

Bite me: Blue tails as a ‘risky-decoy’ defense tactic for lizards

P.W. BATEMAN^{1, 2*}, P.A. FLEMING³, B. ROLEK^{2, 4}

¹ Department of Environment and Agriculture, Curtin University, Bentley, Perth WA 6845, Australia

² Archbold Biological Station, Lake Placid, P.O. Box 2057, Lake Placid, FL 33862 U.S.A.

³ School of Veterinary and Biomedical Sciences, Murdoch University, Murdoch, Perth WA 6150, Australia

⁴ Department of Wildlife Biology, University of Maine, Orono, ME 04469 U.S.A.

Abstract Many lizard species use caudal autotomy to escape entrapment. Conspicuous coloration may increase the likelihood of being attacked, but if that attack can be directed towards the autotomous tail this may ultimately increase the chances of the lizard surviving a predatory attack. We tested the hypothesis that brightly-colored function to divert predatory attention away from the head and body using pairs of blue-tailed and all-brown clay model lizards. Predatory bird attacks on the 24 blue-tailed models occurred sooner ($P = 0.001$) than attacks on the 24 all-brown models, and over 7 days, blue-tailed models were attacked more often than all-brown models ($P = 0.007$). Blue-tailed models were, however, more frequently attacked on the tail than other parts of the body ($P < 0.001$), while all-brown models were more frequently attacked on the head and body ($P = 0.019$) which would be more likely to be fatal for a real lizard. Our results suggest that models with a blue tail were more conspicuous than all-brown models, attracting attacks sooner and more often, but that the attacks were predominantly directed at the tail. It is better for individuals to be attacked unsuccessfully many times, than successfully just once. Having a brightly colored tail may, therefore, act as a ‘risky decoy’. Despite increased conspicuousness, a blue tail increases the likelihood that the lizard would be able to effect escape through caudal autotomy rather than being grabbed by the head or body [*Current Zoology* 60 : – ,].

Key words Autotomy, Skink, Predation, Ontogeny, Dichromatism

Ontogenetic color change occurs in several lizard species: while adults have dull, cryptic colors, juveniles of some skink (e.g. Vitt and Cooper, 1986) and teid (e.g. Fitch, 2003) species have bright blue tails, and juveniles of some lacertids have green or blue tails (e.g. Castilla et al., 1999, Hawlena et al., 2006). This striking difference has been posited to be due to aposematism (i.e. the blue tail is noxious to predators, Arnold, 1984), or intraspecific signaling (i.e. a social signal decreasing aggression towards juveniles, Clark and Hall, 1970). Alternatively, the hypothesis with the most support is that the contrasting tail color acts as a decoy to predators, directing predatory attention towards the tail when the lizard is foraging actively in the open (e.g. Castilla et al., 1999; Vitt and Cooper, 1986; Watson et al., 2012). This difference in coloration is apparently typical of species where ontogenetic stages show differences in foraging patterns and, therefore, face different risks, and juveniles rely on flight rather than crypsis to escape predation (Jackson et al., 1976, Vitt and Cooper, 1986); for example, blue-tailed *Acanthodactylus beershebensis* (Lacertidae) hatchlings are more likely to forage actively in open microhabitats where there is greater risk of predation than the cryptic adults are exposed to (Hawlena et al., 2006).

Received July 12, 2013; accepted Sept.17, 2013.

* Corresponding author. E-mail: bill.bateman@curtin.edu.au

© *Current Zoology* 2014

The benefit for the lizard of the tail being the preferred target is due to it being autotomous. Shedding the tail is a dramatic defense tactic common to many lizard species. While it may come with costs (e.g. to locomotion, energy storage and social behavior; reviewed by Arnold, 1984, 1988, Bateman and Fleming, 2009), caudal autotomy is adaptive in that it increases the chance of a lizard surviving a predatory encounter (although the individual may be more vulnerable in subsequent encounters until the tail has regenerated, Downes and Shine, 2001).

We examined the hypothesis that blue tails act as a decoy for predators, increasing conspicuousness but directing attacks towards the tail. We worked at a site populated by Southeastern five-lined skinks *Plestiodon inexpectatus*, a species which demonstrates an ontogenetic difference in tail color. Hatchlings and juveniles have bright blue tails and dark brown bodies with paler lateral stripes; the tails become brown in adults of both sexes although the stripes are retained by some females. The primary predators that might be attracted to blue body parts are likely to be birds, such as crows (Corvidae) and small hawks (Accipitridae) that see the blue color spectrum well (Håstad et al., 2005). We used clay models of skinks that varied only in the color of the tail. We predicted that blue-tailed models would:

- 1) Be found sooner than all-brown models
- 2) Be attacked more often than all-brown models
- 3) Have more attacks aimed at the tail than other parts of the body than the all-brown models.

