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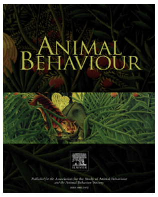

Ontogenetic shifts in risk behaviours are related to body size and coloration in spiny-footed lizards

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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).

During behavioural observations, the observer recorded the exact moment of any of the following activities: moving, stopping, going into the sun, going into the shade and displaying (to move stereotypically) tail and/or limbs. The distance to the closest refuge when the lizard stopped for more than 5 s was also recorded; we defined a refuge as any dense shrub at least 50 cm tall or any crevice or burrow where the animal could hide. Once the focal observation was completed, we recorded local time, geographical coordinates of the place where the lizard was originally detected (with a GPS), temperature as the mean of ground temperatures in the sun and in the shade (with an electronic digital thermometer to the nearest 0.1 °C) and a visual estimation of the percentage of ground covered by shrubs (the main refuge used by this species) in a 10 m radius circle centred at the place where the focal lizard was originally detected.

We attempted to capture each lizard by noosing after recording behaviour. When the focal individual could not be captured, a distance of at least 100 m was kept between each recording place and the next to minimize the risk of recording the same individual twice. This means that the area excluded for subsequent recordings was more than 31 000 m^2 around the previous recording place, an area that is much larger than the mean home range area for juveniles (180 m^2), adult females (550 m^2) or adult males (630 m^2) (Seva, 1982). If the animal was captured, the next lizard found was considered the next focal individual. A total of 95 lizards were observed and their behaviours recorded, and 81 of them were also captured (see Table 1 for age and sex class distribution of samples). Captured lizards were taken to the laboratory (for transport conditions, see Ethical Note), where their SVL and total length were measured (with a ruler to the nearest 0.1 cm). All captured lizards were toe-clipped before release to allow identification in case of recapture. Animals captured in April to June 2011 were kept in captivity for other studies. The rest of the animals were released in exactly the same places where they had been detected on the next visit to the study area (2–7 days after capture). For captivity conditions and other ethical concerns, see Ethical Note.

All data from voice recordings were transferred to Excel worksheets, where time devoted to each behaviour was calculated. Observation time was calculated as the total recording time minus the time the observer was not sure of the exact position of the lizard, for example when it was on the other side of a dense shrub (this time amounted in all cases to less than 5% of total recording time). We then calculated a number of behavioural indices: (1) movements/min (MPM), as the number of times an individual started moving in 1 min; (2) percentage of time spent moving (PTM), as the percentage of the observation time that the focal lizard was moving; (3) mean distance to refuge (MDR), as the average distance (cm) to the closest refuge weighted by the time spent at different distances; (4) tail displays/min (TDM), as the number of tail waving movements in 1 min; and (5) limb displays/min (LDM), as the number of stereotyped movements of any limb in 1 min. MPM and PTM have commonly been used to describe lizard foraging mode (Belliure, Carrascal, & Díaz, 1996; Hawlena, 2009; Hawlena et al., 2006; Perry et al., 1990), assuming that foraging is the main factor affecting activity rates, although social behaviour or thermoregulation might also influence activity levels (Cooper, 2011a). MDR is usually considered a measure of risk-taking behaviour, since the risk of capture after a predator attack is higher when lizards are further from refuge (Blázquez, Rodríguez-Estrella, & Delibes, 1997; Bulova, 1994; Cooper, 1997). TDM and LDM have been previously associated with a pursuit deterrent function (Font, Carazo, & Kramer, 2012; Hasson et al., 1989).

Table 1
Sample sizes for behaviour records and captures for the different age and sex classes of spiny-footed lizards in 2010 and 2011

Age class	Sex	2010		2011	
		Recorded	Captured	Recorded	Captured
Adults	Females	4	4	10	10
	Males	9	7	18	17
Juveniles	–	15	9	24	21
Hatchlings	–	14	12	1	1

