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ARTICLE

Multiple vs. single predator effects: differing experimental responses by the spotted fringe-fingered lizard (*Acanthodactylus maculatus*) facing aerial and terrestrial predators

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Abstract
To survive, prey should assess the level of predation threat and adjust their anti-predator strategy accordingly. We tested this hypothesis by investigating the escape behavior of spotted fringe-fingered lizards (*Acanthodactylus maculatus*) approached by a person (i.e. terrestrial predator), with or without a raptor model (i.e. aerial predator), and recording data on escape agility, display movements and refuge use. We predicted that lizards subjected solely to the terrestrial predator would be more agile, thereby signaling low chances of attack success, whereas lizards exposed to both predators would opt for immobility to be less detectable. Our expectations were supported for males, but not females. Males exposed simultaneously to an aerial and a terrestrial predator tolerated a closer approach of the terrestrial predator and frequently sought to hide in refuges, while males only exposed to a terrestrial predator showed a more agile response, by running away early and fast, conducting frequent display movements and remaining detectable outside refuges. Females tended to rely on the immobility strategy more than males most likely because they were slower. In sum, our results highlight the flexibility of lizard anti-predatory behaviors. Lizards adjusted their escape strategy to the type of predator and intensity of the threat encountered.

Keywords Antipredatory · Escape agility · Lacertid · Multiple predation threats · Sex differences

Introduction

Predation avoidance is a crucial task for prey survival and fitness, often involving different anti-predator tactics based on the predation threat detected. Escape success can depend upon the decisions made by prey concerning when and how to move. The decision to initiate flight in response to a predator attack is determined by a cost–benefit trade-off, in which the perceived risk associated with an imminent predation threat outweighs the benefit of maintaining regular activities. Optimal escape theory asserts that prey should begin to flee when risk of predation is in balance with the cost of escape (Ydenberg and Dill 1986). Possible escape costs include the loss of opportunities to feed, mate, or defend territories (Cooper and Frederick 2007). The optimal flight distance for prey should correspond to the trade-off in the costs and benefits of flight, which is largely determined by the predator's attack speed and angle (Cooper et al. 2004; Samia et al. 2016). Prey should be able to estimate the level of predation risk in the environment at any time and decide how to respond by weighing the cost–benefit balance associated with their escape strategy (Ydenberg and Dill 1986).

Lizards are subject to strong predation pressure from a variety of predators, including terrestrial predators like snakes (Sherbrooke 2008) and mammals (Amo et al. 2004), as well as aerial ones (i.e., birds; Poulin et al. 2001; Carlile et al. 2006). Different predators are associated with different levels of threat and elicit varied escape behaviors (Preisser et al. 2007; Palmer and Packer 2021). Consistent with the predictions of economic escape theory, lizards tend to tolerate a close approach by terrestrial predators, displaying and fleeing only when assault is imminent (Frid and Dill 2002; Cooper 2008; Cooper et al. 2015). By contrast, when avian predators are perceived, lizards often become immobile, presumably to minimize the risk of being detected (Malavasi

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et al. 2008). A common strategy against both terrestrial and aerial predators is hiding in a suitable shelter (Martín and Lopez 1999; Møller 2012).

As lizards often live in communities with multiple terrestrial and aerial predators, predator-specific responses could be required (Bouskila 1995; Caro 2005). Lizards should be able to detect temporal variation in predators activity and adjust their escape behaviors accordingly (e.g., Sherbrooke 2008). In an environment where the assemblage of nearby predators can change rapidly, lizard survival may depend on continuously updating their anti-predation strategy, switching between a strategy of active dissuasion of predator attacks (i.e., signaling low probability of success to predator by moving away and displaying) to one aimed at avoiding being attacked (i.e., reducing the risk of detection, by staying motionless or seeking to hide in a refuge (Cabezas-Cartes et al. 2018)). However, due to the scarcity of empirical studies, detailed data on this issue are still lacking despite the relevance of such data for a better understanding of lizards anti-predatory behavior.

