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Blue tail and striped body: why do lizards change their infant costume when growing up?

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Ontogenetic changes in color and pattern that are not directly related to reproduction are very common yet remain a poorly understood phenomenon. One example is conspicuous colors in the tails of fish, amphibians, and reptiles that fade out later in life. We suggest a novel hypothesis: conspicuous tail colors that appear only in juveniles compensate for an increased activity level, deflecting imminent attacks to the tail. We observed blue-tailed, newly hatched lizards (*Acanthodactylus beershebensis*) in the field and compared 5 behavioral parameters with those of older individuals that had already lost their neonate coloration. In addition, we explored whether tail displays, often assumed to direct a predator's attention to the tail, disappear with the color change. Striped blue-tailed hatchlings foraged more actively than 3-week-old juveniles, spent a longer time in open microhabitats, and performed deflective tail displays. In comparison, 2 other lacertids that do not undergo ontogenetic change did not switch to safer foraging when growing up. The results suggest that activity alteration may be a major factor affecting the ontogenetic color and pattern change. Active lizards that forage in open habitats increase their probability of attack by ambush predators. Conspicuous colors and deflection displays may shift attacks to the expendable tail, increasing the prey's overall probability of surviving attacks. The persistence of both striped body pattern and blue tail fits the active foraging period of neonates and hence may be appropriate for other species that display a conspicuous tail accompanied by a striped pattern. *Key words: Acanthodactylus beershebensis*, antipredatory behavior, autotomy, foraging activity, ontogeny. *[Behav Ecol 17:889–896 (2006)]*

Many vertebrate species belonging to different taxa show age-related (ontogenetic), directional changes in coloring or pattern. For example, Hoffman and Blouin (2000), who reviewed the coloration in 225 polymorphic anuran species, found that 46 of the assessed species went through an ontogenetic color or pattern change. Although the phenomenon is very common, especially in reptiles, the adaptive significance of color change that is not directly related to reproduction has received very little attention (Booth 1990).

Conspicuous colors in juvenile tails that fade during maturation are widespread and are a clear example of ontogenetic color change among amphibians, reptiles, and fish (Caldwell 1982; Cooper 1998; Kynard, Henyey, and Horgan 2002). Brightly colored tails may expose cryptic individuals to increased risk of predation. Such a cost, on top of the energetic cost of the ontogenetic color alteration, should be offset by the advantages that the individual gains from having a conspicuous tail. In the few studies that have addressed the adaptive value of conspicuous tail colors, the most common suggestion was that conspicuous tails deflect predator attacks to expendable or relatively invulnerable body parts in reptiles (Cooper and Vitt 1985; Cooper 1998), amphibians (Caldwell 1982; McCollum and Leimberger 1997), and fish (MacPhail 1977). Other studies suggested that colored tails may serve as a visual signal for social behavior, as a lure to approaching prey, or as a signal to a predator that it has been spotted or that the prey is unpalatable (Clark and Hall 1970; Arnold 1984; Hasson et al. 1989; Andrade et al. 1996; Kynard, Zhuang, et al. 2002).

Typical examples of conspicuous tail colors that contrast with cryptic body coloration can be found in a variety of lizard species belonging to different families (Arnold 1984; Cooper and Vitt 1985; Vitt and Cooper 1986). In most diurnal lizards, the conspicuous tail is colorful (e.g., blue, green, or red); in nocturnal species, contrasting colors (light and dark bands) make the tail noticeable. In most diurnal lizard species, only the juvenile's tail is brightly colored—the contrasting color fades and becomes similar to the cryptic body colors when the lizard approaches the minimal size for sexual maturity (Arnold 1984; Vitt and Cooper 1986). Studying this ontogenetic change may shed some light on the general questions related to ontogenetic color change that are not directly related to mate choice or social hierarchy.

The adaptive value of the conspicuous tail in lizards has been the subject of surprisingly few manipulative studies. Cooper and Vitt (1985) and Vitt and Cooper (1986) showed that blue tails confer protection against snake predation on *Eumeces* hatchlings, that the colored tail is not aposematic for the predator tested, and that the conspicuous tail has no inhibiting effect against aggression and cannibalism by adults. In contrast, Clark and Hall (1970) found that blue tails in juveniles inhibited attacks by aggressive conspecific adults. Castilla et al. (1999) showed that lizard replicas with green tails had more bird beak markings on the tail than those with brown tails, supporting the hypothesis that the adaptive value of a green tail is in reducing predation risk on vital parts of the body. Nevertheless, the obvious question—why do lizards eventually lose their conspicuous colors when growing up?—was rarely addressed in these studies and remains a poorly understood phenomenon. In one case, Clark and Hall (1970) used the process of color change to argue against the role of the blue tail as a mechanism for reducing predation, claiming that if the conspicuous tail is an efficient antipredator mechanism, then it should be retained after maturation. Vitt and Cooper (1986) tried to overcome this apparent paradox by suggesting that the color loss of the tail may reflect differences in the risks to which immature and mature lizards are exposed. Although widely recognized, the

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essential role of the ontogenetic process in explaining the adaptive value of the conspicuous tail was not studied in any of the above-cited studies. We suggest a new approach and address the reasons for the ontogenetic change by focusing on lizard behaviors that may change the costs and benefits of the bright coloration.