Colour Measurements

Colour measurements were taken in the laboratory for 59 individuals: 13 hatchlings, 28 juveniles, 4 adult males and 14 adult females. We quantified the spectral properties of lizard coloration by taking reflectance readings (with a USB 2000 spectrometer and a DT-MINI-2-GS tungsten halogen light source, Ocean Optics, Dunedin, FL, U.S.A.) in the 320–700 nm range (Whiting et al., 2006). Four body regions (rear of both hindlimbs and the ventral part of the tail around 1 cm and 2.5 cm from the cloaca) were measured three times each. Then the reflectance at 1 nm intervals was calculated using AVICOLOR software (Gomez, 2006) and three colour parameters were calculated as follows: brightness as the mean reflectance between 320 and 700 nm, red chroma as the sum of reflectances from 630 to 700 nm divided by the sum of reflectances from 320 to 700 nm, and hue as the wavelength where the maximum reflectance was recorded (Montgomerie, 2006). Since the three measurements in each body part were highly repeatable (repeatability according to Lessells and Boag (1987); brightness: $0.769 \le r \le 0.929$; red chroma: $0.935 \le r \le 0.953$; hue: $0.270 \le r \le 0.850$; $F_{58,118} \ge 2.10$, $P < 0.001$ in the 12 tests), we calculated mean values for each body part. Likewise, as measurements in the four body regions were positively correlated (Pearson correlations: brightness: $0.415 \le r_{57} \le 0.834$, red chroma: $0.368 \le r_{57} \le 0.926$, $P < 0.001$ in the 12 tests; Spearman correlations: hue: $0.307 \le r_S \le 0.668$, $N = 59$, $P \le 0.018$ in five tests, but the correlation between the right hindlimb and the tail at 2.5 cm from the cloaca was marginally nonsignificant: $r_S = 0.233$, $N = 59$, $P = 0.075$), they were all unified in single brightness, red chroma and hue values for each individual (the mean of the four body parts), and these values were then used for further analyses (Cuervo & Belliure, 2013).

Statistical Analyses

As body size (SVL) and age class were strongly correlated (Spearman correlation: $r_S = 0.916$, $N = 95$, $P < 0.001$), we used SVL instead of age class in all analyses, as this variable provided more precise information. However, when SVL was retained in the final model (see last paragraph of this section), this final model was repeated replacing SVL with age class to check which age classes differed in their behaviour. We also found a strong correlation between year (2010 or 2011) and day of the year (Spearman correlation: $r_S = -0.760$, $N = 95$, $P < 0.001$). We decided to include only day of the year in our models because we expected more variability in population composition (proportion of different age classes) and behaviour on different days of the same year than on the same days of different years. Coloration varies with life stages in this species and was therefore related to SVL. In addition, some of the three colour parameters were also related to one another. However, correlations between these four variables (SVL, brightness, red chroma and hue) were not as strong as those mentioned above (the strongest correlation: $r_{57} = 0.656$, $P < 0.001$). We were particularly interested in testing the relationships between behaviour and colour parameters while simultaneously controlling for body size and the other colour traits, so we included the four predictors in our models. Variance inflation factors (VIF) in all models were less than 3.162, so we assumed that collinearity was not a problem in our analyses (O'Brien, 2007).

MPM, PTM and MDR were $\log_{10}(x+1)$ transformed and TDM and LDM fourth-root transformed before subsequent analyses to fulfil parametric assumptions. Relationships between behavioural indices and colour parameters (brightness, red chroma and hue) were tested with general linear models (GLMs). The following predictors were also included in these models: temperature, as behaviour in ectotherms is strongly influenced by ambient temperature (Belliure et al., 1996), body size (SVL) and tail status, as they may affect lizard behaviour (Hawlena et al., 2006; Martín & Avery, 1998), day of the year as an indicator of temporal variability, and percentage of ground covered by shrubs as an indicator of refuge availability in the area.

A backward stepwise procedure was used in all GLMs, retaining only terms associated with P values below 0.10 in final models (Mundry & Nunn, 2009). However, using Akaike's information criterion (Burnham & Anderson, 2002) instead of a backward stepwise procedure to select final models yielded qualitatively identical results regarding the variables of interest (behavioural and colour parameters). When any of the colour variables was retained in a model, only data from the 59 lizards with colour measurements were included in the analysis. When the three colour variables had been eliminated during the stepwise procedure, all 95 lizards were then included in the analysis. All statistical analyses were carried out using STATISTICA 7.1 (StatSoft Inc., 2005). All tests were two-tailed and the significance level was 0.05.

Ethical Note

This study was conducted following the ASAB/ABS (2006) and ASIH (2004) guidelines for the treatment of animals in behavioural research, and complied with the laws of Spain and the Madrid Autonomous Region. Permission to capture, toe-clip and keep spiny-footed lizards in captivity was given by the Madrid Autonomous Region Environment Department (permit number 10/163269.9/10 in 2010 and 10/315072.9/11 in 2011).

