Behav Ecol Sociobiol (2013) 67:1113–1122
DOI 10.1007/s00265-013-1536-3

ORIGINAL PAPER

Ontogenetic switch between alternative antipredatory strategies in the leopard gecko (*Eublepharis macularius*): defensive threat versus escape

Eva Landová · Jitka Jančúchová-Lásková · Veronika Musilová · Štěpánka Kadochová · Daniel Frynta

Received: 19 December 2012 / Revised: 27 March 2013 / Accepted: 28 March 2013 / Published online: 18 April 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract Ontogenetic changes in antipredator behavior optimize survival of growing animals. Leopard geckos (*Eublepharis macularius*) respond to a simulated predator either by postural and vocal threats, sometimes followed by biting, or alternatively by a rapid escape. The former "confrontational" and the latter "avoidance" behavior rarely occurs in a sequence; in fact, they represent mutually exclusive defensive strategies. We examined 552 individuals of a leopard gecko (*E. macularius*) of various ages, from hatching up to adulthood (31 months). Each experimental animal was exposed to a sequence of five "water-spraying" and ten "stick" (stick poking on base of the tail) stimuli, and the emitted behavior was recorded. We analyzed the effects of age, body size, body condition, adult–juvenile coloration, and sex on observed behavioral traits. The results showed that in the case of water-spraying stimulus, the usage of deterrent vocalization or escape tactic was affected by age and condition. In addition to that, using deterrent vocalization was influenced by the coloration of the animal. Stick stimulus evokes antipredator strategies that correspond with age and coloration (deterrent vocalization) and also with standardized body size (escape). Thus, leopard geckos exhibit clear ontogenetic change of defensive strategies, from threat–vocalization–bite strategy prevailing in juveniles to an escape strategy typical for adults. This behavioral change is accompanied by the ontogenetic switch of coloration from presumably warning contrasting light–dark banded pattern of juveniles to a cryptic spotted coloration of the adults.

Keywords Antipredation · Ontogeny · Alternative strategies · Aposematic coloration · Lizard · *Eublepharis macularius*

Introduction

Antipredatory behavior fundamentally contributes to survival, and thus, it may determine fitness in many animals. An extensive research effort has been devoted to the function of antipredatory strategies (for review, see Caro 2005; Lind and Cresswell 2005). The antipredatory skills either emerge gradually during development (Pongracz and Altbacker 2000; Blumstein and Munos 2005; Hollén and Manser 2006) or its efficiency may change substantially in different ages (Fuiman and Magurran 1994; Magrath et al. 2006). Developmental change in the use of alarm calls in specific contexts and the responses to calls produced by others was reported in various taxa, e.g., ground squirrels and marmots (Hanson and Coss 2001; Blumstein and Munos 2005), meerkats (Hollén and Manser 2006; Hollén et al. 2008), and several species of primates and birds (reviewed in Hollén and Randford 2009).

A developmental shift in the preferred antipredatory response, e.g., between confrontation and avoidance, was also reported in some animals. A young skunk (*Mephitis mephitis*) preferred confrontational defensive behavior like a tail-up enhancing the black-and-white warning coloration pattern that was accompanied by chemical defense later during the development. A switch of the prevailing strategies took place during the maturity, when more animals chose to perform

---

Communicated by S. J. Downes

Electronic supplementary material The online version of this article (doi:10.1007/s00265-013-1536-3) contains supplementary material, which is available to authorized users.

E. Landová · J. Jančúchová-Lásková · V. Musilová ·
Š. Kadochová · D. Frynta (✉)
Department of Zoology, Faculty of Science,
Charles University in Prague, Viničná 7,
128 44 Prague, Czech Republic
e-mail: frynta@centrum.cz

the avoidance behavior (Medill et al. 2011). On the other hand, the avoidance behavior in juveniles of many species of fishes reduced the probability of encountering a predator or being attacked by it, and this avoidance strategy was also preferentially used. Older fishes could detect the predator and react to it more effectively, e.g., by joining conspecifics in common defense (Fuiman and Magurran 1994). Moreover, the perceived predator pressure influenced the behavior, growth, and sexual maturation in many species of fishes and frogs; such a phenomenon is called a predator-induced phenotypic plasticity (Bernard 2004). In nine-spined stickleback (*Pungitius pungitius*), the predation-adapted (during ontogeny) marine population showed stronger reactions to predatory cues than competition-adapted pond sticklebacks (Välimäki and Herczeg 2012).

The post-hatching growth and ontogeny of the animals affect almost all morphological, physiological, and behavioral traits. Consequently, selective pressures operating on juveniles and adults may differ considerably. In reptiles, the course of the post hatching ontogeny is associated with changes in vulnerability (Hawlena et al. 2006; Hawlena 2009) related to habitat use (Paulissen 1988a, b; Law 1991; Lind and Welsh 1994; Keren-Rotem et al. 2006) and foraging strategies (Wilson et al. 2007; Eskew et al. 2009). This may trigger acquisition of adaptive ontogenetic changes in affected traits such as age-related change in coloration (see Booth 1990 for review), body size, and shape (Garland 1985; Frynta et al. 2010). Moreover, even subtle changes in behavior may affect the relationship between an animal and its potential predator substantially (Blomberg and Shine 2000; Lind and Cresswell 2005).

In recent years, a considerable research effort was devoted to behavioral mechanisms enabling reptiles to avoid predators such as vigilance (reviewed by Treves 2000), chemical detection (for lizards, see reviews by Cooper 1994; Amo et al. 2004; or see Bealor and Krekorian 2006), and optimality of fleeing distance (reviewed by Cooper 2009 for lizards). The final stage of a predator–prey confrontation was studied by examining real or simulating predator attacks in nature (Castilla et al. 1999; Janzen et al. 2000; Cooper 2008) and laboratory (Shine et al. 2000; Downes 2002; Martín and López 2003; López et al. 2005). A specific mechanism involved in this stage of predator–prey interaction is tail autotomy (see review by Maginnis 2006; Bateman and Fleming 2009).

