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Sex- and performance-based escape behaviour in an Asian agamid lizard, *Phrynocephalus vlangalii*

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Abstract In lizards, males are predicted to sprint faster and run for longer than females by virtue of higher testosterone levels and differences in morphology. Consequently, escape behaviour is also predicted to be associated with sex and locomotor performance, yet these links have rarely been explored. Here, we tested whether escape behaviour is associated with locomotor performance in the toad-headed agama, *Phrynocephalus vlangalii*, and whether it is sex-dependent. This species is also characterized by elaborate tail displays, which we examined as a potential pursuit-deterrent signal. Tail waves were performed by a very small proportion (2/58, 3 %) of individuals during predatory trials, suggesting that tail signalling functions exclusively in a social context. To understand the relationships between sex, escape behaviour and performance, we first measured escape behaviour (flight initiation distance, flight distance—measured differently compared to previous studies of lizard escape behaviour, and refuge use) in the field before measuring maximal sprint speed and endurance on the same individuals in the laboratory. Flight initiation distance did not differ between the sexes and was unrelated to performance capacity (maximal endurance and sprint speed) but was positively related to body size with larger individuals fleeing earlier. Males fled farther than females, but flight distance was also unrelated to either endurance or sprint speed. Interestingly, faster females were less likely to enter a refuge than slower females, whereas sprint speed and the probability of taking refuge were unrelated for males. Our results suggest that when males and females are not obviously sexually dimorphic, they are more likely to overlap in escape tactics.

Keywords Escape behaviour · Locomotor performance · Sprint speed · Endurance · Reptile

Introduction

Physiological performance capacity, how fast and for how long an organism is able to run or how hard an animal is able to bite, is predicted to be shaped by both natural and sexual selection because of their effect on escape behaviour and mating success (Husak and Fox 2008; Irschick et al. 2008). Therefore, selection on performance traits is frequently predicted to be sex-dependent (Lailvaux 2007; Irschick et al. 2008; Van Damme et al. 2008; Noble et al. 2014), and this may in turn influence escape behaviour in different ways for males and females. Typically, males are predicted to delay fleeing and run shorter distances in escaping because males are usually reported to run faster and longer than females by virtue of differences in morphology and higher testosterone levels (Klukowski et al. 1998; Lailvaux et al. 2003; Noble et al. 2014). Conversely, females may adjust their escape behaviour and rely more on crypsis if their performance capacity is reduced (Vanhooydonck et al. 2007; Goodman et al. 2008). We currently have few tests of sex-based differences in escape behaviour or performance capacity in lizards (Lailvaux et al. 2003; Martin et al. 2009; Noble et al. 2014). For example, Lailvaux et al. (2003) found sexual differences in sprint speed but no differences in endurance in the lizard *Platysaurus intermedius wilhelmi*, and males were found to take refuge earlier and flee farther than females.

Various optimality models have been proposed to predict when an animal should flee a predator (Cooper and Frederick

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2007). The most popular of these is an economic model that qualitatively predicts that prey should flee when the risk of predation is equivalent to the cost of escaping (Ydenberg and Dill 1986). In contrast, other optimality models predict that escape behaviour should be flexible and adjusted based on predator search speed and prey locomotor performance (Broom and Ruxton 2005; Cooper and Frederick 2007). The key difference between these models lies in the escape cost. In the Ydenberg and Dill (1986) economic model, the escape cost is the lost opportunity associated with foraging and courtship, whereas in other optimality models, it is alerting the predator to the presence of the prey (Broom and Ruxton 2005; Cooper and Frederick 2007). The latter model best explains flight initiation distance in cryptic species because the likelihood of a predator detecting cryptic prey increases as it gets closer to the prey. Nevertheless, the act of fleeing will alert the predator; therefore, the prey will have to trade-off the benefits of remaining stationary against the cost of being detected (Broom and Ruxton 2005). No matter the model, escape decisions are critical to an individual's fitness (Cooper and Frederick 2007) and these decisions may depend on an individual's intrinsic capacity to escape predation (Clobert et al. 2000; Kullberg et al. 2002; Lailvaux et al. 2003).