Capture methods, captivity conditions and release procedures used in this study seemed to be appropriate as determined by previous experience with this species (Belliure & Carrascal, 2002; Belliure et al., 1996; Cuervo & Belliure, 2013). The capture method we used (noosing) is appropriate for small lizards (Fitzgerald, 2012) and has been used with other lizard species with no apparent detrimental effect (e.g. Healey, Uller, & Olsson, 2007; López, Hawlena, Polo, Amo, & Martín, 2005). Captured lizards were immediately placed in individual cloth bags (23 × 28 cm) in the shade to prevent overheating. After a maximum of 6 h from capture, they were transported by car to the laboratory for colour and size measurements. During transport, which never took longer than 1 h, lizards were kept in their individual cloth bags at a temperature of around 22 °C. All lizards looked healthy when they arrived at the laboratory. During the time lizards were in captivity, they were placed in individual terraria (42 × 26 cm and 19 cm high) with a thin layer of sand on the bottom and cardboard shelter (egg cartons). Room temperature was 25 °C and a bulb hanging over the edge of each terrarium provided a temperature gradient for thermoregulation. Lizards were supplied with food (mealworms, *Tenebrio molitor*, dusted with vitamins) once a day, including the day of arrival at the laboratory, and water ad libitum.

As this population was involved in a long-term study, individual identification was essential. Therefore, the most distal phalanx was clipped in three toes (from different feet) with surgical scissors. In nearly all cases, injuries did not bleed, but when they did, blood loss was minimal and bleeding stopped almost immediately. After clipping, injuries were cleaned with alcohol. When a lizard presented natural toe loss, only two toes were clipped. Toe clipping was preferred over alternative marking methods because it is permanent and reliable (skin shedding makes paint marks not suitable for long-term studies as lizards usually shed their skin several times a year (e.g. Chiu & Maderson, 1980; Maderson & Licht, 1967)), it is not particularly stressful (Langkilde & Shine, 2006), and adverse effects on performance, at least for terrestrial lizards, do not seem to be important (Borges-Landáez & Shine, 2003; Dodd, 1993; Huey, Dunham, Overall, & Newman, 1990). It is very unlikely that natural toe losses could be taken for toe-clip codes given the number of toes clipped (three from different feet) and considering that most often in natural toe losses it is not only the most distal phalanx that is missing.

We observed no adverse effects of noosing, transport to the laboratory, toe clipping or captivity. When lizards were released in the field, they were in good condition and always behaved normally, i.e. they immediately fled to hide under the vegetation and, after a short time (seconds or a very few minutes), began basking or searching for food. No adverse consequences for the studied population were detected, even during the mating season, possibly owing to the small proportion of lizards captured and to the resilience of this species to the extraction of individuals (Busack & Jaksić, 1982). In fact, a reduction in capture rate during the study or in the following seasons was not noticed. The percentage of individuals recaptured (17%) was similar to recapture rates reported for *Acanthodactylus* lizards in other field studies (e.g. Rehman, Ahmed, & Fakhri, 2002). Regarding the period of the annual cycle when lizards were captured, it should be considered that spiny-footed lizards in central Spain usually begin to be active in April, mate in May, females lay eggs in June, eggs hatch in August and hibernation begins in November (Castilla et al., 1992; Pollo & Pérez-Mellado, 1990; B. Fresnillo, J. Belliure & J. J. Cuervo, personal observation). The number of lizards captured each month for each age/sex class is indicated in Table A1 in Appendix 2.

RESULTS

Movements/min (MPM) and percentage of time spent moving (PTM) were not significantly related to lizard coloration, but MPM was related to snout–vent length (SVL), as small animals were more active than large ones (Table 2, Fig. 1a). When SVL was replaced by age class in the final model, we found that hatchlings had significantly higher MPM than adults, while juveniles had intermediate values (age class: $F_{2,92} = 7.04$, $P = 0.001$; Tukey post hoc tests: adults–hatchlings: $P = 0.002$; adults–juveniles: $P = 0.056$; hatchlings–juveniles: $P = 0.164$; Fig. 1b). PTM also tended to be higher in small animals, but the relationship was marginally

Table 2
General linear models testing the relationship between five risk-related behavioural indices and colour parameters in spiny-footed lizards

