

Increased tail length in the King's skink, *Egernia kingii* (Reptilia: Scincidae): an anti-predation tactic for juveniles?

JAMES I BARR^{1,2,*}, RUCHIRA SOMAWEERA², STEPHANIE S GODFREY³ and PHILIP W BATEMAN¹

¹*Behavioural Ecology Lab., School of Molecular and Life Sciences, Curtin University, Kent Street, Bentley, WA 6102, Australia*

²*CSIRO Land and Water, 147 Underwood Avenue, Floreat, WA 6014, Australia*

³*Department of Zoology, University of Otago, 340 Great King Street, North Dunedin, Dunedin 9016, New Zealand*

Received 14 September 2018; revised 19 November 2018; accepted for publication 20 November 2018

Caudal autotomy is an adaptive, but costly, anti-predation strategy used by many lizard species. As predation risk varies with ontogenetic life stage, it can be predicted that the use of costly anti-predation mechanisms would also change if they are no longer required. Here we assess ontogenetic change in relative tail length and degree of caudal autotomy in the King's skink (*Egernia kingii*), a large skink endemic to Western Australia. We found that younger individuals invested more in relative tail length compared to older individuals, with younger individuals also having a higher degree of their tail consisting of regenerated tissue. This appears to reflect an ontogenetic shift in the risk of predation for this species, with larger, more mature individuals capable of actively defending themselves against certain predator types and therefore decreasing their reliance on a costly anti-predation strategy compared to juveniles.

ADDITIONAL KEYWORDS: autotomy – lizard – ontogeny – predation – Scincidae – skink – tail.

INTRODUCTION

Many animals use specialized tactics to escape predators. Autotomy, the ability to shed part of the body to escape a predator, is an extreme example. This anti-predator trait is found across a multitude of taxa (Maginnis, 2006; Fleming *et al.*, 2007). In particular, caudal autotomy – the shedding of part of the tail – is found in many squamates, including lizards, tuatara and some snakes (Arnold, 1988; Cooper & Alfieri, 1993; Clause & Capaldi, 2006; Seligmann *et al.*, 2008). Lizards with advanced caudal autotomy ability possess breakage planes within a series of their caudal vertebrae (Etheridge, 1967; Bellairs & Bryant, 1985). Once autotomized, the tail regenerates with a rigid cartilage rod lacking autotomy planes in place of the vertebrae (Woodland, 1920; Alabardi, 2010). For the

tail to be voluntarily shed again (e.g. following another predator attack), it would need to autotomize at a plane more proximal to the body (Arnold, 1984; Bateman & Fleming, 2009). Thus, it has been suggested that a longer tail could allow for more opportunities of autotomy and escape from predators than would be possible for individuals with shorter tails (Bateman & Fleming, 2009; Fleming *et al.*, 2013).

The adaptive value of caudal autotomy is likely to be context-dependent as it can be energetically costly to regrow the tail (Vitt *et al.*, 1977). The concept that larger species of lizard are more capable of defending themselves than smaller ones, and as a result may not need to rely on such extreme tactics as autotomy, was outlined by Arnold (1984). However, this is highly likely to depend on the individuals' size in relation to their average predator, as well as their risk of predation, as indicated by Fleming *et al.* (2013). In their review, Fleming *et al.* (2013) reported that more gracile lizard species tend to have longer tails compared to robust

*Corresponding author. E-mail: james.barr@postgrad.curtin.edu.au

individuals, reflecting the prediction that investment in tails is influenced by potential predation pressure.

Additionally, anti-predation tactics, including caudal autotomy, can change ontogenetically (Barbosa & Castellanos, 2005; Creer, 2005). Adults often have fewer predators than juveniles due to an increase in body size, and/or the development of defensive weaponry, reducing the number of predatory taxa able to subdue them (Saporito *et al.*, 2010; Stankowich, 2012). Juvenile Balkan green lizard (*Lacerta trilineata*) are willing to rapidly drop their tails, but adults lose the ability (or at least their willingness) to autotomize their tail (Pafilis & Valakos, 2008). The use of autotomy as an anti-predation tactic for juveniles can be enhanced through redirection of predation attempts (Humphreys & Ruxton, 2018). Several species of lizard possess brightly coloured tails, or 'motion dazzling' patterns that help redirect predator attacks away from their bodies as juveniles, but as they mature, the colour fades to become uniform with the rest of the animal (Vitt & Cooper, 1986; Castilla *et al.*, 1999; Fitch, 2003; Hawlena *et al.*, 2006; Bateman *et al.*, 2014; Murali & Kodandaramaiah, 2018). These colour changes may also be associated with behavioural changes. Juvenile lizards that forage in the open more than adults are more exposed to visual predators, and thus having a tail that is more brightly coloured than the body would be adaptive as part of the 'risky decoy' hypothesis (Bateman *et al.*, 2014). Similarly, lizard species that actively forage also tend to have longer tails (Fleming *et al.*, 2013). Therefore, just as investment in tail length as a defence mechanism may alter between species, we hypothesize that this should also be true for life stages: if it were adaptive to invest in a longer tail during the ontogenetic stages that are most vulnerable to predation, then tail length should be proportionally longer in juveniles than in adults in lizard species that rely on other defence tactics when they mature. This is particularly likely if both resource and energy allocation to different body parts for both growth and regeneration are costly (Barbosa & Castellanos, 2005). Here, we assess ontogenetic shifts in tail length and the prevalence of caudal regeneration in the King's skink (*Egernia kingii*), to investigate potential shifts in anti-predation tactics between life stages.