Avoiding predation and escaping from predators may incur a variety of costs including lost foraging and mating opportunities. One way to reduce these costs is to communicate with predators using pursuit-deterrent displays (Dial 1986; Cooper 2001). For example, Anolis cristatellus use push-up displays to convey information about their endurance to a predator (Leal 1999) and wall lizards Podarcis muralis communicate with predators using foot shake displays (Font et al. 2012). Alternatively, animals may freeze or make escape decisions through risk assessment. A typical metric of risk assessment is flight initiation distance, which is frequently adjusted in response to risk (Broom and Ruxton 2005; Cooper and Frederick 2007). For example, conspicuous individuals are predicted to flee earlier than cryptic ones if escape costs are low (Martin et al. 2009). Additional measures of risk assessment during escape include flight distance and latency to enter a refuge (Martin and Lopez 2000; Lailvaux et al. 2003; Martin and Lopez 2010). Locomotor performance capacity (sprint speed and endurance) is potentially a key driver of escape behaviour because of its obvious influence on evading capture by a predator. For example, individuals with higher sprint speed are predicted to flee shorter distances (Lailvaux et al. 2003; Broom and Ruxton 2005). Also, lizards such as Lacerta schreiberi adjust their refuge use based on sprint speed, with faster lizards decreasing their reliance on refuges (Martin and Lopez 2010). Because of differences and constraints in reproductive state (Schwarzkopf and Shine 1992; Olsson et al. 2000; Cooper and Wilson 2007; Vanhooydonck et al. 2007), escape behaviour is frequently sex-specific. For example, male striped plateau lizards, Sceloporus virgatus, pay more

attention to courtship and social interactions during the mating season, thus delaying escape from predators (Cooper and Wilson 2007). In the southern water skink, Eulamprus tympanum, compared to males and nongravid females, gravid females allow predators to approach more closely (Schwarzkopf and Shine 1992). Presently, little is known about the general relationship between sex, performance and escape behaviour, especially outside the mating season.

We used an Asian agamid lizard, Phrynocephalus vlangalii, to test the relationship between escape behaviour, sex and maximal locomotor performance capacity. Because both male and female P. vlangalii are territorial and use complex tail displays during social interactions, we first tested whether their tail displays function as a pursuit-deterrent signal. Males and females are similarly conspicuous with the exception of the underside of the tail tip (orange in females, black in males) precluding a role for sex-specific conspicuousness in escape behaviour. Males tend to be larger than females in both body length and head size, although not by much (Qi et al. 2012). Given that female lizards typically have lower sprint speed and endurance than males (Lailvaux et al. 2003; Noble et al. 2014), we predicted that males will permit predators to approach closer, will flee shorter distances and will be less likely to enter a refuge than females. With respect to locomotor performance capacity, we predicted that sprint speed would be inversely related to flight initiation distance, flight distance and refuge use because faster runners are predicted to be at a lower risk of predation and can more easily escape from predators (Irschick et al. 2008). Similarly, we predicted that individuals with higher endurance would flee sooner (longer flight initiation distance), run longer distances and be less likely to seek refuge (Leal 1999; Le Galliard and Ferriere 2008; Martin and Lopez 2010).

Methods

Study area

We conducted fieldwork during mid-June/July (summer) in 2011 near Xiaman Conservation Station in the Zoige Wetland Nature Reserve in southwestern China (33° 43′ 25.0″ N, 102° 29′ 04.0″ E), at an elevation of ca. 3464 m.a.s.l. P. vlangalii occupy patchily vegetated sand dunes at a density of ca. 0.32/m^2 (Yin Qi, unpublished data). The vegetation on and around these sand dunes is predominantly composed of the grasses Kobresia humilis, Kobresia prattii and Elymus natans and a shrub (Salix sclerophylla).

Escape behaviour

We quantified responses to a predatory threat by using a human 'predator' that directly approached each lizard. For

consistency, the same person performed all approaches from roughly 15 m (comfortably beyond maximum flight initiation distance) and always wore the same clothes. In order to avoid sampling the same individual twice, we systematically moved through a 3-km^2 area and did not work in the same area more than once. To ensure that approach speed was consistent (0.5 m/s), we conducted 17 timed practice trials over 10 m. Our protocol consisted of walking directly towards a lizard and dropping a marker when the lizard fled at least 10 cm (to distinguish this from a postural adjustment) before stopping at the lizard's initial location, after which, we dropped a second marker. Unlike many other studies of lizard escape behaviour, we continued our approach because otherwise lizards fled very short distances that were insufficient to relate to physiological performance capacity. We calculated flight initiation distance (FID) as the distance between markers one and two. We waited 10 s before dropping a third marker at the lizard's final location where it paused for at least 2 s in order to calculate flight distance (FD). We used 2 s between moves to distinguish a single movement from a series. We also recorded the lizard's final destination [refuge or open which we called refuge use (RU) in the following analysis]. All measurements were to the nearest 1 cm. Finally, we also scored whether lizards tail-waved in response to being approached in the event that this behaviour might be a pursuit-deterrent signal. We then caught the focal lizard by noose or by digging a pitfall trap in front of the burrow in which it had sought refuge. All captured lizards were brought back to the field station in order to measure their morphology and maximal performance capacity (sprint speed and endurance).

