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ORIGINAL PAPER

Colorful tails fade when lizards adopt less risky behaviors

Dror Hawlena

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Abstract Colorful tails that become cryptic during ontogeny are found in diverse taxa. Nevertheless, the evolutionary bases for this change remain debated. Recent work suggests that colorful tails, deflective displays, and striped patterns may represent antipredator mechanisms used by immature lizards to compensate for being more active and hence more vulnerable to predation (increased movement hypothesis, IMH). I challenged the generality of IMH by comparing foraging behavior and frequency of tail displays across five *Acanthodactylus* lizards that vary in fundamental life history traits, before and after the tail changed color. As these species underwent changes in tail coloration, they congruently adopted less risky behaviors and reduced the frequencies of tail displays. Contrary to expectation, in two species, the hatchling risky behavior resulted not from increased movements but from longer stay in exposed microhabitats. I suggest that colorful tails and deflective tail displays are synergistic antipredator mechanisms neonates use to minimize the fitness consequences of using various risky behaviors rather than increased movement alone.

Keywords *Acanthodactylus* · Deflective display · Dorsal pigmentation · Movement · Ontogeny · Predation risk · Tail autotomy

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D. Hawlena (✉)
School of Forestry and Environmental Studies, Yale University,
370 Prospect Street,
New Haven, CT 06511, USA
e-mail: dror.hawlena@yale.edu

Introduction

Many species undergo concurrent ontogenetic changes in behavior, color, and body pigmentation (Booth 1990). It has been argued that ontogenetic changes should involve transitions from cryptic coloration and cautious behavior in juveniles to avoid predation risk to conspicuous colors and noticeable displays for mating when reaching sexual maturity (Wilson et al. 2007). Yet, many transitions in amphibians, reptiles, and fish follow an opposite course in which conspicuous colors are apparent in juveniles and the colors fade during ontogeny, often concurrently with dramatic changes in dorsal pigmentation (Caldwell 1982; Cooper 1998; Kynard et al. 2002). This seems counterintuitive because we might expect that conspicuous colors exacerbate already heightened vulnerabilities of juveniles (see Whiting et al. 2003 for details) to visually oriented predators. The purpose of this paper is to offer an integrative explanation for those counterintuitive transitions.

Conspicuous colors in juvenile tails that fade during maturation can be found in various lizard species, belonging to different families (Cooper and Vitt 1985). Often, those lizards have striped dorsal patterns that change coincidently with the tail color change (Arnold 1988). Clark and Hall (1970) suggested that a conspicuous tail serves as a visual signal to reduce intraspecific aggression and cannibalism. This hypothesized function can explain tail color change only in species in which neonates and adults coexist. An alternative explanation holds that conspicuous juvenile tail colors reduce predation risk by deflecting predator attacks to the autotomizable tails (Cooper and Vitt 1985; Cooper 1998; Castilla et al. 1999). This suggested function can explain tail color change if tail loss in juveniles is relatively cheaper than later in life (Vitt and Cooper 1986). In many cases, smaller lizards face higher predation risk from a wider range of predators than larger lizards. Consequently, selection may additionally favor ontogenetic differences in tail coloration as an active way to deflect predation attacks and thus reduce predation risk in highly vulnerable age classes (Arnold 1984; Vitt 2000).

More recently, Hawlena et al. (2006) suggested that neonate lizards may also have conspicuous tails to compensate for elevated predation risk caused by their more active foraging behavior (from here on: "increased movement hypothesis" (IMH)). Specific physiological constraints (e.g., high-energy demands for rapid somatic growth, thermoregulation) may force foraging neonates to move more than adults (Nagy 2000; Herczeg et al. 2007). This heightened activity increases the likelihood of detection and attack by ambush predators (Lima 1998; Lima and Bednekoff 1999; Sheffield et al. 2001) and reduces the probability to escape an attack (Fleishman 1986), increasing the risk of predation above the already elevated risk due to the small hatchling size (Webb et al. 2003). Thus, a conspicuous tail accompanied by deflective tail displays should redirect the predator toward the autotomizable tail, increasing the neonates chance to escape inevitable attacks. Not like alternative hypotheses that assume tail color change only when lizards approach maturation (e.g., Clark and Hall 1970; Vitt and Cooper 1986), the IMH is not age or size dependent and can explain tail color change even in species that undergo color change a few weeks after hatching and in annual species with virtually no overlap between succeeding cohorts. Moreover, IMH suggests an integrative explanation for why ontogenetic changes in tail color and body pattern so often concur. Dorsal patterns that lack reference points (i.e., stripes or uniform pattern) may hinder the visual predator ability to estimate lizard's velocity (Jackson et al. 1976; Brodie 1989). After adopting less active foraging behavior, striped pattern can become disadvantageous since it can increase the probability that the otherwise cryptic lizard will be detected and attacked. Consequently, striped and uniform dorsal patterns may serve as a complementary antipredator mechanism to reduce the probability that the active neonate will be intercepted while moving. Although appealing, the strength of IMH as a general explanation for tail color and dorsal pattern changes among lizards has never been examined. Moreover, no data (rather than Hawlena et al. 2006) are available on ontogenetic changes in foraging behavior in species that undergo changes in tail coloration to allow such examination.