In lizards, the colored tail is frequently accompanied by a striped body pattern, which fades concurrently with the loss of the bright tail coloration (Arnold 1984; Vitt and Cooper 1986). In other contexts, it has been suggested that reptile dorsal pigmentation correlates with escape behavior and foraging mode (Brodie 1989, 1993). Jackson et al. (1976) found that the striped pattern in North American snakes is associated with an antipredator defense mechanism that emphasizes flight, whereas the blotched-spotted patterns emphasize camouflage and active defense. In addition, Jackson et al. (1976) showed that for North American snakes and lizards, the dorsal pigmentation pattern is also correlated with foraging mode. Active foraging movements may attract more predators than sit-and-wait foraging, and thus, active foragers need a high escape speed and often display the striped pattern accompanied with flight as their antipredator strategy. On the other hand, species that tend to be closer to the sit-and-wait side of the foraging mode continuum were predicted to have a camouflaging blotched-spotted pattern. Because the association between the change in tail color and body pattern is so widespread in lizards, we suggest grouping the 2 phenomena together, and we propose a hypothesis that will address both.

We hypothesized that juvenile lizards with a striped pattern will forage more actively prior to color change. Active foragers may be more susceptible to predation because moving prey can be detected more easily and can devote less time to vigilance than static prey (Lima 1998; Lima and Bednekoff 1999). Active hatchlings should thus increase their probability of surviving encounters with a predator by attracting the predator's attention to the autotomizable brightly colored tail (possibly also by a behavioral tail display). According to this hypothesis, the ontogenetic change in pattern and coloration is associated with different behaviors: high mobility is associated with a striped body and conspicuous tail when young, and lower mobility later on should be associated with crypticity, and with a reduction in deflective tail displays.

To test this idea, we examined whether the alteration in body pattern and tail color is associated with behavioral differences before and soon after the ontogenetic change. To simplify the interpretation of the results, we concentrated on a very simple system, in which a lizard goes through the change very early in life. The hatchlings of *Acanthodactylus beershebensis* have a bright blue tail and dark and yellowish stripes on their dorsal body. The hatchling's blue tail was found to reflect ultraviolet (UV) light more than the body, generating a sharp contrast between the hatchling's tail and body (Figure 1). This pattern changes within a few weeks posthatching: the tail becomes brownish gray, and the pattern on the dorsum turns to the typical blotch coloration of adult *A. beershebensis*. This special pattern gave the name to the *Acanthodactylus pardalis* group, to which *A. beershebensis* belongs (in Greek, pardalis = leopard) (Moravec et al. 1999). The species lives less than a year on average, and thus, there is almost no overlap between cohorts (D Hawlena, unpublished data). The rapid change in tail color, the transformation of body pattern from stripes to blotches, and the fact that all lizards belong to the same cohort render *A. beershebensis* an ideal model species on which to test our hypothesis while ruling out several of the alternative hypotheses suggested previously as explanations for ontogenetic color and pattern change.

Figure 1
A blue-tailed *A. beershebensis* hatchling photographed through an UV filter (B+W UV Black 403 Glass Filter) on black and white film (Kodak BW400CN 135-36, 400 ASA). The tail reflects in the UV range and is very conspicuous in comparison to the natural substrate (loess soil) and to the body. The striped body pattern (in human visual range) reflects UV uniformly and very similarly to the reflectance of the soil.

We present a field study that describes for the first time the ontogenetic change in tail color, body pattern, and deflective display in *A. beershebensis*. The results show that these changes are associated with changes in foraging behavior that expose the hatchlings to different predation pressures. In addition, we show that risky foraging behavior is not a general phenomenon in lizard hatchlings by comparing the results with other species that do not show ontogenetic color change.

METHODS

Study site and animals

The study was performed in a loess plain west of Beer-Sheva, Northern Negev desert, Israel (31°14′N, 34°38′E). The small woody perennial shrub *Noea mucronata* dominates the study area, creating an open-scrub landscape. *Acanthodactylus beershebensis* is the most abundant diurnal lizard in the study site. This recently described species is endemic to Israel, inhabiting loess plains with sparse vegetation in the Northern Negev desert (Moravec et al. 1999). The hatchlings hatch synchronically at the end of May and live less than 1 year. Lizards seem to go through a short period of spatial redistribution during the second week after hatching (early June) but later in the season become sedentary in small home ranges. The species undergoes rapid growth and reaches adult size by October, less than 5 months after hatching. The Great Gray Shrike (*Lanius excubitor*) is the main lizard predator in the study area

(D Hawlena, unpublished data). Shrikes are ambush predators that hunt exclusively from perches, have excellent color vision (Yosef 1993), and have been shown to use UV vision to improve their hunting efficiency (Probst et al. 2002).