Morphology and performance capacity

We measured snout-vent length (SVL) from the tip of the snout to the posterior edge of the cloaca to the nearest 1 mm using a clear plastic ruler.

We quantified two measures of performance capacity: sprint speed and endurance. We first warmed lizards to a body temperature of ca. 30 °C (actual range 22–37.5 °C) by floating them in plastic bags on warm water. Prior to all performance measurements, we measured the lizard body temperature using a cloacal thermometer (Miller-Weber, USA) to the nearest 1 °C and we used these measurements to statistically control for any effects temperature had on performance. After measuring body temperature, lizards were enticed to sprint down a 1.5-m racetrack by lightly touching them with an artist's paintbrush on the base of their tail (Noble et al. 2014). Four 100-W incandescent lights were suspended above the racetrack to provide illumination. Fine lightly compacted sand from their habitat was used as substrate to provide natural traction for the lizard. The floor of the racetrack was marked every 25 cm, and all runs were recorded using a high-speed digital camera [Casio High Speed Exlim camera (EX-FH100), 240 fps].

Immediately following sprinting, lizards were placed in a circular racetrack (circumference 180 cm, width 13 cm) with a sand substrate to measure endurance. Lizards were enticed to run around this track by gently touching them on the base of their tail using an artist's paintbrush. We regarded the lizard as exhausted if after ten light taps with the paintbrush, the lizard no longer ran. The time the lizard started running until the last tap was considered the lizard's endurance.

Each lizard's sprinting speed and endurance were measured once/day over three consecutive days before releasing them at their point of capture. We used the lizard's maximal performance capacity in all analyses because lizards can perform highly variably based on motivation and other factors (Losos et al. 2002).

Data analysis

All data analyses were carried out in R software version 2.14 (R-Core-Team 2013). Before analysis, we excluded lizards without locomotor performance and/or which did not have temperature data. Sample sizes for each of the analyses are indicated throughout. To test whether the sexes differed significantly in sprint speed and running endurance, we compared the difference in log sprint speed and log endurance between the sexes using analysis of covariance (ANCOVA) after controlling for log body temperature and SVL. We included interactions between sex and SVL and temperature because the relationships between these variables and performance appeared to vary between the sexes. Models were then simplified by excluding interactions and testing model fit using F tests. We tested for a trade-off between sprint speed and endurance along with log FD and log FID using a Pearson's product-moment correlation test.

We tested the relationships between escape behaviours (FID, FD and RU), sex and physiological performance capacities (sprint speed and endurance) by creating models that included all main effects (sprint speed, endurance, sex) and important interactions related to our questions. We also included SVL as a covariate in models because body size has been linked with escape behaviours in many ectotherms (Cooper 2000; Miller et al. 2011; Sagonas et al. 2013). Given that temperature affected endurance measurements, and this varied between the sexes, we used residuals from a model with sex, SVL, temperature and a sex*temperature interaction as our measure of endurance in the FID, FD and RU models. Given that none of these variables affected sprint speed, we included our raw sprint speed data as a predictor. Only sex*residual endurance and sex*sprint speed interactions were tested because we were explicitly interested in whether the relationships between performance and escape behaviours differed between males and females. We used log-transformed FID and FD and

assumed a Gaussian error distribution (identity link function) whereas we modelled RU using a binomial error distribution (logit link function). We tested whether over-dispersion affected inferences in RU models by fitting a quasi-binomial model; however, this had little effect on estimates. Using backwards elimination procedures, we excluded higher-order interactions ($P > 0.15$) from the global models using F tests (FID and FD) or likelihood ratio tests (refuge use). We present estimates from the full main effects models regardless of significance because these parameters directly related to our predictions. Using our models, we predicted the response surface to test how model predictions were related to our verbal predictions. Model residuals in both the FID and FD models were normally distributed; however, there was a highly influential point in FID models. Exclusion of this point did not affect the overall inferences from this model, and we include it in our final analysis. All continuous predictor variables were standardized (mean=0, SD=1) to make model parameters more comparable and to make main effects easier to interpret in the presence of interactions. To quantify the goodness of fit, we also calculated the R^2 of our models (Nakagawa and Schielzeth 2013). All means are reported as mean±1 SE.

