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Antipredatory reaction of the leopard gecko *Eublepharis macularius* to snake predators

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Abstract

Ability to recognize a risk of predation and react with adaptive antipredatory behavior can enhance fitness, but has some costs as well. Animals can either specifically react on the most dangerous predators (threat-sensitive avoidance) or they have safe but costly general wariness avoiding all potential predators. The level of threat may depend on the predator's foraging ecology and distribution with the prey with sympatric and specialist species being the most dangerous. We used 2 choice trials to investigate antipredatory behavior of captive born and wild-caught leopard geckos confronted with different snake predators from 2 families (Colubridae, Boidae) varying in foraging ecology and sympatric/allopatric distribution with the geckos. Predator-naïve subadult individuals have general wariness, explore both chemically and visually, and perform antipredatory postures toward a majority of snake predators regardless of their sympatry/allopatry or food specialization. The most exaggerated antipredatory postures in both subadult and adult geckos were toward 2 sympatric snake species, the spotted whip snake *Hemorrhois ravergeri*, an active forager, and the red sand boa *Eryx johnii*, a subterranean snake with a sit-and-wait strategy. In contrast, also subterranean but allopatric the Kenyan sand boa *Eryx colubrinus* did not elicit any antipredatory reaction. We conclude that the leopard gecko possesses an innate general antipredatory reaction to different species of snake predators, while a specific reaction to 2 particular sympatric species can be observed. Moreover, adult wild caught geckos show lower reactivity compared with the captive born ones, presumably due to an experience of a real predation event that can hardly be simulated under laboratory conditions.

Key words: allopatric, antipredation, lizard, posture, sympatric, 2 choice trial.

Predation poses a major risk for most organisms and presents a strong selective pressure on prey to avoid dangerous predators as failure to do so can result in death or injury. Predator recognition and evaluation of potential threat is important when animals must balance between the safety and cost of defense against predators (Lima and Dill 1990) which in lizards may include reduced foraging (Cooper 2000), mating (Cooper 1999), or basking activity (Burger and Gochfeld 1990).

Overall, the predation risk varies with time and across different habitats (Sih et al. 1998; Ferrari et al. 2008) due to presence of

multiple predator types and their fluctuating population density (McCoy et al. 2012). However, if the environment is stable, specific predator recognition and a quick behavioral response may be fixed genetically. For instance, a newly hatched Atlantic salmon *Salmo salar* responds stronger to odor of a high-risk predator (the northern pike *Esox lucius*) than to a low-risk one (the minnow *Phoxinus phoxinus*) (Hawkins et al. 2007). Similarly, a naïve hatchling of the rock-dwelling velvet gecko *Oedura lesueurii* demonstrates a typical anti-snake tactic such as tail waving in presence of the broad-headed snake *Hoplocephalus bungaroides* despite absence of any prior

experience (Downes and Adams 2001). Finally, some avian species show innate avoidance to the ringed pattern of deadly coral snakes (Smith 1975).

Snakes are often among the most important predators of lizards (Downes and Shine 1998; Balderas-Valdivia and Ramírez-Bautista 2005; Webb et al. 2009), hence the recognition ability of many lizard species (e.g., *O. lesueurii*: Downes and Shine 1998; skinks *Carlia rostralis*, and *Carlia storri*: Lloyd et al. 2009). Theoretically, sympatric distribution with a particular snake should give the prey an opportunity to learn the level of threat it poses (Van Damme et al. 1995; Ferrari et al. 2005). Interestingly, only sympatric populations of the wreath tree iguana *Liolaemus lemniscatus* under heavy predation pressure showed less chemical exploration behavior (tongue flicking) and more antipredatory behavior reducing its detection when exposed to the saurophagous long-tailed snake *Philodryas chamissonis*. On the other hand, some studies reported that lizard prey might also express antipredatory behavior to chemicals of allopatric snake predators (Balderas-Valdivia and Ramírez-Bautista 2005).

Nevertheless, it is not just the sympatric distribution, but also the length of co-evolution that may influence an adaptive antipredatory response (Brock et al. 2014). For example, the wall lizard *Podarcis muralis* from a mainland population with heavy predation pressure recognizes dangerousness of saurophagous and piscivorous snakes, unless they have lived isolated for 7 million years (Durand et al. 2012, but see Amo et al. 2004b). Furthermore, sympatric predator recognition may sometimes be conditioned by the predator's diet specialization and foraging tactic (Amo et al. 2004a). The desert iguana *Dipsosaurus dorsalis* can discriminate between chemicals of saurophagous snakes and species feeding mainly on arthropods (Bealor and Krekorian 2002; Amo et al. 2004b). In contrast, some species (e.g., *O. lesueurii*) displayed a generalized antipredatory response to chemicals of 5 syntopic elapid snakes with various foraging ecology and activity pattern (diurnal and nocturnal, active or ambush foragers), thus posing a various degree of threat to them (Webb et al. 2009, 2010).

In this study, we aimed to investigate antipredatory behavior of captive born and wild caught leopard geckos *Eublepharis macularius* during a direct confrontation with a live snake predator kept in a small cage. Although we may expect, that the geckos are able to detect their predators even when chemical cues only are present, we chose to simulate a situation that is much similar to what happens in the wild, when a predator is already present in the prey's close proximity, preparing for an attack. In this case, the potential prey has complex information about the predator (visual as well as chemical cues) that allows it to assess the threat and chose an optimal antipredatory strategy (Helfman 1989).

The leopard gecko inhabits various environments from rocky semi-desert habitats to subtropical forests of Afghanistan, Pakistan, and India (Seufer et al. 2005) where it is sympatric with various snake predators adopting different foraging tactics (Khan 2002; Whitaker and Captain 2004), thus it is a suitable model for studying specificity of antipredatory reaction which still remains inconclusive.

We hypothesize that the leopard gecko will show preferential avoidance or expresses higher level of other antipredatory behaviors in response to sympatric rather than allopatric snake predators. Furthermore, we predict that the predator's foraging ecology may also influence the level of threat to its prey with saurophagous snakes being more dangerous than generalists. To determine the role of experience on risk evaluation we also compared antipredatory behavior of wild and captive born animals. We assume that wild born animals should show more specific antipredatory reaction than

individuals coming from a laboratory stock. Finally, by testing captive-born subadults we could assess the level to which the innate antipredatory reactions are predator specific.

Materials and Methods

Studied animals

In this study we used 585 leopard geckos during breeding seasons 2007–2012 to test their antipredatory behavior toward various snake (and control) species. Three different populations of geckos were available: 1) those originated from the wild (2 independent imports of adult individuals from western Pakistan (P), 2) their first generation born in laboratory (PAKF1), and 3) individuals from a laboratory stock (LAB) that has been kept for several generations in the Czech Republic since 1970. We compared antipredatory reactions of adult animals coming from the wild (P) with the captive born adults and subadults (PAKF1, LAB). It is noteworthy, that the wild born animals (P) only might have had a direct experience with sympatric snake predators.

The leopard gecko demonstrates a shift of antipredatory strategies, the youngsters usually vocalize, while escape is a preferred strategy of adults (Landová et al. 2013). However, 7-month-old subadults already chose an antipredatory strategy similar to that of adults. In order to avoid this developmental effect of antipredatory behavior we tested laboratory born subadult individuals ($n=316$) between the age of 210 and 300 days and fully adult animals (2 years and older, $n=269$). We confronted at least 28 subadults with each predator species (14–17 animals per each population PAKF1 and LAB) and at least 52 adults (20 animals per each population PAKF1 and LAB, 12–15 animals per population P). The number of animals confronted with each predator is given in Table 1; every individual was tested only once.