Therefore, our study aimed to investigate how lizards may adjust their escape behavior in response to variation in predator pressure by adopting predator-specific strategies. Our main hypothesis was that lizards exposed simultaneously to an aerial predator and a terrestrial predator would be more likely to engage in behavior consistent with avoiding detection by staying motionless or hiding in a refuge, while lizards facing a terrestrial predator only would rather exhibit behaviors signaling low probability of success to predator by moving away while displaying. We tested these predictions by using the spotted fringe-fingered lizard (*Acanthodactylus maculatus*) inhabiting an arid desert area in southern Tunisia as a study model. We conducted field experiments by approaching active lizards with or without a raptor model, recording a set of behavioral variables describing escape agility, display movements and refuge use. We used an observer to simulate a mammalian predator (Frid and Dill 2002), and an observer with a raptor model to simulate simultaneous threats by a mammalian and an avian predator. Concretely, we expected that lizards approached by a mammalian predator alone would exhibit an agile escape response, fleeing early and fast and conducting frequent display movements while remaining detectable outside refuges. However, lizards exposed to both mammalian and raptor predators simultaneously would respond less actively by staying immobile, displaying less and seeking more often to hide in a refuge. As sex can also affect lizard behavior (Stuart-Fox et al. 2003), we compared males and females in our experiments. Because *A. maculatus* males are faster than females (unpublished data), and consistent with the general trend among lacertids (e.g., Braña 1993; Capizzi et al. 2007; Brecko et al. 2008), we expected males to be more agile and respond more actively to predation threats than females.

Methods

Study species and site

The spotted fringe-fingered lizard is a small diurnal lizard (Lacertidae) endemic to northwest Africa, occurring in dry shrublands and sandy shores (Joger et al. 2006). It is an insectivorous lizard that does not exhibit sexual dichromatism (Joger et al. 2006). The species is abundant in southeastern Tunisia, mainly inhabiting sparse desert steppes and using shrubs as shelters (Nouira and Blanc 2003).

Our study took place in a desert plain located northwest of the Gabès oasis in southern Tunisia (33°53'N -10°01'E), an area characterized by an arid Mediterranean climate (Jemai et al. 2017) and vegetated with sparse steppe shrubs, dominated by *Astragalus armatus* (Fabaceae) and *Deverra tortuosa* (Apiaceae) (Dhief et al. 2022). Other diurnal lizard species that coexist on the site include Bosk's fringe-toed lizard (*Acanthodactylus boskianus*), Olivier's sand lizard (*Mesalina olivieri*), Ocellated skinks (*Chalcides ocellatus*), and less commonly the Mediterranean chameleon (*Chameleo chameleon*), Schneider's skink (*Eumeces schneiderii*), Desert monitor (*Varanus griseus*) and Desert agama (*Trapelus mutabilis*) (Nouira and Blanc 2003; Escoriza 2018). Their main avian predators on the site include the Common kestrel (*Falco tinnunculus*) and the Southern grey shrike (*Lanius meridionalis*) (Nasri et al. 2018). Potential diurnal mammalian predators are feral cats (*Felis catus*) and dogs (*Canis familiaris*). Humans, especially shepherds, frequently move through the study site (pers. obs.).

Experimental design and data collection

Our study was conducted in October 2022, approximately one month before the hibernation season in our study area (pers. obs.). Fieldwork was usually carried out from 10:00 h to 14:00 h, covering the peak activity of spotted fringe-fingered lizards (unpublished data). We investigated the escape behavior of lizards by experimentally approaching them in one of two treatments: (1) a single observer approached the target lizard (i.e., exposure to a mammalian predator alone) (Vitt et al. 2002), or (2), the same observer approached the lizard while a second person, hidden by a shrub two to three meters behind the observer, held a long pole carrying a plastic wing-flapping raptor model (Fig. 1), so that the raptor model was approximately 5 m above the target lizard (i.e., simultaneous exposure to a mammalian predator and an avian predator) (Ventura et al. 2017). The raptor model used was actually a battery-operated falcon-sized toy. We emphasize here that in

Fig. 1 Photo of the raptor model used in the experiments

our study design, an 'avian predator alone' treatment was inconceivable because the presence of an observer was always required to approach the targeted lizard and make observations.

We searched for lizards along 12 parallel 600 m long transects separated by 70 m. Each transect was traveled only once throughout the course of the study, and the studied lizards were captured and individually marked after the trials were conducted (see below) so that each lizard was only used once. Moreover, we alternated randomly which experimental treatment we introduced to the encountered lizards. To reduce potential observer biases, all experiments were conducted by the same observer (O. C.), wearing apparel of the same color while walking at a steady pace (approximately 80 m/min). The experiments were always conducted on clear days, under suitable meteorological conditions. Only large lizards (SVL exceeding 35 mm), which were presumably adults (Schleich et al. 1996; del Mármol et al. 2019), were included in the experiments. In addition, because tail loss affects sprint speed in some lizards (Gillis et al. 2009; Libby et al. 2012; McElroy and Bergmann 2013), we did not include lizards with recently lost or incompletely regenerated tails.