The King's skink is a large (up to 550 mm total length), uniformly coloured skink endemic to Western Australia (Storr, 1978; Cogger, 2014). At birth, individuals measure 60–80 mm with a mean mass of 7 g. Individuals take approximately 5 years to mature, reaching a snout to vent length (SVL) of up to 244 mm (Storr, 1978) with an average weight of between 220 and 360 g, resulting in a 30- to 50-fold increase in weight (Dilly, 2000; Arena & Wooller, 2003). Juveniles have been found to experience higher predation risk than adults (Aubret *et al.*, 2004), and adults have

been reported to actively chase and defend themselves against certain predators (Masters & Shine, 2003). For long-lived species, like *E. kingii*, where there is a change from relatively small, gracile juveniles to larger, robust adults, we hypothesize that there will be an ontogenetic change in investment in tail length that reflects predictions based on potential predation pressure and concomitant reliance on autotomy (Fleming *et al.*, 2013). Specifically, we predict that:

1. As *E. kingii* individuals grow, they will reduce their investment in their tail, such that adults will have proportionally smaller tails, reflecting reduced reliance on the tail as an anti-predator device through autotomy.
2. If the adaptiveness of autotomy varies with life stage, this will be reflected in patterns of tail regeneration. That is, more adults will show evidence of regeneration than juveniles, due to a longer period of time available to them in which to lose tails, but will also have a lower relative proportion of their tail consisting of regenerated tissue, indicating that autotomy occurred when they were younger.

MATERIAL AND METHODS

We studied 300 preserved specimens from the Western Australia Museum. For each specimen, we recorded SVL, tail length (TL) and any regeneration length (RL) to the nearest millimetre using a flexible material tape measure. The incidence of regeneration (the proportion of samples with regeneration) was calculated for each age class, as was the proportion of regeneration (RL/TL). Mass was not recorded due to potential inaccurate measurements from preservation methods. Tail regeneration was identified from multiple morphological indications including evident colour change in a region of the tail, change in scale pattern of a caudal region or narrowing of a tail segment. Specimens that had their tail tip or part of the tail missing were excluded from analysis as this might reflect post-mortem tail loss. Individuals that had their complete (intact), original (without regeneration) tail were used to assess SVL and TL correlation, and their relative tail lengths (TL/SVL) were calculated for comparison between the age classes.

As *E. kingii* are long-lived species, individuals were classified into four age categories to comprehensively investigate ontogenetic changes: neonates (SVL 60–80 mm), <2 years old (80 mm < SVL < 150 mm), 2–4 years old (150 mm < SVL < 180 mm) and 4+ years old (SVL > 180 mm), as indicated by Arena (1986). *Egernia kingii* lack evident secondary sexual characteristics; therefore, sex was determined from head width (HW) to SVL ratios for adults only

(SVL ≥ 185 mm) as indicated by Arena & Wooller (2003) for males (≥ 0.163) and females (≤ 0.154). A total of 24 individuals fell between these ratios and as a result had their sex classified as unknown, and were not included in analyses when comparing the sexes.

All analyses were conducted in R studio v.1.1.383 (R Development Core Team, 2013). Linear models (LMs) were used to assess the effect of age class on relative tail length (TL/SVL) and correlation between SVL and TL for the age classes. Regression statistics for the SVL and TL model were acquired via the summary function, and residuals were extracted via the residual function. To understand if age classes had similar variation within their age groups, homogeneity of variance was assessed using a Levene test. Comparison of relative tail length between the sexes was assessed via t-test. General linear models (GLMs) were used to assess the influence of age class on the incidence of regeneration (binomial family) and the proportion of regeneration (Gamma family) and Wilcoxon tests were used to compare these measures between sexes.