Behavioral observations

We observed the behavior of juvenile *A. beershebensis* during the first week of June 2003, less than 1 week after they hatched, and then in the third week of June, when most lizards lost their hatchling coloration. During the second observation period, we observed only lizards that had already lost the blue tail coloration. The same observer wearing the same clothes made all observations. We limited our observations to between 07:30 AM and 10:00 AM to decrease the variation in lizard activity resulting from nonforaging behaviors (e.g., thermoregulation, Cooper et al. 2001; Perry forthcoming). Perry (forthcoming) concludes that short observation times might not provide a representative sample of lizard foraging behavior; we therefore performed preliminary observations to select the best observation length. We used a method similar to the collector's curve and found that 20 min is the minimal time needed to represent lizard activity. A lizard was located by random search and was then observed, from a distance, for 23 min. To allow for habituation of the lizard to the observer, we deleted the first 3 min of every observation during analysis. We recorded the foraging mode and the microhabitat use on a palmtop with the software FIT (Held and Manser 2005). This software allowed us to record accurately the timing of each of the lizard behaviors while constantly observing lizard activity, to record various parameters at the same time, and to download the data directly into Excel files. Only lizards with intact tails were observed, in order to decrease the variability in activity that may result from tail autotomy (Martin and Salvador 1997). Observations on lizards that were engaged in thermoregulation or lizards that showed a strong response to the observer (e.g., escape behavior and intensive refuge use) were stopped after 10 min and were not included in the analysis. During data analysis, movements that lasted less than 3 s were deleted. We calculated the most commonly used foraging mode indices, movements per minute (MPM) and proportion of time spent moving (PTM), to quantify the lizard foraging mode (Cooper et al. 1999; Perry forthcoming). Perry et al. (1990) recommended using both indices, considering them to be complementary measures, because the use of only one can mask important biological differences. We quantified the lizard microhabitat use by calculating the percent of time spent in the open gaps between shrubs (PTO). We placed a colored flag with sequential numbers each time the lizard changed its movement direction. To determine the lizard's course at the end of the observation, we used a 50-m measuring tape to measure the total distance traveled (TD) and the net distance between the lizard's position at the beginning and at the end of the observation (ND). The second measurement only roughly estimates the pattern of movements because a short ND may represent movement within a certain radius around an activity center (e.g., burrows). Ambient temperature was measured at the beginning and at the end of every observation, and the average of these values was used during data analysis. Ambient temperature affects all aspects of reptile behavior and physiology, especially in active foragers (Cooper et al. 2001). Thus, checking for an effect of ambient temperature on lizard behavior and removing it during data analysis, if it exists, may reduce the variance in activity measurements. We measured the temperature using a digital thermometer, whose thermistor was suspended within a horizontal cardboard cylinder wrapped in aluminum foil, 2 cm above the ground. The direction in which the cylinder was positioned allowed free flow of wind yet prevented direct sunlight from reaching the thermistor.

To investigate whether tail displays are correlated to the ontogenetic color change, we observed the behavior of juvenile *A. beershebensis* during the first week of June 2004 and then in the first week of July when the lizards lost their hatchling coloration. We used a palmtop with FIT software to record the tail display events using exactly the same observational procedure used for the foraging observations. We distinguished between 2 tail displays: delicate vibration and robust undulation and calculated the number of events per minute as indices (DVM and RUM, respectively).

Lizard morphology and color

All lizards were captured in 3 trapping sessions between the 26th of May 2001 and the 23rd of June 2001, in 5 separate plots. The first trapping session was conducted less than a week after the lizards hatched, the second after 9 days, and the third after a further 11 days. Lizards were captured for 3 consecutive days per session using 64 pitfall traps per plot. During trapping periods, the pitfall traps were checked at least once every 3 h to prevent loss of animals due to overheating. Between trapping periods, pitfall traps were tightly closed with lids. We measured lizard body size with a transparent ruler [snout-vent length (SVL) to the nearest 1 mm] and their mass (to the nearest 0.1 g) with an electronic field scale. Tail color was estimated by the same researcher and was classified into 1 of 3 groups: bright blue, faded blue, and adult coloration, when it changed to brownish gray. The animals were not individually marked because individual recapture probability of *A. beershebensis* hatchlings in the same field site was found in a previous study to be much less than 0.1 (D Hawlena, unpublished data). The trapped lizards were released at the location of capture within 24 h.