The particular factors affecting antipredatory response may differ considerably between juveniles and adults (Creer 2005; Hawlena 2009). These include intrinsic factors such as experience with the predator (Marcelini and Jenssen 1991), a running performance (Irchick 2000; Nelson et al. 2006), possession of cryptic (Wilson et al. 2007; Hawlena 2009) or signaling contrast coloration (Clark and Hall 1970; Huey and Pianka 1977; Hawlena et al. 2006) or the ability of an active defense (Hertzog and Burghardt 1986), etc. Due to extrinsic factors such as social context, habitat, predator type, and density (Roth and Johnson 2004), a predator preference for smaller prey can be included as well (Blomberg and Shine 2000; Janzen et al. 2000).

A different antipredator strategy used by adults and juveniles in connection with color change has been frequently demonstrated in reptiles. In snakes, *Coluber constrictor*, the juveniles bearing disruptive color patterns are cryptic and aggressive when uncovered, whereas the adult snakes possessing striped or plane color patterns choose the escape as an antipredator strategy (Creer 2005). Newly hatched lizards *Acantodactylus beershebensis* with striped pattern and blue tails forage more actively in open space than 3-week-old juveniles, and thus, they are more vulnerable to predators. Conspicuous color and deflection displays attract a predator's attention to the tail (distinctively colored only in juveniles) which can be autotomized, thus enabling the hatchlings to survive the predator attack (Congdon et al. 1974; Cooper and Vitt 1985; Hawlena et al. 2006).

The leopard gecko (*Eublepharis macularius*) belonging to the family of Eye-lid geckos (Eublepharidae) is a long-lived animal coming from the desert and semidesert areas of Pakistan, Afghanistan, Iran, and NW India (Seufer et al. 2005), and it can be routinely bred in captivity. Its popularity currently increases as a lizard model in laboratory experiments. It seems to be a promising model species for studying ontogenetic change in coloration which can theoretically be accompanied by a switch in the antipredatory behavior. Generally, there are three types of coloration: the juveniles possess contrasting yellowish dark pattern with distinctive stripes (see Fig. 1a), subadults possess similar pattern with more disruptive stripes (see Fig. 1b), and adults possess similar color except the pattern is blotchy like in a leopard (see Fig. 1c). Hatchlings in our dataset (unpublished results) possessed the juvenile coloration for up to 70–90 days of life (three of relatively smaller individuals possessed juvenile coloration for up to 124, 173, 210 days). The subadult color pattern coincides with visible sexual organs (hemipenises) in males aged between 90 and 450 days. Fully adult coloration emerges individually between 150 and 954 days of age, and it is not tightly connected with weight or age. Reproductive maturity is attained between 280 and 350 days of age, and it depends on the incubation temperature, season, and individual variation (Tousignant et al. 1995; Sakata and Crews 2004).

In this paper, we used simple procedures simulating predatory attack to examine whether the leopard gecko exhibits ontogenetic changes in defensive behavior, and if so, we asked whether these changes are associated with the actual: (1) age, (2) body size, (3) body condition, and (4) change in coloration from the contrasting striped juvenile to the disruptive and more cryptic adult pattern.

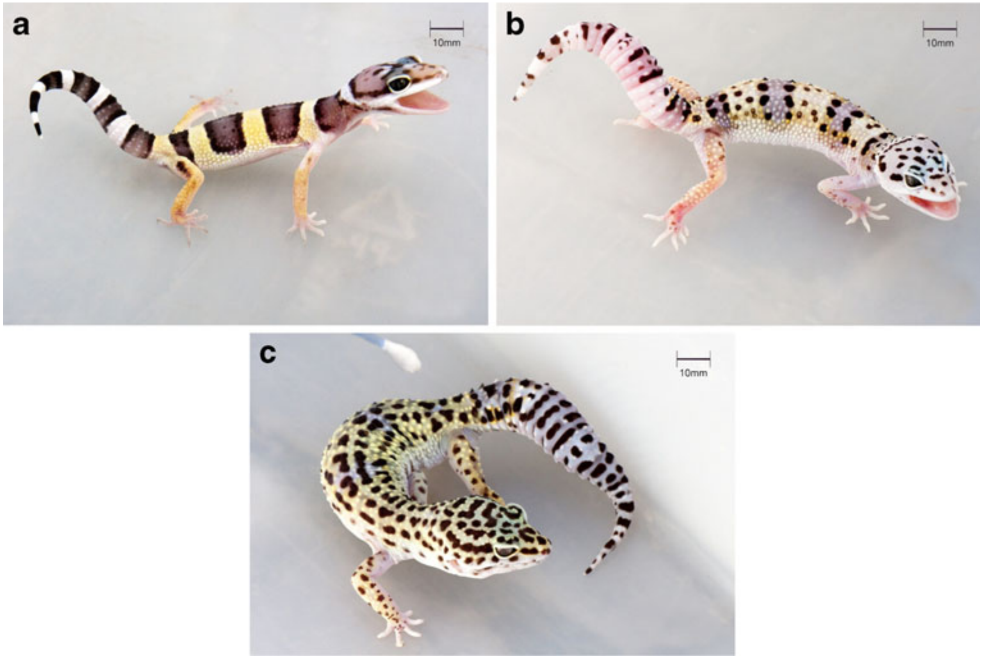

Fig. 1 **a** High defensive posture (the gecko is standing on tight legs with ventrum raised, sometimes with an arched back) and deterrent vocalization in juvenile gecko. The posture is usually accompanied by tail waving. Juvenile coloration persists up to 70–90 days of life. **b** Low defensive posture (the gecko remains motionless with its ventrum pressed against the floor of arena) and deterrent vocalization in subadult gecko. This posture is sometimes accompanied by tail waving. Subadult color pattern coincides with visible sexual organs (hemipenises) in males (of the age of 90–450 days). **c** Escape. The gecko reverses rapidly and moves quickly from the stimulus. This serves as a defensive strategy in adult geckos. Full adult coloration emerges individually between 150 and 954 days of age, not tightly connected with weight or age

Materials and methods

Animals and morphological variables

We studied 552 leopard geckos (*E. macularius*, Eublepharidae) hatched during the breeding seasons 2007–2010. The studied species has temperature-dependent sex determination (Viets et al. 1993), and the incubation temperature may also affect behavioral traits of these animals (cf. Flores et al. 1994; Sakata and Crews 2004). In order to avoid possible incubation effects and to bias the sex of experimental animals in favor of non-territorial females, we set the incubation temperature to 28, 5 °C±0.5, ±, which is close to the temperature (approximately 29 °C) preferred by the females of *E. macularius* for eggs laying (Bull et al. 1988; Bragg et al. 2000). At the time of testing, the experimental animals were of various ages from the period of hatching to adulthood. For the purpose of data presentation, we defined the following nine age categories: up to 60, 120, 180, 240, 300, 360, 420, 530, and 950 days; each was represented by 63, 61, 62, 74, 68, 48, 49, 64, and 63 individuals, respectively.