P-values were derived using either F-tests (for LMs) or Wald chi-square tests (for GLMs), calculated using the function 'Anova' in the package 'car' (Fox et al., 2017). Differences between age groups were analysed using post-hoc Tukey tests via the 'glht' function in the package 'multcomp' (Hothorn et al., 2017). The distribution of data was examined using frequency histograms, with residual and QQ plots for appropriateness of LMs and GLMs.

RESULTS

BODY SIZE AND TAIL LENGTH CORRELATIONS

Of the 300 *E. kingii* specimens assessed, 110 (36.7%) had a complete original tail, 130 (43.3%) showed evidence of regeneration and 60 (20.0%) were missing varying degrees of their tail (excluded from analysis). Of the 110 individuals with their intact, original tail a strong significant correlation between SVL and TL was observed, but this varied for the individual age classes (Table 1). Correlation strength increased from neonates to individuals < 2 years old, followed by a

gradual decrease thereafter as the animals matured (Fig. 1). Residuals extracted from the linear model showed a significant difference in variation between the age groups ($F = 25.6$, d.f. = 1, $P < 0.001$) (Fig. 3), with the 2–4 years and 4+ years age groups showing much greater variation than the neonates and the < 2 years age categories. Skink age classes differed significantly in their average relative tail lengths (TL/SVL ratios) ($F = 15.1$, d.f. = 3, $P < 0.001$). The < 2 year olds ($t = 6.291$, $P < 0.001$) and 2–4 year olds ($t = 2.96$, $P < 0.05$) had significantly larger relative tail lengths compared to the 4+ age category, with relative tail length clearly decreasing as the animal matured (Fig. 2). There was no significant difference in relative tail length between adult males and females ($t = -1.18$, d.f. = 21.7, $P = 0.251$).

INCIDENCE AND DEGREE OF REGENERATION

The incidence of regeneration was significantly different between age classes ($\chi^2 = 54.0$, d.f. = 3, $P < 0.001$) for the 130 specimens that had regenerated tails. It increased with age, with a lower incidence of regeneration in the neonate and <2-year-old categories than the 2–4-year-old and 4+ years age categories (Fig. 4). Younger *E. kingii* had a larger proportion of their total tail length that comprised regenerated tissue compared to those of more mature skinks (Fig. 5); however, the difference between age classes was not significant ($\chi^2 = 5.43$, d.f. = 2, $P = 0.143$). There was no significant difference in the incidence of regeneration ($W = 936$, $P = 0.124$, $N = 81$) or the proportion of tail regenerated ($W = 438$, $P = 0.319$, $N = 55$) between males and females.

DISCUSSION

Our results suggest that there is an ontogenetic shift in relative tail length as *E. kingii* age, with younger individuals investing more in tail length, but that there is no difference between adult males and females. Our predictions that patterns of tail regeneration reflect ontogenetic variation in reliance on autotomy in *E. kingii* were also supported: younger individuals (not

Table 1. Tail length and snout–vent length relationship equation, correlation and significance for *Egernia kingii* and their specific age categories as displayed in Figure 1

Age category	Sample size	Linear relationship	Correlation (R^2 value)	R^2 significance
All age classes	110	$y = 1.06x + 27.2$	0.838	$P < 0.001$
Newborn	23	$y = 0.934x + 27.8$	0.277	$P < 0.001$
< 2 years	34	$y = 1.31x + 8.32$	0.816	$P < 0.001$
2–4 years	20	$y = 2.77x - 246$	0.474	$P = 0.001$
4+ years	33	$y = 1.23x - 14.6$	0.206	$P < 0.01$

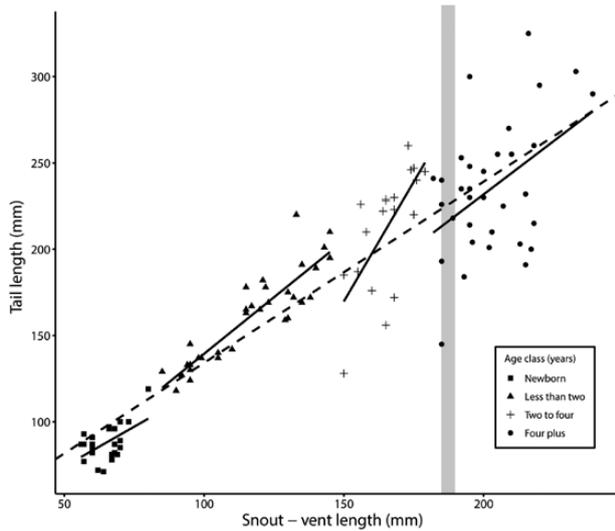


Figure 1. Correlation between snout to vent length (SVL) and tail length for all samples (dashed line) and different *Egernia kingii* age classes (solid lines) with intact tails ($N = 110$). The shaded area represents the SVL range of skinks when they reach maturity (Arena & Wooller, 2003).