Furthermore, the studied species belongs to a group of lizards with temperature-induced sex determination (Viets et al. 1993). There are several studies showing that incubation temperature does not only determine the sex but may also affect behavior (Flores et al. 1994; Sakata and Crews 2003). Thus, in order to control for such variability and to ascertain that different behaviors would not be a result of different hatching conditions, all eggs were incubated under the same constant temperature. The incubator was set to $28.5^{\circ}\text{C} \pm 0.5$, which is an optimal temperature for incubation preferred by females themselves (Bragg et al. 2000) and under which more female hatch. For all tested animals the natural circadian rhythm of daylight was preserved. Temperature was maintained stable around 28°C , while a heat cable was placed under each terrarium. Adults were placed individually or in couples (male-female or 2 females) in glass terrariums $30 \times 30 \times 20$ cm. Offspring until 1 year of age were housed individually in plastic boxes measuring $20 \times 20 \times 15$ cm. All animals were fed *ad libitum* with crickets, mealworms dusted with vitamins and minerals (Nutri Mix, AD₃, and E). The geckos were confronted with 9 species of snake predators from Boidae and Colubridae family and the glass lizard *Pseudopus apodus* from Anguidae as a control (see Table 1 summarizing their distribution with the gecko, food specialization, and foraging tactic).

Experimental design and testing apparatus

Experiments took place in a glass terrarium $30 \times 60 \times 30$ cm with constant temperature of $28 \pm 0.5^{\circ}\text{C}$ which is preferred by the gecko in nature (Bergmann and Irschick 2006). The bottom of the testing arena was covered with white paper that was removed after each trial and the whole arena was washed with 70% ethanol and water.

Table 1. Information on activity pattern, distribution, and foraging ecology of the tested snake predators from 2 families (Colubridae, Boidae) and 1 control lizard species, *P. apodus*

Predator species	n	Activity	Distribution with the leopard gecko	Feeding type	Foraging strategy	Number of tested geckos					
						Subadults			Adults		
						P	PAKF1	LAB	P	PAKF1	LAB
<i>Eryx johnii</i>	3	Nocturnal	Sympatric	Generalist	Sit-and-wait, subterranean	—	17	17	15	20	20
<i>Eryx colubrinus</i>	4	Nocturnal	Allopatric	Generalist	Sit-and-wait, subterranean	—	17	17	15	20	20
<i>Hemorrhois ravergieri</i>	6	Diurnal	Sympatric	Saurophagous	Active forager	—	16	16	12	20	20
<i>Hemorrhois hippocrepiis</i>	2	Diurnal	Allopatric	Saurophagous	Active forager	—	15	15	—	—	—
<i>Spalerosophis atriceps</i>	2	Nocturnal	Sympatric	Generalist	Combining	—	16	16	12	20	20
<i>Spalerosophis diadema</i>	3	Nocturnal*	Allopatric	Generalist	Combining	—	16	16	—	—	—
<i>Malpolon monspessulanus</i>	2	Diurnal	Allopatric	Saurophagous	Active forager	—	16	16	—	—	—
<i>Lampropeltis californiae</i>	2	Diurnal	Allopatric	Generalist	Active forager	—	15	15	—	—	—
<i>Elaphe quatuorlineata</i>	4	Diurnal	Allopatric	Generalist	Combining	—	16	16	—	—	—
<i>Pseudopus apodus</i>	4	Diurnal	Allopatric	Generalist	Active forager	—	14	14	15	20	20

Number of geckos presented to each stimulus species is included. Subadults (210–300 days old) were confronted with 10 species of predators while adults (2 years and older) were tested with a subset of 5 species only. P: wild caught leopard geckos imported from Pakistan, PAKF1: first generation of offspring born in laboratory to wild caught animals, LAB: individuals from a laboratory stock. **S. diadema* changes its activity period according to the season - it is diurnal during the winter, autumn, and spring, but becomes nocturnal and crepuscular during the summer.

Experiments were running in the evening hours as it is a period when the leopard gecko starts being active. We also avoided testing during a reproduction season (January and February).

The geckos were first weighed and then placed into the testing arena 2 days prior to the experiment to habituate (López et al. 2000). Paper shelters were provided in the arena during the habituation period but these were removed just before a trial started. The geckos were then put through a preferential 2-choice test with a box containing a live snake (stimulus box) on one side of the testing arena and a control empty box on the other side. The 2 boxes (both novel to the gecko) were of the same size 14 × 20 × 13 cm and made of perspex with a front wire mesh. The right/left position of each box was randomized.

A chosen predator was put in the stimulus box just before the trial and put back into its terrarium immediately after the trial ended. The box was then properly washed before being used again. Subadult geckos were confronted with all 10 species of predators while the adults were tested with a subset of 5 species only (the red sand boa *Eryx johnii*; the Kenyan sand boa *Eryx colubrinus*; the spotted whip snake *Hemorrhois ravergieri*; the blackheaded royal snake *Spalerosophis atriceps*; and the glass lizard *P. apodus*).

Each trial lasted 30 min, enabling the tested animals to express a range of antipredatory behavior. The trials were illuminated by a single blue 25 W light bulb and filmed from the side with the JVC Everio S, memory camcorder (Victor Company of Japan). The recordings were then assessed using the OBS30 software (Noldus Information Technology 1993). Selected components of antipredatory behavior were evaluated either by their frequency or time length.

Antipredatory behavioral variables

We modified the list of behaviors previously used by Landová et al. (2013) according to the current experimental design: (1) active exploring: the gecko is walking in the arena and visually and chemically exploring its environment (see below for explanations), especially the stimulus and control box; (2) inactivity near a box: the gecko is passive and showing no apparent interest, lying inactively in a safe area; the animal's position in regards to the predator plays a crucial role here, that is, whether the individual is lying in the part

with the predator or by the empty control box (Labra and Hoare 2015) (for this purpose, the testing arena was divided into equal quarters by the larger side (each 15 cm large) and preference for either a control or stimulus box was registered only when the head or most of the gecko's body was in the respective outer quarters where the boxes were placed; (3) tongue flicking: chemical exploration when the animal is directly licking the object of its interest or sniffing around (the head is lifted and the nostrils directed toward the snake/empty box or pressed against the mesh) to detect a potential predator (Amo et al. 2004b); and (4) an antipredatory posture that involves various types of behaviors: a) high posture: the gecko is standing on tight legs with the abdomen raised, sometimes with the arched back, and this posture is usually accompanied by tail waving (Caro 2014), that is, the tail is slowly moving from side to side (Webb et al. 2009); b) low posture: the gecko is crouched with its legs bent, keeping the back straight and pressing the abdomen against the surface, the tail is waving; c) freezing: the gecko remains motionless, the abdomen may be pressed against the arena floor; d) tail vibration: the tail is wiggled from side to side (Downes and Shine 1998); e) binocular fixation: the gecko gazes directly at the predator and keeps it in the binocular receptive fields.