The ambient temperature of the breeding room was about 28 °C with permanent presence of basking cables under each terrarium to maintain a temperature gradient. The juveniles were housed singly in plastic boxes 20×20×15 cm, and adults were housed in glass terrariums 30×30×20 cm. Food and water was provided ad libitum. Hatchlings were fed with crickets; since 3 months of their age, the diet was supplemented by mealworms (cf. Gauthier and Lesbarrères 2010). The insects were dusted with vitamins and minerals (Nutri Mix); AD_3 and E vitamins were provided weekly. After testing the defensive response, the experimental animals were weighed and measured (snout-vent length, SVL; tail width, TW) to assess the actual body size and condition.

E. macularius is a capital breeder depositing energetic reserves in the form of fat tissue on the basal part of the tail (Gauthier and Lesbarrères 2010; see also Dial and Fitzpatrick 1981 in another eublepharid *Coleonyx brevis*). The tail can be autotomized, but only in life-threatening situations such as a predator attack (Bateman and Fleming 2009; Cooper and Frederick 2010; Higham and Russell 2010). The relative width of the basal part of the tail reflects the actual energetic reserves in these geckos more properly than the indices of body condition. In order to avoid problems with scaling, we expressed relative tail width as a residual from the allometric relationship between the TW and the SVL that is described by equation $\ln(TW)=1.588\times\ln(SVL)-4.704$.

We recognized three distinct categories of coloration: juvenile, subadult, and adult (see “Introduction” and Fig. 1a–c). Coding of the coloration was performed blindly by three different researchers (with inter-observer reliability exceeding 95 %), and the majority rule was adopted in the cases of disagreement.

Methods of testing

We conducted behavioral trials in a temperature-controlled breeding room (28 °C) illuminated by a single blue 25-W light bulb. We used milk polycarbonate boxes as test arenas of the size 15.5×15.5×11 cm (length, width, and height) for juveniles up to 4 months of age and 24.5×19.5×16 cm high for the older animals including the adults. The test arena was large enough to permit the leopard gecko of appropriate age to reverse and run away of the place where it was exposed to the stimuli that simulated predator attack. We gently placed the geckos into the arena using a piece of a cardboard, and the box was then slowly covered for several (usually three) seconds. All animals were calm and did not react defensively at the beginning of the trials.

Because the defensive behavior may differ between amorphous and acute threats (cf. Curio 1993), we exposed each tested animal successively to the water-spraying and stick stimuli. The former stimulus is indirect and difficult to localize while the latter stimulus simulates an immediate attack of the predator with direct contact. In rodents, it is known that these two types of contextually dependent threats influence a risk assessment as well as the preferred defensive strategy flight vs. defensive threat/attack or freezing (Eilam 2005).

To evoke a defensive reaction to the amorphous stimulus which is difficult to locate, we water-sprayed the animal on its side five times in the first 10 s of the trial with an interval 1 s between consecutive stimuli. The hand of the experimenter was on the edge of the testing arena. Previously, we observed that water-spraying released defensive behavior of moderate intensity accompanied with attempts to localize the source of the disturbing stimulus in several species of reptiles, e.g., a Cuban boa (*Epicrates angulifer*), mangrove-dwelling monitor lizard (*Varanus indicus*), and geckos of the genera *Teratoscincus* and *Eublepharis* (unpublished results).

Under natural situation, the prey is usually warned by the presence of various non-specific stimuli elevating alertness (Curio 1993, p. 143). Thus, the stick touching was introduced after water spraying to ensure the alertness of the tested animal. The whole sequence of stimulation consisted of water spraying (5×), followed by 3 s of an inter-trial interval which preceded the final stick stimulation part in which we touched the back of the gecko by a plastic stick with a cotton tip in the sacral part ten times. The whole trial lasted 30 s, enabling the animals to express a range of defensive (antipredator-like) behavior. The trials were all videotaped and the presence or absence of the recorded behavior was scored.

Defensive behavior

We recorded the following nine elements of defensive behavior. All of them were also previously observed in experiments examining the responses of *E. macularius* to the presence of live snakes or snake odors (Landová et al., unpublished data): (1) tail wave: the leopard gecko raises its tail above the horizontal (Fig. 1a, b) and holds it stationary or slowly moves it from side to side; (2) tail vibration: the tail is wiggled from side to side, but it is not raised above the horizontal plane; (3) high posture: the gecko is standing on tight legs with the ventrum raised, sometimes with an arched back (Fig. 1b), and this posture is usually accompanied by tail waving; (4) freezing: the gecko remains motionless with its ventrum pressed against the arena floor. When an animal stands in the defensive (5) high posture, they may either (6) vocalize (vocalization with open mouth, Fig. 1a) or escape; the terminal reaction was usually either attack the stick; or (7) escape, when the gecko reverses rapidly and moves quickly from the stimulus (Fig. 1c) or (8) the animal suddenly runs and attempts to escape from the test arena; (9) trying to climb the wall of the tested arena.

We pooled these elements into three distinct categories: defensive posture (elements 1–5), vocalization (element 6), and escape (elements 7–9). In our experiments, these broader categories of behavior occurred in sufficient frequencies, and their presences/absences in each trial were given as dependent variables in further analyses.

Statistical analysis

In order to perform formal tests of the above-described ontogenetic patterns, we performed GLMs, in which the presence of a particular category of responses (defensive posture, vocalization, and escape) was given as a dependent variable with binomial distribution and logit link function; log-transformed age, residual SVL (i.e., relative body size at given age), and residual tail width (indication of condition) were introduced as continuous explanatory variables. The coloration was used as a categorical explanatory variable. Initial full models were reduced according to the Akaike information criterion (command step). The calculations were performed in the R package (R Developmental Core Team 2010). Graphs and alternative models were computed in STATISTICA 6.0 (StatSoft, Inc. 2001).