As soon as a lizard was detected, the observer turned towards it and ensured that the target lizard stopped activity and was paying attention to the observer's position. Lizards that fled immediately when encountered were not tested. After recording start time, the observer walked towards the focal lizard until an escape attempt was made, placing small markers at (1) the observer's location when the lizard began to move, (2) the lizard's starting location and (3) the escape destination (i.e., location where the lizard first stopped after fleeing). To record flight time (FT, s; = time elapsed between the flight beginning and end), and to note the occurrence of displays prior to flight (head, limb and/or tail movements), as well as the type of escape destination (i.e., in a bush or in the open), the observer used a Dictaphone to describe the lizard's behavior.

At the end of the trial, the lizard was captured with a lasso attached to the end of an extendable pole, measured (snout-vent length (SVL)), sexed based on morphology (i.e., hemipene eversion and femoral pore characters (wider and darker in males)), and uniquely marked with non-toxic paint prior to release at the site of capture. Using a measuring tape, we recorded flight initiation distance (FID, m; = distance separating the observer from the lizard when the lizard began escaping), and flight distance (FD, m; = distance moved by the lizard during its flight). For lizards that fled into a bush, FD was determined as the distance between the starting location and the bush's edge. Flight speed (FS, m/s), calculated as the ratio of FD to FT, and was subsequently preferred over FT as a descriptor of escape behavior as it was more meaningful in the context of our study.

The date and time at which each experiment started were always recorded. Furthermore, since lizard behavior may be influenced by ambient temperature (Samia et al. 2016), this parameter had to be taken into account. Unfortunately, we did not record air temperature in the field, but we used online meteorological data from Weather Spark (2024), considering the nearest weather station (Gabès station, 6 km from the study site) and the precise time of the experiments.

Statistical analysis

Because the investigated escape variables (FID, FD and FS) were inter-correlated (see results), we used Principal Components Analysis (PCA) to summarize escape variables into a composite index of escape agility (IEA), then developed a general linear model (GLM) with normal error distribution to investigate whether IEA varied according to treatment (i.e., one predator or two-predator exposure), sex, and SVL, while also accounting for time of day (centered from midnight) and air temperature as covariates. SVL data were standardized to a mean of zero and unit variance for each sex separately, as to obtain a sex-independent size measure. In a first step, a model accounting for all possible interactions among main effects was conducted. Non-significant interactions were then removed and the model rerun. Similarly, we used a logistic regression to assess the relevance of treatment and sex as predictors of 1) the probability of

displaying when approached by the observer, and 2) fleeing into a refuge. All tests and analyses were conducted using SAS (SAS Institute 2008).

Results

We experimentally tested 120 lizards, 59 females and 61 males (Table 1). Air temperature at the moment of the experiment ranged from 23 to 31 °C (mean ± SD = 27 ± 2 °C). All three escape variables (FID, FD, FS) were positively intercorrelated (FID and FD: $r = 0.513$, $P < 0.001$; FID and FS: $r = 0.379$, $P < 0.001$; FD and FS: $r = 0.523$, $P < 0.001$). A PCA summarized them into a single factor accounting for 65% of the original variance, with an eigenvalue of 1.955. The PCA factor was positively correlated with all three initial escape variables, providing a composite index of escape agility (IEA) (FID: $r = 0.777$, $P < 0.001$; FD: $r = 0.854$, $P < 0.001$; FS: $r = 0.783$, $P < 0.001$). High IEA scores occurred in lizards that responded earlier by running a greater distance and at greater speed, whereas low scores characterized more immobile, slower-moving lizards.

IEA was significantly related to treatment and lizard sex, as well as the interaction between treatment and sex, but it did not vary according to SVL, time of day and air temperature (GLM; Table 2). In particular, males exposed to the two-predator treatment showed significantly lower IEA scores compared to males exposed to one predator, but no similar trend was detected in females (Table 3, Fig. 1). Moreover, males always had higher IEA scores than females (Fig. 2).