Statistical analyses

The count variables were either treated as variables with a negative binomial distribution (postures) or square root transformed to achieve normality (tongue flicking). Duration of binocular fixation of the snake was expressed as a proportion of total time of the experiment (1,800 s) and square root arcsin transformed. Similarly, preference measures (time spent close to the control box versus that close to the snake, time spent exploring the snake versus that exploring the control box) were calculated as $A/(A + B)$, where A and B are compared time scores; the resulting proportion was then square root arcsin transformed to improve normality and divided by arcsin (square root 0.5) to obtain intuitive values ranging from 0 (total avoidance) to 2 (total preference) with a balanced proportion corresponding to value 1. Residuals dispersion and other graphic model diagnostics were visually checked.

The response variables with a normal distribution were treated by linear models (function lm) while those exhibiting a binomial or

negative binomial distribution by generalized linear models (functions `glm` for quasibinomial model and `glm.nb` of the MASS package, respectively; for a list of models see Table 2). The stimulus species (snake), population (wild vs. laboratory), and gecko's body weight were introduced as fixed factors. The initial full models were further reduced according to the Akaike information criterion (AIC) using a step function. The log-likelihood ratio test was applied to compare the reduced models with the full ones in order to approve the model reduction. The reduced linear models (analysis of variance and coefficients) are further shown under the results. All the calculations were performed in R environment (R Core Team 2013).

Results

Antipredatory behavior of subadult geckos

The preference to stay inactive close the control box (i.e., in the safe area) was influenced only by the snake predator species ($F_{9,306} = 2.15$; $P = 0.0255$). Apart from experiments with *S. atriceps*, these preferences tended to be positive, that is, the geckos preferred to stay on the safe side far from the snake predator (Figure 1). Compared with a reference experiment with the lizard predator *P. apodus*, preferences for inactivity close to the control box were elevated in the case of sympatric *E. johnii* and the allopatric horseshoe whip snake, *Hemorrhhois hippocrepsis* (Figure 1, for coefficients see Table 3). Preference for exploring the snake (risky behavior) was affected exclusively by the gecko's body weight, heavier individuals were more prone to perform predator inspection ($F_{1,315} = 3.95$; $P = 0.0477$).

Linear models revealed that time the subadult geckos spent by binocular fixation of the predator varied significantly with different species ($F_{9,306} = 2.30$; $P = 0.0166$). Compared with the binocular fixation of *P. apodus*, the geckos gazed longer especially on the allopatric diadem snake, *Spalerosophis diadema*, saurophagous sympatric *H. ravergeri*, and allopatric *H. hippocrepsis* (Figure 2A, Table 4).

Similarly, the total number of antipredatory postures was significantly affected by the predator species ($df = 9,306$; $P = 0.0037$) only. In comparison to the control species *P. apodus*, the geckos performed more postures when in the presence of nearly all snake predators, but the most prominently with sympatric *H. ravergeri* and *S. atriceps*, allopatric *S. diadema* and *H. hippocrepsis*, and the allopatric saurophagous California kingsnake, *Lampropeltis californiae* (Figure 3A, Tables 3 and 4). When particular antipredatory postures were analyzed separately, the only variables that could explain differences in high posture frequency was the predator species ($df = 9,306$; $P = 0.0006$) and gecko's body weight ($df = 1,305$; $P = 0.0095$). Interestingly, it was only the snake species that significantly affected the frequency of low postures ($df = 9,306$; $P < 0.0001$). Compared with what was recorded in the presence of *P. apodus*, the subadult geckos performed considerably more low postures when encountering sympatric *H. ravergeri*, *E. johnii*, *S. atriceps*, allopatric *S. diadema*, *Elaphe quatuorlineata*, and *L. californiae* (Figure 3A, Tables 3 and 4). Variability in frequency of freezing was explained only by the stimulus species ($df = 9,306$; $P = 0.0024$). The geckos used this antipredatory strategy significantly more often in the presence of *H. ravergeri* and *S. diadema* when compared with the frequency elicited by *P. apodus* (Figure 3A, Tables 3 and 4).

The geckos responded to the predator's presence by tail waving depending on the particular snake ($df = 9,306$; $P = 0.0013$). Most snake species (all except *E. colubrinus* and the Montpellier snake,

Table 2. Description of the statistic models used for data analyses

Age	Model (function)	Distribution	Link function	Response variable	Transformation	Full model predictors	Reduced model predictors
Subadults	Lm	Normal	identity	Exploring the snake (preference)	Square root arcsin	Species, population, body weight, sympatry	Body weight
	Lm	Normal	identity	Inactivity near the control box (preference)	Square root arcsin	Species, population, body weight, sympatry	Species
	Lm	Normal	identity	Binocular fixation (time)	Square root arcsin	Species, population, body weight	Species
	Lm	Normal	identity	Tongue flicking (frequency)	Square root	Species, population, body weight	Species
	glm.nb	Negative binomial	log	All posture (frequency)	—	Species, population, body weight	Species, body weight
	glm.nb	Negative binomial	log	High posture (frequency)	—	Species, population, body weight	Species
	glm.nb	Negative binomial	log	Low posture (frequency)	—	Species, population, body weight	Species
	glm.nb	Negative binomial	log	Freezing (frequency)	—	Species, population, body weight	Species
	glm.nb	Negative binomial	log	Total tail waving (frequency)	—	Species, population, body weight, sympatry	No predictor
	Adults	Lm	Normal	identity	Exploring the snake (preference)	Square root arcsin	Species, population, body weight, sympatry
Lm		Normal	identity	Inactivity near the control box (preference)	Square root arcsin	Species, population, body weight, sympatry	No predictor
Lm		Normal	identity	Binocular fixation (time)	Square root arcsin	Species, population, body weight	Species
Lm		Normal	identity	Tongue flicking (frequency)	Square root	Species, population, body weight	Species, body weight
glm.nb		Negative binomial	log	All posture (frequency)	—	Species, population, body weight, sex	No predictor
Glm		Quasibinomial	logit	Presence/absence of any posture	—	Species, population, body weight, sex	Species, population
glm.nb		Negative binomial	log	High posture (frequency)	—	Species, body weight, sex	Sex NS
glm.nb		Negative binomial	log	Low posture (frequency)	—	Species, population, body weight, sex	Population NS
glm.nb		Negative binomial	log	Freezing posture (frequency)	—	Species, population, body weight, sex	Species, population NS
glm.nb		Negative binomial	log	Total tail waving (frequency)	—	Species, population, body weight, sex	No predictor