Results

The leopard geckos readily responded to the experimental stimuli. The incidence of defensive posture, vocalization, and escape was affected by the strength of the experimental stimuli (water spray versus stick); however, it followed a clear ontogenetic pattern (Fig. 1a–c).

The strong stimuli caused an apparent defensive response (i.e., vocalization, posture, and/or escape) in 87 % of experimental animals; the values computed for the first three age classes (up to the age of 5 months) were markedly lower (62–73 %) than those computed for higher age categories (89–100 %). In contrast, the water-spraying stimuli induced the response in only 49 % of the animals; the highest mean values (65 and 70 %) belonged to the highest age category.

The ontogenetic patterns are even more apparent when individual categories of defensive behavior are treated separately. The incidence of escape after exposure to the stick stimuli increased sharply, but continuously from zero (in animals up to the age of 1 month) up to the peak value of 87 % (in the age class of 8–9 months) followed by a slow decline to 61 % in the animals of the class of 27–32 months. In contrast, only 5 % of tested animals escaped after the exposure to the water-spraying stimulus (Fig. 2).

The ontogenetic patterns of vocalization are inversed to those of escape. Vocalization in the response to the water-spraying stimulus is relatively frequent in juveniles, but it is almost absent in the animals over the age of 5 months. Although the stick stimulus also evokes vocalization in animals of higher age classes, the representation of this behavior still apparently decreases with the age of the tested animals (Fig. 3). The incidence of the defensive posture exhibits less consistent age variation than that found in the case of escape or vocalization.

The predictors included in GLMs were the age, parameters reflecting growth (SVL residual) and fat reserves (tail-width residual), as well as the presence of juvenile and adult coloration patterns. The results confirmed that in response to both mild and stick stimuli, the fleeing behavior sharply increases and vocalization decreases with the age of the tested animal (GLMs; the command ANOVA in R package; all P's<0.001); the incidence of posture response remained independent on age (Table 1). In response to the water-spraying stimuli, the tail-width residuals also contributed positively to escape ($P=0.026$) and negatively to vocalization ($P=0.001$). The effects of SVL residuals were significant only in the case of models concerning the responses to the stick stimuli. These residuals were positively associated with the escape response ($P<0.001$) and posturing ($P=0.030$). Moreover, coloration affected vocalization ($P<0.001$; JUV>SAD>AD) and posture response ($P<0.001$, SAD<AD, JUV) to the water-spraying stimuli. It also affected the escape response ($P<0.001$, JUV<SAD, AD) and vocalization ($P=0.010$, AD<SAD, JUV) in the response to stick stimuli.

Discussion

According to Niko Tinbergen (1963), the ontogeny itself represents one of four distinct, equally relevant and mutually independent categories of causes and explanations of behavior. Although ontogeny has been defined and treated as a fourth pillar of Tinbergen's causes five decades ago, it has remained in the shadow of the remaining ones, i.e., causation (proximate causes), survival value (ultimate causes), and evolution (macroevolutionary patterns). Recently, the ontogenetic causes of complex behavior have received more attention (Hogan and Bolhuis 2009), and *E. macularius* has been repeatedly used as a model species enabling to manipulate the developmental process by alteration of incubation temperature and hormonal profiles (Crews and Groothuis 2009 and references herein).

An ontogeny of the leopard geckos is associated with mutually correlated changes of multiple morphological and physiological traits. We attempted to explain the main ontogenetic changes in antipredator strategies by age, body size, body condition, and coloration pattern. The age (time since hatching) is a reliable proxy of the developmental

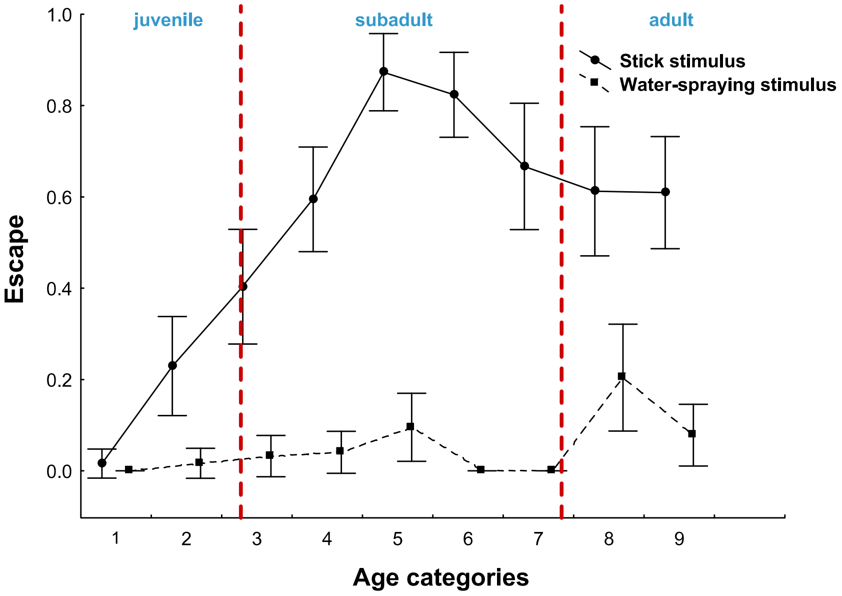

Fig. 2 Frequency of escape behavior in response to water-spraying (*dashed line*) and stick (*continuous line*) stimuli within particular age category: *1* up to 60 days (N=63), *2* up to 120 days (N=61), *3* up to 180 days (N=62), *4* up to 240 days (N=74), *5* up to 300 days (N=68), *6* up to 360 (N=48), *7* up to 420 days (N=49), *8* up to 530 days (N=64), *9* up to 950 days (N=63). Weighted means+ 95 % confidence intervals predicted from GLM model