including neonates) had a larger relative proportion of the tail consisting of regenerating tissue than older individuals, with the overall incidence of regeneration increased as the animals aged. Regenerated tissue mainly accumulated within the first 2 years of life (only one neonate showed evidence of regeneration) and regeneration eventually plateaued. Although multiple factors can influence tail length and regeneration patterns (Vitt *et al.*, 1977; Bateman & Fleming, 2009; Fleming *et al.*, 2013), we suggest that this change in relative tail length and regeneration is most likely to be influenced by a change in predation risk during ontogeny, which we discuss below.

Egernia kingii ontogenetically change from small, gracile lizards to large robust ones (Arena & Wooller, 2003). Arena (1986) found that after *E. kingii* reach maturity they go through a period of reduced SVL growth, but a marked rate of evenly distributed growth in body mass, resulting in a larger and more robust animal. As a result, adults seem to be large enough to actively defend themselves against some predators. Adult *E. kingii* have been recorded fighting with and chasing away both tiger snakes (*Notechis scutatus*) (Masters & Shine, 2003) and Rottnest Island dugites (*Pseudonaja affinis exilis*) (J. Barr, pers. obs.). Juvenile *E. kingii* are reported to experience higher predation risk than adults (Arena, 1986; Aubret *et al.*, 2004), and are more likely to flee quicker from threats compared to adults (Masters & Shine, 2003; J. Barr, pers. obs.). Additionally, caudal autotomy is used as an anti-predation tactic in life, with minimal function and purpose until the individual is

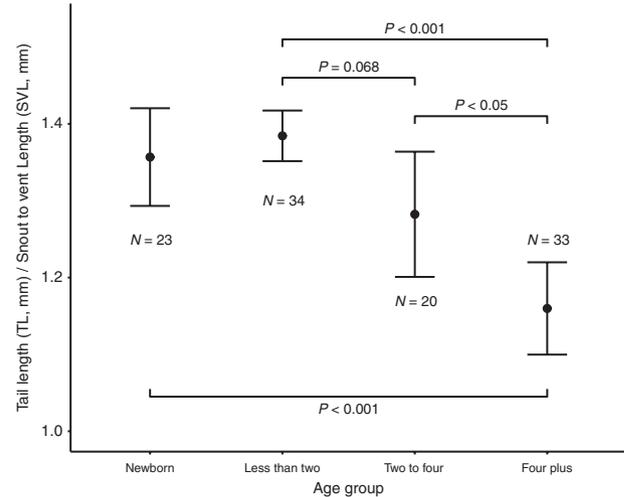


Figure 2. Comparison of relative tail length [tail length (TL)/snout to vent length (SVL)] for different *Egernia kingii* age classes with intact tails ($N = 110$). The mean \pm 95% confidence interval is shown with number of specimens in each age class (N). P -values are as indicated from a post-hoc Tukey test of the model.

born (Moffat & Bellairs, 1964). Our data suggest that investment in tail length is most important within the first 2 years of their life for *E. kingii*, perhaps when they are most vulnerable, where use of autotomy would be most valuable. As they mature, ontogenetic increases in size and robustness may allow adult *E. kingii* to adopt more active anti-predation behavioural defence strategies, and as a result they may not need to resort to the costlier process of caudal autotomy.

However, once mature, *E. kingii* are still susceptible to some predators, and have been recorded in the stomachs of south-west carpet python (*Morelia spilota imbricata*) (Pearson *et al.*, 2002). Although younger *E. kingii* individuals showed greater investment in their relative tail length than older skinks (Fig. 1), the residual data (Fig. 3) indicate that there is substantial variation in relative tail length among older individuals (4+ age class), with some individuals having longer tails than others. This variation in relative tail length among older individuals might reflect differences in predation risk between different environments; if some populations are exposed to high predation pressure from different types of predators once mature, caudal autotomy may still be used an effective anti-predation mechanism.