Behavioural index	Predictor	Adjusted R^2	F	P	β±SE
MPM	SVL	0.114	13.11	<0.001	−0.352±0.097
PTM	SVL	0.028	3.68	0.058	−0.195±0.102
MDR	Hue	0.103	7.67	0.008	0.344±0.124
TDM	–	–	–	–	–
LDM	–	–	–	–	–

MPM: movements/min; PTM: percentage of time spent moving; MDR: mean distance to refuge; TDM: tail displays/min; LDM: limb displays/min. Only predictors retained after a backward stepwise procedure ($P < 0.10$) are shown. Complete models included day of the year, tail status (complete or incomplete), snout–vent length (SVL), shrub cover, temperature, brightness, red chroma and hue. $N = 59$ when a colour parameter was included in the model and $N = 95$ when none of the colour parameters was included.

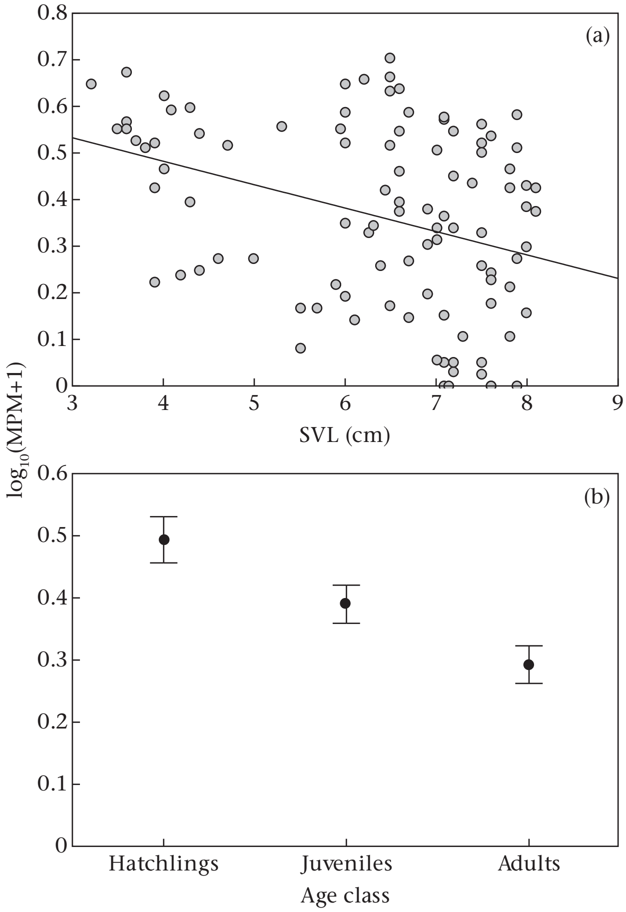

Figure 1. (a) Relationship between $\log_{10}$(movements/min (MPM) + 1) and snout–vent length (SVL) and (b) mean (±SE) $\log_{10}$(MPM + 1) for three age classes (hatchlings, juveniles and adults) of spiny-footed lizards ($N = 95$). For the statistical tests, see Results.

nonsignificant (Table 2). Mean distance to refuge (MDR) was related to lizard coloration, as lizards with higher hue values (redder, less orange) stayed further away from refuge for longer periods of time (Table 2, Fig. 2). This was the case even when SVL was forced into the model (hue: $F_{1,56} = 5.95$, $\beta \pm SE = 0.317 \pm 0.130$, $P = 0.018$). One adult male showed hue values much lower than the rest of the lizards (Fig. 2), but removing this individual from the analysis resulted in a qualitatively identical result ($F_{1,56} = 13.21$, $\beta \pm SE = 0.437 \pm 0.120$, $P < 0.001$; forcing SVL into the model: hue: $F_{1,55} = 11.12$, $\beta \pm SE = 0.413 \pm 0.124$, $P = 0.002$). Although only four adult males were included in this analysis, we do not think that inclusion of more adult males would change the result, because adult males generally show lower hue and MDR values than other age/sex classes (for more details on the shortage of adult males in the sample, see Appendix 1). Tail displays/min (TDM) and limb displays/min (LDM) were not significantly related to lizard coloration or to any other predictor (Table 2). Tail status was not retained in final models (Table 2), suggesting that lizards with complete or incomplete tails did not differ in their risk-taking behaviour. However, the small number of lizards with incomplete tails in our sample (13 of the 95 lizards, and only eight of the 59 lizards with colour information) does not allow us to draw firm conclusions on this issue.