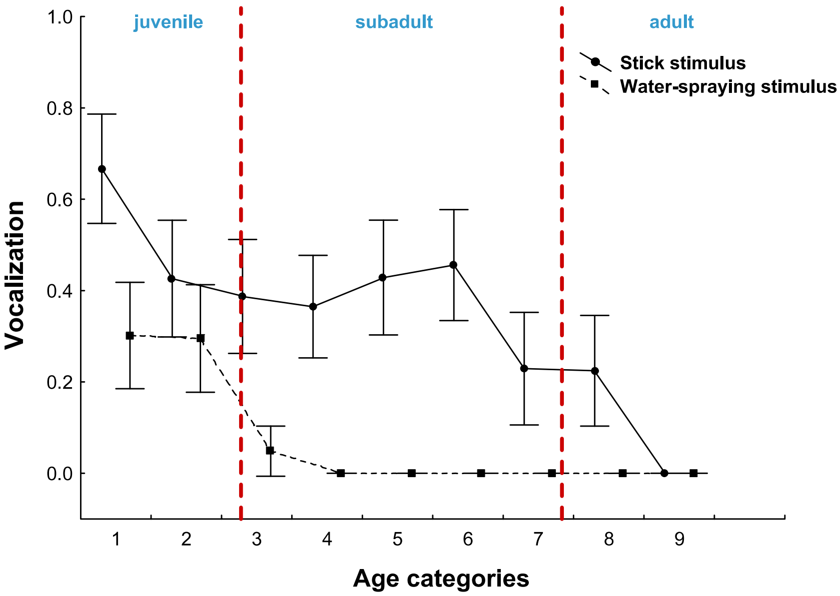

Fig. 3 Frequency of deterrent vocalization behavior in particular age category. Weighted means; 95 % confidence intervals predicted from GLM model. For age categories tested, see Fig 2

stage. The morphological traits are also relevant for its estimation. The residual body size reflects the acceleration or arrest of the somatic growth, and the body condition may reflect the actual prospect of further somatic growth; the coloration pattern (coded as juvenile, subadult, and adult) is a visible manifestation of subjective ontogenetic stage.

We found that the defensive responses of *E. macularius* recorded in our experiment follow a clear ontogenetic pattern. Deterrent vocalization representing a typical defensive response of the young animals gradually disappears with an increasing age. In contrast, an escape response nearly absent in juveniles becomes increasingly important in adulthood. Age was invariably the best predictor of these behavioral traits. Nevertheless, both threat vocalization and escape were usually preceded and/or accompanied by defensive posture that was not clearly dependent on age of the tested animal.

The function of vocalization is obviously to confuse and deter the predator on site, while the function of the escape response is a fast withdrawal out of the range of the predator. In our experiment simulating direct attack of a predator and recording an immediate response of the lizard, the escape was an alternative tactic to deterrent vocalization.

Functional interpretation of the observed ontogenetic shift in the preferred defensive tactic requires uncovering of an age-specific mechanisms favoring one tactic over another. The efficiency of escape is obviously determined by running speed and other parameters of locomotory performance of the attacked animal. Because most morphological and physiological variables are tight to the body size by allometric, rather than isometric relationships, somatic growth is unavoidably associated with a change of the derived traits (ratios) that may affect performance considerably. For example, small juvenile snakes possess a reduced endurance capacity compared to adults because of a lower blood oxygen-carrying capacity and lower stamina (Pough 1977, 1978). Moreover, the increased body size enables absolutely faster running performance in some reptiles, e.g., the sprint speed of a lizard [*Stellio* (*Agama*) *stellio* (Huey and Hertz 1982)] or a tuatara (*Sphenodon punctatus*). Tuataras were affected by size at given age: The older and thus absolutely longer juveniles ran faster than the smallest juveniles (Nelson et al. 2006). This positive relationship between body size and running speed of the lizard may provide reliable explanation for the observed preference of the escape strategy by the adults of *E. macularius*. In leopard gecko, the walking speed of adults is about 0.18–0.24 m s^{-1} (McElroy et al. 2008; Fuller et al. 2011), the running speed is 0.29 m s^{-1} (McElroy et al. 2008), and the somatic growth results in a substantial (two-fold) increase of the body size: SVL increases from 53.9 mm in hatchlings up to an asymptotic SVL of about 113.7 mm (these means were computed from the current dataset).

The putative role of body size itself on the preferred defensive tactic was supported by the fact that body size was a successful predictor of escape behavior elicited by stick stimuli. The animals bigger than their conspecifics of the same age showed a tendency to choose the escape strategy more frequently.

Vocalization can be viewed as a distress reaction performed by the animals when they have low prospects to flee from the predator because they are too small (juveniles) or are in a bad physical condition. In a response to water-spraying stimuli, the occurrence of deterrent vocalization was associated with poor condition (relative width of the tail base). Similar change of defensive strategy dependent on the actual state of the animal was reported by Hertz et al. (1982) for two agamid lizards *Agama savignyi* and *Agama pallida*. At high body temperature (analogically to leopard geckos in good

Table 1 The parameters of the full and reduced generalized linear models (GLMs; function glm, binomial distribution, logit link function) examining the effects of age (in days; log transformed), body size (log transformed snout-vent length in millimeters), condition (residuals of the allometric relationship between tail width and snout-vent length), color pattern (juvenile, subadult, and adult) on dependent variables reflecting the presence/absence of particular defensive responses

Stimulus	Response	Full model	*df*	Deviance	Resid.Df	Resid.Dev	*P*(>|chi|)	Estimate
Spray	Vocalization	Null			551	287.00		
		ln age	1	60.87	550	226.14	<0.000	−0.346
		Tail width resid	1	11.63	549	214.50	0.001	−1.830
		Pattern	2	18.38	547	196.13	<0.000	
		Pattern (subadult)						17.019
		Pattern (juvenile)						18.582
		(Intercept)						−18.449
	Posture	Null			551	761.40		
		Tail width resid	1	1.39	550	760.01	0.240	0.803
		Pattern	2	15.45	548	744.55	<0.000	
		Pattern (subadult)						−0.684
		Pattern (juvenile)						0.014
		(Intercept)						0.117
	Escape	Null			551	215.61		−8.269
		ln age	1	11.50	550	204.12	0.001	0.929
		Pattern	1	4.93	549	199.19	0.026	3.405
Stick	Vocalization	Null			551	721.70		
		ln age	1	46.38	550	675.32	<0.000	−0.265
		Pattern	2	8.91	548	666.40	0.010	
		Pattern (subadult)						0.714
		Pattern (juvenile)						0.978
		(Intercept)						0.267
	Posture	Null			551	755.82		
		SVL resid	1	4.93	550	750.89	0.030	2.140
		Pattern	2	4.48	548	746.41	0.110	
		Pattern (subadult)						−0.078
		Pattern (juvenile)						0.432
		(Intercept)						0.230
	Escape	Null			551	762.33		
		ln age	1	122.52	550	639.82	<0.000	0.766
		SVL resid	1	8.67	549	631.15	0.003	3.238
		Pattern	2	17.01	547	614.14	<0.000	
		Pattern (subadult)						0.312
		Pattern (juvenile)						−1.358
		(Intercept)						−3.901

In the left part of the table, results of chi-square tests of ANOVA tables (GLMs, the command ANOVA in R package), while in the right part, the coefficients of the models and their significance are provided

condition), the lizards flee rapidly from predators. At lower body temperature (analogically to our geckos in poor condition), which reduces the sprint speed, the agamid lizards rarely run and behave aggressively trying to attack the predator (Hertz et al. 1982).