I report on an evaluation of the IMH in five *Acanthodactylus* (Lacertidae) lizards that undergo ontogenetic change in tail coloration but differ in dorsal patterns and in life history traits (e.g., longevity, hatching synchrony, etc.; Table 1). Using related species that share a focal trait but differ in other fundamental traits is a conservative way to challenge the generality of a hypothesis when data needed for a phylogenetically informed comparative analysis are unavailable. Such an approach cannot reveal the adaptive value of a specific trait but allow hypotheses that are not applicable to all tested species to be rejected. I examine whether ontogenetic changes in tail color, dorsal pattern, and frequency of tail displays are associated with changes in movement behavior as predicted by IMH, specifically asking (a) whether all species move more while having conspicuous tails than after the conspicuous tail coloration has faded, (b) whether all lizards with conspicuous tails use tail display more often before than after the tail fades to cryptic coloration, and (c) whether striped and uniform dorsal patterns are associated with increased movements. Additionally, I examined whether ontogenetic changes in color and pattern correspond to changes in microhabitat use without predicting a specific association.

Methods

Species and study sites

I observed the behavior of five *Acanthodactylus* species in four field sites in central and southern Israel. In order to allow meaningful comparisons between age classes, I used two different experimental schemes that fit the differences in lizard life history traits (e.g., hatching synchrony, longevity, growth rate; Table 1). I observed hatchling (neonate soon after hatching) and adult behavior simultaneously when both age classes coexist. But when studying annual species that hatch synchronously (i.e., no overlap between cohorts), I observed the neonate lizard behavior before the tail color turned cryptic (hereafter referred to as hatchlings) and soon after the tail color turned cryptic (here after referred to as juveniles). I also observed adult behavior of annual species to allow comparing all species on equal bases. Lizards were defined as adults when I could visually determine their sex.

I observed *Acanthodactylus longipes* Boulenger 1918 in Holot Mashash nature reserve (31°05′ N, 34°46′ E) during May (adults, n=9) and August (hatchling, n=12) 2006. This species undergoes only moderate and gradual changes in tail color. Thus, I used it to examine whether increased movement is a general trend among *Acanthodactylus* hatchlings. Because of the gradual changes in tail coloration, I was able to compare only the behavior of hatchlings and adults. The habitat in Holot Mashash is characterized by semistabilized dunes scattered by *Artemisia monosperma* and *Retama raetam* bushes and by stabilized interdunal depressions that support denser vegetation. In the same field site, I observed also *Acanthodactylus*

Table 1 Trait comparison between the five *Acanthodactylus* species (based on Baha El Din (2006) and Hawlena personal observations)

Species	Cohort overlap	Hatching synchrony	Tail color change (weeks)	Tail color		Dorsal pigmentation		Sympatry
				Hatchling	Adult	Hatchling	Adult	
A. longipes	Medium	Medium	No	Yellow	Straw	Finely speckled	Finely speckled	*A. scutellatus*
A. scutellatus	Very low	High	12	Blue	Sand	Finely speckled	Spots–vermiculation	*A. longipes* *A. schreiberi*
A. beershebensis	Very low	Very high	3	Blue	Sand-gray	Stripes	Blotches	–
A. boskianus	High	Low	5	Blue	Sand-gray	Stripes	Stripes	–
A. schreiberi	High	Medium	6	Red	Sand	Stripes	Stripes	*A. scutellatus*

A. longipes, *A. scutellatus*, and *A. beershebensis* are annual species and *A. boskianus* and *A. schreiberi* are perennial species. Cohort overlap indicates a situation in which adults and hatchlings coexist. Hatchling synchrony refers to differences in hatching timing within the same reproductive season. Several populations of *A. boskianus* do not undergo ontogenetic changes in tail color

scutellatus Audouin 1829 during April (adults, n=9), June (hatchling, n=12), and September (juvenile, n=9) 2006. I observed *Acanthodactylus beershebensis* (Moravec et al. 1999) in the Loess Park (31°14′ N, 34°35′ E) during May–June 2003 (hatchling, n=20), late June 2003 (juvenile, n=13), and October 2006 (adults, n=15). This study site is a loess plain dominated by the small woody perennial shrub *Noea mucronata* that creates an open scrubland. I observed *Acanthodactylus boskianus* Daudin 1802 in Holot Ephee nature reserve (31°03′ N, 35°08′ E) on a bare sandy plain scattered with big *Retama raetam* and *Calligonum comosum* perennials during May, July, and September 2006 (adults, n=13) and during August and September 2006 (hatchlings, n=16). I observed *Acanthodactylus schreiberi* Boulenger 1878 in Keisaria costal dunes (38°28′ N, 34°54′ E) during May and August 2006 (adults, n=10) and August 2006 (hatchling, n=11). This site is characterized by high and mostly stabilized dunes with dense vegetation cover of *Pistacia lentiscus* and *Retama raetam* and interdunal depressions with very dense vegetation. The main predators of *Acanthodactylus* lizards in those habitats are avian predators that hunt mostly from perches (e.g., shrikes and kestrels).