Predators of *E. kingii* include highly venomous elapids (Aubret *et al.*, 2004), which use a combination of their highly potent venom and constriction to subdue their prey (Shine & Schwaner, 1985). In addition to active defence against such predators, *E. kingii* may also possess immunity to venomous

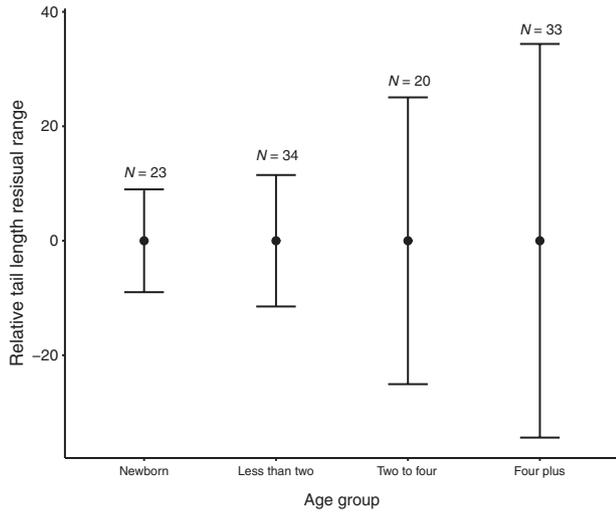


Figure 3. Variation in the residuals of the relative tail length of *Egernia kingii* age classes with intact tails ($N = 110$) extracted from the linear model. The mean \pm SD is shown with the number of specimens in each age class (N).

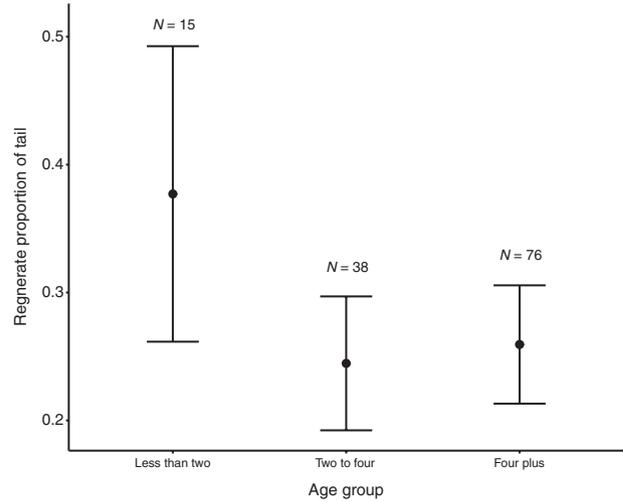


Figure 5. Comparison of the proportion of regeneration for the age classes of *Egernia kingii* that exhibited caudal regeneration. The mean \pm 95% confidence interval is shown with number of specimens in each age class (N). Neonates are not included; only one skink in this category showed evidence of tail regeneration.

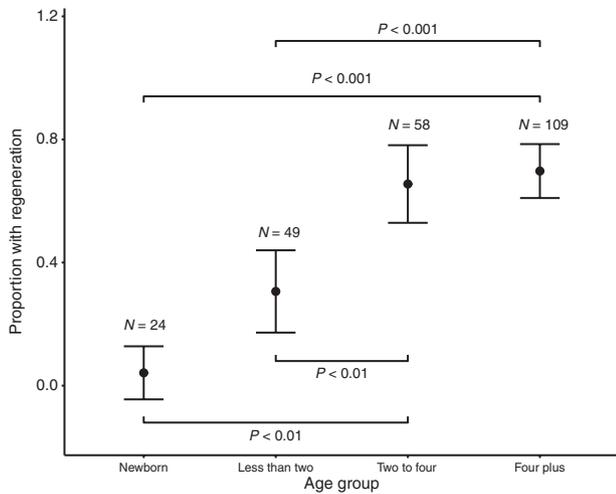


Figure 4. Proportion of *Egernia kingii* specimens exhibiting regeneration for each age class. The mean \pm 95% confidence interval is shown with the number of specimens in each age class (N). P -values are as indicated from a post-hoc Tukey test.

predators. Three relatives of *E. kingii* (*E. striolata*, *E. cunninghami* and *E. whitii*) all have high resistance to large doses of sympatric snake venom, including the tiger snake (*Notechis scutatus*) and the eastern brown snake (*Pseudonaja textilis*) (Minton & Minton, 1981). Lizards that escape venomous snakes may still receive a considerable dose of venom if bitten, but may have sufficient immunity to survive the encounter (Minton & Minton, 1981). The ontogenetic

stage or mass of the test animals were not reported by Minton & Minton (1981), and therefore inference of ontogenetic resistance in lizard species could not be assessed. However, many elapids undergo ontogenetic shifts in their venom composition and potency, linked to dietary shifts, with saurophagous juvenile snakes having a more potent venom against lizards compared to adults, which have more generalist diets (Cipriani *et al.*, 2017; Wolfe *et al.*, 2018). If younger *E. kingii* are more susceptible to sympatric elapid venom, and have a reduced ability to struggle free, it would be adaptive to provide a larger relative tail target, directing the attack away from the body and allow the use of caudal autotomy to stop venom entering the bloodstream, and to escape from the predator.