The effect of coloration involving the preferred reaction of adult, subadult, and juvenile animals needs to be discussed separately. The adult leopard geckos possess coloration that might also be considered as cryptic (Marcelini 1977; see Fig. 1c). The coloration of adults probably includes colors similar to those found in a desert/sub-desert environment, which is an important characteristic of cryptic coloration (for crypsis, see Ruxton et al. 2004). The color–pattern variation is also highly variable within species (Seufer et al. 2005), and thus, the adults may match the background of different areas. However, the preferred defensive strategy of the adult geckos is escape. Using of escape tactic when a predator attacks the prey has been observed also in cryptic horned lizards *Phrynosoma cornutum* (Sherbrooke 2008).

Such behavior increases the probability of being detected (Cooper and Sherbrooke 2010, 2011), but during the situation simulated by our experiments, the tested animals have already been detected by the predator. Another role of the mottled coloration of the adults might be the formation of disruptive coloration pattern (Thayer 1909; Cott 1940), breaking the animal's periphery outline and causing it to be less detectable by a predator. Similarly, an effect when repetitive pattern on moving animal brakes down animal's periphery outline was demonstrated, e.g., on snakes (Pough 1976). The disruptive effect of the pattern is even thought to provide a general advantage over simple crypsis (Cuthill et al. 2005). However, the frequently used escape strategy of an adult leopard gecko is surprising because the phylogenetic reconstructions of locomotion mode in lizards suggest that these species have evolved low-speed locomotion (McElroy et al. 2008) in addition to cryptic/disruptive coloration and nocturnal activity.

Several hypotheses have been proposed for the function of the conspicuous juvenile coloration in lizards. The first two hypotheses concern the blue tails of juvenile lizards (Cooper and Vitt 1985; Hawlena 2009). One of them states that the conspicuous coloration together with defensive posture (tail waving) deflects predator attacks from a body to tail, which can be easily autotomized. This hypothesis was demonstrated to be effective in the case of *Eumeces fasciatus* and *Eumeces laticeps*. Another hypothesis considers the blue tail coloration to play role in the conspecific communication as a signal stimulus inhibiting an attack by conspecific adult males or females (Cooper and Vitt 1985). The juveniles of the leopard geckos use similar tail waving in response to simulated predatory attacks as the above-mentioned lizards, but they are conspicuously striped as a whole, including both body and tail (Marcelini 1977; see Fig. 1a). However, during the development of an adult coloration in the subadult state, the bodily coloration pattern scatters into the adult-like mottled pattern, while the tail stripes remain contrasting and conspicuous and change the last; thus, the subadult *E. macularius* may present a similar case as the blue-tailed lizards. Another famous example of complex adaptation can be found in juvenile lizards *Eremias lugubris* that in coloration and movement mimic noxious beetles (Huey and Pianka 1977). The yellowish-dark striped color pattern of juvenile *E. macularius* may theoretically mimic some species (e.g., *Bungarus caeruleu*, Elapidae) of warningly colored and poisonous snakes living in sympatry (Pakistan, India). The color pattern mimicking a warning coloration may enhance the synergic deterrent effect of vocalization accompanied by the defensive posture of juveniles *E. macularius*.

In this study, we examined exclusively the internal factors (features of the animal); however, selective pressures determining the survival of the lizard under natural conditions are also influenced by external factors like features of the predators and the degree of an exposure to them in a given habitat. Thus, the external factors should also be considered. Juvenile and adult lizards face different kind of predation pressure because the smaller the prey animal, the larger is the spectrum of its predators, as small animals present a suitable prey for an assemblage of both large- and small-sized predators, e.g., juvenile *Eulamprus heatwolei* avoided odors not only of vertebrate (snake) predators but also of the invertebrate ones (Head et al. 2002). Typically, the predation pressure of juvenile lizards is extreme, e.g., in lacertid lizards *Psammodromus algirus*, only 8 % of males and 14 % of females survive from hatching to maturity (Civantos and Forsman 2000). This brings about a strong selection force optimizing an antipredatory response set to the juvenile stage. The juvenile antipredatory strategy does not necessarily have to be effective in the adult stage. Thus, especially long living animals, such as the *E. macularius* (with maximum life span in captivity exceeding 25 years; Frynta, unpublished data), may profit from adopting an age-specific antipredatory strategy set to the adulthood. The evolution of age-specific antipredatory strategies may be further enhanced by the fact that the same behavioral response performed by juveniles and adults in the same situation may be differently efficient even against the same or similar predator.

Acknowledgments The research was supported by the Grant Agency of the Academy of Sciences of the Czech Republic project no. IAA 601410803.

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All performed experiments were allowed by Ethical Committee of the Charles University in Prague, Czech Republic and approved by Ethical Committee of Ministry of Education, Youth and Sports, license no. 27667/2007-30.