Among the 120 lizards approached, 56 (47%) displayed before fleeing, and displaying was more likely among lizards exposed to a single predator treatment compared to lizards exposed to the two-predator (Table 4; Fig. 3). Moreover, 46/120 lizards (38%) took refuge in a shrub, the probability of which was significantly related to both treatment, sex, and also time of day (Table 4). Lizards that were exposed to the two-predator treatment tended to hide in a shelter more frequently than those exposed to one predator, and females fled to shrubs more often than males (Fig. 4). However, under the conditions of our experiments, neither displaying nor hiding probability varied according to air temperature (Table 4).

Table 2 Results of GLM investigating lizard escape agility (IEA) as a function of treatment (2 classes: terrestrial predator vs terrestrial-aerial predator combination), sex (2 classes), SVL (standardized by sex), time of day (centered from midnight) and air temperature. Non-significant interactions were removed. Model $R^2 = 70\%$, $F_{6,113} = 43.460$, $P < 0.001$

Source	DF	*F-ratio*	*P-value*
Treatment	1	32.790	< 0.001
Sex	1	174.130	< 0.001
SVL	1	2.460	0.120
Time of day	1	0.070	0.796
Air temperature	1	2.760	0.099
Treatment × Sex	1	32.810	< 0.001

Discussion

Our hypothesis that lizards exposed simultaneously to an aerial predator and a terrestrial predator would be more likely to become immobile and engage in behavior consistent with avoiding detection than those facing a terrestrial predator only was partially supported. Exposure to multiple predation threats was associated with decreased escape agility in males (i.e., lower IEA), but not females. Regardless of predation threat, females were always less agile and more prone to hide in refuges than males.

The tendency towards immobility we observed in males exposed to an aerial predator is consistent with the idea that prey adjust their anti-predatory behavior to predator type and

Table 1 Descriptive statistics of lizard SVL and investigated escape variables

Treatment	Variable	Females					Males				
		n	Min	Max	Mean	SD	n	Min	Max	Mean	SD
Observer	SVL (mm)	30	40.17	51.50	45.21	2.83	30	40.31	56.74	47.29	4.44
	FID (m)	30	0.270	1.430	0.662	0.279	30	0.610	2.100	1.389	0.444
	FD (m)	30	0.280	3.100	0.796	0.617	30	0.330	5.000	2.267	1.312
	FT (s)	30	0.370	3.920	1.206	0.910	30	0.47	3.240	1.461	0.839
	FS (m/s)	30	0.301	1.123	0.691	0.165	30	0.589	2.561	1.561	0.537
Observer + Raptor	SVL (mm)	29	40.46	50.99	45.25	2.27	31	42.05	57.54	48.42	3.82
	FID (m)	29	0.320	1.040	0.543	0.176	31	0.480	1.460	0.860	0.245
	FD (m)	29	0.310	1.140	0.523	0.200	31	0.520	1.370	0.845	0.231
	FT (s)	29	0.310	1.100	0.575	0.182	31	0.300	1.620	0.645	0.229
	FS (m/s)	29	0.540	1.823	0.930	0.254	31	0.789	2.275	1.381	0.391

FID flight initiation distance, *FD* flight distance, *FT* flight time, *FS* flight speed

Table 3 Results of GLMs investigating lizard escape agility (IEA) as a function of treatment (2 classes), SVL (standardized), time of day (centered from midnight) and air temperature, in females and males separately. Non-significant interactions were removed

Source	Females ($R^2 = 0.5\%$, $F_{3,55} = 0.090$)			Males ($R^2 = 47\%$, $F_{3,57} = 17.050$)		
	DF	*F-ratio*	*P-value*	DF	*F-ratio*	*P-value*
Treatment	1	0.060	0.801	1	36.840	< 0.001
SVL	1	0.050	0.828	1	3.140	0.082
Time of day	1	0.450	0.507	1	0.000	0.954
Air temperature	1	1.580	0.214	1	2.120	0.151