Results

We found no support for tail waving as a pursuit-deterrent signal in *P. vlangalii*. Only two *P. vlangalii* tail-waved upon approach [2/58 total 3 %, males (N=1/31) and female (N=1/27)], most likely due to other factors (possibly other lizards not seen by us).

Males had a tendency to be larger (mean=56.29±0.43 mm, n=31), on average, over females (mean=54.70±0.77 mm, n=28), but this was not significant (Wilcoxon test: W=300.5, P=0.07). Sprint speed was not significantly different between the sexes (male mean 0.54±0.03 m/s, n=28; female mean 0.50±0.03 m/s, n=22), when body size and body temperature were controlled for (sex: F=0.45, P=0.50; SVL: F=0.72, P=0.40; body temperature: F=1.98, P=0.17; Table 1), and there was no evidence that the relationship varied between the sexes (SVL*sex: F=0.07, P=0.79; log temp*sex: F=0.67, P=0.42). Endurance was also not significantly different between the

sexes (male mean 39.40±2.60 s, n=29; female mean 42.84±2.02 s, n=19; Table 1), when body size and body temperature were controlled. Temperature positively influenced log endurance, and its effects on endurance varied between the sexes (sex*log temp: F=6.56, P=0.01) with temperature more strongly affecting males than females (Table 1).

Mean FID for males was 268.23±36.56 cm (n=31) and for females 248.44±33.07 cm (n=28) (Fig. 1a). We found no evidence for an interaction between sex*sprint speed (F=0.02, P=0.90) or sex*endurance (F=0.84, P=0.37). FID did not differ significantly between males and females (F=0.01, P=0.92; Table 2) and was not related to endurance (F=0.57, P=0.46; Table 2) or sprint speed (F=0.02, P=0.89; Table 2); however, it was positively related to SVL (F=5.42, P=0.03; Table 2; Fig. 2a).

Mean FD for males was 105.97±20.81 cm (n=31) and for females 59.00±14.21 cm (n=28) (Fig. 1b). We found no evidence for a significant sex*endurance interaction (F=0.58, P=0.45) and a marginally nonsignificant sex*sprint speed interaction (F=3.36, P=0.07; Table 2). FD was significantly greater in males than in females (Table 2, Fig. 1b) but was not a function of individual endurance (F=1.30, P=0.26; Table 2) or SVL (F=0.41, P=0.53; Table 2).

Seventeen of 31 (54.8 %) males and 16 of 27 (59.26 %) females took refuge in a burrow when approached (Fig. 1c). The probability of refuge use was not a function of individual endurance, and there was no evidence that this differed between the sexes (sex*residual endurance: χ^2=0.24, P=0.62; residual endurance: χ^2=2.00, P=0.16; Table 2). The probability of refuge use was also not related to SVL (χ^2=0.04, P=0.85; Table 2). The relationship between the probability of taking refuge and sprint speed depended on sex (sex*sprint speed: χ^2=6.21, P=0.01; Table 2), and this was true even after accounting for over-dispersion (quasi-binomial GLM—sex*sprint speed: F=4.73, P=0.035). Slower females were predicted to take refuge with a higher probability compared to faster females, whereas there was no strong relationship between the probability of taking refuge and sprint speed for males (Fig. 2b).

Log sprint speed was not associated with log endurance (r=0.09, P=0.52, n=51). Log FID was negatively associated with log FD, but the relationship was not significant (r=−0.12, P=0.39, n=58).