References

Amo L, López P, Martín J (2004) Wall lizards combine chemical and visual cues of ambush snake predators to avoid overestimating risk inside refugees. Anim Behav 67:647–653

Bateman PW, Fleming PA (2009) To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. J Zool 277:1–14

Bealor MT, Krekorian CO'N (2006) Chemosensory response of desert iguanas (*Dipsosaurus dorsalis*) to skin lipids from a lizard-eating snake (*Lampropeltis getula californiae*). Ethology 112:503–509

Bernard MF (2004) Predator-induced phenotypic plasticity in organisms with complex life. Ann Rev Ecol Evol Syst 35:651–673

Blomberg SP, Shine R (2000) Size-based predation by kookaburras (*Dacelo novaeguineae*) on lizards (*Euamprus tympanum*: Scincidae): what determines prey vulnerability. Behav Ecol Sociobiol 48:484–489

Blumstein DT, Munos O (2005) Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. Anim Behav 69:353–361

Booth CL (1990) Evolutionary significance of ontogenetic colour change in animals. Biol J Linn Soc 40:125–163

Bragg WK, Fawcett JD, Bragg TB, Viets BE (2000) Nest-site selection in two eublepharid gecko species with temperature-dependent sex determination and one with genotypic sex determination. Biol J Linn Soc 69:319–332

Bull JJ, Gutzke WHN, Bulmer MG (1988) Nest choice in a captive lizard with temperature dependent sex determination. J Evol Biol 2:177–184

Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago

Castilla AM, Gosá A, Galán P, Pérez-Mellado V (1999) Green tails in lizards of the genus *Podarcis*: do they influence the intensity of predation? Herpetologica 55:530–537

Civantos E, Forsman A (2000) Determinants of survival in juvenile *Psammodromus algirus* lizards. Oecologia 124:64–72

Clark DR, Hall RJ (1970) Function of blue tail-coloration of the five-linked skink (*Eumeces fasciatus*). Herpetologica 26:271–274

Congdon JD, Vitt LJ, King WW (1974) Geckos: adaptive significance and energetics of tail autotomy. Science 184:1379–1380

Cooper WE (1994) Chemical discrimination by tongue flicking in lizards: a review with hypotheses on its origin and phylogenetic relationship. J Chem Ecol 20:439–487

Cooper WE (2008) Visual monitoring of predators: occurrence, cost and benefit for escape. Anim Behav 76:1365–1372

Cooper WE (2009) Fleeing and hiding under simultaneous risks and costs. Behav Ecol 20:665–671

Cooper WE, Frederick WG (2010) Predator lethality, optimal escape behaviour, and autotomy. Behav Ecol 21:91–96

Cooper WE, Sherbrooke WC (2010) Plesiomorphic escape decisions in cryptic horned lizards *Phrynosoma* having highly derived antipredatory defenses. Ethology 116:920–928

Cooper WE, Sherbrooke WC (2011) Crypsis influences escape decisions in the round-tailed horned lizard *Phrynosoma modestusm*. Can J Zool 88:1003–1010

Cooper WE, Vitt LJ (1985) Blue tails and autotomy: enhancement of predation avoidance in juvenile skink. Z Tierpsychol 70:265–276

Cott HB (1940) Adaptive coloration in animals. Methuen, London

Creer DA (2005) Correlations between ontogenetic change in color pattern and antipredator behaviour in the racer, *Coluber contrictor*. Ethology 111:287–300

Crews D, Groothuis T (2009) Tinergen's four questions, ontogeny: sexual and individual differentiation. In: Bolhuis JJ, Verhulst S (eds) Tinbergen's legacy: function and mechanism in behavioral biology. Cambridge University Press, UK, pp 54–81

Curio E (1993) Proximate and developmental aspects of antipredator behaviour. Adv Study Behav 22:135–238

Cuthill I, Stevens M, Sheppard J, Maddock T, Párraga CA, Troscianko TS (2005) Disruptive coloration and background pattern matching. Nature 434:73–74

Dial BE, Fitzpatrick LC (1981) The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). Oecologia 51:310–317

Downes JS (2002) Does responsiveness to predator scents affect lizard survivorship? Behav Ecol Sociobiol 52:38–42

Eilam D (2005) Die hard: a blend of freezing and fleeing as a dynamic defence—implications for the control of defensive behaviour. Neurosci Biobehav Rev 29:1181–1191

Eskew EA, Willson JD, Winne CT (2009) Ambush site selection and ontogenetic shifts in foraging strategy in a semi-aquatic pit viper, the eastern cottonmouth. J Zool 277:179–186

Flores D, Tousignant A, Crews D (1994) Incubation temperature affects the behavior of adult leopard geckos (*Eublepharis macularius*). Physiol Behav 55:1067–1072

Frynta D, Frýdlová P, Hnízdo J, Šimková O, Cikánová V, Velenský P (2010) Ontogeny of sexual size dimorphism in monitor lizards: males grow for a longer period, but not at a faster rate. Zool Sci 27:917–923

Fuiman LA, Magurran AE (1994) Development of predator defences in fishes. Rev Fish Biol Fish 4:145–183

Fuller OP, Higham TE, Clark AJ (2011) Posture, speed, and habitat structure: three-dimensional hindlimb kinematics of two species of padless geckos. Zoology 114:104–112

Garland T (1985) Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchlis*. J Zool 207:425–439

Gauthier C, Lesbarrères D (2010) Growth rate variation in captive species: the case of leopard geckos, *Eublepharis macularius*. Herpetol Conserv Biol 5:449–455

Hanson MT, Coss RG (2001) Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to conspecific alarm calls. Ethology 107:259–275

Hawlena D (2009) Colorful tails fade when lizards adopt less risky behaviors. Behav Ecol Sociobiol 64:205–213

Hawlena D, Boochnik R, Abramsky Z, Bouskila A (2006) Blue tail and striped body: why do lizards change their infant costume when growing up. Behav Ecol 17:889–896

Head ML, Keogh JS, Doughty P (2002) Experimental evidence of an age-specific shift in chemical detection of predators in a lizard. J Chem Ecol 28:541–554

Hertz PE, Huey RB, Nevo E (1982) Fight versus flight: body temperature influences defensive responses of lizards. Anim Behav 30:676–679

Hertzog HA Jr, Burghardt GM (1986) Development of antipredator responses in snakes: I. Defensive and open-field behaviors in newborns and adults of three species of garter snakes (*Thamnophis melanogaster*, *T. sirtalis*, *T. butleri*). J Comp Psychol 100:372–379

Higham TE, Russell AP (2010) Flip, flop and fly: modulated motor control and highly variable movement patterns of autotomized gecko tails. Biol Lett 6:70–73

Hogan JA, Bolhuis JJ (2009) Tinergen's four questions and contemporary behavioural biology. In: Bolhuis JJ, Verhulst S (eds) Tinbergen's legacy: function and mechanism in behavioral biology. Cambridge University Press, UK, pp 25–35