Behavioral observations

I conducted all observations between 07:30 and 10:30 wearing similar clothing to control for variation in lizard activity resulting from nonforaging behaviors (e.g., thermoregulation, Perry 2007) or from lizard responses to differences in my appearance. I located a lizard by random search and then observed it from a distance of approximately 4 m, for 23 min. I deleted the first 3 min of every observation during analysis to decrease variation resulting from transient behaviors before habituation of the lizard to me (Hawlena et al. 2006). I recorded the foraging behavior, the microhabitat use, and three distinct tail displays (delicate vibration, robust undulation, and robust undulation accompanied with limbs waving) on a palm-top with the software FIT (Held and Manser 2005). This software enabled me to record event times while observing lizard behavior continuously. I observed only lizards with intact tails in order to decrease variability associated with changes in activity that may result from tail autotomy (Martin and Salvador 1997). I omitted observations of lizards that were engaged in thermoregulation (basking or transient movements between shaded spots) or lizards that showed a strong response to the observer (i.e., escape behavior and intensive refuge use) from the analysis.

I calculated the foraging indices movements per minute (MPM) and percentage of time spent moving (PTM) to quantify lizard foraging behavior (Cooper et al. 1999). Both indices together can reveal important behavioral differences that could be concealed using only a single index (Huey and Pianka 1981; Perry 2007). I estimated lizard microhabitat use by calculating the percent of time spent in open gaps between shrubs (percentage time open, PTO) and number of transitions between shrub and open microhabitat per minute (microhabitat change per minute, MCM). I considered a lizard to be in a shrub when at least part of it was concealed under the shrub canopy. To investigate whether tail displays are correlated to ontogenetic color change, I calculated the number of each kind of discrete tail display event per minute as indices of tail display (delicate vibration per minute (DVM), robust undulation per minute (RUM), and robust undulation accompanied with limb waving per minute (UWM)). Some of the data for *A. beershebensis* were taken from Hawlena et al. (2006) and did not distinguish between RUM and UWM. Thus, I considered every robust tail undulation for this species as RUM, whether it was accompanied with limb movement or not. The distinction between those two displays in this species is the least obvious of all the species used in this study. I measured ambient temperature at the beginning and the end of every observation 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. I used the average temperature of each observation during data analysis to reduce intraspecific variation in lizard foraging behavior.

Data analysis

I used linear regression to examine the effect of temperature on all behavioral variables. When a significant association was found, I used the linear regression unstandardized residuals for all further analysis.

I used a mixed model multivariate analysis of variance with age class (hatchlings vs. adults) as a fixed factor and species (only the four species that undergo dramatic changes in tail coloration) as a random factor to challenge the main prediction of the IMH that tail color change should be associated with behavioral changes from more active to less active foraging. A significant age class effect would support the hypothesis and a significant age class by species interaction would suggest that the hypothesis is not adequate for all observed species.

To assess the overall changes in lizard foraging behavior between hatchlings and adults (*A. boskianus*, *A. schreiberi*, and *A. longipes*) or between hatchling, juveniles, and adults (*A. beershebensis* and *A. scutellatus*), I used a nonparametric randomization multivariate analysis of variance (RAMANOVA) test (RAMAN program, Alford 1999), based on algorithms provided by Manly (1991), because not all behavioral variables fulfilled the assumption of parametric procedures (normal distribution or homoscedasticity). A one-way ANOVA with Tukey's post hoc comparison was applied to determine which behavioral index contributes to the significant multivariate effect. In cases where the data failed to fulfill the assumption of parametric tests, I used Wilcoxon–Mann–Whitney *U* test or the Kruskal–Wallis one-way ANOVA by ranks to compare between hatchlings and adults or hatchling, juveniles, and adults, respectively (Siegel and Castellan 1988). The nonparametric procedure for multiple comparisons with unequal sample sizes was applied to determine between which of the samples significant differences occur. Since the data were analyzed in a protected framework (i.e., multivariate analysis revealed significant effect), I did not have to use the sequential Bonferroni adjustment to decrease the chance of type I errors derived from family-wise error (Scheiner 2001).