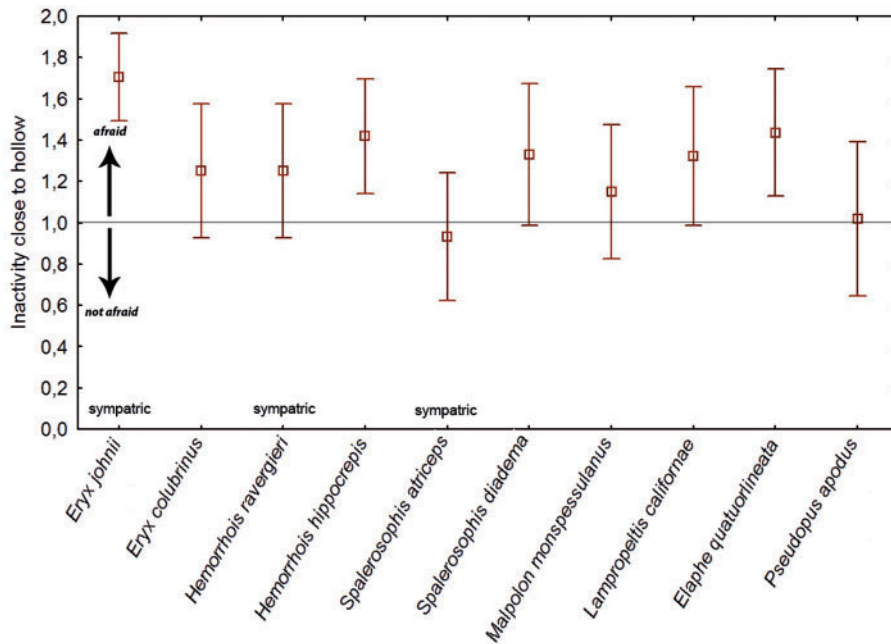


Figure 1. Preference scores of inactivity close to the control box (“hollow”; square root arcsin transformed to improve normality and divided by arcsin (square root 0.5) to obtain intuitive values ranging from 0 (total avoidance) to 2 (total preference) with a balanced proportion corresponding to value 1—straight line) for subadult leopard geckos confronted with different types of predators. Sympatric distribution to the leopard gecko is noted, other snake species are allopatric.

Malpolon monspessulanus) elicited this behavior more frequently than the control lizard species *P. apodus*, especially sympatric *H. ravergieri* and *S. atriceps* (Figure 3A, Tables 3 and 4). Linear models revealed that the frequency of tongue flicking was significantly affected exclusively by the stimulus species ($F_{9,306} = 2.30$, $P < 0.0001$). Except *E. johnii* and the 4-lined snake, *E. quatuorlineata*, all other snake species elevated tongue flicking frequency in geckos when compared with behaviors elicited by the control species *P. apodus* (Tables 3 and 4).

Antipredatory behavior of adult geckos

Duration of binocular fixation of the predator was significantly affected by the stimulus species ($F_{4,264} = 5.05$, $P = 0.0006$). Compared to the control species, this was higher for *E. johnii* and lower for *S. atriceps*.

Presence of postures was significantly affected mainly by the predator species ($F_{4,264} = 3.41$, $P = 0.0096$), and also the gecko's origin (laboratory vs. wild; $F_{2,262} = 5.58$, $P = 0.0042$). Animals from the wild (Pakistan) were slightly less prone to perform postures than their descendants bred in laboratory (Table 3). Compared with the control stimulus (*P. apodus*), the proportion of adults responding by antipredatory postures was elevated in the presence of *H. ravergieri* (Tables 3 and 4). Variability in frequency of freezing was explained by the predator species ($df = 4,264$; $P = 0.0006$). Freezing occurred less frequently in the presence of allopatric *E. colubrinus* than in the control experiments (Tables 3 and 4).

As for the subadults, linear models revealed that the frequency of tongue flicking in adult geckos was significantly affected by the stimulus species ($F_{4,263} = 8.32$, $P < 0.0001$); the gecko's body weight was also included in the reduced model, but its effect was non-significant ($F_{1,263} = 2.42$, $P = 0.1211$). We found out that *H. ravergieri* and *S. atriceps* elevated the tongue flicking frequency compared with that elicited by *P. apodus*. Contrary to that, *E. johnii* and *E.*

colubrinus reduced the tongue flicking frequency in geckos compared with what was observed in the presence of *P. apodus* (Tables 3 and 4).

Discussion

The leopard geckos tested in our experiments exhibited various antipredatory behaviors to all stimulus species and none of these behaviors was confined to a specific species. Compared with responses to the control lizard species, the occurrence of at least one element of antipredatory behavior was significantly elevated in the presence of 7 out of 9 snake species (i.e., except *M. monspessulanus* and *E. colubrinus*, see Table 5 summarizing these results). Responses to the colubrid genera *Hemorrhhois* and partially also *Spalerosophis* were among the most pronounced ones and especially included elements of active defense, for example, low and high postures (with or without tail waving), binocular fixation, and exploration of the snake predator. This may be related to the fact that the majority of other colubrid snakes are agile, fast predators that can actively chase their prey. As reported in another eye-lid geckos of a related North American genus *Coleonyx*, distant chemical detection and active defense exhibited in direct confrontation with a snake is beneficial (Dial and Schwenk 1996). It is noteworthy that in our experiments some of the heavier individuals explored carefully the box with a predator from close proximity, often staying just in front of the wire mesh, sometimes escaping after a while. This behavior which is similar to the “predator inspection” occurs in the case of uncertainty in risk assessment (cf. Dugatkin and Godin 1992). In contrast to this, responses to *E. johnii* included particularly staying motionless in the safer part of the arena sometimes accompanied by binocular fixation and tongue flicking, which can graduate into low postures (see the discussion below).

When multiple predators occur in the prey's habitat, an optimal antipredator response may be determined by the attack

Table 3. Parameters of the full and reduced linear models examining the effects of predator species (intercept = *P. apodus*), gecko's population (P, PAKF1, LAB), and its body weight on response variables: exploring the snake, inactivity near the control box, and binocular fixation (preference score (time), square root arcsin transformation); total number of postures, high and low posture, freezing, tale waving, and tongue flicking (frequency, square root transformation)