Anti-predation mechanisms such as tail autotomy may also be used to escape conspecific aggression (Pafilis *et al.*, 2009). For example, autotomy rates in two gecko species, *Hemidactylus turcicus* and *Mediodactylus kotschy*, were positively correlated with gecko density, suggesting that increased intraspecific aggression was the main driver (Itescu *et al.*, 2017). Reliance on tail autotomy and therefore investment in relative tail length may aid younger lizards of species that are subject to conspecific aggression. Skinks in the *Egernia* radiation (Gardner *et al.*, 2008) range from solitary to highly stable family groups (Chapple, 2003). Although not studied in *E. kingii*, infanticide of young is known to occur in related group-living species such as *E. stokesii* (Lanham & Bull, 2000; O'Connor & Shine, 2004). *Egernia kingii* is a group living lizard, with up to four adults sharing a common

core home-range, in addition to multiple subadults and juveniles (Chapple, 2003; Masters & Shine, 2003; Barr, 2016). Increased investment in relative tail length may help younger skinks to escape both from predators and from aggressive mature conspecifics.

Lizard tails can have a wide range of specialized functions, including in intraspecific competition (Murphy & Mitchell, 1974; Schall *et al.*, 1989; Tsellarius & Tsellarius, 1997) and signalling (Johnson & Brodie, 1974; Vitt & Cooper, 1986; Cooper, 2001), and can be used for prehensile gripping (Losos *et al.*, 1993). Tail specializations can also undergo ontogenetic changes; for example, several skink species have bright, conspicuously coloured tails as juveniles that appear to have a role in directing attacks toward the tail and away from the body (Cooper & Vitt, 1985; Hawlena *et al.*, 2006; Pafilis & Valakos, 2008; Bateman *et al.*, 2014; Fresnillo *et al.*, 2016). As the skinks mature, this deflecting coloration is lost. Although the original tails of *E. kingii* do not show a distinct contrast from their bodies, regenerated tails in juvenile *E. kingii* are much darker in colour than the intact parts (J. Barr, pers. obs.). As the individual and the regenerated portion of the tail matures, the distinct colour contrast appears to fade, resembling the colour of the original tail (J. Barr, pers. obs.). In juveniles, this distinct contrast, in both *E. kingii* and other species that exhibit similar contrasting regeneration, may act to redirect subsequent predator attacks towards the regenerating distal tail. This in turn would minimize the amount of remaining original tail that would be lost in subsequent attacks, contributing towards an adaptive economy of autotomy (Cromie & Chapple, 2013). However, further investigation is needed to identify if the contrasting colour of the regenerated portion aids in redirecting attacks away from their original tail, as seen in other lizard species.

In conclusion, our study of *E. kingii* indicates that they undergo an adaptive ontogenetic shift in tail investment, with greater use of caudal autotomy within the first 2 years of life. Individuals have a longer relative tail length when younger, which provides a larger target for predators to attack, and rely on caudal autotomy to allow escape. As they mature, they are more capable of active defence, having relatively shorter tails and are more able to escape predation events without relying on autotomy. However, this is likely to have a degree of plasticity, and be influenced by the type or diversity of predator(s) present in their environment (Pearson *et al.*, 2002).

ACKNOWLEDGEMENTS

We would like to thank the Western Australian Museum for granting us access to their collection,

specifically Rebecca Bray and Paul Doughty, as well as Stephen Ferguson for his valuable input. We would also like to thank three anonymous reviewers for their valuable comments. JIB was supported by an RTS scholarship from the Australian government and a CRS scholarship from Curtin University.