I used the nonparametric Wilcoxon–Mann–Whitney *U* test or Kruskal–Wallis one-way ANOVA by ranks test because all tail display indices (DVM, RUM, and UWM) failed to fulfill the assumptions of parametric tests. Since the different tail displays can be used in different ontogenetic stages and their exact function is not yet fully understood, I analyzed each display index separately and then used sequential Bonferroni adjustment. The adjusted alpha level for each test is reported in brackets. Otherwise, significance tests were two-tailed at $\alpha=0.05$. For all analyses except for RAMANOVA, I used SPSS 12.0. RAMAN version 1.73 was used to conduct RAMANOVA.

Results

Ontogenetic changes in time allocation and microhabitat use

Ambient temperature had no significant effects on the foraging behavior and microhabitat use of the five *Acanthodactylus* species observed in this study, except for a weak positive effect of ambient temperature on *A. longipes* MPM and PTO ($R^2=0.199$, $P=0.043$; $R^2=0.385$, $P=0.003$, respectively).

As expected due to the lack of dramatic change in tail coloration, *A. longipes* behavior (e.g., PTM, MPM, PTO, MCM) did not differ between hatchling and adults (*Euclidean dist*=48.244, $P=0.412$; Figs. 1 and 2). All species that undergo ontogenetic changes in tail coloration (i.e., all species except *A. longipes*) differed between ontogenetic stages*:* *A. scutellatus* (Euclidean dist=55.908; $P=0.001$), *A. beershebensis* (Euclidean dist=86.801; $P=0.007$), *A. boskianus* (Euclidean dist=58.679; $P<0.001$), and *A. schreiberi* (Euclidean dist=40.712; $P=0.016$).

Not all species that undergo ontogenetic changes in tail coloration altered their movement behavior in a similar way (age class by species interaction; *Pillai's trace*= 0.302, *df*=6,178, $P<0.001$). *A. schreiberi* foraging behavior did not differ between hatchling and adults (PTM: $F_{1,18}=0.162$, $P=0.692$; MPM: $F_{1,18}=0.507$, $P=0.485$). Comparison of changes in the percent time moving (e.g., PTM) among the five lizards is illustrated in Fig. 1a. PTM was significantly affected by the lizard's age class in *A. scutellatus* ($F_{2,16}=7.045$, $P=0.004$), *A. beershebensis* ($F_{2,37}=5.878$, $P=0.006$), and *A. boskianus* (PTM: $F_{1,27}=7.471$, $P=0.011$). As predicted by IMH, hatchlings of *A. scutellatus* and *A. beershebensis* moved more before than soon after the tail colors changed ($P=0.04$; $P=0.032$, respectively) and in both species hatchlings also moved more than adults ($P=0.004$; $P=0.008$, respectively). Surprisingly, although *A. boskianus* hatchling and adults differed in PTM, adults moved more than hatchling contradicting the IMH main prediction. Comparison of changes in movement frequency (i.e., MPM) among the five *Acanthodactylus* species is illustrated in Fig. 1b. Here too, MPM was significantly affected by the lizard's age class in *A. scutellatus* ($F_{2,16}=7.627$, $P=0.002$), *A. beershebensis*

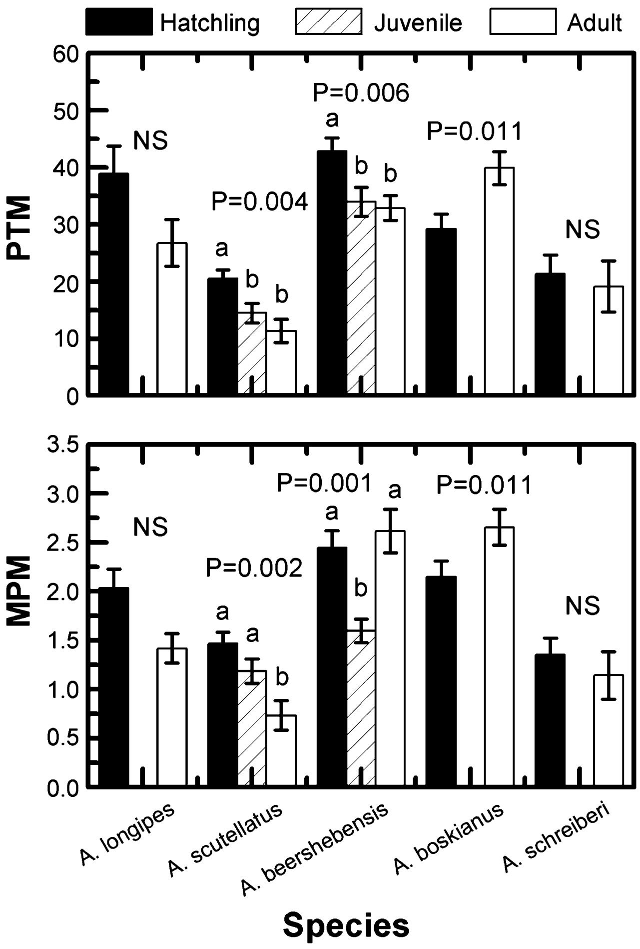

Fig. 1 Comparison of the two foraging mode indices: *PTM* proportion of time spent moving, *MPM* movements per minute. The *error bars* represent 1 standard error. The *values above each species* represent the significant level (*NS* nonsignificant) obtained from a univariate test (see Methods). When three age categories were used, the *letters above each age group columns* represent differences between groups as found in post hoc tests