Reference species

To examine whether ontogenetic behavioral changes in *A. beershebensis* are general phenomena shared with other desert lizards that do not undergo ontogenetic changes in pattern and coloration, we observed the behavior of 2 lacertid species that overlap in their distribution with *A. beershebensis.* Because no distinct color transformation exists in these species, different periods can be compared in order to reveal behavioral changes. We used 2 approaches: for the annual lizard *Mesalina guttulata* (that co-occur in the same habitat as *A. beershebensis*), we compared the behavior of newly hatched lizards with the behavior of 1-month-old juveniles; for *Acanthodactylus boskianus*, we compared the behavior of juveniles with the behavior of adults during the same period. In both cases, we repeated the same procedure described earlier for *A. beershebensis.* For *M. guttulata*, we measured MPM, PTM, and PTO, but for *A. boskianus*, we measured only the 2 foraging mode indices MPM and PTM.

Statistical analysis

The data were checked for all relevant assumptions before performing statistical analysis (Zar 1998). Some variables were log transformed to normalize the variance and to achieve homogeneity of the variance. Temperature is known to affect reptile behavior (Huey 1982). We therefore checked for the effect of ambient temperature on all behavioral variables using linear regressions. We used a 1-way ANOVA with Tukey honestly significant difference (HSD) post hoc comparison to compare the SVL of the lizards between the 3 tail-color groups. All combinations of behavioral characters measured were tested for correlation using Pearson's correlation test. In order to assess the changes in hatchling behavior before and after the tail color and body pattern change, we compared all 5 indices: MPM, PTM, PTO, TD, and ND. Because all hatchling activity indices were correlated except for ND, we used multivariate analysis of variance (MANOVA) to analyze the overall change in hatchling activity before and after the color change. A univariate F-test for each dependent variable was performed in order to determine which individual dependent variables contribute to the significant multivariate effect. Because the data was analyzed in a protected framework, we did not have to use the sequential Bonferroni adjustment (Rice 1989) to decrease the chance of type I errors derived from familywise error (Scheiner 2001). Because ND did not correlate with the other behavioral parameters, a 1-way ANOVA was used to assess the changes in ND before and after the change in tail color and body pattern occurred.

Because both tail display indices DVM and RUM failed to fulfill the assumption of parametric tests, we used the nonparametric Mann–Whitney U test (Siegel and Castellan 1988). We analyzed both tail display indices before and after the color change separately and then used sequential Bonferroni adjustment (Rice 1989) to decrease the chance of type I errors derived from familywise error. For the analysis of the foraging data of the 2 reference species, we repeated exactly the same procedure as for *A. beershebensis.* We compared *A. boskianus* hatchlings MPM and PTM with those of blue-tailed *A. beerhebensis* hatchlings using a 1-way ANOVA. For all analyses we used SPSS 10.0 (Coakes and Steed 2001).

RESULTS

All hatchlings hatched with a bright blue tail ($n = 57$). After about 10 days, 60% of the hatchlings had lost their bright blue tail, and in about 25% of the individuals, color had already changed to adult tail coloration. By the third week posthatching, 85% of the individuals had lost their blue tail coloration (Figure 2). The fading of the striped hatchling pattern coincided with the loss of the blue tail coloration.

A comparison of hatchling SVL between the 3 tail-color groups revealed significant differences (1-way ANOVA: $F = 247.1$, df = 2, error df = 162, $P < 0.001$). A Tukey HSD post hoc test revealed significant differences between all 3 tail-color groups ($P < 0.001$ for all groups, Figure 3). Ambient temperature had no significant effect on any behavioral variable, allowing for further analysis without the need to correct for temperature (for all analysis $R^2 < 0.06$, $P > 0.246$). Strong and significant correlations were found between all behavioral measurements except for ND (Table 1). MANOVA testing for differences in MPM, PTM, PTO, and TD between blue-tailed newly hatched lizards and 3-week-old individuals with brown tails, using Pillai's Trace criterion, revealed highly significant differences (df = 20, Pillai's Trace = 0.514, $F = 5.297$, $P = 0.004$). A univariate F-test for each dependent variable showed that PTM, MPM, and PTO are significantly affected by the lizard's maturation stage (Table 2 and Figure 4). An ANOVA to compare ND between newly hatched lizards with blue tails and 3-week-old lizards with brown tails revealed no significant difference (df = 1, $F = 1.018$, $P = 0.324$).

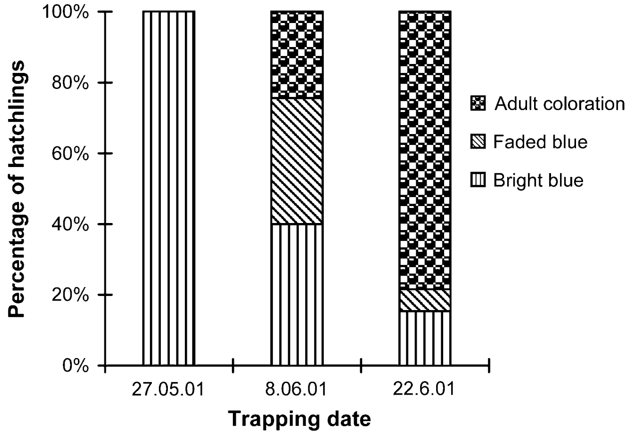

Figure 2
Relative abundance of the 3 tail-color groups during each of the 3 trapping sessions.