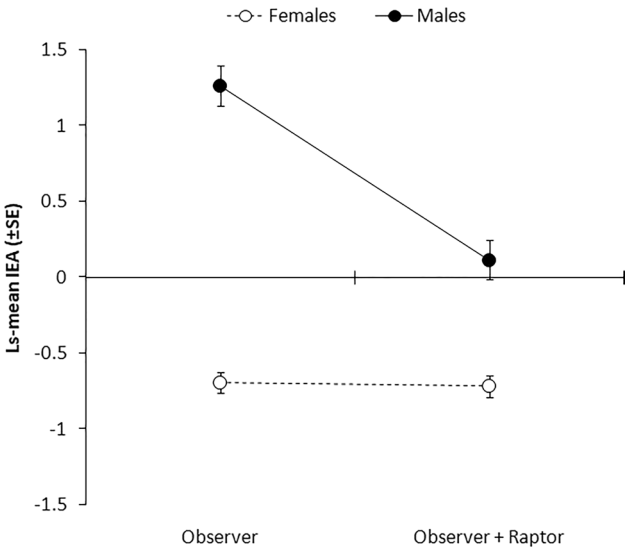

Fig. 2 Least-square means (±SE) index of escape agility in females (white circles and dashed line) and males (black circles and bold line), as estimated from a GLM investigating the relevance of treatment, sex, SVL (standardized by sex), time of day (centered from midnight) and air temperature as predictors of lizard escape agility

threat intensity (Hopper 2001; Blumstein 2006; Langridge et al. 2007; Rundus et al. 2007; Sherbrooke 2008), particularly among lizards living in elevated-risk environments (e.g., Downes 2002; Hawlena and Pérez-Mellado 2009). Staying motionless and delaying escape until the threat of predation becomes lower can be an effective defensive strategy, especially against aerial predators that attack faster than terrestrial predators, as movements can increase the likelihood of being detected and survival can depend on remaining motionless and blending into the surroundings (Webster et al. 2009; Cooper and Sherbrooke 2010). Prey that rely on camouflage and crypsis as an anti-predatory tactic should be particularly prone to using immobility as a strategy, and should utilize immobility more often against diurnal aerial predators that mainly use visual cues to detect prey and can approach faster than terrestrial predators (Blumstein 2006). Spotted fringe-fingered lizards mainly adopted immobility as an anti-predator tactic when an aerial predator was detected. With their beige dorsal coloration interspersed with black and white marks, motionless individuals are well-camouflaged in their sparsely vegetated desert habitat (pers. obs.).

Exposure to two types of predators simultaneously was also associated with increased refuge use by both sexes, which was rare among lizards facing only one predator. Because of possible unsuitable conditions for thermoregulation and foraging inside refuges, the use of refuges can be costly (Amo et al. 2006). Lizards should only enter refuges when the outside is particularly dangerous, such as when the presence of terrestrial predators, to which the lizards must respond by fleeing, is aggravated by the presence of aerial predators that are particularly effective at detecting and capturing prey moving in open areas. A terrestrial predator alone may not be perceived as a serious threat, which could explain why lizards tended to avoid refuges, moving away as a precaution to maintain a safe distance (Cooper 1997).

Consistent with predictions of the pursuit-deterrence hypothesis (Caro 1995), head and forelimb movements

Table 4 Results of logistic regressions investigating the relevance of treatment (2 classes), sex (2 classes), SVL (standardized by sex), time of day (centered from midnight) and air temperature as predictors of the probability of conducting display movements and the probability of hiding in a shelter. Non-significant interactions were removed

Source	Display movements			Hiding in a shelter		
	DF	Wald χ^2	*P-value*	DF	Wald χ^2	*P-value*
Treatment	1	19.440	< 0.001	1	10.630	0.001
Sex	1	2.970	0.085	1	12.960	< 0.001
SVL	1	0.090	0.770	1	1.790	0.181
Time of day	1	0.170	0.676	1	5.170	0.023
Air temperature	1	2.560	0.103	1	0.510	0.475

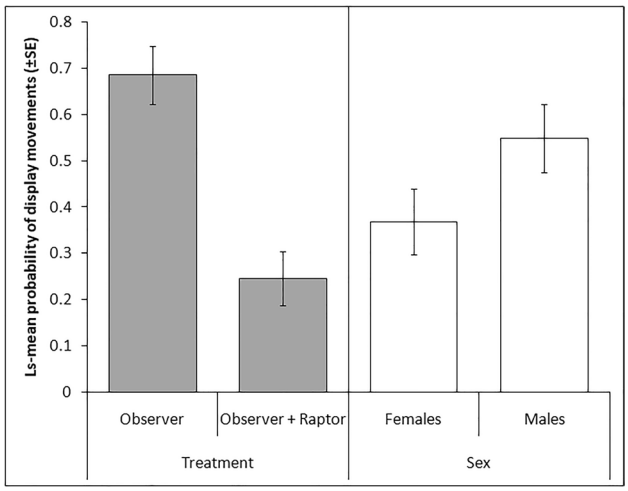

Fig. 3 Least-square means (±SE) probability of conducting display movements before fleeing, as estimated from a logistic regression models investigating the effects of treatment, sex, SVL (standardized by sex), time of day (centered from midnight) and air temperature