($F_{2,37}$=8.958, P=0.001), and *A. boskianus* ($F_{2,16}$=4.266, P=0.05). Hatchlings of *A. scutellatus* did not differ in movement frequency (i.e., MPM) before and after the tail color changed but hatchlings move more frequent than adults (P=0.002; Fig. 1). *A. beershebensis* hatchlings moved more often before than soon after the tail color changed (P=0.004), but hatchling and adults did not differ in movement frequencies (P=0.868; Fig. 1). Here too, *A. boskianus* hatchlings moved less frequently than adults contradicting the predicted behavioral change expected by the IMH.

Comparison of changes in microhabitat use (i.e., PTO, MCM) among the five *Acanthodactylus* species is illustrated in Fig. 2. I did not detect differences in microhabitats use between the three age classes of *A. scutellatus* (PTO: χ^2=1.823; df=1; P=0.177, MCM: χ^2=3.12; df=1; P=0.077) or *A. beershebensis* (PTO: $F_{2,37}$=0.873, P=0.426; MCM: $F_{2,37}$=1.796, P=0.180), but found significant differences in PTO between hatchlings and adults of *A. boskianus* (Z=−2.325, P=0.02) and *A. schreiberi* (Z=−3.386, P=0.001). In both *A. boskianus* and *A. schreiberi*, hatchling spent significantly more time than adults in exposed microhabitats. Hatchlings and adults of *A. schreiberi* did not differ in MCM (Z=−1.296, P=0.195) but *A. boskianus* adults shuttled more frequently between microhabitats than did hatchlings (Z=−2.501, P=0.012).

Ontogenetic changes in tail displays

Ambient temperature had no significant effects on the frequencies of the three tail display indices: delicate vibration (DVM), robust undulation (RUM), and robust undulation accompanied with hand waving (UWM) of the five *Acanthodactylus* species observed in this study, except

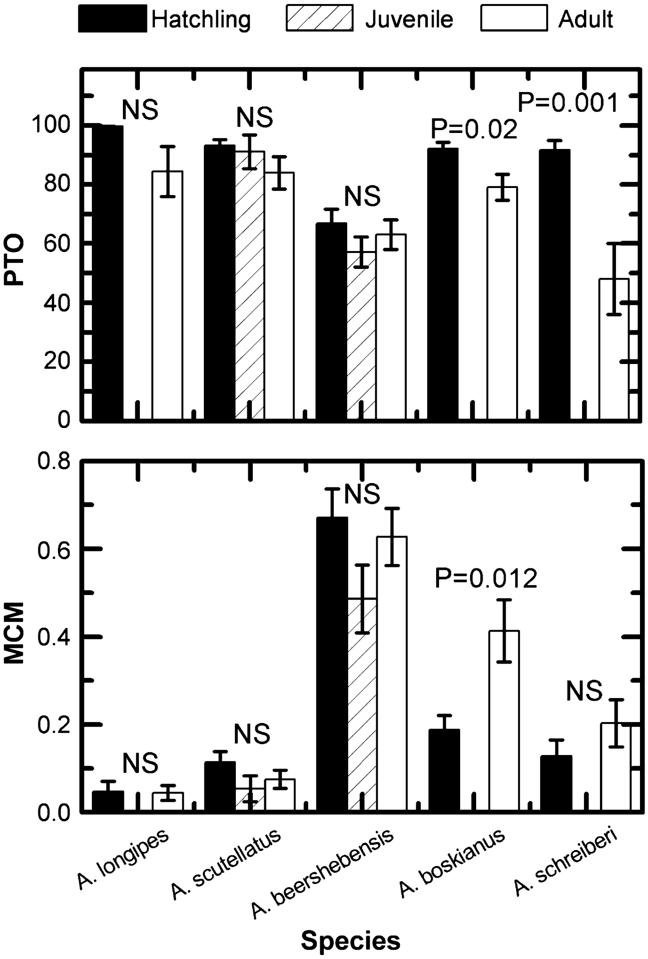

Fig. 2 Comparison of the two microhabitat-use indices: *PTO* percent of time spent in the open gaps between shrubs, *MCM* the microhabitat change (shrub vs. open) per minute. The *error bars* represent 1 standard error. The *values above each species* represent the significance level (*NS* nonsignificant) obtained from a univariate test (see Methods)

for weak positive effect of ambient temperature on RUM in both *A. scutellatus* (R^2=0.437, *P*=0.018) and *A. beershebensis* (R^2=0.292, *P*=0.046).