Age	Response	Parameters	Estimate	Std. error	z-value	Pr(> z)
Subadults	Exploring the snake	(Intercept) ^a	0.705374	0.103429	6.820	4.8e-11***
		Weight	0.007185	0.003614	1.988	0.0477*
	Inactivity near the control box	(Intercept)	1.287038	0.234270	5.494	8.75e-08***
		<i>Eryx johnii</i>	0.686509	0.219661	3.125	0.00196**
		<i>Elaphe quatuorlineata</i>	0.323312	0.237232	1.363	0.17401
		<i>Eryx colubrinus</i>	0.234626	0.219661	1.068	0.28637
		<i>Hemorrhois hippocrepis</i>	0.523081	0.238475	2.193	0.02909*
		<i>Hemorrhois ravergieri</i>	0.377232	0.240039	1.572	0.11717
		<i>Lampropeltis californiae</i>	0.438139	0.242582	1.806	0.07195
		<i>Malpolon monspessulanus</i>	0.136766	0.222712	0.614	0.53965
		<i>Spalerosophis atriceps</i>	0.047422	0.237369	0.200	0.84180
		<i>Spalerosophis diadema</i>	0.224782	0.236129	0.952	0.34193
		Weight	-0.011408	0.007051	-1.618	0.10682
	Binocular fixation (time) ^b	(Intercept) ^a	0.193172	0.036198	5.337	1.85e-07***
		<i>Eryx johnii</i>	0.061201	0.048881	1.252	0.21151
		<i>Elaphe quatuorlineata</i>	0.080694	0.049566	1.628	0.10455
		<i>Eryx colubrinus</i>	0.038522	0.048881	0.788	0.43126
		<i>Hemorrhois hippocrepis</i>	0.099331	0.050331	1.974	0.04933*
		<i>Hemorrhois ravergieri</i>	0.115863	0.049566	2.338	0.02005*
		<i>Lampropeltis californiae</i>	0.062078	0.050331	1.233	0.21837
		<i>Malpolon monspessulanus</i>	-0.001836	0.049566	-0.037	0.97048
		<i>Spalerosophis atriceps</i>	0.023955	0.049566	0.483	0.62924
		<i>Spalerosophis diadema</i>	0.160702	0.049566	3.242	0.00132
		Total number of postures	(Intercept) ^a	-0.1967	0.3897	-0.505
	<i>Eryx johnii</i>		1.2755	0.5011	2.546	0.01091*
	<i>Elaphe quatuorlineata</i>		1.1130	0.5091	2.186	0.02879*
	<i>Eryx colubrinus</i>		0.6593	0.5095	1.294	0.19563
	<i>Hemorrhois hippocrepis</i>		1.3805	0.5130	2.691	0.00712**
	<i>Hemorrhois ravergieri</i>		2.1291	0.5012	4.248	2.15e-05***
	<i>Lampropeltis californiae</i>		1.4205	0.5126	2.771	0.00559**
	<i>Malpolon monspessulanus</i>		0.8085	0.5134	1.575	0.11530
	<i>Spalerosophis atriceps</i>		1.5350	0.5048	3.041	0.00236**
	<i>Spalerosophis diadema</i>		1.4405	0.5056	2.849	0.00439**
High posture	(Intercept) ^a		-19.30	1781.46	-0.011	0.991
	<i>Eryx johnii</i>	16.47	1781.46	0.009	0.993	
	<i>Elaphe quatuorlineata</i>	18.54	1781.46	0.010	0.992	
	<i>Eryx colubrinus</i>	16.47	1781.46	0.009	0.993	
	<i>Hemorrhois hippocrepis</i>	18.54	1781.46	0.010	0.992	
	<i>Hemorrhois ravergieri</i>	18.61	1781.46	0.010	0.992	
	<i>Lampropeltis californiae</i>	18.61	1781.46	0.010	0.992	
	<i>Malpolon monspessulanus</i>	17.92	1781.46	0.010	0.992	
	<i>Spalerosophis atriceps</i>	18.93	1781.46	0.011	0.992	
	<i>Spalerosophis diadema</i>	19.06	1781.46	0.011	0.991	
	Low posture	(Intercept) ^a	-2.51020	0.72182	-3.478	0.000506***
<i>Eryx johnii</i>		2.22833	0.66490	3.351	0.000804***	
<i>Elaphe quatuorlineata</i>		1.91767	0.69597	2.755	0.005862**	
<i>Eryx colubrinus</i>		0.67404	0.72741	0.927	0.354119	
<i>Hemorrhois hippocrepis</i>		1.54797	0.70361	2.200	0.027804*	
<i>Hemorrhois ravergieri</i>		2.55876	0.68691	3.725	0.000195***	
<i>Lampropeltis californiae</i>		1.84927	0.69852	2.647	0.008111**	
<i>Malpolon monspessulanus</i>		1.25269	0.69893	1.792	0.073084	
<i>Spalerosophis atriceps</i>		1.97088	0.69266	2.845	0.004436**	
<i>Spalerosophis diadema</i>		1.99132	0.069127	2.881	0.003968**	
Population		0.23854	0.22217	1.074	0.282955	
Freezing	Weight	0.01651	0.01625	1.016	0.309620	
	(Intercept) ^a	-1.3863	0.4867	-2.848	0.00440**	
	<i>Eryx johnii</i>	1.0788	0.5952	1.812	0.06993	
	<i>Elaphe quatuorlineata</i>	0.8650	0.6097	1.149	0.15601	
	<i>Eryx colubrinus</i>	1.0788	0.5952	1.812	0.06993	

(continued)

Table 3. Continued

Age	Response	Parameters	Estimate	Std. error	z-value	Pr(> z)
Adults	Total number of tale-waving	<i>Hemorrhois hippocrepis</i>	0.9295	0.6142	1.513	0.13019
		<i>Hemorrhois ravergieri</i>	2.2900	0.5760	3.975	7.02e-05***
		<i>Lampropeltis californiae</i>	1.0296	0.6101	1.688	0.09150
		<i>Malpolon monspessulanus</i>	0.9651	0.6056	1.594	0.11104
		<i>Spalerosophis atriceps</i>	0.8650	0.6097	1.419	0.15601
		<i>Spalerosophis diadema</i>	1.3863	0.5920	2.342	0.01919*
		(Intercept) ^a	-0.5596	0.4007	-1.397	0.16254
		<i>Eryx johnii</i>	0.3373	0.5048	2.649	0.00807**
		<i>Elaphe quatuorlineata</i>	1.0451	0.5154	2.028	0.04257*
		<i>Eryx colubrinus</i>	0.4006	0.5252	0.763	0.44564
		<i>Hemorrhois hippocrepis</i>	1.3779	0.5165	2.668	0.00764**
		<i>Hemorrhois ravergieri</i>	2.0065	0.5037	3.983	6.79e-05***
		<i>Lampropeltis californiae</i>	1.4489	0.5156	2.810	0.00495**
		<i>Malpolon monspessulanus</i>	0.5904	0.5260	1.122	0.26169
		<i>Spalerosophis atriceps</i>	1.5937	0.5074	3.141	0.00169**
		<i>Spalerosophis diadema</i>	1.2370	0.5121	2.416	0.01571*
		(Intercept) ^a	6.6104	0.8516	7.763	1.26e-13***
		<i>Eryx johnii</i>	0.5462	1.1500	0.475	0.635147
	<i>Elaphe quatuorlineata</i>	0.6334	1.1661	0.543	0.587377	
	<i>Eryx colubrinus</i>	2.7600	1.1500	2.400	0.016989*	
	<i>Hemorrhois hippocrepis</i>	4.5378	1.1841	3.832	0.000154***	
	<i>Hemorrhois ravergieri</i>	3.7223	1.1661	3.192	0.001559**	
	<i>Lampropeltis californiae</i>	3.7569	1.1841	3.173	0.001663**	
	<i>Malpolon monspessulanus</i>	2.5774	1.1661	2.210	0.027821*	
	<i>Spalerosophis atriceps</i>	5.1716	1.1661	4.435	1.29e-05***	
	<i>Spalerosophis diadema</i>	4.4595	1.1661	3.824	0.000159***	
	(Intercept) ^a	0.30181	0.03178	9.496	<2e-16***	
	<i>Eryx johnii</i>	0.09611	0.04495	2.138	0.0334*	
	<i>Eryx colubrinus</i>	-0.01062	0.04495	-0.236	0.8134	
	<i>Hemorrhois ravergieri</i>	-0.05371	0.04559	-1.178	0.2398	
	<i>Spalerosophis atriceps</i>	-0.09768	0.04559	-2.149	0.0331*	
	Posture	(Intercept) ^a	-8.321e-01	3.443e-01	-2.417	0.01635*
		<i>Eryx johnii</i>	4.161e-01	4.134e-01	1.007	0.31506
		<i>Eryx colubrinus</i>	-2.664e-16	4.245e-01	-6.28e-16	1.00000
		<i>Hemorrhois ravergieri</i>	1.295e+00	4.209e-01	3.076	0.00232**
		<i>Spalerosophis atriceps</i>	5.604e-01	4.159e-01	1.347	0.17904
Type P		-6.697e-01	3.533e-01	-1.896	0.05912	
Type PAK F1		4.688e-01	2.960e-01	1.584	0.11448	
(Intercept) ^a		-0.4613	0.2989	-1.543	0.12273	
<i>Eryx johnii</i>		0.1067	0.3534	0.302	0.76277	
<i>Eryx colubrinus</i>		-1.5628	0.4807	-3.251	0.00115**	
Freezing	<i>Hemorrhois ravergieri</i>	0.3099	0.3509	0.883	0.37717	
	<i>Spalerosophis atriceps</i>	-0.1351	0.3674	-0.368	0.71301	
	Type P	-0.3864	0.3315	-1.166	0.24373	
	Type PAK F1	0.3473	0.2709	1.282	0.19996	
	(Intercept) ^a	6.92052	1.18220	5.854	1.43e-08***	
	<i>Eryx johnii</i>	-0.12449	0.88230	-0.141	0.887901	
	<i>Eryx colubrinus</i>	-1.27742	0.88007	-1.451	0.147835	
	<i>Hemorrhois ravergieri</i>	1.71318	0.90519	1.893	0.059505	
	<i>Spalerosophis atriceps</i>	3.20962	0.89652	3.580	0.000409***	
	Weight	0.03077	0.01978	1.555	0.121053	
Tongue flicking	(Intercept) ^a	6.92052	1.18220	5.854	1.43e-08***	
	<i>Eryx johnii</i>	-0.12449	0.88230	-0.141	0.887901	
	<i>Eryx colubrinus</i>	-1.27742	0.88007	-1.451	0.147835	
	<i>Hemorrhois ravergieri</i>	1.71318	0.90519	1.893	0.059505	
	<i>Spalerosophis atriceps</i>	3.20962	0.89652	3.580	0.000409***	
	Weight	0.03077	0.01978	1.555	0.121053	