Hollén LI, Clutton-Brock T, Manser MB (2008) Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suricatta*): adaptations or constraints?. Behav Ecol Sociobiol 62:821–829

Hollén LI, Manser MB (2006) Ontogeny of alarm call responses in meerkats (*Suricata suricata*): the roles of age, sex, and nearby conspecifics. Anim Behav 72:1345–1353

Hollén LI, Randford AN (2009) The development of alarm call behaviour in mammals and birds. Anim Behav 78:791–800

Huey RB, Hertz PE (1982) Effects of body size and slope on sprint speed of a lizard (*Stellio* (*Agama*) *stellio*). J Exp Biol 97:401–409

Huey RB, Pianka ER (1977) Natural selection for juvenile lizards mimicking noxious beetles. Science 195:201–203

Irchick DJ (2000) Effects of behaviour and ontogeny on locomotor performance of a West Indian lizard, *Anolis lineatopus*. Funct Ecol 14:438–444

Janzen FJ, Tucker JK, Paukstis GL (2000) Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. J Evol Biol 13:947–954

Keren-Rotem T, Bouskila A, Geffen E (2006) Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). Behav Ecol Sociobiol 59:723–731

Law BS (1991) Ontogenetic habitat shift in the eastern Australian water skink (*Eulamprus quoyii*)? Copeia 1991:1117–1120

Lind J, Cresswell W (2005) Determining the fitness consequences of antipredation behavior. Behav Ecol 16:945–956

Lind AJ, Welsh HH (1994) Ontogenic changes in foraging behavior and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. Anim Behav 48:1261–1273

López P, Hawlena D, Polo V, Amo L, Martín J (2005) Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards. Anim Behav 69:1–9

Maginnis LT (2006) The costs of autotomy and regeneration in animals: a review and framework for future research. Behav Ecol 17:857–872

Magrath RD, Platzen D, Kondo J (2006) From nestling calls to fledgling silence: adaptive timing of change in response to aerial alarm calls. Proc R Soc Lond B 273:2335–2341

Marcelini D (1977) Acoustic and visual display behavior of gekkonid lizards. Am Zool 17:251–260

Marcelini DL, Jenssen TA (1991) Avoidance learning by the curly-tailed lizards, *Leiocephalus schreibersi*: implication for antipredator behaviour. J Herpetol 25:238–241

Martín J, López P (2003) Ontogenetic variation in antipredator behavior of Iberian rock lizards (*Lacerta monticola*): effects of body-size-dependent thermal-exchange rates and costs of refuge use. Can J Zool 81:1131–1137

McElroy EJ, Jockey KL, Reilly SM (2008) The correlated evolution of biomechanics, gait and foraging mode in lizards. J Exp Biol 211:1029–1040

Medill SA, Renard A, Larivière S (2011) Ontogeny of antipredator behaviour of striped skunks (*Mephitis mephitis*). Ethol Ecol Evol 23:41–48

Nelson JN, Thompson MB, Pledger S, Keal SN, Daugherty CH (2006) Performance of juvenile tuatara depends on age, clutch and incubation regime. J Herpetol 40:399–403

Paulissen MA (1988a) Ontogenetic and seasonal comparisons of daily activity patterns of the six-lined racerunner, *Cnemidophorus sexlineatus* (Sauria: Teiidae). Am Midl Nat 120:355–361

Paulissen MA (1988b) Ontogenetic and seasonal shifts in microhabitat use by the lizard *Cnemidophorus sexlineatus*. Copeia 1988:1021–1029

Pongracz P, Altbacker V (2000) Ontogeny of the responses of European rabbits (*Oryctolagus cuniculus*) to aerial and ground predators. Can J Zool 78:655–665

Pough HF (1976) Cryptic effects of crossbanded and ringed patterns of snakes. Copeia 1976:834–836

Pough HF (1977) Ontogenetic change in blood transport capacity and endurance in garter snakes (*Thamnophis sirtalis*). J Comp Physiol B 116:337–345

Pough HF (1978) Ontogenetic changes in endurance in water snakes (*Natrix sipedon*): physiological correlates and ecological consequences. Copeia 1978:69–75

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Roth ED, Johnson JA (2004) Size-based variation in antipredator behavior within a snake (*Agkistrodon piscivorus*) population. Behav Ecol 15:365–370

Ruxton GD, Sherratt TN, Speed MP (2004) Avoiding attack. Oxford University Press, Oxford

Sakata JT, Crews D (2004) Developmental sculpting of social phenotype and plasticity. Neurosci Biobehav Rev 28:95–112

Seufer H, Kaverkin H, Kirschner A (2005) The eyelash geckos. Kirschner & Seufer, Karlsruhe

Sherbrooke WC (2008) Antipredator responses by Texas horned lizards to two snake taxa with different foraging and subjugation strategies. J Herpetol 42:145–152

Shine R, Olsson MM, Lemaster MP, Moore IT, Mason RT (2000) Effects of sex, body size, temperature, and location on the antipredator tactics of free-ranging gartersnakes (*Thamnophis sirtalis*, Colubridae). Behav Ecol 11:239–245

StatSoft, Inc (2001) STATISTICA for Windows [Computer program manual]. StatSoft, Tulsa, http://www.statsoft.com

Thayer GH (1909) Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries. Macmillan, New York

Tinbergen (1963) On aims and methods of ethology. Z Tierpsychol 20:410–433

Tousignant A, Viets BE, Flores D, Crews D (1995) Ontogenetic and social factors affect the endocrinology and timing of reproduction in the female leopard gecko (*Eublepharis macularius*). Horm Behav 29:141–153

Treves A (2000) Theory and method in studies of vigilance and aggregation. Anim Behav 60:711–722

Välimäki K, Herczeg G (2012) Ontogenetic and evolutionary effects of predation and competition on nine-spined stickleback. J Anim Ecol 81:859–867

Viets BE, Tousignant A, Ewert MA, Nelson CE, Crews D (1993) Temperature-dependent sex determination in the leopard gecko, *Eublepharis macularius*. J Exp Zool 265:679–683

Wilson D, Heinsohn R, Endler A (2007) The adaptive significance of ontogenetic colour change in tropical python. Biol Lett 3:40–43