Comparison of changes in the three tail display indices among the five *Acanthodactylus* species is illustrated in Fig. 3. *A. longipes* was the only species in which the frequencies of DVM, RUM, and UWM were not affected by age (*Z*=−0.714, *P*=0.508; *Z*=−1.066, *P*=0.310; *Z*=−0.426, *P*=0.702, respectively).

A. scutellatus differed in frequencies of DVM, RUM, and UWM between the three age classes (χ^2=12.23, *df*=2, *P*=0.002 (α=0.05); χ^2=11.643, *df* =2, *P*=0.003 (α=0.025); χ^2=9.604, *df* =2, *P*=0.008 (α=0.017), respectively). Hatchlings used all tail displays more often than adults and used RUM more often before than soon after the tail color changed. Similarly, *A. beershebensis* differed in frequencies of a DVM and RUM between the three age classes (χ^2=30.286, *df*=2, *P*<0.001 (α=0.05); χ^2=21.402, *df*=2, *P*<0.001 (α=0.025), respectively). Hatchlings used both tail displays more often than adults and used DVM more often before than soon after the tail color changed (Fig. 3). Hatchling *A. boskianus* used UWM more often than adults (*Z*=−2.587, *P*=0.009), but did not differ in the frequency of DVM (*Z*=−1.804, *P*=0.071) or RUM (*Z*=−1.886, *P*=0.059). Similarly, *A. schreiberi* hatchling used only DVM more often than adults (*Z*=−2.86, *P*=0.005) but did not display RUM (*Z*=−0.43, *P*=0.667) and UWM (*Z*=−1.549, *P*=0.121) in different frequency from adults.

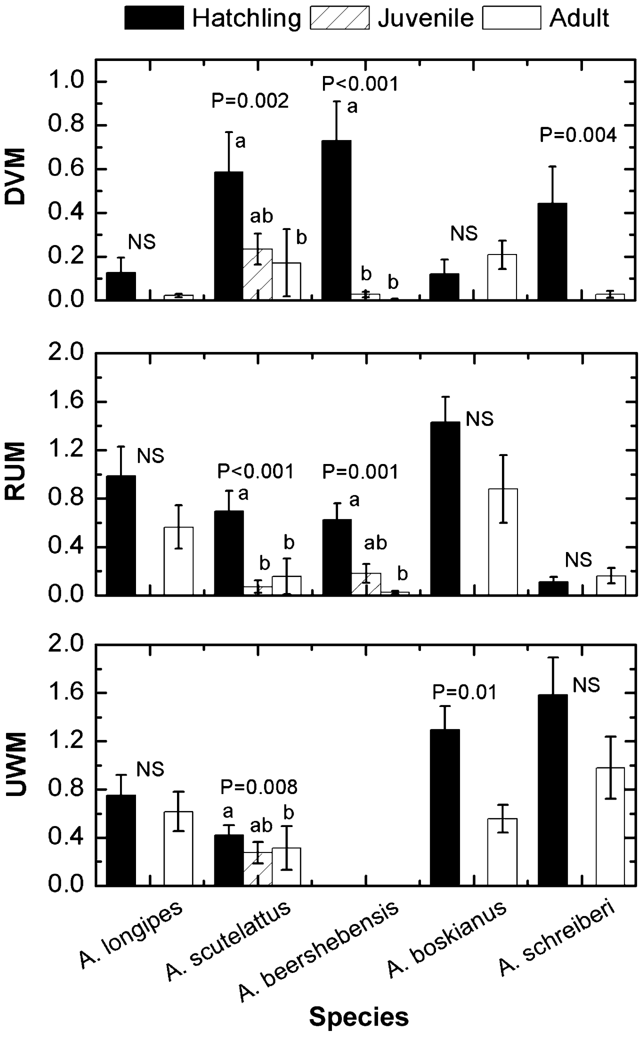

Fig. 3 Comparison of the three tail display indices: *DVM* delicate vibration per minutes, *RUM* robust undulation per minutes, *UWM* robust undulation accompanied with hand waving per minutes. The *values above each species* represent the significance level (*NS* nonsignificant) obtained from a univariate test (see Methods). When three age categories were used, the *letters above each age group columns* represent differences between groups as found in post hoc tests

Discussion

Ontogenetic changes in time allocation

The increased movement hypothesis suggests that ontogenetic changes in tail color, body pattern, and frequency of tail displays should be associated with ontogenetic changes in lizard movement behavior. I used five *Acanthodactylus* lizards that vary in life history traits and differ in tail coloration and dorsal patterns to challenge IMH.