Table 1 Effect of sex, log temperature and snout-vent length (SVL) on log sprint speed and log endurance. Estimates are standardized (mean=0, SD=1). Confidence intervals are provided from profiled likelihoods of model parameters. Confidence intervals not overlapping 0 are in italics

Parameter	Log sprint speed (n=50)			Log endurance (n=48)		
	Std. est	L 95 % CI	U 95 % CI	Std. est	L 95 % CI	U 95 % CI
Intercept	−0.72	−0.85	−0.60	3.72	3.60	3.85
Sex	0.06	−0.11	0.23	−0.13	−0.29	0.04
Log temperature	0.06	−0.02	0.14	0.03	−0.06	0.13
SVL	−0.04	−0.12	0.05	−0.06	−0.14	0.02
Sex*log temperature	–	–	–	*0.21*	*0.05*	*0.38*
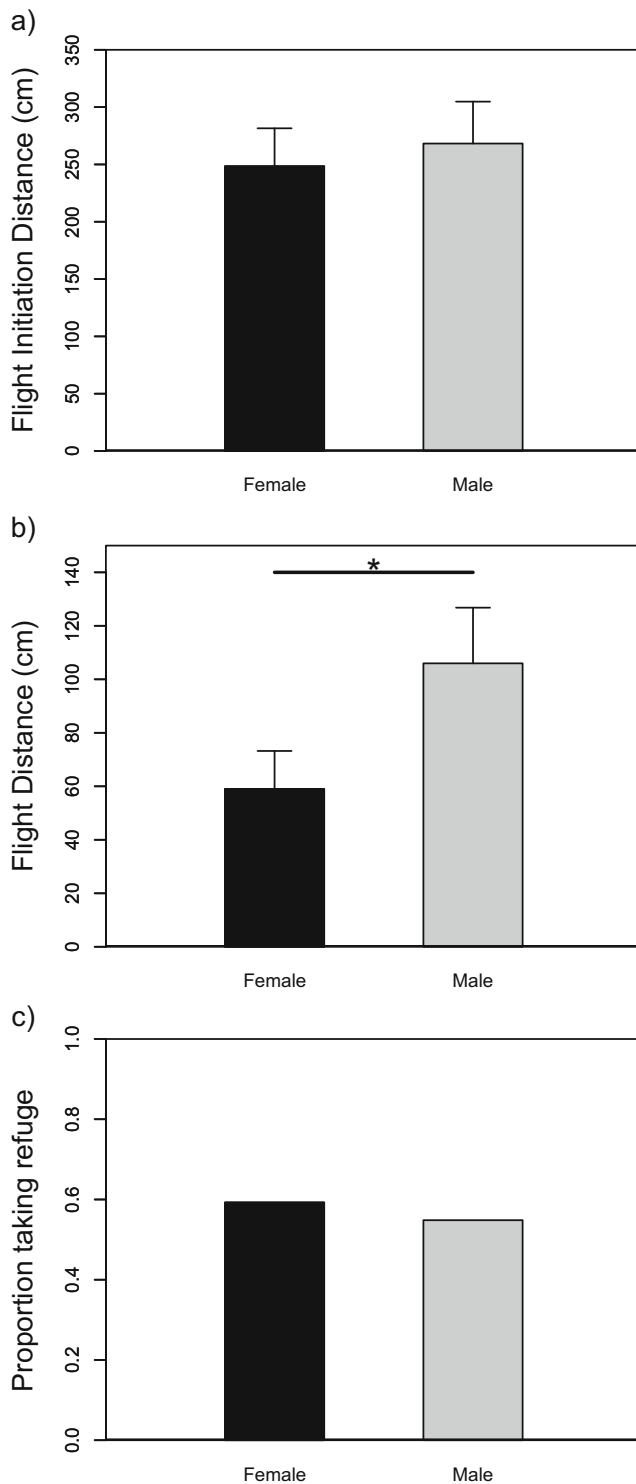
Fig. 1 Comparison of escape behaviours between the sexes. **a** Flight initiation distance. **b** Flight distance (*$P<0.05$). **c** Proportion of refuge use. Means±1 SE

Discussion

P. vlangalii did not tail-wave in response to simulated predatory approaches and therefore does not use any obvious pursuit-deterrent signals. In terms of performance capacity, maximal sprint speed and maximal endurance were not significantly different for males and females. Also, males and females exhibited similar escape behaviour with one exception: males fled farther than females. Escape behaviours were, however, related to body size and locomotor performance. First, flight initiation distance increased as SVL increased. Second, the association between refuge use and sprint speed was sex-dependent such that slower females were more likely to take refuge than faster females whereas the same was not true for males.

