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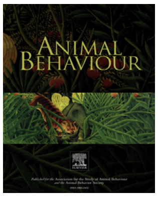

Ontogenetic shifts in risk behaviours are related to body size and coloration in spiny-footed lizards

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Ontogenetic colour changes in animals generally involve cryptic juveniles developing conspicuous coloration when they achieve sexual maturity. However, there are several species in which juveniles develop conspicuously coloured tails that become cryptic in adults. In lizards, colourful tails may act as an antipredator mechanism, either by diverting predator attacks from vital body parts to the expendable tail (decoy hypothesis) or, when associated with tail movements, by signalling to the potential predator that it has been spotted and an attack will probably not succeed (pursuit deterrent hypothesis). In both cases, the antipredator function would allow lizards with colourful tails to show more risk-taking behaviours. The aim of this study was to test whether conspicuous coloration was related to risk behaviours in spiny-footed lizards, *Acanthodactylus erythrurus*, a species with red-tailed juveniles. Behaviour was recorded in free-ranging lizards and several risk-related behavioural indices were calculated. As predicted, risk behaviour and tail coloration were found to be related, as redder (less orange) lizards stayed further from refuge, maybe because redder coloration was associated with a perception of lower predation risk. Coloration was not related to any other behavioural index, including tail displays, but the level of activity was negatively related to lizard size, suggesting a change towards less active behaviour associated with growth, probably because energy and thermoregulatory requirements depend on body size. In conclusion, the link between red coloration and risk-taking behaviour in spiny-footed lizards supports the antipredator function of this coloration that enables more colourful lizards to take more risks when necessary. Moreover, the nonsignificant association between coloration and tail displays is not consistent with the pursuit deterrent hypothesis, thus making the decoy hypothesis more probable.

Changes in coloration across different life stages of an organism (ontogenetic changes) are relatively common in animals (Booth, 1990). Very often there is a change from cryptic to conspicuous coloration when animals reach sexual maturity which appears to be associated with sexual selection, for example when conspicuous colours signal dominance or attractiveness (e.g. Blount & McGraw, 2008; Senar, 2006). However, some ontogenetic colour changes involve a change from conspicuous coloration in juveniles to cryptic coloration in adults (Landová, Jančúchová-Lásková, Musilová, Kadochová, & Frynta, 2013; Londei, 2005; Thresher, 1978). This change may seem counterintuitive for nonaposematic species, as cryptic coloration is generally expected to minimize predation risk by reducing the possibility of being detected by predators (Wilson, Heinsohn, & Endler, 2007). Various hypotheses have been presented to explain ontogenetic colour change from conspicuous juveniles to cryptic adults (Booth, 1990). For example, the mimicry of aposematic models that are similar in size to juveniles but not to adults (Huey & Pianka, 1977; Jackson & Drummond, 1974; Pough, 1974), the change from gregarious juveniles, which might use conspicuous coloration to draw group members together, to solitary adults (Rowell, 1967), or changes in palatability or vulnerability to predators from one life stage to another (Booth, 1990).

A dramatic example of ontogenetic colour change occurs in some lizard species characterized by conspicuous colours in juvenile tails that fade away as they grow (Hawlena, 2009; Hawlena, Boochnik, Abramsky, & Bouskila, 2006). Several nonexclusive hypotheses have been postulated to explain conspicuous tail coloration in juvenile lizards. First, it might inform conspecific adult males of the age class (i.e. sexual immaturity) of the bearer, reducing adult male aggressiveness (aggression avoidance hypothesis; Clark & Hall, 1970; Fresnillo, Belliure, & Cuervo, 2015a; Werner, 1978). Second,

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it might have a pursuit deterrent function, if associated with behaviours that make this coloration more visible, by signalling to the potential predator that it has been spotted (pursuit deterrent hypothesis; Cooper, 2011b; Hasson, Hibbard, & Ceballos, 1989; Ruxton, Sherratt, & Speed, 2004). The lizard would signal that the pursuit may be costly, because the chances of capturing an alert prey are low. Third, it might deflect predator attacks from head and body towards expendable body parts, for example the tail in the case of species with tail autotomy (decoy hypothesis; Bateman, Fleming, & Rolek, 2014; Fresnillo, Belliure, & Cuervo, 2015b; Hawlena et al., 2006). The last two hypotheses involve interspecific communication and imply that the conspicuous colour of juvenile tails in some lizard species might have an antipredator function by reducing the number of predator attacks or the impact of such attacks on survival. Conspicuous coloration has also been proposed as an antipredator mechanism by the pursuit deterrent hypothesis or the decoy hypothesis in other animal taxa such as insects (e.g. Kodandaramaiah, Lindenfors, & Tullberg, 2013), fish (e.g. Ikeda & Kohshima, 2009), amphibians (e.g. Van Buskirk, Aschwanden, Buckelmüller, Reolon, & Rüttiman, 2004), birds (e.g. Alvarez, 1993) or mammals (e.g. Caro, Lombardo, Goldizen, & Kelly, 1995).