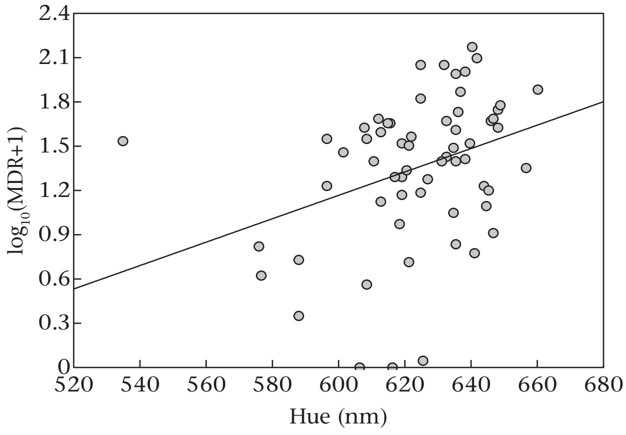

Figure 2. Relationship between $\log_{10}$(MDR + 1) (MDR is mean distance (in cm) to the closest refuge weighted by the time spent at different distances) and hue for the 59 spiny-footed lizards in which coloration was measured.

DISCUSSION

The main aim of this study was to test the hypothesis that red coloration on the hindlimbs and tail in spiny-footed lizards is an antipredator mechanism. The hypothesis was tested by checking the prediction that individuals showing redder coloration will perform more risk-taking behaviours. Indeed, we found that lizards with redder (less orange) coloration took more risks by staying further from refuge for longer periods of time, a result that is consistent with the antipredator function of the red colour. Several studies have suggested a link between colour patterns and antipredator behaviours in lizards (Carretero et al., 2006; Forsman & Shine, 1995; Ortega, López, & Martín, 2014), with more conspicuously coloured individuals generally acting more cautiously (e.g. Cabido, Galán, López, & Martín, 2009; Ortega et al., 2014). However, our results support a negative not a positive association between conspicuousness and shyness. A number of differences between this and previous studies might help explain the different results. First, sexually immature spiny-footed lizards show bright coloration, in contrast with other lizard species that develop conspicuous colours only in adulthood (e.g. Cabido et al., 2009). Second, we observed behaviour in free-ranging lizards, whereas other studies were performed in captivity (e.g. Ortega et al., 2014), which implies the previous capture and/or handling of the lizards, with possible effects on their behaviour. Third, we studied risk-taking behaviour of lizards at a distance (4–6 m), while most previous studies simulated predator attacks, with the observer directly approaching the lizards until they fled (e.g. Carretero et al., 2006).

To have a pursuit deterrent function, coloration needs to be associated with behaviours that make the colour more visible when the predator has been spotted. If this is not the case, the colour will not provide honest information to the predator, the predator will not know whether it has been spotted or not, and the attack will not be prevented. Consequently, more tail and limb displays were expected in redder lizards if the red coloration contributed to deter predator attacks by making tail and limbs more conspicuous to predators (pursuit deterrent hypothesis; Cooper, 2011b; Font et al., 2012; Hasson et al., 1989). However, our results do not confirm this expectation, and thus make other mechanisms explaining the antipredator function of coloration (i.e. the decoy hypothesis; Bateman et al., 2014; Fresnillo et al., 2015b; Hawlena et al., 2006) more probable. Conspicuously coloured lizard tails have been suggested to divert attacks from vulnerable body parts (Castilla, Gosá, Galán, & Pérez-Mellado, 1999; Watson, Roelke, Pasichnyk, & Cox, 2012), and, indeed, this seems to be the case in spiny-footed lizards (Fresnillo et al., 2015b). The red tail would contrast more with the background than the rest of their body, thus producing a lure effect (Arnold, 1984). Diverting predators' attacks to the tail may result in tail loss, which entails significant costs (Arnold, 1984; Bateman & Fleming, 2009), but receiving attacks on other body parts such as head or trunk would probably decrease the probability of surviving the attacks. Moreover, for young lizards, becoming less conspicuous to predators by decreasing their activity rates would also reduce their growth rates (Clobert et al., 2000), what might cost more in terms of fitness than losing the tail. Although our results suggest that red coloration might function as a decoy for predators, this is probably restricted to the tail colour, because limbs cannot be autotomized and limb injuries seriously compromise locomotion and therefore survival. A possible function for red coloration on limbs would be to reduce aggressiveness by conspecific adults (Fresnillo et al., 2015a). Alternatively, red coloration on limbs might have no specific function, and simply be a side-effect of selection for red tails, for example if tail and limb coloration are genetically linked. It should also be noted that we are not arguing against the pursuit deterrent function of tail/limb displays, but against the pursuit deterrent function of the red coloration. Tail/limb waving might deter predator attacks in this lizard species, as it does in others (e.g. Cooper, 2011b; Font et al., 2012), but might also be involved in thermoregulation or intraspecific communication (Magnusson, 1996), functions that are not directly related to predation.