1 Materials and Methods

1.1 Construction of models

We made a plaster cast of a plastic toy lizard that appeared to be based on the cast of an actual scincid lizard and conformed to the general proportions of Southeastern five-lined skinks (SVL = 55 mm, SVL of *P. inexpectatus* = 58.6 mm, Vitt and Cooper, 1986) and used it to produce 48 models made of commercially available modeling clay (Plastalina, Van Aken International, Rancho Cucamonga, CA, USA). Tails were made separately and were attached to the lizards' bodies with small lengths of wooden toothpicks, and the clay smoothed together: this was intended to allow us to see more clearly if the models' tails were targeted or even removed. The tails were the same length as the models' SVL. 24 models were made entirely of Plastalina 'brown' clay and 24 had tails made of Plastalina 'ultra blue' clay that was close to the blue of a skink tail. Each model was attached to the center of a paper plate (235 mm diameter) with a loop of fishing line. By burying the plate under the sand/leaf litter and leaving the lizard on the surface we hoped to prevent any predator carrying the model away entirely (since 81% of the models put out by Castilla et al. 1999 disappeared entirely).

1.2 Placement of models in habitat

Dyads of model lizards (1 all-brown, 1 blue-tailed) were placed at 24 locations (each location ~300 m apart) in the Lake Wales scrub at Archbold Biological Station (27.1806° N, 81.3500° W). At each location the two models were 25 m apart, on similar substrate (white sand and leaf litter) and placed in semi-open conditions. The vegetation cover at the study site was very low, and in order to strike a balance between the models being completely exposed or entirely concealed by vegetation, we placed them where they were shaded by vegetation 0.2–0.5 m above the models. This also broadly reflects what is known of favored sites for *P. inexpectatus*: semi-open areas (Watson and Gough, 2012) with sufficient cover and leaf litter for shelter and foraging (Mushinsky, 1992).

1.3 Recording damage to models

We checked each model daily for a week (7 days) and recorded type of damage (pecks from birds or chew marks from rodents) and location of damage: 1. head; 2. body and limbs; 3. tail base (proximal third), 4. midway (mid third) or 5. tip of tail (distal third). The most extensive damage to models was repaired (e.g. any tails that had been removed were replaced). Damage was only recorded on the first day it was observed and we distinguished between damage that left the model otherwise intact or removed a body part.

1.4 Statistical analyses

The number of days that a model was damaged (both removal and pecking damage) was totaled and compared for blue-tailed and all-brown models by Wilcoxon Matched Pairs Test. We also compared damage to the tail or head/body between blue-tailed and all-brown models by Wilcoxon Matched Pairs Test.

Time (days) until first damage was recorded for a model was compared by Sign Test for matched pairs. Models that were not damaged at all by the end of the week were assigned a value of 8 days and data were excluded for two sites (one where there was no damage to either model and the other due to tied data) making $n = 22$ non-tied pairs of models.

To test for differences in damage count between the three tail positions, we used by repeated-measures Friedman ANOVA with total count of days that the tails were damaged at the base, midway, or tip as the three repeated dependent measures.

2 Results

At 23 of the 24 locations, we recorded damage to one or both models over the week. A total of 65 incidences of damage were recorded to these models. Only one mark on an all-brown model and only 4 on blue-tailed models could be attributed to rodent chewing; the rest were distinctive peck marks (V-shaped indentations or tears), almost certainly from birds (e.g. Daly et al., 2008), and most likely from Florida scrub jays *Aphelocoma coerulescens* which were relatively common at the site and are known lizard predators (Sprunt, 1946).

Significantly more blue-tailed (28%) models were attacked than the all-brown models (11%) (Wilcoxon Matched Pairs Test: $Z_{n=24} = 2.71$, $P = 0.007$). Blue-tailed models were also attacked significantly sooner than all-brown models (Sign Test $Z_{n=22} = 3.20$, $p = 0.001$; Fig. 1a). There was, however, a significant difference in the location of damage to blue-tailed and all-brown models. Blue-tailed models were attacked more often on the tails ($Z_{n=24} = 3.60$, $P < 0.001$) than on other parts of the body, while all-brown models were more often attacked on the head or body ($Z_{n=24} = 2.34$, $P = 0.019$; Fig. 1b).