REFERENCES

- Alabardi L. 2010.** *Morphological and cellular aspects of tail and limb regeneration in lizards: a model system with implications for tissue regeneration in mammals*. Berlin: Springer-Verlag.
- Arena P. 1986.** *Aspects of the biology of the King's skink Egernia kingii (Gray)*. Honours thesis, Murdoch University.
- Arena PC, Wooller RD. 2003.** The reproduction and diet of *Egernia kingii* (Reptilia: Scincidae) on Penguin Island, Western Australia. *Australian Journal of Zoology* **51**: 495–504.
- Arnold E. 1984.** Evolutionary aspects of tail shedding in lizards and their relatives. *Journal of Natural History* **18**: 127–169.
- Arnold E. 1988.** Caudal autotomy as a defense. *Biology of the Reptilia* **16**: 235–273.
- Aubret F, Bonnet X, Maumelat S, Bradshaw D, Schwaner T. 2004.** Diet divergence, jaw size and scale counts in two neighbouring populations of tiger snakes (*Notechis scutatus*). *Amphibia-Reptilia* **25**: 9–17.
- Barbosa P, Castellanos I. 2005.** *Ecology of predator-prey interactions*. Oxford: Oxford University Press.
- Barr J. 2016.** *Social structure and the influence of personality traits in the King's skink (Egernia kingii) on Penguin Island, Western Australia*. Honours thesis, Murdoch University.
- Bateman P, Fleming P. 2009.** To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *Journal of Zoology (London)* **277**: 1–14.
- Bateman P, Fleming P, Rolek B. 2014.** Bite me: blue tails as a 'risky-decoy' defense tactic for lizards. *Current Zoology* **60**: 333–337.
- Bellairs A, Bryant S. 1985.** Autotomy and regeneration in reptiles. *Biology of the Reptilia* **15**: 301–410.
- Castilla AM, Gosa A, Galan P, Perez-Mellado V. 1999.** Green tails in lizards of the genus *Podarcis*: do they influence the intensity of predation? *Herpetologica* **55**: 530–537.
- Chapple DG. 2003.** Ecology, life-history, and behaviour in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs* **17**: 145–180.
- Cipriani V, Debono J, Goldenberg J, Jackson TNW, Arbuckle K, Dobson J, Koludarov I, Li B, Hay C, Dunstan N, Allen L, Hendrikx I, Kwok HF, Fry BG. 2017.** Correlation between ontogenetic dietary shifts and venom variation in Australian brown snakes (*Pseudonaja*). *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology* **197**: 53–60.
- Clause AR, Capaldi EA. 2006.** Caudal autotomy and regeneration in lizards. *Journal of Experimental Zoology* **305**: 965–973.