Tail displays do not have an anti-predator function

Both male and female *P. vlangalii* frequently use complex tail waves during social interactions. The tail tip is orange in females and black in males, and because the tail is prehensile, they are able to dorsally curl and then uncurl their tails. Tail waving is conspicuous and could therefore function as a pursuit-deterrent signal to potential predators to discourage pursuit (Dial 1986; Cooper 2001). However, a very low percentage of individuals tail-waved during our predatory approaches, and as such, the tail display is only likely to be used in social signalling. While it is possible that some aspect of our approach failed to elicit tail waving, this protocol has been used to successfully test pursuit-deterrent signals in lizards in the past (Font et al. 2012). Cooper (2001) suggested that the lizard *Callisaurus draconoides* tail-waved based on predator approach distance, with fewer individuals signalling at longer or shorter distances. We think this is unlikely for *P. vlangalii* because we began approaching from a distance beyond which they respond (ca. 15 m), and the very low incidence of tail waves simply suggests that this behaviour has no clear link to anti-predatory behaviour.

Sex-dependent escape behaviour and influence of locomotor performance

No sexual differences were apparent in mean flight initiation distance and refuge use; however, flight distance was significantly greater for males than females. The lack of any difference in flight initiation distance and refuge behaviour might be a consequence of the cryptic coloration of both sexes. Males are larger than females, but this relationship is not significant and only the underside of the tail tip is sexually dimorphic. Therefore, it is likely that they experience similar predator-driven selection pressures as a consequence of their shared degree of conspicuousness. At the time of this study, female *P. vlangalii* were likely to be in an early stage of pregnancy while males were still defending territories. The similarity of flight initiation distance and refuge use between the sexes suggests an absence of any effect of reproductive state (at that point in time) on escape behaviour unless sex-specific effects cancel each other out. Conversely, the longer

Table 2 Models examining relationships between escape behaviours [flight initiation distance (FID), flight distance (FD) and refuge use (RU)], locomotor performance capacity (sprint speed and endurance) and sex

	Log flight initiation distance (FID)			Log flight distance (FD)			Refuge use (RU)		
				(n=45)			(n=45)		
	(n=45)			R^2=0.13			R^2=0.14		
	R^2=0.05								
Parameter	Std. est.	L 95 % CI	U 95 % CI	Std. est.	L 95 % CI	U 95 % CI	Std. est.	L 95 % CI	U 95 % CI
Intercept	*5.37*	*5.03*	*5.71*	*2.95*	*2.29*	*3.61*	0.92	−0.32	2.34
SVL	*0.26*	*0.04*	*0.48*	−0.14	−0.56	0.28	0.07	−0.67	0.84
Sex (M)	−0.02	−0.49	0.43	*1.08*	*0.22*	*1.93*	−0.76	−2.41	0.76
Sprint speed	0.02	−0.21	0.24	0.63	−0.12	1.38	*−1.46*	*−3.47*	*−0.13*
Res. endurance	0.08	−0.13	0.30	0.25	−0.18	0.68	−0.52	−1.31	0.20
Sex*sprint speed	–	–	–	−0.87	−1.80	0.06*	*1.99*	*0.39*	*4.18*
Sex*res. endurance	–	–	–	–	–	–	–	–	–

All variables have been standardized (mean=0, SD=1). We present the results of excluding interactions using *F* or LRT tests (see "Results") and present all estimates along with their lower and upper 95 % confidence intervals ('L 95 % CI' and 'U 95 % CI'). Confidence intervals not overlapping 0 are in italics

R^2 adjusted R^2, *Std. est.* standardized coefficient for model predictors

*$P<0.08$

flight distance of males may be related to some difference in physiological state.

Individuals are predicted to adjust their flight initiation distance based on the risk of capture and the cost of initiating a chase as a function of their locomotor performance (Broom and Ruxton 2005; Cooper and Frederick 2007; Martin et al. 2009). Running too soon may be costly because it alerts predators, and being able to run faster or longer would be