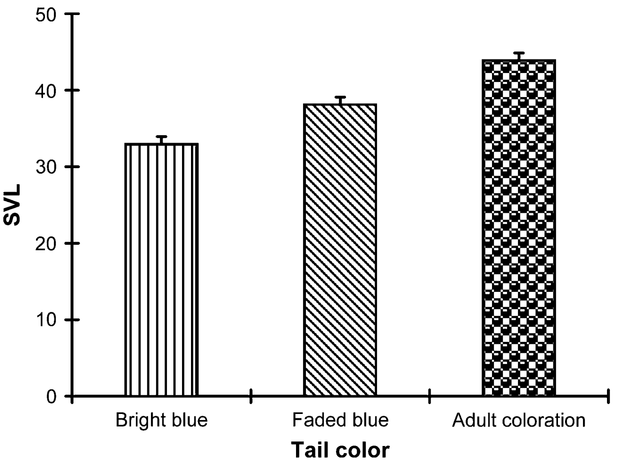

Figure 3
SVL of the 3 tail-color groups (mean ± SE).

Newly hatched blue-tailed *A. beershebensis* had a significantly higher DVM compared with the movements of 4-week-old brown-tailed individuals (Mann–Whitney U test, $Z = -4.251$, $P < 0.001$; Figure 5a). This display is most obvious during hatchling movements and especially when passing between dissimilar microhabitats. A significant difference was also found between the RUM of blue-tailed and brown-tailed lizards (Mann–Whitney U test, $Z = -2.295$, $P = 0.022$; Figure 5b). This tail display is most obvious when hatchlings perch on a stone or on an exposed branch, especially immediately after stopping and before resuming movement.

Ambient temperature had no significant effect on any behavioral variable measured from the 2 reference species, *M. guttulata* and *A. boskianus,* allowing for further analysis without the need to correct for temperature. No significant correlations were found between the 3 indices measured

Table 1

Summary of Pearson correlation results assessing the relationship between all combinations of behavioral measurements

	ND	PTM	MPM	PTO
TD	−0.201	0.51	0.625	0.526
	0.336	**0.009**	**0.001**	**0.007**
ND		−0.268	−0.146	−0.001
		0.195	0.485	0.997
PTM			0.779	0.478
			<0.001	**0.016**
MPM				0.681
				<0.001

The upper value in each cell represents the Pearson correlation value. The bold P values indicate significant effects.

Table 2
Univariate *F*-test for each dependent variable

	ANOVA			
Source	df	Mean square	*F*	*P*
Tail color				
PTM	1	493.048	8.056	**0.009**
PTO	1	1194.509	5.237	**0.032**
TD	1	75.628	0.7	0.411
Log (MPM)	1	0.206	16.802	<**0.001**

This was performed in order to indicate which individual dependent variables contribute to the significant multivariate effect. The bold *P* values indicate significant effects.

for *M. guttulata.* MANOVA testing for differences in MPM, PTM, and PTO between *M. guttulata* newly hatched lizards and 1-month-old individuals, using Pillai's Trace criterion, revealed no significant differences (df = 27, Pillai's Trace = 0.064, $F = 0.612$, $P = 0.613$). Strong and significant correlations were found between MPM and PTM of *A. boskianus* ($r = 0.646$, $P < 0.001$). MANOVA testing for differences in MPM and PTM between *A. boskianus* juveniles and adults, using Pillai's Trace criterion, revealed highly a significant difference (df = 23, Pillai's Trace = 0.296, $F = 4.847$, $P = 0.018$). A univariate *F*-test for each dependent variable showed that PTM is significantly affected by lizard age (df = 1, $F = 6.102$, $P = 0.021$): juvenile *A. boskianus* move less (mean = 15.5%, SE = 1.8%) than adults (mean = 22.9%, SE = 2.4%). In contrast, there was no significant difference in MPM between age groups (df = 1, $F = 0.079$, $P = 0.781$).

Newly hatched *A. beershebensis* PTM differed from that of *A. boskianus* hatchlings ($F = 152.62$, df = 1, $P < 0.001$). However, we found no difference comparing the MPM between hatchling of the 2 species ($F = 0.281$, df = 1, $P = 0.6$). *Acanthodactylus beershebensis* hatchlings spent longer time moving than hatchlings of *A. boskianus* (Figure 4).

DISCUSSION

Tail coloration, body pattern, and foraging activity

Our results indicate that newly hatched lizards move more and spend more time in the open microhabitat than hatchlings that have already undergone the ontogenetic color change. Our results are congruent with the general principle found at the species level by Arnold (1984) and Vitt and Cooper (1986), who stated that bright tail coloration is generally associated with actively foraging species.