- Cogger HG.** 2014. *Reptiles and amphibians of Australia*. Victoria: CSIRO Publishing.
- Cooper WE.** 2001. Multiple roles of tail display by the curly-tailed lizard *Leiocephalus carinatus*: pursuit deterrent and deflective roles of a social signal. *Ethology* **107**: 1137–1149.
- Cooper WE, Alfieri KJ.** 1993. Caudal autotomy in the eastern garter snake, *Thamnophis s. sirtalis*. *Amphibia-Reptilia* **14**: 86–89.
- Cooper WE, Vitt LJ.** 1985. Blue tails and autotomy: enhancement of predation avoidance in juvenile skinks. *Zeitschrift für Tierpsychologie* **70**: 265–276.
- Creer DA.** 2005. Correlations between ontogenetic change in color pattern and antipredator behavior in the racer, *Coluber constrictor*. *Ethology* **111**: 287–300.
- Cromie GL, Chapple DG.** 2013. Is partial tail loss the key to a complete understanding of caudal autotomy? *Austral Ecology* **38**: 452–455.
- Dilly ML.** 2000. *Factors affecting the distribution and variation in abundance of the King's skink (Egernia kingii) (Gray) in Western Australia*. Honours thesis, Murdoch University.
- Etheridge R.** 1967. Lizard caudal vertebrae. *Copeia* **1967**: 699–721.
- Fitch HS.** 2003. A comparative study of loss and regeneration of lizard tails. *Journal of Herpetology* **37**: 395–399.
- Fleming PA, Muller D, Bateman PW.** 2007. Leave it all behind: a taxonomic perspective of autotomy in invertebrates. *Biological Reviews* **82**: 481–510.
- Fleming PA, Valentine LE, Bateman PW.** 2013. Telling tails: selective pressures acting on investment in lizard tails. *Physiological and Biochemical Zoology* **86**: 645–658.
- Fox J, Weisberg S, Adler D, Bates D, Baud-Bovy G, Ellison S, Firth D, Friendly M, Gorjanc G, Graves S.** 2017. *Package 'car'*. Available at: <https://cran.r-project.org/web/packages/car/car.pdf>.
- Fresnillo B, Belliure J, Cuervo JJ.** 2016. Ontogenetic shifts in risk behaviours are related to body size and coloration in spiny-footed lizards. *Animal Behaviour* **119**: 165–172.
- Gardner MG, Huggall AF, Donnellan SC, Hutchinson MN, Foster R.** 2008. Molecular systematics of social skinks: phylogeny and taxonomy of the *Egernia* group (Reptilia: Scincidae). *Zoological Journal of the Linnean Society* **154**: 781–794.
- Hawlena D, Boonchik R, Abramsky Z, Bouskila A.** 2006. Blue tail and striped body: why do lizards change their infant costume when growing up? *Behavioral Ecology* **17**: 889–896.
- Hothorn T, Bretz F, Westfall P, Heiberger RM, Schuetzenmeister A, Scheibe S, Hothorn MT.** 2017. *Package 'multcomp'*. Available at: <http://cran.stat.sfu.ca/web/packages/multcomp/multcomp.pdf>.
- Humphreys RK, Ruxton GD.** 2018. What is known and what is not yet known about deflection of the point of a predator's attack. *Biological Journal of the Linnean Society* **123**: 483–495.
- Itescu Y, Schwarz R, Meiri S, Pafilis P, Clegg S.** 2017. Intraspecific competition, not predation, drives lizard tail loss on islands. *Journal of Animal Ecology* **86**: 66–74.
- Johnson JA, Brodie Jr ED.** 1974. Defensive behaviour of the western banded gecko, *Coleonyx variegatus*. *Animal Behaviour* **22**: 684–687.
- Lanham EJ, Bull C.** 2000. Maternal care and infanticide in the Australian skink, *Egernia stokesii*. *Herpetological Review* **31**: 151–152.
- Losos JB, Walton BM, Bennett AF.** 1993. Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Functional Ecology* **7**: 281–286.
- Maginnis TL.** 2006. The costs of autotomy and regeneration in animals: a review and framework for future research. *Behavioral Ecology* **17**: 857–872.
- Masters C, Shine R.** 2003. Sociality in lizards: family structure in free-living King's Skinks *Egernia kingii* from southwestern Australia. *Australian Zoologist* **32**: 377–380.
- Minton SA, Minton MR.** 1981. Toxicity of some Australian snake venoms for potential prey species of reptiles and amphibians. *Toxicon* **19**: 749–755.
- Moffat LA, Bellairs ADA.** 1964. The regenerative capacity of the tail in embryonic and post-natal lizards (*Lacerta vivipara*). *Journal of Embryology and Experimental Morphology* **12**: 769–786.
- Murali G, Kodandaramaiah U.** 2018. Body size and evolution of motion dazzle coloration in lizards. *Behavioral Ecology* **29**: 79–86.
- Murphy JB, Mitchell LA.** 1974. Ritualized combat behavior of the pygmy mulga monitor lizard, *Varanus gilleni* (Sauria: Varanidae). *Herpetologica* **30**: 90–97.
- O'Connor DE, Shine R.** 2004. Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). *Animal Behaviour* **68**: 1361–1369.
- Pafilis P, Meiri S, Foufopoulos J, Valakos E.** 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Naturwissenschaften* **96**: 1107–1113.
- Pafilis P, Valakos ED.** 2008. Loss of caudal autotomy during ontogeny of Balkan green lizard, *Lacerta trilineata*. *Journal of Natural History* **42**: 409–419.
- Pearson D, Shine R, How R.** 2002. Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). *Biological Journal of the Linnean Society* **77**: 113–125.
- R Development Core Team.** 2013. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Saporito RA, Isol AM, Maccachero VC, Condon K, Donnelly MA.** 2010. Ontogenetic scaling of poison glands in a dendrobatid poison frog. *Journal of Zoology (London)* **282**: 238–245.
- Schall JJ, Bromwich CR, Werner YL, Midlege J.** 1989. Clubbed regenerated tails in *Agama agama* and their possible use in social interactions. *Journal of Herpetology* **23**: 303–305.
- Seligmann H, Moravec J, Werner YL.** 2008. Morphological, functional and evolutionary aspects of tail autotomy and regeneration in the 'living fossil' *Sphenodon* (Reptilia: Rhynchocephalia). *Biological Journal of the Linnean Society* **93**: 721–743.
- Shine R, Schwaner T.** 1985. Prey constriction by venomous snakes: a review, and new data on Australian species. *Copeia* **1985**: 1067–1071.

- Stankowich T. 2012.** Armed and dangerous: predicting the presence and function of defensive weaponry in mammals. *Adaptive Behavior* **20**: 32–43.
- Storr G. 1978.** The genus *Egernia* (Lacertilia, Scincidae) in Western Australia. *Records of the Western Australian Museum* **6**: 147–187.
- Tsellarius A, Tsellarius E. 1997.** Behavior of *Varanus griseus* during encounters with conspecifics. *Asiatic Herpetological Research* **7**: 108–130.
- Vitt LJ, Congdon JD, Dickson NA. 1977.** Adaptive strategies and energetics of tail autonomy in lizards. *Ecology* **58**: 326–337.
- Vitt LJ, Cooper Jr WE. 1986.** Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): age-specific differences in costs and benefits. *Canadian Journal of Zoology* **64**: 583–592.
- Wolfe AK, Bateman PW, Fleming PA. 2018.** Does urbanization influence the diet of a large snake? *Current Zoology* **64**: 311–318.
- Woodland W. 1920.** Memoirs: some observations on caudal autotomy and regeneration in the Gecko (*Hemidactylus flaviviridis*, Rppel), with notes on the tails of *Sphenodon* and *Pygopus*. *Journal of Cell Science* **2**: 63–100.