beneficial in escaping predators (Irschick et al. 2008; Le Galliard and Ferriere 2008). We found no evidence of associations between flight initiation distance and sprint speed or endurance in *P. vlangalii*, but larger individuals ran earlier when scared compared with smaller individuals. We tentatively suggest this might be because of the relationship between body size and heating rates. Ydenberg and Dill (1986) predicted that flight initiation distance and body
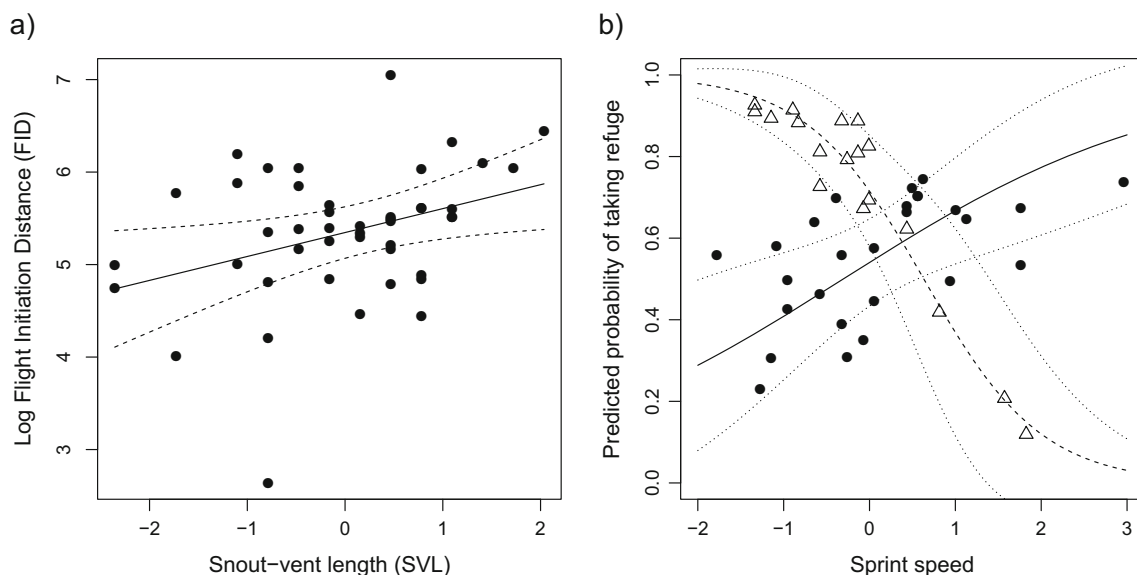
Fig. 2 Relationship between **a** log flight initiation distance and snout-vent length (SVL) and **b** predicted probability of taking refuge and sprint speed. The *filled circles* and *solid line* represent males, while the *clear* *triangles* and *dashed line* represent females along with standard errors (*dotted lines*). Model predictions are based on models in Table 2

temperature should be inversely related because of higher predation risk at lower temperature. Therefore, larger lizards might flee earlier because they are compensating for lower body temperature, and this behavioural anti-predator response has been shown in multiple species (e.g. *Anolis lineatopus*) (Rand 1964). Nonetheless, this needs to be tested in the field.

The relationship between sprint speed and flight distance was marginally nonsignificant and likely influenced by low statistical power. Nonetheless, there is good theoretical reason to believe that individuals should adjust their flight distance based on locomotor performance (Lailvaux et al. 2003), such that individuals that run faster and/or longer may be more likely to evade capture (Clobert et al. 2000; Irschick et al. 2008; Le Galliard and Ferriere 2008). Running too far can be energetically costly, while not running far enough can increase predation risk (Ydenberg and Dill 1986; Cooper and Frederick 2007), and these trade-offs are predicted to vary depending on sex. Different selection pressures as a consequence of differences in reproductive state may shape these trade-offs (Irschick et al. 2008). However, future work will be required to rigorously test this hypothesis in *P. vlangalii*.

The association between refuge use and sprint speed was sex-dependent. Taking refuge leads to a loss of foraging time and carries thermal costs (Martin and Lopez 2000; Martin and Lopez 2003; Blumstein and Pelletier 2005; Martin and Lopez 2010), and as such, individuals are predicted to make decisions on refuge use based on their locomotor performance (Martin and Lopez 2010). In *P. vlangalii*, faster females were less likely to enter burrows when scared compared with slower females, whereas there did not appear to be a strong relationship between performance and refuge use in males.

In summary, we found no evidence that tail displays function as pursuit-deterrent signals in *P. vlangalii*. Male and female lizards had similar sprint speed and endurance capacity. Sex differences in escape behaviour appear limited to flight distance (males run farther), while there were no differences in flight initiation distance and refuge use. Our study addresses the potentially important role of physiological performance capacity in responding to predation risk and demonstrated that when both sexes are cryptically coloured and territorial (aggressive), there is likely to be a significant overlap in both locomotor capacity and escape behaviour.

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