Twice an all-brown model lost half of its tail, while 11 times blue-tailed models lost their tails (6 the tail tip, 3 half the tail and 2 the entire tail), but there was no significant difference in incidence of damage between these three positions for blue-tailed models: Friedman ANOVA $\chi^2_2 = 2.49$, $P = 0.288$ (or all-brown models: $\chi^2_2 = 0.75$, $P = 0.687$). All-brown models incurred more damage to the head and body than blue-tailed models ($Z_{n=24} = 2.19$, $P = 0.028$; Fig. 1b).

3 Discussion

All of our predictions were supported: attacks on blue-tailed models occurred sooner than on all-brown models, blue-tailed models were attacked more often than all-brown models and blue-tailed models were more likely to be attacked on the tail than were all-brown models. There was no difference in frequency of attacks towards the tail base or tip. Despite blue tails inducing more attacks than brown tails, this increased risk of attack may be adaptive if the lizard is more likely to survive any particular attack through autotomy.

Blue-tailed models were significantly more likely to be attacked on the tail than on the head or body than were the all-brown models, supporting the decoy-hypothesis that contrasting tails act to divert attacks away from the head and body (vital body parts that would translate to potentially fatal attacks in live lizards) to the autotomous tail (Watson et al., 2012). All-brown models were attacked more often on the head and body than blue-tailed models; caudal autotomy would be ineffective against such attacks. Similarly, monochromatic clay models of *Podarcis sicula* exposed to bird predation tended to be attacked on the head and neck (Vervust et al., 2011).

In live lizards, caudal autotomy is likely to be more effective against some predators than others due to how the predator captures and handles the lizard. For example, of three predators feeding upon three *Liolaemus* (Iguanidae) species under controlled conditions, a falcon was the most deadly (100% success; falcons attacked the lizard's head or body from above, precluding use of caudal autotomy), whereas 10%–20% of the lizards attacked by a teiid lizard or colubrid snake (which would pursue the lizards and try and grab them by their tails) escaped by autotomizing their tail (Medel et al., 1988). How the predator handles prey also influences the incidence of tail loss between conspecific populations. For example, brown anoles *Anolis sagrei* (Polychrotidae) showed approximately equal incidence of tail damage/regeneration in populations predated on by feral cats *Felis catus* that were 'efficient' hunters that killed and ate the anoles and populations where there were no cats, while the highest incidence of tail damage/regeneration occurred where well-fed pet cats acted as 'inefficient' predators, inducing caudal autotomy but not necessarily killing the lizards (Bateman and Fleming, 2011). These studies indicate that the behavior of the predator is one of the most important factors in determining the efficacy of tail autotomy as an escape tactic. This is supported by the present study, which shows how birds vary the position of their attacks on models according to the model's coloration. Watson et al. (2012) found that lizard models with blue parts (heads, bodies, tails) were more likely to be attacked on the blue parts, suggesting that the color attracts predatory attention, regardless of where it is on the body. As birds are likely to be 'efficient' predators (Medel et al., 1988, Vervust et al., 2011), any trait that increases the chance of an attack being directed towards the tail, and hence affording the opportunity to use caudal autotomy, is likely to be adaptive.

Neither Watson et al. (2012, recording over a 48-h period) nor Castilla et al. (1999, recording every 24 h over a week) found a difference in total numbers of attacks on dichromatic or monochromatic lizard models. Our study is the first to show that brightly-colored tails pose additional risk for the lizard in that both a higher number of attacks and a higher rate of attacks (attacked sooner) occurred for blue-tailed models compared to all-brown models, reflecting their greater conspicuousness. It seems counterintuitive that a prey organism should make itself more obvious to predators through behavior or coloration and this was the main reason for the emphatic dismissal of a decoy function of the blue tail by Clark and Hall (1970), who pointed out that "loss of the tail ... is probably advantageous only if the alternative is death, and possession of a bright blue tail would seem to increase the probabilities of both death and loss of tail".