All *Acanthodactylus* species that undergo dramatic ontogenetic changes in tail coloration performed congruent behavioral changes. However, those changes differed between species. *A. longipes*, the only species included in this study that underwent only modest changes in tail coloration (at least within the human visual range), did not exhibit significant ontogenetic changes in foraging behaviors and microhabitat use (Figs. 1 and 2), supporting the conclusion of Hawlena et al. (2006) that increased movement is not a general trend among hatchling lizards. *A. longipes* shares its habitat and presumably predators with *A. scutellatus*. This closely related (Harris and Arnold 2000), but larger annual species, undergoes noticeable changes in tail color and body pattern, demonstrating the implausibility that taxonomy, body size, longevity, or environmental conditions (e.g., predators) can solely account for tail color change. As predicted by IMH, hatchlings of *A. scutellatus* and *A. beershebensis* spent more time moving than juveniles that had already changed their tail coloration or than adults (Fig.1a) and used more movement bouts before than soon after the tail changed color (Fig. 2b). Because *A. scutellatus* and *A. beershebensis* are annual species with almost no overlap between cohorts, it is unlikely that conspicuous tails evolved to reduce intraspecific aggression and cannibalism between hatchlings and adults. Conspicuous tailed hatchlings of *A. boskianus* and *A. schreiberi* differed in their foraging activity from cryptic tailed adults. However, contrary to the main prediction of the IMH, hatchlings did not move more than adults (Fig. 1). Consequently, although all *Acanthodactylus* lizards that undergo dramatic changes in tail coloration exhibited ontogenetic changes in behavior, my results were inconsistent with the predicted association between conspicuous tail coloration and increased movements.

Ontogenetic changes in tail displays

Tail displays were suggested by the IMH to serve as complementary antipredator mechanisms to conspicuous tails, aiming to minimize fitness consequences of risky hatchling behavior (Hawlena et al. 2006). Many species try to minimize fitness loss by deflecting predatory attack from head or trunk toward expendable or relatively invulnerable body parts (e.g., autotomizable appendages of amphibians and reptiles) using a combination of special marks or conspicuous colors and noticeable behavioral displays (Robbins 1981; Wourms and Wasserman 1985; Van Buskirk and Schmidt 2000; Ruxton et al. 2004). All *Acanthodactylus* species that undergo dramatic ontogenetic changes in tail coloration used at least one tail display more often when having conspicuous tails than after their tail coloration turned cryptic (Fig. 2). *A. longipes* did not undergo remarkable ontogenetic changes in tail coloration and hatchlings did not use tail displays more often than adults, emphasizing that frequent tail displays do not necessarily characterize all neonate lizards. Changes in frequency of tail displays were especially clear in *A. scutellatus* and *A. beershebensis*. Hatchlings of both species used tail displays very frequently before changing the tail coloration but as adults used tail display very rarely. Interestingly, adults of *A. boskianus* and *A. schreiberi*, which do not alter their basic dorsal pigmentation, used tail displays more often than adults of *A. scutellatus* and *A. beershebensis*. The results of the current study verified the predicted association between conspicuous tails and high frequency of tail display.

Behavior and dorsal pigmentation

Striped, finely speckled, or uniform patterns are often associated with active foraging and with flight as the dominant antipredator strategy (Brodie 1993; Creer 2005; Carretero et al. 2006). It was suggested that because these patterns lack reference points, visual predators may have difficulties in estimating a lizard's velocity, consequently improving the lizard's probability to escape predator attack (Jackson et al. 1976; Brodie 1989). The IMH is based, in part, on this association, predicting that hatchling dorsal pigmentation would change concurrently with foraging behavior, from a pattern associated with high movement to one associated with less active foraging (i.e., blotches, spots, and reticulation). As predicted by their pattern alteration, *A. scutellatus* and *A. beershebensis* hatchlings forage more actively when displaying stripes than after their pattern transformed to reticulation or blotches, respectively. *A. longipes* and *A. schreiberi* that did not alter their movement behavior during ontogeny retained their "active" patterns of finely speckled or striped, respectively. The only species for which the association between pattern and behavior was less conclusive was *A. boskianus*. Both hatchlings and adults have striped pattern but hatchlings were less mobile than adults.