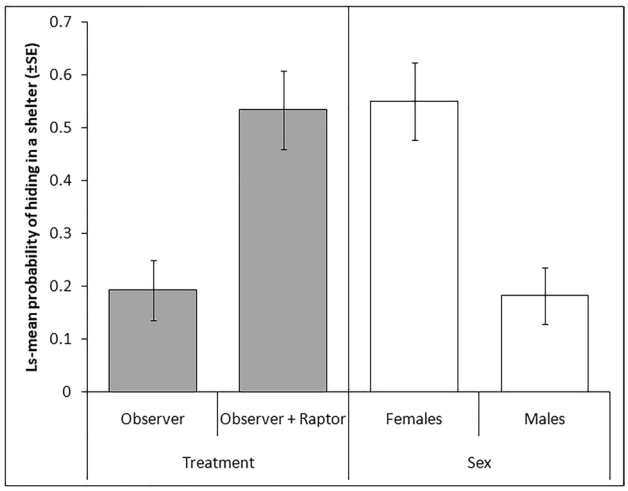

Fig. 4 Least-square means (±SE) probability of hiding in a bush, as estimated from a logistic regression models investigating the effects of treatment, sex, SVL (standardized by sex), time of day (centered from midnight) and air temperature

were recorded in lizards exposed to both predation threat treatments. Nonetheless, display movements occurred more frequently when lizards were facing a terrestrial predator only than when an aerial predator also was detected. Displays could be an adaptive defensive response as their use depended on the identity of the predators involved and the intensity of threat encountered, which is consistent with other lizard studies showing decreased display movements with predation threats (e.g., Leal and Rodríguez-Robles 1997; Cooper et al. 2004). Overall, our findings support the notion that prey use displays when the predation threat is low to demonstrate their ability to escape, such as when the predator is further away or attacks slowly (Blumstein and Daniel 2005; Pafilis et al. 2009; Cooper and Martin 2016). Prey display to indicate that predators are detected and the chance of successfully attacking them is low (perceptual advertising), or that they are difficult to catch or control (advertising of quality) (Caro 2005). Display movements may also provide an unexpected and sudden stimulus designed to induce fear or confusion in the predator and result in hesitation in its attack (Sherratt et al. 2004).

In accordance with trends reported for other lacertids, male *A. maculatus* were more agile and less conspicuous in their escape, hiding in refuges less than females (e.g., Braña 1993; Capizzi et al. 2007; Brecko et al. 2008). Sex-based differences could be related to size and speed differences between males and females, with the fastest lizards being more agile (Cullum 1998; Lailvaux et al. 2003; Qi et al. 2014). Females might adopt the strategy of immobility more than males because they are slower and cannot rely on speed to avoid capture. When exposed to elevated predation threats (i.e., aerial and terrestrial predators) males hid in refuges even more. Males were often reluctant to enter available bushes even when there was a high risk of predation, possibly because of the presence of other predators in bushes that we could not detect, like snakes and larger lizard species. Bush occupation by larger conspecifics could also cause bush avoidance as has been observed in juvenile Bosk's fringe-toed lizards that were often attacked by adults (Nasri et al. 2018). Indeed social interactions are known to play important roles in shaping lizard anti-predatory behaviors (e.g., Díaz-Uriarte 1999; Ventura et al 2021). This is an appealing issue that deserves further attention. We also highlight that under the conditions of our experiments, lizards' anti-predatory responses were not sensitive to air temperature, but this could simply be due to our study design. As specified above, we always strived to have the experiments run under suitable meteorological conditions, thus avoiding extreme temperatures under which significant behavioral changes may have occurred.

Our experiment highlights the flexibility of lizard anti-predatory behaviors. Lizards adjusted their escape strategy to the intensity of the threat encountered. In particular, they are more vigilant in the presence of two predators to which they responded by increasing wariness and seeking refuges. However, sex differences, particularly regarding how escape agility varies with predation risk, remain poorly understood and require further investigation.

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Data availability Data are available from the authors on reasonable request.

Declarations

Conflicts of interest No conflicts of interest to be declared.

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