The foraging behavior of newly hatched lizards of the reference species, *M. guttulata,* did not differ from that of 1-month-old lizards. The foraging behavior of juvenile *A. boskianus,* our second reference species, did differ from that of adults. However, in contrast to *A. beershebensis,* in *A. boskianus* the juveniles move less and thus present a safer foraging mode. A relatively safer foraging mode in juveniles is also seen among juveniles of a third lizard, *Chamaeleo chamaeleon* (Keren-Rotem et al. 2005). In the latter 2 species, the safer foraging mode of juveniles is compatible with a behavioral attempt to reduce predation risks. Thus, *A. beershebensis* does not simply follow a general trend among lizards: the only 3 other lizards whose foraging mode have been quantified at different ages neither follow the behavioral change from risky to safer foraging with maturity nor show an ontogenetic change in tail color.

The alteration of hatchling behavior at the same time as alterations in dorsal pattern and tail color raises the question: What mechanism can relate behavior to coloration and pattern?

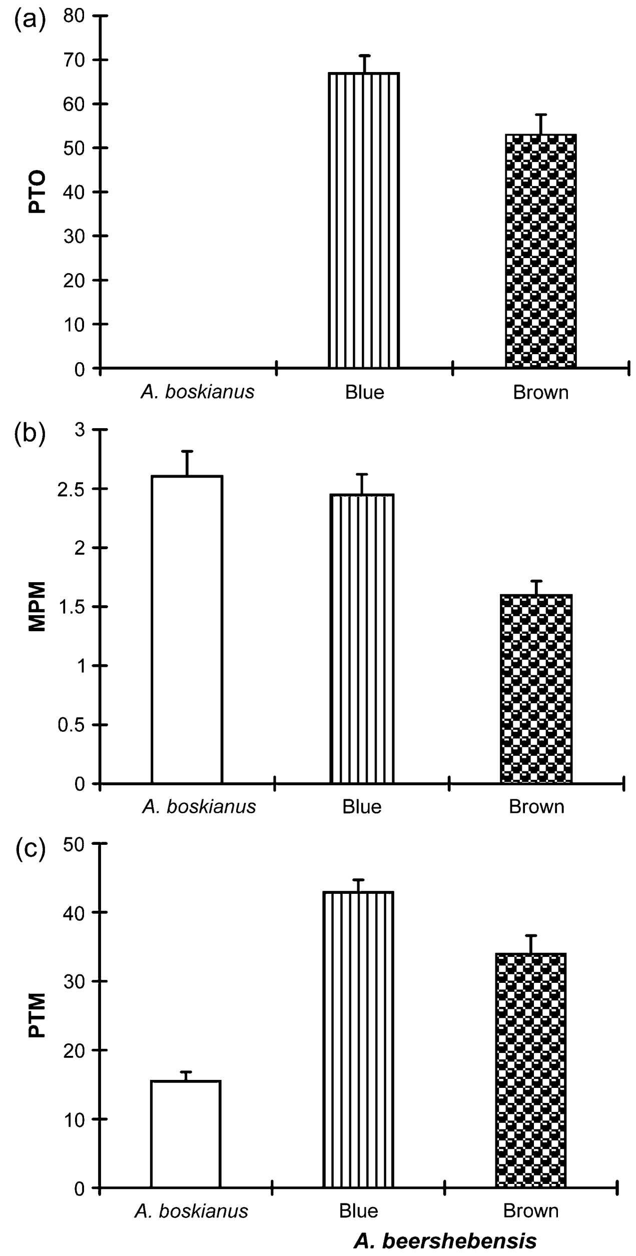

Figure 4
Comparison of the mean values of the behavioral indices that were significantly different before and soon after the ontogenetic tail color change (Table 2) to those of *A. boskianus* hatchlings: (a) PTM, (b) PTO, and (c) MPM. Error bars represent SE except for (c) in which 95% confidence intervals are given because the results were inverse log transformed.

Predation risk as a possible explanation

The risk of predation to which a prey individual is exposed can be expressed as the product of the time vulnerable to attack, the probability of encounter with predators, and the probability of escaping an attack (Lima and Dill 1990). The behavior of *A. beershebensis* hatchlings involves a large number of movements, a large total amount of time spent moving, and a large amount of time spent in open microhabitats; the