In comparison to static models, live lizards may show behavior that reduces their conspicuousness, although this does not seem to be the case, since in many lizards, the brightly-colored, autotomous tails that make individuals explicitly obvious seem to be linked with ontogenetic stages that forage in the open (Castilla et al., 1999, Fitch, 2003; Hawlena et al., 2006; Vitt and Cooper, 1986). Such lizards further increase the likelihood of the tail being seen by writhing it, both when predators are present (Cooper and Vitt, 1991) and even when they are not (i.e. when moving and foraging; this is referred to as the 'anticipatory deflective display', Cooper, 2001). Our finding that blue-tailed models were more conspicuous than all-brown models is, therefore, likely to reflect a real difference in vulnerability to attack between juvenile and adult *P. inexpectatus*.

Because of increased conspicuousness to predators, bright coloration could also counteract sexual selection. For example, models of ‘bright’ male *Ctenophorus* lizards of sexually dimorphic species were attacked more often than ‘dull’ models (Stuart-Fox et al., 2003; although attack rates varied with how familiar the predators at each site were with the prey species). It would be of value to explore this further with ontogenetic color differences, take into account prey density and identity of predators present, as well as making species-specific models that accurately mimic natural variation in spectral reflectance as lizards age.

In conclusion, our data support the hypothesis that ontogenetic differences in tail color in lizards have a function in diverting predatory attacks to the autotomous tail, but we also find evidence, *contra* some previous studies (Castilla et al., 1999; Watson et al., 2012), that, at least in some environments, blue tails may increase the risk of being attacked sooner and more often by predators. This ‘risky-decoy’ hypothesis is supported by a study on a very different kind of organism: *Cyclosa mulmeinensis* (Tseng and Tso, 2009). These orb-web spiders decorate their webs with clusters of prey remains and silk that act as ‘decoy spiders’. An increasing number of decoys (increasing conspicuousness) results in more attacks by predatory wasps, but these attacks are more likely to be directed against the decoys and consequently less likely to be fatal (Tseng and Tso, 2009). Ultimately, it would be adaptive for individuals to risk multiple unsuccessful attacks, than to suffer just one successful attack.

Acknowledgments P.W.B & B.R. thank Dr R. Bowman and the Avian Ecology Program at Archbold Biological Station for allowing us to expose their jays to model lizards. P.W.B. was at Archbold Biological Station as a research affiliate in the Herpetology Laboratory and thanks Dr Betsie Rothermel and the Restoration Ecology and Herpetology Program for assistance and hospitality. We thank two anonymous reviewers for helpful comments on the manuscript.

References

- Arnold EN, 1984. Evolutionary aspects of tail shedding in lizards and their relatives. *Journal of Natural History* 18: 127–169.
- Arnold EN, 1988. Caudal autotomy as a defence. In: Gans C, Huey R ed. *Biology of the Reptilia*. New York: Alan R. Liss, 235–273.
- Bateman PW, Fleming PA, 2009. To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last twenty years. *Journal of Zoology* 277: 1–14.
- Bateman PW, Fleming PA, 2011. Frequency of tail loss reflects variation in predation levels, predator efficiency, and the behaviour of three populations of brown anoles. *Biological Journal of the Linnean Society* 103: 648–656.
- Castilla AM, Gosá A, Galán P, Pérez-Mellado V, 1999. Green tails in lizards of the genus *Podarcis*: Do they influence the intensity of predation? *Herpetologica* 55: 530–537.
- Clark DR, Hall RJ, 1970. Function of the blue tail-coloration of the five-lined skink *Eumeces fasciatus*. *Herpetologica* 26: 271–274.
- Cooper WEJ, 2001. Multiple roles of tail display by the curly-tailed lizard *Leiocephalus carinatus*: Pursuit deterrent and defective roles of a social signal. *Ethology* 107: 1137–1149.
- Daly BG, Dickman CR, Crowther MS, 2008. Causes of habitat divergence in two species of agamid lizards in arid central Australia. *Ecology* 89: 65–76.
- Downes SJ, Shine R, 2001. Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology* 82: 1293–1303.
- Fitch HS, 2003. A comparative study of loss and regeneration of lizard tails. *Journal of Herpetology* 37: 395–399.
- Håstad O, Victorsson J, Ödeen A, 2005. Differences in color vision make passerines less conspicuous in the eyes of their predators. *Proceedings of the National Academy of Science, USA* 102: 6391–6394.
- Hawlena D, Bochnik 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.
- Jackson JF, Ingram W, Campbell HW, 1976. Dorsal pigmentation pattern of snakes as an anti-predator strategy—multivariate approach. *American Naturalist* 110: 1029–1053.