Subadult geckos (210–300 days old) were confronted with 10 species of predators while adults (2 years and older) were tested with a subset of 5 species only. Results of linear models in R package, the coefficients of the models, and their significance are provided. Significance codes: 0 “***” 0.001 “**” 0.01 “*” 0.05 “.”, 0.1 “ ” 1.

^aIntercept is a reaction to the control species *P. apodus*. Responses to all other stimuli species were compared with it.

^bAll the variables are expressed as frequencies apart from the binocular fixation that was recorded as time spent staring at the predator (in this case *t*-values and Pr(>|*t*|) are reported in the last 2 columns instead of *z*-values and Pr(>|*z*|) which are applicable for all the remaining variables).

probability. This can be more expected from a specialist rather than generalist predator. Furthermore, if predator–prey arm races have taken a place for some evolutionary time we can assume that the prey is adapted to react more specifically to the most

dangerous sympatric predators (Webb et al. 2009). Many studies have already mentioned that apart from sympatry or allopatry it is diet preferences that are crucial in the predator detection (Cooper 1990; Dial and Schwenk 1996; Van Damme and Quick

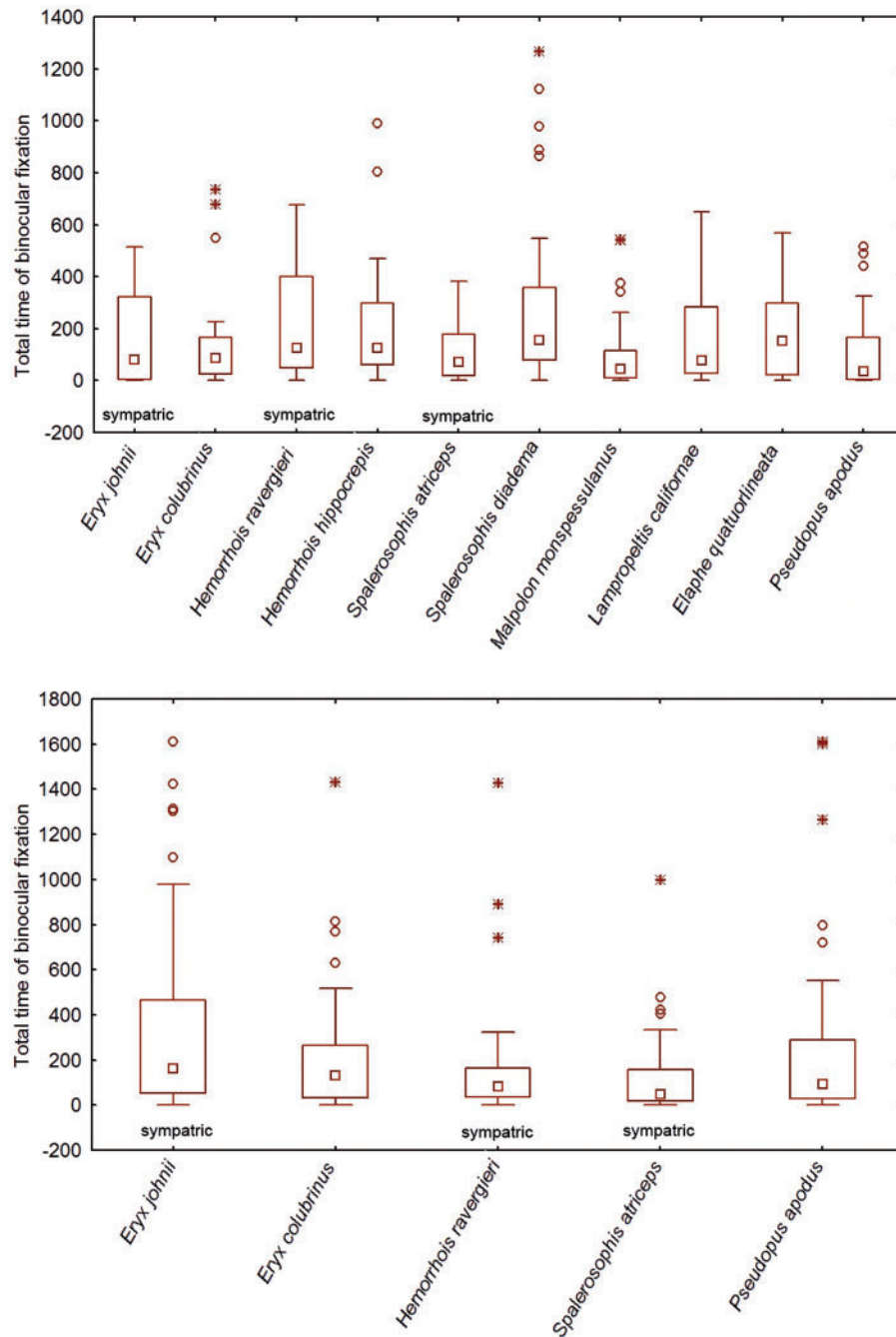


Figure 2. Total time of binocular fixation (square root arcsin transformed) depending on the type of predator. Outliers are depicted as circles, extreme values as stars. Sympatric distribution to the leopard gecko is noted, other snake species are allopatric. A) subadults and B) adults.

2001). Such a trend may also be seen in our results as the geckos (both adults and subadults) performed more antipredatory postures when confronted with saurophagous actively foraging *H. ravergieri*. However, this was not a general trend apparent with other saurophagous predators used in our study. The geckos explored by visual and chemical senses 7 snake and 1 lizard predator species from distance as well as in closer proximity, showing no clear systematic difference regardless of the predator's sympatry/allopatry or food specialization (Figure 2A, B; Table 4). Such a result is in contrast to findings of other studies (Dial et al. 1989; Van Damme and Quick 2001) that considered

the level of saurophagous specialization as a key factor when anticipating snake predator dangerousness.

