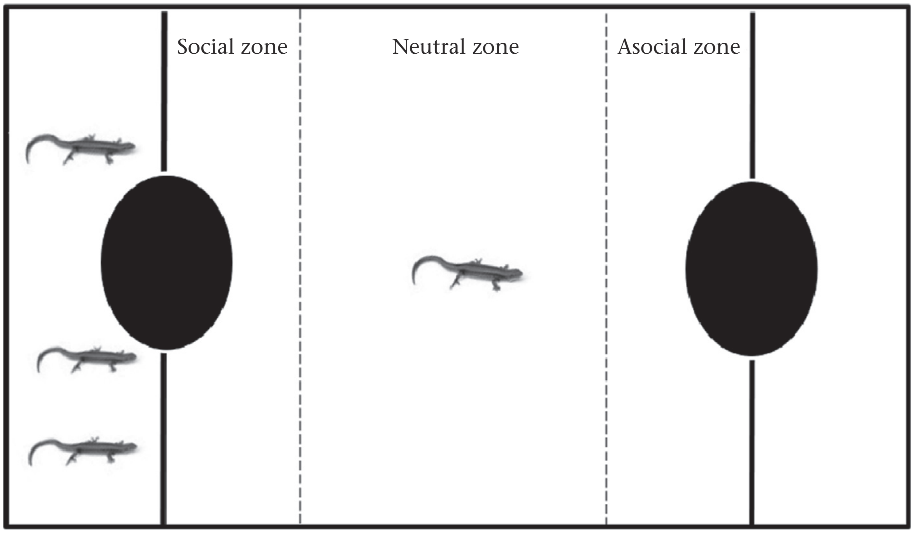

Figure A2. Diagrammatical representation of the sociability test. The experimental arena was split into three zones: social, asocial and neutral (dashed lines). A black marker pen was used to draw five 11 cm segments along the length of the experimental arena to create the three zones. A basking site (black oval) under a 40 W heating lamp was placed at the end of each arena, on the inner edge of the exterior segments. Each basking site was divided in half by a clear Perspex partition (11 cm high), which ran the width of the arena (solid lines). Three stimulus lizards were placed within the peripheral sections, enabling focal lizards to see but not physically interact with them. The inner segments adjoining the basking sites were designated as either the ‘social zone’ (containing the stimulus lizards) or the ‘asocial zone’ (containing no lizards) and the central segment was considered a ‘no choice’ or neutral zone. The temperature underneath the heat lamps (ca. 35 °C) was substantially higher than the ambient temperature (ca. 20 °C), prompting the lizards to use the basking sites.