Regardless of which hypothesis is best suited to explain the antipredator function of red coloration in spiny-footed lizards, the specific mechanism underlying the relationship between red coloration and distance to refuge is unknown. We can speculate that redder lizards had a perception of lower predation risk, which would explain why they stayed further away from refuge. This perception of lower predation risk would be based on their redder coloration either deterring the attacks more effectively (pursuit deterrent hypothesis) or resulting in higher survival rates after an attack (decoy hypothesis) than less red colours. The perception of lower predation risk, in turn, would influence the decision-making process (Lima & Dill, 1990) by reducing the trade-offs between escaping from a predator and devoting their time to other activities. This would allow lizards that are more protected against predation because of their redder colour to take more risks and to have access to more resources, for example basking far from shrubs to get direct insolation or feeding not only in the safest areas, but also far from refuge. In any case, risk perception by lizards would not necessarily have to be involved in the process (e.g. if lizards requiring more resources showed redder colour, and they were more active simply to fulfil their needs, not because they perceived lower risk), so more research is needed to clarify whether this speculative explanation has any basis.

Rate of movements, one of the behavioural parameters indicating lizard activity and foraging mode (Belliure et al., 1996; Hawlena, 2009; Hawlena et al., 2006; Perry et al., 1990), was related to body size, but not to lizard coloration. The relationship with body size could be the consequence of the high energy needs of smaller/younger lizards, which are immersed in intense somatic growth processes, and indeed, hatchlings moved more often than adults (Fig. 1b). However, increased movement in smaller lizards could also be reflecting lizard thermoregulatory needs, as smaller lizards, which have higher heat exchange rates (Martín & López, 2003), would need to move more to maintain their optimum body temperature. Behavioural differences between individuals of different age/size have already been hypothesized (Nagy, 2000) and observed (Hawlena, 2009; Hawlena et al., 2006; Herczeg et al., 2007) in other reptile species.

As more active individuals probably undergo a higher predation risk (Jackson et al., 1976), we expected redder lizards, presumably more protected from predators because of their redder colouring, to have higher levels of activity. However, our results do not confirm this prediction, maybe because lizards were as active as they needed to be to meet their energetic or thermoregulatory requirements regardless of the effectiveness of their antipredator mechanisms. Red coloration may decrease predation risk, but a better strategy is probably to take as few risks as possible. An association between conspicuous tails and high levels of activity has previously been found in other lizard species (Arnold, 1984; Vitt & Cooper, 1986), but these studies might not have controlled for lizard size as we did. Therefore, previous relationships found between activity rates and coloration could simply be the result of correlations between activity rates and age/size.

Our finding that redder individuals behaved more riskily (stayed further from refuge for longer periods of time) supports the hypothesis that red coloration has an antipredator function in a lizard species that shows ontogenetic colour change from conspicuous juveniles to cryptic adults. This interpretation of the results is based on a number of assumptions that, although reasonable in our opinion, have not been fully tested. We assumed that there was an inherent predation risk (e.g. from birds) at any time during the observations, and also, based on current knowledge (Cooper, 2003; Cooper et al., 2009), that the presence of the human observer imitated well the presence of a predator, and thus predation risk. We also assumed that behaving less riskily, and thus obtaining less resources, would reduce growth rates (Clobert et al., 2000) and might be more detrimental in terms of fitness than behaving more riskily and obtaining more resources, at least for juvenile lizards. This would imply that juvenile lizards cannot rely on crypsis to avoid predation due to their high activity rates (Jackson et al., 1976). The incorrectness of any of these assumptions might weaken our conclusion and make alternative explanations more likely (e.g. red coloration might be involved only in intraspecific communication, Fresnillo et al., 2015a). Future studies should focus on an experimental approach with free-ranging lizards, manipulating (painting) tail coloration in individuals already showing red tails, and creating at least two experimental groups, one with redder tails (mimicking natural colours) and the other with less red tails. If red coloration has an antipredator function, we expect that the experimental group with redder tails will suffer lower predation rates. In this experiment, it would also be important to check (e.g. with video recordings to avoid human interference) whether the experimental colour has any effect on lizard behaviour, because lizards with experimentally reduced tail redness might perceive higher predation risk and behave less riskily. If the antipredator function is confirmed, further observations should clarify whether lizards with manipulated redder tails are attacked at a lower rate (thus supporting the pursuit deterrent hypothesis) or are attacked at the same or even higher rate but mainly on the expendable tail (thus supporting the decoy hypothesis).