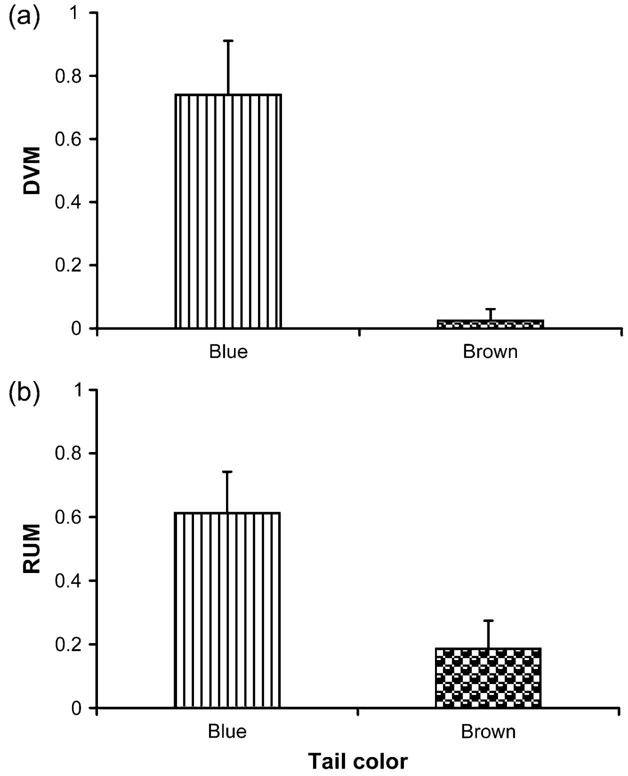

Figure 5
Comparison of the mean values of tail display indices before and soon after the ontogenetic tail color change. (a) Comparison of the delicate vibration per minutes (DVM). (b) Comparison of the robust swing per minute (RUM). The error bars represent the standard error.

hatchlings therefore bear a high probability of encounter with a predator, particularly a visually oriented predator (Lima 1998; Sheffield et al. 2001). At the same time, the probability of detecting an attack and avoiding the encounter is lower because a moving prey has reduced abilities to detect approaching predators and to respond accordingly (Lima and Bednekoff 1999). Altogether, survival of active foragers is predicted to be lower than that of less active foragers (Webb et al. 2003). In our system too, the survival probability of *A. beershebensis* hatchlings during the phase of active foraging is much lower than their survival probability later on, when they adopt the more sedentary mode (active = 0.357, SE = 0.153; sedentary = 0.781, SE = 0.035, respectively) (D Hawlena, unpublished data). The need of *A. beershebensis* to accumulate energy for rapid growth (see below) limits the ability of hatchlings to use a safe foraging mode. Therefore, the major component of predation risk that can be managed by the prey is the probability of surviving an attack.

A striped pattern is associated with active foraging and with flight as the dominant antipredator strategy, and it was suggested that because this pattern lacks reference points, visual predators may have difficulties in estimating the lizard's velocity (Jackson et al. 1976; Brodie 1989). Our results support this relationship between pattern and behavior and expand its applicability from a comparison between species or populations of the same species (Brodie [1989] and Jackson et al. [1976], respectively) to an intraindividual comparison during different ontogenetic stages. We suggest that the striped pattern in newly hatched *A. beershebensis* increases the probability of a successful escape, if detected. Because the striped pattern is associated with colorful tails, we need to examine how tail color fits into this suggested hypothesis.

Blue tail increases the probability of surviving attacks

Many species try to deflect predator attacks to expendable or relatively invulnerable body parts by parasematism, that is, special marks or conspicuous colors (Cooper 1998). Species that present parasematism often use behavioral displays to direct the predator's attention further to the targets of deflection, such as autotomizable appendages of lizards (Arnold 1984; Cooper and Vitt 1985; Vitt and Cooper 1986), salamander larvae (Van Buskirk and Schmidt 2000) and anuran tadpoles (Caldwell 1982), or posterior wing margins of butterflies (Robbins 1981; Wourms and Wasserman 1985). An attack on such anatomical targets causes a much lower loss in fitness than attacks on the head or trunk. A few prey species perform anticipatory deflection, that is, a display performed even when they have not detected any predator, probably to induce attacks by ambush predators when the prey is more vigilant and has better chances of escaping (Magnusson 1996; Cooper 1998). The 2 tail displays frequently exhibited by blue-tailed hatchlings of *A. beershebensis* are significantly reduced when lizards lose their conspicuous coloration. Both displays seem to attract the attention of potential predators: the fast delicate vibration is often coupled with tail lifting when lizards are moving, and the slow tail undulation is performed soon after stopping on exposed perches and just before resuming movement.

The main lizard predator in our field site is the Great Gray Shrike (*Lanius excubitor*), a sit-and-wait predator, that hunts exclusively from perches and has excellent color and UV vision (Cooper and Vitt 1985; Yosef 1993; Yosef and Grubb 1993). The active foraging of newly hatched *A. beershebensis* exposes them to high risk from ambushing shrikes and may favor parasematism coupled with deflection displays to divert the attacks toward the tail or to induce attacks while the lizards are vigilant. Three weeks later, when lizards reduce their movements and increase the time spent in refuge, the shrikes' ability to detect the more static prey is reduced, and the tradeoff between costs and benefits of parasematism may therefore favor a different antipredator mechanism, for example, the camouflaging pattern of spots and blotches (Jackson et al. 1976; Brodie 1993). The fact that *A. boskianus* hatchlings present less active foraging than hatchlings of *A. beershebensis* and have a camouflaged tail further supports this notion.