We may hypothesize that the effect of food specialization is not conclusive because the studied geckos might have identified chemically, that the snake predators had not been feeding on their conspecifics. It is well known, for example, that the northern damselfly larvae *Enallagma* spp. can chemically detect from diet cues, whether their predator *E. lucius* fed on other damselflies or another (hetero-specific) prey (Chivers et al. 1996). Similarly, naïve individuals of the fathead minnow *Pimephales promelas* reacted to diet cues (and subsequently capture-released alarm cues) of *E. lucius* only when it

Table 4. Frequency and preference scores of particular antipredatory behaviors expressed by the leopard gecko face to predators with sympatric and allopatric occurrence and various foraging ecology

Age	Species	Sympatric/allopatric	Preference score (time)		Frequency					
			Exploring the snake Mean (SE)	Binocular fixation Mean (min, max)	Total postures Mean (min, max)	High posture Mean (min, max)	Low posture Mean (min, max)	Freezing Mean (min, max)	Total waving Mean (min, max)	Tongue flicking Mean (min, max)
Subadults	<i>Eryx johnii</i>	S	0.36 (±0.061)	2.8 (0, 11)	2.94 (0, 16)	0.11 (0, 1)	2.37 (1, 7)	1.32 (0, 8)	3.89 (1, 14)	67.24 (5, 362)
	<i>Eryx colubrinus</i>	A	0.43 (±0.057)	3.71 (0, 10)	1.59 (0, 13)	0.2 (0, 1)	0.9 (0, 3)	2.5 (1, 8)	2.9 (1, 10)	108.82 (7, 363)
	<i>Hemorrhois ravergieri</i>	S	0.44 (±0.064)	2.97 (0, 9)	6.9 (0, 54)	0.67 (0, 5)	2.83 (0, 8)	3.29 (0, 51)	5.67 (1, 21)	123.97 (18, 357)
	<i>Hemorrhois hippocrepis</i>	A	0.44 (±0.052)	4.1 (0, 9)	3.27 (0, 12)	0.82 (0, 6)	1.44 (0, 6)	1.12 (0, 3)	4.53 (1, 9)	143.4 (8, 554)
	<i>Spalerosophis atriceps</i>	S	0.54 (±0.058)	3.38 (0, 14)	3.81 (0, 20)	1.38 (0, 13)	2.13 (0, 12)	1.19 (0, 3)	5.62 (1, 15)	167.19 (5, 525)
	<i>Spalerosophis diadema</i>	A	0.39 (±0.068)	3.66 (0, 14)	3.47 (0, 16)	1.47 (0, 13)	1.71 (0, 6)	1.88 (0, 7)	3.94 (1, 8)	145.63 (9, 473)
	<i>Malpolon monspessulanus</i>	A	0.55 (±0.061)	3.03 (0, 10)	1.84 (0, 11)	0.73 (0, 3)	1.45 (0, 5)	1.91 (1, 6)	3.3 (1, 9)	100.03 (7, 304)
	<i>Lampropeltis californiae</i>	A	0.41 (±0.061)	4.00 (0, 10)	3.4 (0, 16)	0.94 (0, 6)	1.94 (0, 11)	1.31 (0, 4)	4.87 (1, 16)	126.77 (6, 392)
	<i>Elaphe quatuorlineata</i>	A	0.36 (±0.068)	2.52 (0, 11)	2.5 (0, 16)	0.94 (0, 7)	1.69 (0, 8)	1.19 (0, 6)	3.25 (0, 15)	70.72 (0, 276)
	<i>Pseudopus apodus</i>	A	0.52 (±0.079)	2.18 (0, 7)	0.82 (0, 7)	0 (0, 0)	0.8 (0, 2)	1.4 (0, 2)	3.2 (1, 5)	62.32 (0, 471)
Adults	<i>Eryx johnii</i>	S	0.53 (±0.048)	4.58 (0, 16)	2.31 (0, 13)	0.02 (0, 1)	0.76 (0, 7)	0.73 (0, 7)	1.56 (0, 8)	92.42 (0, 359)
	<i>Eryx colubrinus</i>	A	0.46 (±0.049)	3.2 (0, 13)	1.76 (0, 13)	0.02 (0, 1)	1.02 (0, 8)	0.15 (0, 2)	1.67 (0, 16)	74.05 (0, 321)
	<i>Hemorrhois ravergieri</i>	S	0.44 (±0.048)	3.12 (0, 9)	3.31 (0, 12)	0.04 (0, 2)	1.81 (0, 9)	0.6 (0, 4)	2.42 (0, 11)	128.21 (2, 414)
	<i>Spalerosophis atriceps</i>	S	0.44 (±0.044)	3.38 (0, 11)	2.85 (0, 18)	0.02 (0, 1)	1.17 (0, 10)	0.92 (0, 8)	2.38 (0, 16)	158.35 (8, 456)
	<i>Pseudopus apodus</i>	A	0.44 (±0.049)	3.36 (0, 9)	2.58 (0, 34)	0 (0, 0)	1.02 (0, 10)	0.67 (0, 7)	1.96 (0, 29)	96.15 (0, 407)

fed on their conspecifics (Ferrari et al. 2007). Therefore, the predator's diet may influence antipredatory behavior of its prey. Whether this is also applicable for the leopard gecko would need to be further assessed in a separate experiment. The other possible explanation for the negative results is that we do not have the accurate information on food biology of the predator species in the wild or the prey identifies its predator based on other cues (e.g., the type of predator locomotion, etc.).

In our study, we tested pairs of predator species with similar food specialization and foraging tactic, differing only in their distribution, that is, one living in sympatry with the gecko, while the other one in allopatry. Surprisingly, we found striking differences in antipredatory behavior only in response to 2 generalist snake species with subterranean ecology, sympatric *E. johnii* and allopatric *E. colubrinus*. In the presence of *E. johnii* the geckos remained for most of the time in the safe area avoiding any closer exploration. If any postures were exhibited at all, these were made near the control box. Contrary to that, *E. colubrinus* sometimes elicited even weaker reaction than the lizard control *P. apodus*. Therefore, it seems that the subterranean life cannot be the only explanatory factor. *E. johnii* is a generalist snake species commonly found in Pakistan, where it overlaps with the leopard gecko's distribution. It is a strong constrictor adopting a sit-and-wait strategy ambushing its prey with a fast attack from very close proximity. The gecko lives in small mammals' burrows or rocky interstices which makes it a difficult habitat to escape when encountering the snake. However, if they meet in the open field, the gecko can flee (D. Frynta, personal communication). We may speculate that a visual detection (adults) as well as tongue flicking (subadults) of this dangerous predator was crucial in our experiments and took over any direct exploration.

In contrast to the predator inspection many lizard species reduce their activity in the presence of a dangerous predator or its chemicals, for example, *P. muralis* (Amo et al. 2006), the Chilean tree lizard (*Liolaemus chiliensis*: Labra and Hoare 2015), or *O. lesueurii* (Webb et al. 2009, 2010). This corresponds to inactivity near the control box observed in our experiments. Distance the geckos kept from the threat was reflecting the level of avoidance of a particular species. Compared with inactivity associated with the lizard control, subadult geckos reduced their exploratory behavior and preferentially stayed inactive close to the control box when a generalist snake *E. johnii*, as well as a saurophagous actively foraging predator *H. hippocrepis* were used as a stimulus (Figure 1). Thus, we may suppose that these predators were evaluated as dangerous and were avoided as much as possible in the current experimental conditions when no shelters were available. This further corroborates the results of Webb et al. (2010) who found that *O. lesueurii* avoids crevices scented by snake chemicals.