The antipredator function of conspicuous tail coloration in lizards would be more important in juveniles than in adults, as the former need to move more for thermoregulation (Herczeg, Török, & Korsós, 2007; Martín & López, 2003) and/or for acquisition of enough resources for somatic growth (Nagy, 2000). High activity rates may imply easy detectability (Jackson, Ingram & Campbell, 1976) and a reduced ability to detect a predator (Lima & Dill, 1990). The increased predation risk cannot be diminished by cryptic coloration in juveniles, as crypsis requires the potential prey to be immobile (Jackson et al., 1976). Nor would it be possible to reduce the activity rate as it might seriously compromise juvenile growth (Clobert et al., 2000) and have adverse effects on future survival and/or reproductive success. Therefore, deterring attacks or deflecting them towards an expendable body part such as the autotomous tail might be the best solution to increase their survival rates (Cooper, 1998). A change towards more cryptic coloration may be advantageous when lizards achieve the minimum body size for sexual maturation and their activity decreases (Hawlena, 2009).

The spiny-footed lizard, *Acanthodactylus erythrurus*, a medium-sized lizard inhabiting the Iberian Peninsula and northern Africa, is a good model organism for studying the relationship between behaviour and colour design across life stages. Coloration in this species undergoes ontogenetic changes: the ventrolateral part of their tail and the rear part of their hindlimbs are conspicuously red in young lizards, but this coloration is lost in adulthood (Seva, 1982; for more details on ontogenetic colour changes in this species, see Appendix 1). Red coloration in juveniles of this species reduces aggressiveness from adults (Fresnillo et al., 2015a), but has been also suggested to act as an antipredator mechanism (Fresnillo et al., 2015b). If red coloration had an antipredator function in this species, redder individuals would be more protected against visually directed predators (mainly birds) and would be able to perform more risk-taking behaviours without increasing the probability of predation. Birds commonly prey on this lizard species (Martín & López, 1990) and are known for their fine discrimination (Sillman, 1974) and even attraction (Møller & Erritzøe, 2010) for red hues. The decoy hypothesis has been suggested as the antipredator mechanism of red tails in spiny-footed lizards (Fresnillo et al., 2015b), but this species often moves tail and limbs stereotypically (B. Fresnillo, J. Belliure & J. J. Cuervo, personal observation), so the pursuit deterrent hypothesis is also possible. Both adults and young of this species show caudal autotomy, because the tail breaks off easily when a lizard is caught by its tail (B. Fresnillo, J. Belliure & J. J. Cuervo, personal observation).

In this study, we analysed the behaviour of free-ranging spiny-footed lizards of different ages to test the hypothesis that red coloration on hindlimbs and tail is an antipredator mechanism in this species. One prediction of the hypothesis is that redder animals will take more risks, i.e. they will (1) be more active (spend more time moving), (2) move further away from refuge and/or (3) display their tail and limbs more often. In addition, the study of the possible association between coloration and tail and limb displays will also allow us to determine whether the pursuit deterrent hypothesis could be the mechanism behind the hypothetical antipredator function of red coloration.

METHODS

Behavioural Observations

Lizard behaviour was studied from July to September 2010 and from April to August 2011 in Chapinería, southwestern Madrid Region, Spain (40°22′N, 4°13′W). In the study area, all spiny-footed lizards hibernate during autumn/winter (Castilla, Barbadillo, & Bauwens, 1992), so their behaviour was not studied during this period. We searched for lizards from 1000 to 1830 hours, on sunny days only, but avoiding the early afternoon when temperatures were high (mainly in summer), as lizard activity is reduced under these conditions (Seva & Escarré, 1980). The activity of focal individuals was followed by one observer (always the same person, B.F., wearing clothes of similar colours) at a distance of 4–6 m, dictating behavioural observations in real time to a portable digital voice recorder. Recording did not begin until the animal's movement appeared to be uninfluenced by the observer's presence, normally 2–3 min after its location. If the focal individual reacted strongly to the observer, recording was suspended. Recordings lasted a maximum of 20 min, as this is considered sufficient to describe lizard behaviour well (Hawlena et al., 2006). Any recordings less than 10 min long were discarded. We assume lizards faced certain predation risk when their behaviour was observed for two reasons. First, an indeterminate level of predation risk is inherent in free-ranging lizards, because predators (particularly avian predators) could suddenly appear at any moment. Second, the presence of a potential predator (the observer) at a relatively close distance (4–6 m) was probably perceived as a moderate predation risk by the lizard as the lizards' response to humans is consistent with predictions of optimal escape theory (Cooper, 2003; Cooper, Hawlena, & Pérez-Mellado, 2009).

When a lizard was found, and before behaviour recording started, the observer noted down the following information. (1) Age class: this was defined as hatchling, juvenile or adult according to the physical characteristics of the lizards (colour design, snout–vent length (SVL) and corpulence) and season, as newborn lizards in populations in central Spain appear in mid-August, hatchlings become juveniles during their first winter and juveniles become adults during their second winter (Bauwens & Díaz-Uriarte, 1997; Castilla et al., 1992; Pollo & Pérez-Mellado, 1990). (2) SVL estimate (at 4–6 m from the lizard): field-recorded estimates were found to be fairly well correlated with SVL measured in the laboratory (Pearson correlation: $r_{79} = 0.780$, $P < 0.001$), so SVL data from lizards observed but not captured were included in statistical analyses. (3) Tail status (complete or incomplete): tails of captured lizards that were regenerating were considered incomplete when they were at least 1 cm shorter than the minimum tail length for that particular age class. Tails of lizards that could not be captured were considered incomplete when part was clearly missing, even though tail regeneration had started. (4) Sex was determined (only in adults) according to the base of the tail, which is much wider in males than in females (Blasco, 1975).