Ontogenetic changes in microhabitat use

The increased movement hypothesis does not predict ontogenetic changes in microhabitat use (Hawlena et al. 2006). No differences in the microhabitat use were observed between hatchlings, juveniles, and adults of the two annual species *A. scutellatus* and *A. beershebensis* (Fig. 3). Unexpectedly, hatchlings and adults of the two perennial species *A. boskianus* and *A. schreiberi* differed in their microhabitat use. Hatchlings of both species spent significantly more time in open microhabitats than adults and *A. boskianus* adults also shuttled more often between microhabitat than hatchlings (Fig. 2). Maybe the transitions in microhabitat use of both perennial species resulted from hatchling attempts to reduce intraspecific aggression and cannibalism from adults that are active in or around bushes (R. Boochnik and D. Hawlena, unpublished data). A prey that spends a long time in an open microhabitat can experience an increased probability of being detected and attacked by an ambush predator. Being away from a refuge prolongs the time needed to reach a retreat, increasing the probability that the prey would be intercepted by a predator while fleeing (Cooper and Frederick 2007). Thus, hatchlings of *A. boskianus* and *A. schreiberi* may experience elevated predation risk by staying longer in exposed microhabitats, even without being more active than adults.

The compensatory hypothesis

Lack of association between ontogenetic changes in tail color and movement behavior in *A. boskianus* and *A. schreiberi* suggests that IMH cannot serve as a general explanation for ontogenetic tail color changes among lizards. However, alteration of the microhabitat use in these two species congruently with changes in tail coloration suggests that other behavioral changes rather than changes in movement pattern alone are making neonates more vulnerable to predation. Consequently, I expanded IMH to accommodate those changes.

The risk of predation to which a prey individual is exposed is a function of the probability of being detected and attacked by a predator coupled by the probability of surviving the attack (Lima and Dill 1990). Different morphological characteristics and behavioral expressions may affect components of predation risk in different ways. Under similar environmental conditions, the prey can use various combinations of behaviors and physical characteristics, each of which may differently impact its probability of being detected, attacked, or surviving the encounter, but which may result in similar predation risk outcomes. Increased movements or activity in exposed microhabitat may expose hatchlings to elevated predation risk. Those risky behaviors could result from specific physiological or ecological constraints that are relevant only for neonate lizards and can differ between species (e.g., cannibalism, rapid somatic growth, thermoregulation, etc.; Nagy 2000; Herczeg et al. 2007). By increasing the efficiency of antipredatory mechanisms, a prey can compensate, or at least minimize, the negative consequences of performing risky behaviors (Lind and Cresswell 2005). I suggest that to balance the severe consequences of risky behaviors, hatchlings should increase the efficiency of other antipredator mechanisms that are not advantageous under lower risk levels. Conspicuous tail colors accompanied by behavioral displays may deflect the unavoidable predator attack toward the autotomizable tail (i.e., improving probability to survive an attack), allowing the hatchling to move more or to stay away from cover without considerably increasing the overall risk of predation. After adopting safer behavior, the compensatory antipredator mechanisms (i.e., conspicuous tails and deflective displays) can become disadvantageous since they can increase the probability that the otherwise cryptic lizard will be detected and attacked.

Risky behaviors that make neonate lizards more detectable may favor fast escape as a main defense strategy. Thus, frequent association between higher movement and striped or uniform pattern could indirectly result from the increased need to flee and not exclusively as a mechanism to reduce risk while actively foraging. Following these lines, I propose that lizards that maintain their general striped pattern are subjected to higher risk of predation as adults and hence retain compensatory mechanisms that improve the probability to escape predation attempts. This hypothesis could explain why *A. boskianus* and *A. schreiberi* have stripes as adults and use more frequent tail displays than species that have camouflage pattern as adults.

The expanded hypothesis (= compensatory hypothesis) is not mutually exclusive of previous hypotheses. Other factors that make hatchlings more vulnerable to predation (e.g., cannibalism, cheaper tail autotomy, impede escape performances, etc.) may favor conspicuous tail accompanied by tail display as well. However, the “compensatory hypothesis” supplies an integrative explanation for ontogenetic changes in color, pattern, and behavior that is not based on absolute size, longevity, or environmental conditions and hence can be applicable for many species that share those ontogenetic changes but differ in fundamental life history traits and in the habitats they use.

Conclusions

Tight association between ontogenetic changes may suggest synergistic functions or compensatory roles that correspond to unique set of ecological and evolutionary conditions. The compensatory hypothesis is using the association between behavior, dorsal patterns, and tail coloration to suggest a general ecological evolutionary explanation for ontogenetic changes in neonate vertebrate tail coloration. The possibility that neonate lizards use similar set of antipredator mechanisms to compensate for different risky behaviors raises the question whether this set is conservative among lizards or evolved independently as response to different constraints. To explore this question, future studies will have to examine the synergistic or complementary functions of multiple traits and to reveal the ecological and physiological constraints on neonate behavior rather than focus solely on the adaptive value of an individual trait (e.g., tail color, dorsal pattern). Ultimately, those research efforts will produce enough data to test the compensatory hypothesis using phylogenetically informed comparative analyses. Moreover, to better understand the evolutionary ecological significance of tail color change, future research should investigate the physical characteristics of tail color and motion and explore how predators perceive the mutual changes in color, pattern, and behavior in natural environments.

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