It has also been shown previously that antipredatory behavior may change ontogenetically (Head et al. 2002; Landová et al. 2013). Generally, the adults were less reactive than the subadult geckos, but their antipredatory reaction was much more threat specific reacting only to sympatric species. However, this tendency was further masked by behavioral pattern of wild caught individuals that were less reactive than the captive born ones. We may hypothesize that the wild animals might have been experienced with a predator event from their early life and evaluated the snake's dangerousness in our experimentally set up differently than the captive born individuals. Thus, antipredatory behavior of the wild animals is probably more state dependent as they can better assess the potential threat of a direct predator attack, a situation that can be hardly simulated in laboratory conditions.

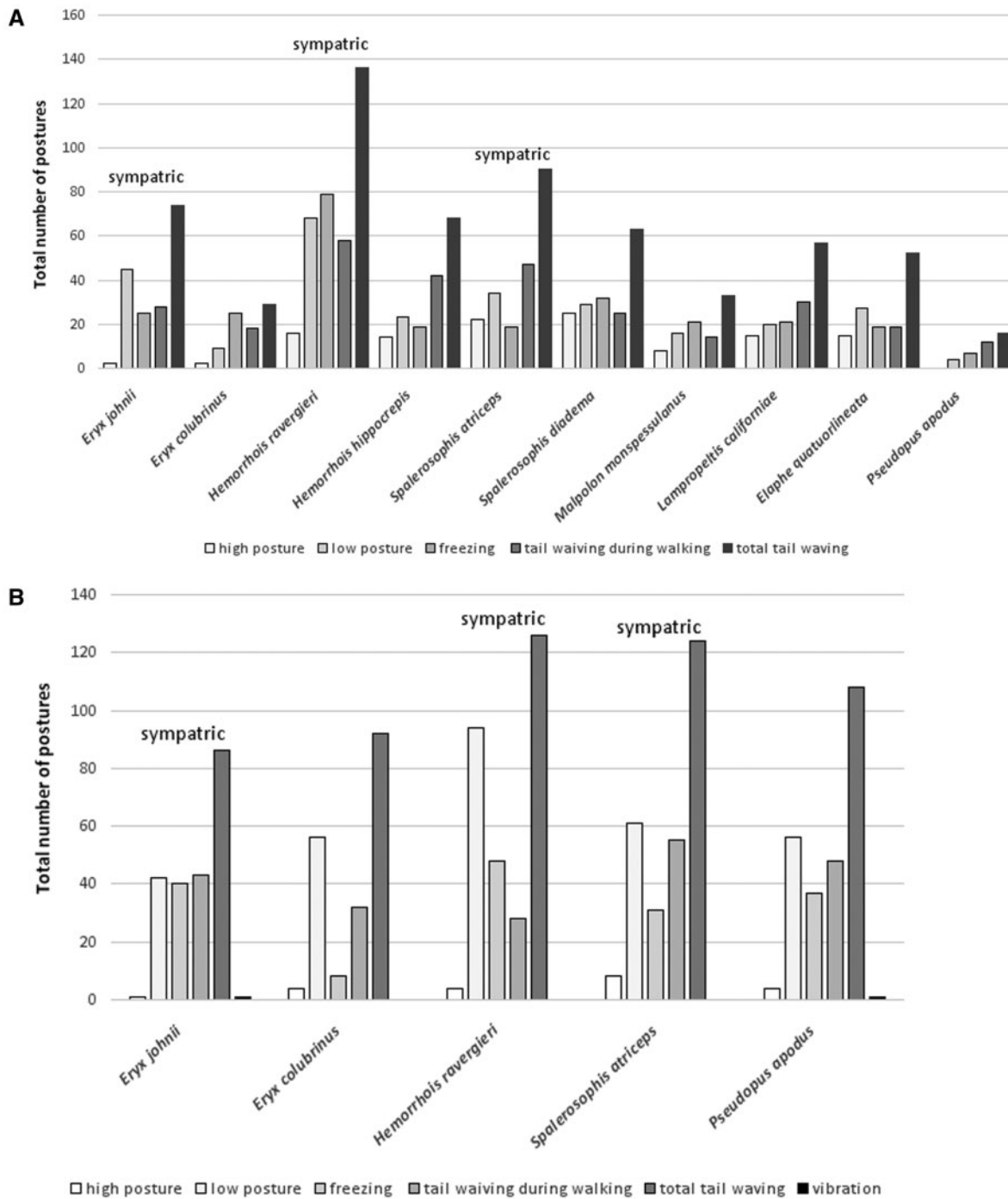


Figure 3. Total frequency of selected antipredatory postures in response to different types of predators. Sympatric distribution to the leopard gecko is noted, other snake species are allopatric. A) subadults and B) adults.

We conclude that the leopard gecko possesses generalized antipredatory reaction to snake predators of different species. They explore them both chemically and visually and use the same variety of other behavioral strategies in response to snakes posing a different level of threat. However, intensity of these reactions varies according to different species and reaches the extreme levels only with some of colubrid and booid snakes (especially *E. johnii* and *H. ravergeri*). This reaction pattern is innate which could be advantageous when novel predators are met (Cisterne et al. 2014). As the animal

gets more experienced with its predators in the wild, this general concept of threat may become more specific and the reaction less intensive and targeted only to the real danger. That could explain why the wild caught animals which were probably more experienced with real predator events were less reactive in response to a predator inside the cage in our study. Interestingly, in the absence of any experience, as in the case of laboratory animals, the antipredatory reaction can still be modulated and mature with aging. Compared with the subadults, the adult captive born geckos reacted only to the

Table 5. Summary table showing which response variables in confrontation with individual predator species were significantly different compared with the control experiments with *P. apodus*

Age	Species	Distribution	Food specialization	Close to the control box	Exploring snake	Binocular fixation	Postures	High posture	Low posture	Freezing	Tail waving	Tongue flicking
Subadults	<i>E. jobnii</i>	S	Generalist	Yes	—	—	—	—	Yes	—	Yes	Yes
	<i>E. colubrinus</i>	A	Generalist	—	—	—	—	—	—	—	—	—
	<i>H. ravergieri</i>	S	Saurophagous	—	—	Yes	Yes	—	Yes	Yes	Yes	—
	<i>H. hipocrepis</i>	A	Saurophagous	Yes	—	Yes	Yes	—	—	—	Yes	—
	<i>S. atriceps</i>	S	Generalist	—	—	—	Yes	—	Yes	—	Yes	—
	<i>S. diadema</i>	A	Generalist	—	—	Yes	Yes	—	Yes	Yes	Yes	—
	<i>M. monspessulanus</i>	A	Saurophagous	—	—	—	—	—	—	—	—	—
	<i>L. californiae</i>	A	Saurophagous	—	—	—	Yes	—	Yes	—	Yes	Yes
Adults	<i>E. quatuorlineata</i>	A	Generalist	—	—	—	—	—	Yes	—	Yes	—
	<i>E. jobnii</i>	S	Generalist	—	—	Yes	—	—	—	—	—	—
	<i>E. colubrinus</i>	A	Generalist	—	—	—	—	—	—	—	—	—
	<i>H. ravergieri</i>	S	Saurophagous	—	—	—	Yes	—	—	—	—	—
	<i>S. atriceps</i>	S	Generalist	—	—	Yes	—	—	—	—	—	—

sympatric, most dangerous predators either by expressing postures or by binocular fixation.

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