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APPENDIX 1

Ontogenetic changes in coloration

The dorsal body pattern in spiny-footed lizards changes from strongly marked dark and light bands in hatchlings to a reticulated pattern in adults (Seva, 1982). Hatchlings and juveniles of both sexes develop red coloration on the ventrolateral part of the tail, and juveniles on the rear part of the hindlimbs as well (Carretero & Llorente, 1993; Seva, 1982). The red coloration in hatchlings and small juveniles is clearly visible from above (B. Fresnillo, J. Belliure & J. J. Cuervo, personal observation). Juvenile males lose the red coloration when they are around 1 year old while juvenile females retain it through adulthood (Seva, 1982). Adult males show white coloration on the rear part of the hindlimbs and the ventrolateral part of the tail throughout the reproductive season (Seva, 1982). In adult females the intensity of the red coloration in the rear part of the hindlimbs and the ventrolateral part of the tail increases at the beginning of the reproductive season, when they are sexually receptive, but is less obvious later on, when females are gravid, and the red coloration becomes pale yellow, nearly white (Cuervo & Belliure, 2013). It remains unclear whether females regain red coloration after reproduction.

Shortage of information on adult male coloration

Only four adult males had their colour quantified in this study, so the robustness of the positive relationship found between MDR and hue (see Fig. 2) might be questioned. For example, if adult males showed high values of one parameter and low values of the other (i.e. high MDR and low hue, or low MDR and high hue), the inclusion of more adult males in the analysis might make the above-mentioned relationship nonsignificant. Therefore, we first checked whether adult males differed in hue values from other age/sex classes by including in the analysis (1) all 59 individuals with spectrophotometric measurements in this study, (2) two adult males from the same population but that were not part of this study, and (3) 36 adult males from another population whose colours were measured for a previous study (Cuervo & Belliure, 2013). In all adult males of both populations, the ventrolateral part of their tail and the rear part of their hindlimbs appeared white to the naked eye. We found that adult males had significantly lower hue values than hatchlings, juveniles and adult females (one-way ANOVA: $F_{3,93} = 20.29$, $P < 0.001$; Tukey post hoc tests: comparison between adult males and any other class: $P < 0.001$ in the three tests; comparison between the rest of the classes: $P \geq 0.917$ in the three tests). We then checked whether the 27 adult males recorded in this study differed in MDR from other age/sex classes and found that adult males presented significantly lower MDR values than the rest of the lizards pooled ($F_{1,93} = 5.07$, $P = 0.027$), although when analysing the four age/sex classes separately, the difference was only statistically significant between adult males and hatchlings (mean ± SE MDR (cm): adult males 20.18 ± 3.83; adult females 45.83 ± 10.26; juveniles 30.73 ± 5.32; hatchlings 36.00 ± 4.38; one-way ANOVA; $F_{3,91} = 2.98$, $P = 0.035$; Tukey post hoc tests: comparison between adult males and hatchlings: $P = 0.046$; rest of between-classes comparisons: $P \geq 0.141$ in the five tests). Therefore, adult males did not show high values of one parameter and low values of the other, but low values in both parameters. Assuming that hue values do not differ greatly between adult males of different populations, the inclusion of more adult males in the analysis would probably provide a similar result or even make the positive relationship between MDR and hue stronger.

APPENDIX 2

Table A1
Number of lizards from each age/sex class captured each month throughout the study period

Month	Adult males	Adult females	Juveniles	Hatchlings
July 2010	4	4	5	0
August 2010	3	0	4	4
September 2010	0	0	0	8
April 2011	4	0	4	0
May 2011	3	4	4	0
June 2011	2	3	8	0
July 2011	8	2	5	0
August 2011	0	1	0	1