- Medel RG, Jiménez JE, Fox SF, Jaksic FM, 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos* 53: 321–324.
- Mushinsky HR, 1992. Natural history and abundance of southeastern five-lined skinks, *Eumeces inexpectatus*, on a periodically burned sandhill in Florida. *Herpetologica* 48: 307–312.
- Sprunt AJ, 1946. *Aphelocoma coerulescens coerulescens* (Bosc) Florida Jay. In: Bent AC (ed). Life histories of North American jays, crows, and titmice: U.S. Natl. Mus. Bull. 191: 77–86.
- Stuart-Fox DM, Moussalli A, Marshall NJ, Owens IPF, 2003. Conspicuous males suffer higher predation risk: Visual modelling and experimental evidence from lizards. *Animal Behaviour* 66: 541–550.
- Tseng L, Tso IM, 2009. A risky defence by a spider using conspicuous decoys resembling itself in appearance. *Animal Behaviour* 78: 425–431.
- Vervust B, Van Loy H, Van Damme R, 2011. Seeing through the lizard's trick: Do avian predators avoid autotomous tails? *Central European Journal of Biology* 6: 293–299.
- Vitt LJ, Cooper WEJ, 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.
- Watson CM, Gough L, 2012. The role of temperature in determining distributions and coexistence of three species of *Plestiodon*. *Journal of Thermal Biology* 37: 374–379.
- Watson CM, Roelke CE, Pasichnyk PN, Cox CL, 2012. The fitness consequences of the autotomous blue tail in lizards: An empirical test of predator response using clay models. *Zoology* 115: 339–344.

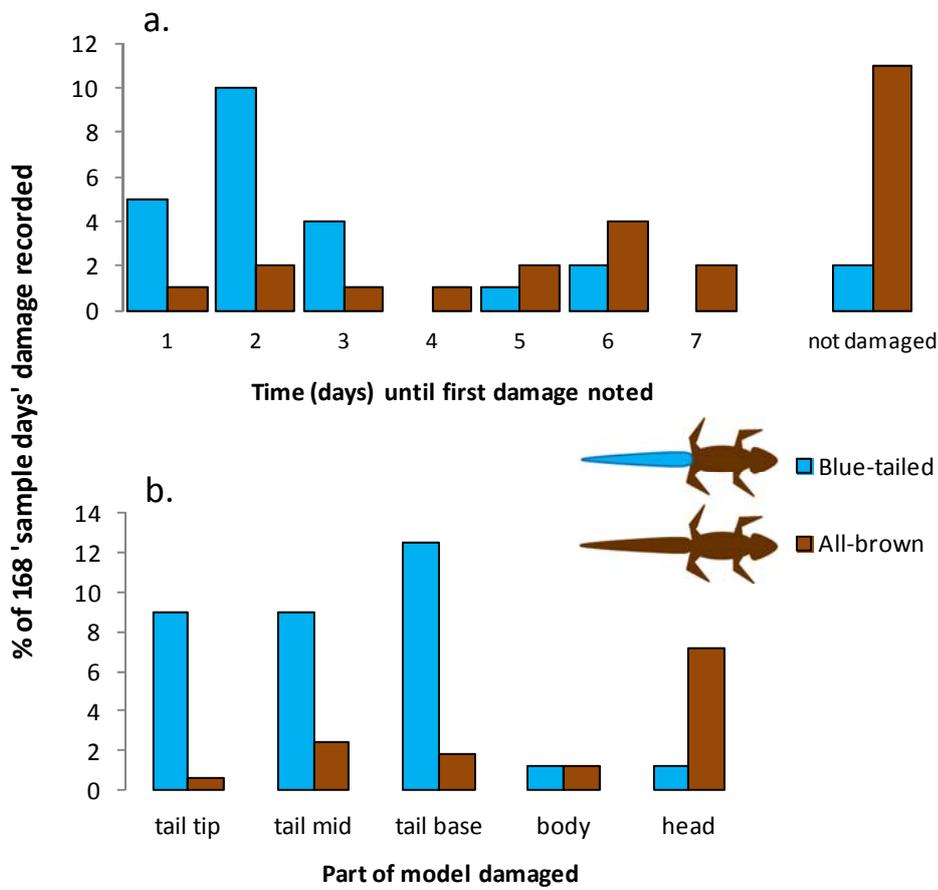


Fig. 1 Time (days) until the first damage by predators on blue-tailed and all-brown models of skinks was noted (A), and distribution of attacks according to position on the model (B)
 Values are expressed in terms of 'sample days' (i.e. 24 models of each color, each checked over 7 days).