Reducing the risk of predation by attracting predators' attacks to the tail demonstrates a widespread situation in which prey animals use antipredatory behaviors or morphological mechanisms to partially compensate for behaviors that expose the prey to higher predation risk (for review see Lind and Cresswell 2005). Therefore, studies of the evolution and the ecological significance of antipredatory mechanism should consider the complete range of behaviors and morphological mechanisms at the same time rather than focus on a single antipredatory mechanism (Lind and Cresswell 2005).

Why do newly hatched lizards move more?

Based on the previous sections, we suggest that the ontogenetic change in tail color and body pattern in *A. beershebensis* results from the increased predation risk that accompanies a change in foraging activity. This raises the question: Why do young hatchlings of this species move more in contrast to the other 3 species used as a comparison? It is well acknowledged that initial size advantages at early stages may lead to adult characteristics that bear higher fitness and can be considered as a "silver spoon effect" (Grafen 1988). In our system, larger hatchlings of *A. beershebensis* survived better and ended up as larger adults (D Hawlena, unpublished data). Because *A. beershebensis* hatchlings emerge in synchrony and have a very narrow size distribution (D Hawlena, unpublished data), their only chance to take control over the "silver spoon" is by using more active foraging. The newly hatched lizards should use the risky, but more profitable, mode (Webb et al. 2003). Other sympatric lacertids demonstrate less synchronized hatching and have a longer period to reach adult size and thus do not need to take greater risks as hatchlings (D Hawlena, unpublished data). Similarly, *A. boskianus* lives on average for more than one season, and as a result, hatchlings need not take very high risks in order to reach adult size before the reproduction period. Two to three weeks after *A. beershebensis* hatches, individuals that have managed to survive and to maintain size superiority face lower intraspecific competition due to the low number of survivors and their size advantage. At this time, the foraging behavior of the hatchlings switches to a safer mode, centering more on reducing predation risk than gaining an advantage over their competitors.

Alternative hypotheses for ontogenetic change in color and pattern

Although not experimentally tested, several alternative explanations have been offered to account for the ontogenetic change in lizard tail colors. In many species, conspicuous coloration of the tail is lost at about the size at which sexual maturity is reached. As a result, researchers suggested that different costs and benefits apply to juveniles and adults. For example, Vitt and Cooper (1986) suggested that tail loss in juveniles is cheaper. This possibility is probably not applicable to *A. beershebensis*, which reaches sexual maturity size at the age of 5 months. Due to the early change in tail color, it is unlikely that there is a difference between newly hatched lizards and 3-week-old hatchlings in the costs and consequences of tail autotomy, such as energy loss (Vitt et al. 1977), limited performance (Brown et al. 1995), and the loss of further ability to autotomize the tail (Martin and Avery 1998; Cooper 2003).

Arnold (1984) and later Vitt (2000) suggested that small lizards suffer a higher risk of predation from a wider range of predators than larger lizards. This higher risk may favor parasematism and deflection displays; however, the rapid change in tail color in *A. beershebensis* reduces the likelihood that some predators specialize only on hatchlings during their first 2 weeks of life.

Clark and Hall (1970) suggested that the conspicuous tails might function as an intraspecific social signal to reduce intraspecific aggression and cannibalism (but for a different view, see Cooper and Vitt 1985). This explanation is not applicable to *A. beershebensis* because its synchronous annual life cycle allows almost no encounter between juveniles and adults.

CONCLUSIONS AND FUTURE DIRECTIONS

Our study suggests that the ontogenetic changes in tail color and body pattern result mainly from alterations in their adaptive value due to changes in foraging behavior. At the age of about 3 weeks, hatchlings switch to safer foraging, and the risk of predation decreases. For the simple system we studied, we were able to reject most of the alternative hypotheses suggested in previous studies as possible explanations for the ontogenetic color and pattern change. Although we cannot directly transfer our inferences from *A. beershebensis* to all other cases, this study demonstrates that on top of all other suggested factors for ontogenetic changes in coloration, a modification in foraging mode is another possible explanation, and it may operate together with some of the previous ones (e.g., communication with adult conspecifics in species that have overlapping generations). We hypothesize that constraints on the ability of species to reduce activity in order to decrease the risk of predation explain why hatchlings of certain species, but not others that share the same habitat, have conspicuous tail coloration. Our hypothesis is the first supported hypothesis to include explanations for the adaptive value of the ontogenetic change both in tail color and in the dorsal-striped pattern that so often accompanies it. The ultimate experiment to explore our hypothesis further would be to manipulate tail color and to examine survival consequences when lizards use either of the 2 foraging modes. Unfortunately, the qualities of hatchling tails prevent us from conducting such experiments on *A. beershebensis*. Any artificial color both limits the very delicate tail movements and does not reflect in the UV range, as natural tails do. We call on researchers who study different systems to accumulate comparative data from additional species in order to explore the generality of the pattern we found.

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